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Leadership in elephants: the adaptive value of age

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The value of age is well recognized in human societies, where older individuals often emerge as leaders in tasks requiring specialized knowledge, but what part do such individuals play in other social species? Despite growing interest in how effective leadership might be achieved in animal social systems, the specific role that older leaders may play in decision-making has rarely been experimentally investigated. Here, we use a novel playback paradigm to demonstrate that in African elephants (*Loxodonta africana*), age affects the ability of matriarchs to make ecologically relevant decisions in a domain critical to survival—the assessment of predatory threat. While groups consistently adjust their defensive behaviour to the greater threat of three roaring lions versus one, families with younger matriarchs typically under-react to roars from male lions despite the severe danger they represent. Sensitivity to this key threat increases with matriarch age and is greatest for the oldest matriarchs, who are likely to have accumulated the most experience. Our study provides the first empirical evidence that individuals within a social group may derive significant benefits from the influence of an older leader because of their enhanced ability to make crucial decisions about predatory threat, generating important insights into selection for longevity in cognitively advanced social mammals.

Keywords: leadership; cognitive abilities; playback experiment; social mammals; longevity; *Loxodonta africana*

1. INTRODUCTION

Despite theoretical predictions that democratic decision-making should predominate in animal groups [1–4], it is becoming clear that specific leaders commonly appear to guide the actions of other group members [5–8]. Leaders are therefore increasingly seen as important in coordinating social organization, and there is now growing interest in parallels between leadership in humans and animals that suggest common evolutionary origins, with the same morphological and behavioural traits predicting leadership across species [3]. Understanding the benefits to individual group members of accepting a leader's decision is critical to uncovering the evolutionary basis of leadership, and hence increasing our knowledge of the role leaders play in human and animal societies [3,9]. One situation in which individuals may gain from following a leader is if older leaders possess some form of superior knowledge enabling better decisions in response to environmental or social triggers [10–12].

Mathematical models of group decision-making have indicated that it may pay individuals in small groups to accept the decision of a knowledgeable leader where large disparities exist in the information possessed by different group members [1]. Indeed, research on humans indicates that age is correlated with leadership in domains that require specialized knowledge [13], and there is recent evidence that decisions about social conflicts improve with age despite declines in many forms of cognitive processing [14]. In animal societies, it has most often been suggested that older leaders provide a vital source of ecological knowledge (e.g. about the location of scarce resources or migration routes), but direct tests of this in natural populations are lacking because of the difficulties in quantifying the relevant skills [6,11,15,16].

A key facet of ecological knowledge that is more amenable to experimental investigation is the ability to respond appropriately to the threat of predators. Moreover, as anti-predator response strategies are often costly and may involve an element of risk [17], the experience to discern when such strategies should be implemented would have critical energetic and survival benefits for individual group members. By using a novel playback paradigm where lion roars were broadcast to simulate varying levels of predatory threat—presented by different numbers and sexes of lions—we were able to investigate

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directly how groups of African elephants (*Loxodonta africana*) with leaders of different ages performed at assessing fine-scaled differences in the risk involved. In doing so, we built on techniques previously developed to assess the factors affecting social knowledge in elephant groups [10].

Female African elephants live in matrilineal family units led by the oldest female, or matriarch, who plays a key role in coordinating group movements and responses to threat [10,18–20]. Other than humans, lions are the main natural predators of African elephants [21–23], typically preying on calves of less than 4 years of age [23,24]. Although it is often assumed that lionesses do most of the hunting, male lions are in fact considerably more effective and successful predators when it comes to targeting the largest prey—namely elephants and buffalo [23,25,26]. These large-bodied species often react to lion attacks with cooperative and aggressive defence mechanisms, presenting formidable opponents given their combined strength and dangerous weaponry [25,27]. In such situations, male lions, being on average 50 per cent larger in body mass and considerably more powerful than females [28], are at a distinct advantage. It is notable that the mean group size for successful male lion hunts on elephants is dramatically smaller than that for successful female hunts (1.8 versus 7 in one key study [23]), a finding also reflected in data on lion hunts of buffalo [25]. Moreover, while hunting success typically increases with group size [22,23], it has been demonstrated that male lions have the capability of overpowering a young elephant even when hunting alone [19,23]. Older elephant matriarchs should be more experienced in facing lion encounters than younger matriarchs, and hence we might expect them to be better able to identify the greater risk posed by larger groups of lions and by male lions in particular. Our study, using individually known elephants in Amboseli National Park, Kenya (see §2), provides an unusual opportunity to examine directly how the age of a leader may influence this vital ecological knowledge in a wild population.

Abilities to discriminate between different levels of predatory threat were tested by giving elephant family units playbacks of three lions versus a single lion roaring and, within these categories, roaring from male versus female lions (see §2). In a wide range of social species, individuals may benefit through increased attentiveness, group-defensive behaviour and, in some cases, even approaches to harass predators (mobbing), which can serve both to directly discourage attack and to gain further information about the threat involved [19,29,30]. While mobbing is not widespread among mammals [17], elephants are sufficiently large and well coordinated to search out and direct group attacks on potential predators [19,27,31]. In conjunction with our previous research on social knowledge in African elephants [10], we predicted that groups led by older matriarchs would show greater attentiveness, defensive bunching behaviour and increased likelihood of mobbing approach when faced with lion groups (as opposed to singletons) and with males (as opposed to females).

2. MATERIAL AND METHODS

(a) *Study population*

All playback experiments were conducted on a natural population of African elephants in Amboseli National Park in Kenya between May 2007 and July 2009. This study population encompasses approximately 1500 elephants, with 58 distinct family groups. The Amboseli Elephant Research Project (AERP; http://www.elephanttrust.org) has long-term demographic and behavioural data on the entire population, including detailed ages for all elephants born after 1971, while ages for older individuals were estimated using criteria that are accepted as standard in studies of African elephants [18,32]. All elephants in the population are habituated to the presence of AERP research vehicles.

(b) *Playback procedure*

A total of 72 playbacks were conducted on 39 elephant family groups (1–4 playbacks per group), with a mean of five adults (±2.6 s.d.) in each family. All of the playbacks were carried out between 16.00 and 19.00 h, the time at which lions become active.

The lion roars used in the study had been recorded in the Serengeti National Park, Tanzania using Sennheiser MKH816T microphones and Panasonic SV-250 digital audio tape recorders [33,34]. Eight different playback exemplars were presented, consisting of two matched pairs of one lion versus three lions roaring for both male and female lions [33,34].

In each playback, a single bout of lion roars (mean duration: males, 39 ± 7 s; females, 40 ± 5 s) was broadcast to the subjects from a fieldwork vehicle that was located 100 m from the periphery of the family group. The lion roars were played through custom-built loudspeakers manufactured by Bowers & Wilkins, Steyning, UK and Intersonics Inc., Northbrook, IL, USA. The Bowers & Wilkins loudspeaker was powered by Alpine PDX-1.1000 and MRP-T222 amplifiers and the Intersonics loudspeaker by a Kenwood KAC-PS400M amplifier. In all playbacks the peak sound pressure level at 1 m from the loudspeaker was standardized at 116 dB, comparable with that of natural lion roars [33]. Sound pressure levels were measured with a CEL-414/3 sound level meter.

The first exemplars played to family groups were randomized; repeat playbacks for each sex of lion were then systematically paired with the first exemplars presented, so that across playbacks two factors (number of lions and sex of lion) were systematically varied in turn, while holding others constant. To avoid habituation, a minimum period of 7 days was left between playbacks to the same family. Playbacks were not given to groups with calves of less than one month as our previous work had indicated that the presence of such very young calves may result in abnormally high sensitivity to perceived threats over this short time period [10].

The behavioural responses of the elephants to playback were observed through binoculars and recorded on video, alongside live commentary, using a Canon XM2 video camera. From video analysis, we assessed five key behavioural measures that described the responses of the family group with particular reference to the matriarch (developed from [10]):

- *Matriarch prolonged listening*. Matriarch continues to exhibit evidence of listening response for more than 3 min after playback, where ears are held in a stiff extended position, often with the head slightly raised.
- *Matriarch bunching*. Defensive response to perceived threat by adult females (including the matriarch) and their young, which results in the diameter of the family

group decreasing after the broadcast of the playback stimulus (calculated in terms of elephant body lengths).

— *Matriarch bunching intensity*. The rate at which a defensive bunch of adult females (including the matriarch) and their young occurs. This measure classifies the overall level of threat response, scoring bunching intensity on a 4-point scale as follows:
  (i) 0: No bunching occurred.
  (ii) 1: Subtle reduction in the diameter of the group, elephants remain relaxed and continue with pre-playback behaviours (>3 min for bunch formation).
  (iii) 2: Group forms a coordinated bunch, pre-playback behaviours such as feeding interrupted (1–3 min for bunch formation).
  (iv) 3: Fast and sudden reduction in the diameter of the group, elephants very alert (<1 min for bunch formation).

— *Matriarch approach*. Distinct change in the direction and approach of the matriarch towards the source of playback.

— *Group to matriarch*. Adult females and/or their young respond to playback by moving towards the matriarch.

An independent observer who did not have access to the video commentary and was blind to the playback sequence second-coded 15 per cent of the video records; an overall agreement of 95 per cent was achieved on the binary response variables and the Spearman's ρ correlation on the scores for matriarch bunching intensity was 0.940 ($p < 0.001$). A video clip illustrating the highest level of bunching and mobbing approach is available as electronic supplementary material S1.

(c) *Statistical analyses*

The data were analysed using generalized linear mixed models (GLMMs) in R (www.r-project.org). To test the responses of elephants to lion playbacks as a function of predatory threat (number and sex of the lions) and the age of the matriarch, five key behaviours were used as dependent variables (see above), while the identity of the elephant group was entered as a random factor. Model selection was performed using Akaike's information criterion (AIC) [35], with lower AIC scores indicating better models; however, a more complex model with more degrees of freedom was only selected over a simpler model when the AIC differed by 2 or more [35]. In our main analysis, matriarch age was entered as a continuous variable in each of the GLMMs. A second analysis compared the behavioural responses of the oldest age class of matriarchs (≥ 60 years) with those ≤ 59 years. In all analyses, potentially confounding variables—the number of adult female elephants in the group and their average age [10]—were excluded during model selection as they generated higher AIC scores, with no significant main effects for the variables nor for interactions between them and the sex and number of lions.

3. RESULTS

In all cases, the best model (see §2) to describe the responses of elephants to playbacks included the number of lions, lion sex, matriarch age, and the interaction between lion sex and matriarch age (electronic supplementary material S2). The number of lions had significant effects on four out of five of our behavioural measures, with playback of three lions generating elevated responses as predicted (table 1 and figure 1). The ability to make this basic distinction did not depend on the age of the matriarch, with no significant interactions occurring between matriarch age and the number of lions for any of our response variables. However, matriarch age (entered as a continuous variable) had marked effects on behaviour in response to playbacks of male versus female lions, with significant interactions between age of matriarch and sex of lions (electronic supplementary material S2 and table 1). More specifically, sensitivity to male (versus female) lions increased with matriarch age, matriarchs being more likely to engage in prolonged listening and defensive bunching, and showing a higher bunching intensity when faced with male lion roars as they get older (table 1 and figure 2*a*; see electronic supplementary material S3 for scatter plots of raw data). Groups with older matriarchs were also more likely to approach the source of playback when male roars were presented (table 1 and figure 2*b*). In addition, as reproductive activity shows a marked decline in female elephants between the ages of 55 and 60 years [18,36,37], we investigated the sensitivity of the oldest age class (60 years and above) to the particular threat posed by male lions in a secondary analysis. Comparing these with matriarchs of 59 years and younger (matriarch age was categorical in this analysis: age ≤ 59, $n = 53$; age 60+, $n = 19$), there were significant interactions between matriarch age class and lion sex in our measures of attentiveness and defensive bunching (table 1). The oldest matriarchs were more likely to engage in prolonged periods of listening and exhibited greater defensive bunching (higher probability of bunching and greater bunching intensity) in response to male versus female roars, demonstrating their key role in identifying and responding to this most serious threat (table 1 and figure 2*c*,*d*). Other potentially confounding variables—number of females in the group and mean age of females other than the matriarch—were excluded from the final models because their inclusion produced poorer results when model selection was carried out using AIC scores (see §2).

4. DISCUSSION

These results demonstrate that while elephant family groups react more strongly to three lions than a single lion roaring irrespective of matriarch age, those led by older matriarchs show a greater sensitivity to the more serious threat posed by male lions across all our behavioural responses, including measures of attentiveness, bunching and mobbing approach. The superior ability to detect the presence of male lions at an early stage—evident in the greater probability of older matriarchs engaging in prolonged periods of listening and defensively bunching with their groups—is likely to have significant survival benefits affording better protection for vulnerable calves in particular. Previous researchers have speculated that elephant groups can derive fitness benefits from the improvement in ecological knowledge conferred by an older matriarch, suggesting that this enables better utilization of scarce resources and predator avoidance during periods of drought [15]. Our work provides the first direct experimental evidence that older matriarchs are in fact able to make better decisions when faced with ecological challenges—in this case, the presence of dangerous predators. It thus bridges an important gap between

Table 1. Results of GLMMs investigating matriarch behavioural responses to lion roar playbacks (*a*) with matriarch age entered as a continuous variable and (*b*) with two age classes of matriarchs—the oldest age class (60 years and over) and all younger matriarchs (≤59 years).

dependent variable	parameters	estimate	s.e.	*Z*-value	*p*-value
(*a*)					
matriarch prolonged listening	lion number	1.128	0.336	3.357	0.0008
	lion sex	−5.897	2.903	−2.031	0.04
	matriarch age	−0.005	0.032	−0.157	0.88
	lion sex × matriarch age	0.102	0.054	1.890	0.06
matriarch bunching	lion number	1.237	0.329	3.758	0.0002
	lion sex	−9.567	3.095	−3.091	0.002
	matriarch age	−0.034	0.031	−1.092	0.27
	lion sex × matriarch age	0.166	0.058	2.862	0.004
matriarch bunching intensity	lion number	0.565	0.148	3.814	0.0001
	lion sex	−5.554	1.503	−3.695	0.0002
	matriarch age	−0.014	0.013	−1.113	0.27
	lion sex × matriarch age	0.094	0.026	3.589	0.0003
matriarch approach	lion number	0.076	0.359	0.211	0.83
	lion sex	−7.020	3.780	−1.857	0.06
	matriarch age	−0.030	0.045	−0.659	0.51
	lion sex × matriarch age	0.148	0.070	2.114	0.03
group to matriarch	lion number	1.269	0.375	3.387	0.0007
	lion sex	−6.258	3.053	−2.050	0.04
	matriarch age	−0.007	0.034	−0.219	0.83
	lion sex × matriarch age	0.115	0.057	2.011	0.04
(*b*)					
matriarch prolonged listening	lion number	1.991	0.363	3.302	0.001
	lion sex	−4.808	2.028	−2.370	0.02
	matriarch age class	−0.874	0.962	−0.909	0.36
	lion sex × matriarch age class	3.234	1.457	2.221	0.03
matriarch bunching	lion number	1.279	0.351	3.635	0.0003
	lion sex	−6.597	2.137	−3.088	0.002
	matriarch age class	−1.374	0.965	−1.424	0.15
	lion sex × matriarch age class	4.194	1.532	2.739	0.006
matriarch bunching intensity	lion number	0.542	0.152	3.567	0.0004
	lion sex	−3.016	0.900	−3.350	0.0008
	matriarch age class	−0.409	0.401	−1.020	0.31
	lion sex × matriarch age class	1.825	0.593	3.079	0.002
matriarch approach	lion number	0.028	0.346	0.081	0.94
	lion sex	−1.723	2.139	−0.806	0.42
	matriarch age class	−0.083	1.220	−0.068	0.95
	lion sex × matriarch age class	1.850	1.522	1.216	0.22
group to matriarch	lion number	1.174	0.364	3.224	0.001
	lion sex	−0.361	1.826	−0.198	0.84
	matriarch age class	0.406	0.913	0.444	0.66
	lion sex × matriarch age class	0.042	1.326	0.032	0.98

theoretical predictions about how knowledge might be expected to affect leadership [1,9] and empirical studies, which to date have been largely confined to observational accounts [6,7,15].

It has recently been suggested that prey species with large brains relative to their body size may be better at evading predators because they can more effectively adjust their behavioural responses to specific encounters [38]. Our results indicate that elephants can indeed make important distinctions between threat levels even within a predator class, in parallel with research showing their ability to distinguish human ethnic groups that pose different levels of threat on the basis of olfactory and visual cues [39]. Moreover, the results demonstrate how the accumulated knowledge of the oldest individuals may have an overriding influence on the effectiveness of anti-predator decisions made by the social group as a whole, and they highlight the vital role of such individuals in natural populations [10]. This is a particularly important consideration where relatively large-brained social species have the opportunity to accumulate ecological information over long lifespans and considerable disparities in knowledge between different individuals are therefore likely to arise.

While we cannot be sure that matriarch age will correlate with experience of lions in every instance, it is reasonable to assume that as matriarchs get older they will accumulate exposure to the particular risks posed by lions. Although elephants are relatively impregnable to most predators by virtue of their large body size and aggressive group defence, lions remain a very significant

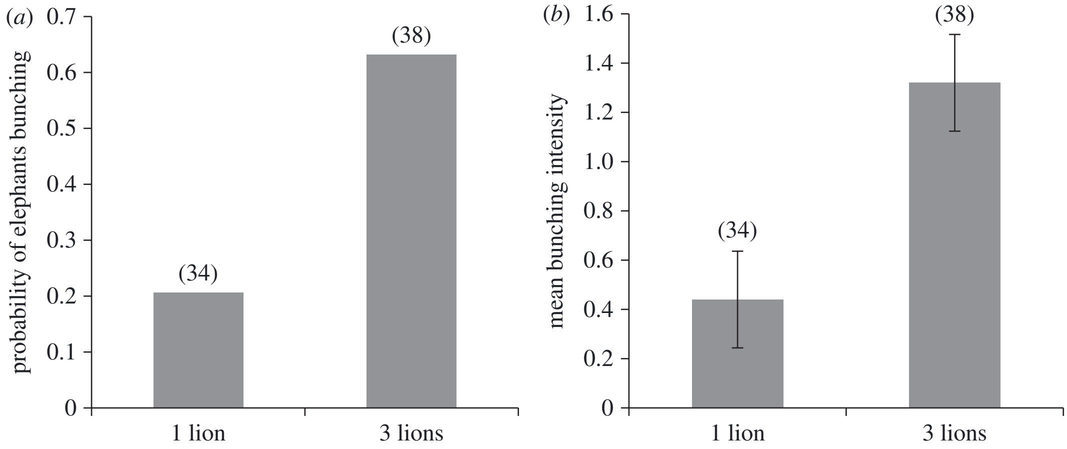

Figure 1. Elephant response to the scale of predation threat as simulated by one versus three roaring lions: (*a*) probability of matriarch bunching and (*b*) matriarch bunching intensity (mean ± s.e.m.). Number of playbacks given in parentheses.

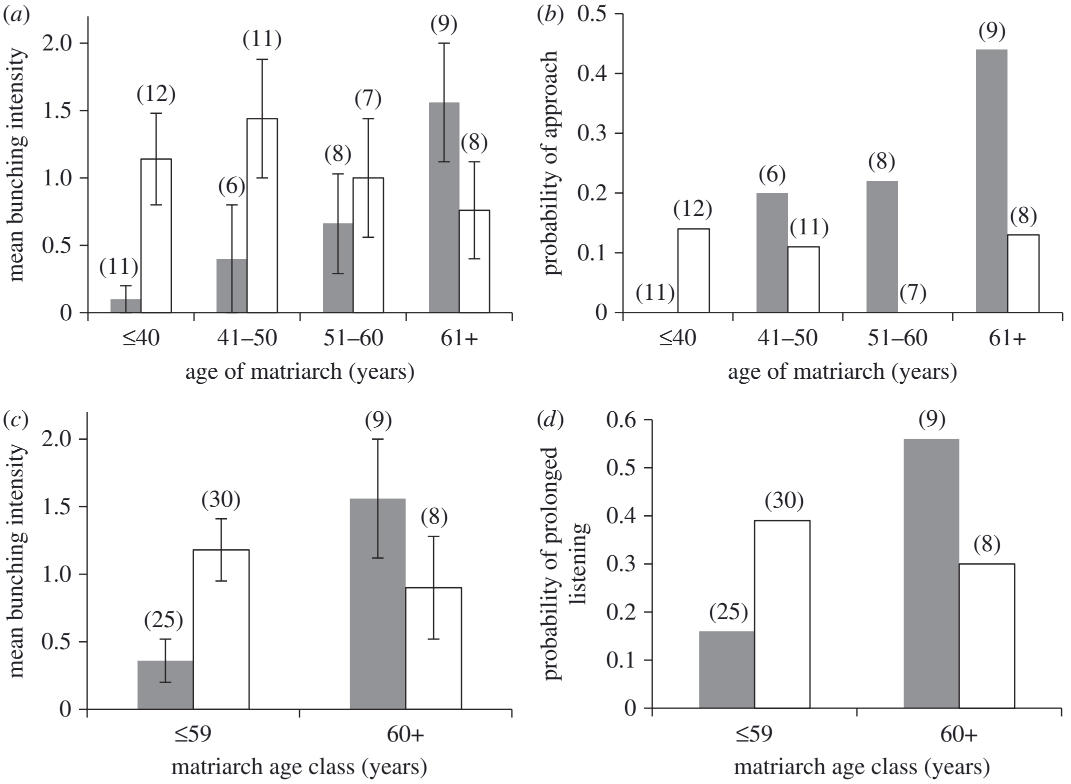

Figure 2. Behavioural responses of matriarchs and their family groups to male (grey bars) versus female (white bars) lions depicted as a function of increasing matriarch age for illustration (see table 1 for detailed analysis and electronic supplementary material S3 for raw data). (*a*,*c*) Mean bunching intensity (±s.e.m.); (*b*) probability of approach; and (*d*) probability of prolonged listening. Number of playbacks given in parentheses.

threat and have the potential to shape the evolution of specific anti-predator behaviour [23,27]. Despite this, the occurrence of lion predation on elephants is typically a rare event [24]. Moreover, the sex ratio of adult lions in most populations is heavily female-biased [40,41], with a 1 M : 1.8 F ratio in the Amboseli population [42], which may lower the exposure to male-specific cues further still. Our experiments test elephant abilities to make a rather subtle distinction—between characteristics defining male and female roars—and while sex-specific acoustic differences have been documented in lion roars [43], these are not overtly obvious to human listeners. It is perhaps not surprising therefore that considerable experience, built up over a long lifespan, should enable older individuals to perform better in this task.

In common with humans and certain other social animals, in particular pilot and killer whales, female elephants can have a significant post-reproductive lifespan—although it is currently unclear whether they exhibit menopause [18,37,44,45]. While reproductive activity declines among this oldest age class, they show no signs of increased vulnerability to predators, and in fact are often the largest individuals within family groups [31]. Indeed, our results suggest that this oldest age class of females can provide significant benefits for their groups in the context of decision-making about predators. As a result of typically no longer having young offspring, they may be able to take a more active role in group defence and could be more attentive to ecological signals. However, if families with older matriarchs were simply more reactive, we would predict an overall increase in sensitivity to lion roars rather than the greater differential response to male versus female roars reported here. Instead, older matriarchs appear more adept at associating male lion roars with a greater level of threat. Observational data also indicate that it is individuals of 60 years and older who have the greatest success in leading large-scale foraging movements [16]—again suggesting that in decisions relating to ecological knowledge, the level of experience that these oldest individuals possess may prove critical. Recent research on humans has demonstrated the key role that grandmothers can play in enhancing the reproductive success of their offspring by assisting in child-rearing after their own reproduction has ceased [46,47]. Our findings indicate that through their greater ecological knowledge, older females can also represent a crucial resource in other long-lived cognitively advanced mammals that live in kin-based social groups.

Leadership is known to be crucial in the coordination of human groups, but we are only now beginning to appreciate its role in animal societies [3,4]. In order to fully understand how animal groups are organized and achieve collective action, it is vital to determine the advantages that a leader may bring to group decision-making. Our study provides the first empirical evidence that individuals within a social group may benefit directly from the influence of an older leader because of their enhanced ability to make crucial decisions about predatory threat. It thus generates important insights into selection for longevity and the evolution of a sophisticated social structure that supports the coordinating role of a single older leader. Such abilities are likely to be highly relevant in other large-brained, long-lived social species where older individuals play a key role in coordinating group activities.

This work complies with the Association for the Study of Animal Behaviour/Animal Behaviour Society guidelines for the use of animals in research, and received approval from the Ethical Review Committee at the University of Sussex.

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REFERENCES

1 Conradt, L. & Roper, T. J. 2003 Group decision-making in animals. *Nature* **421**, 155–158. (doi:10.1038/nature01294)

2 Conradt, L., Krause, J., Couzin, I. D. & Roper, T. J. 2009 'Leading according to need' in self-organizing groups. *Am. Nat.* **173**, 305–312. (doi:10.1086/596532)

3 King, A. J., Johnson, D. D. P. & Van Vugt, M. 2009 The origins and evolution of leadership. *Curr. Biol.* **19**, 911–916. (doi:10.1016/j.cub.2009.07.027)

4 King, A. J. 2010 Follow me! I'm a leader if you do; I'm a failed initiator if you don't? *Behav. Proc.* **84**, 671–674. (doi:10.1016/j.beproc.2010.03.006)

5 King, A. J., Douglas, C. M. S., Huchard, E., Isaac, N. J. B. & Cowlishaw, G. 2008 Dominance and affiliation mediate despotism in a social primate. *Curr. Biol.* **18**, 1833–1838. (doi:10.1016/j.cub.2008.10.048)

6 Maransky, B. P. & Bildstein, K. L. 2001 Follow your elders: age related differences in the migration behavior of broad-winged hawks at hawk mountain sanctuary, Pennsylvania. *Wilson Bull.* **113**, 350–353. (doi:10.1676/0043-5643(2001)113[0350:FYEARD]2.0.CO;2)

7 Wright, R., Stone, R. E. & Brown, N. 2003 Communal roosts as structured information centres in the raven, *Corvus corax*. *J. Anim. Ecol.* **72**, 1003–1014. (doi:10.1046/j.1365-2656.2003.00771.x)

8 Lusseau, D. & Conradt, L. 2009 The emergence of unshared consensus decisions in bottlenose dolphins. *Behav. Ecol. Sociobiol.* **63**, 1067–1077. (doi:10.1007/s00265-009-0740-7)

9 Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. 2005 Effective leadership and decision-making in animal groups on the move. *Nature* **433**, 513–516. (doi:10.1038/nature03236)

10 McComb, K., Moss, C., Durant, S. M., Baker, L. & Sayialel, S. 2001 Matriarchs as repositories of social knowledge in African elephants. *Science* **292**, 491–494. (doi:10.1126/science.1057895)

11 Greve, W., Kierdorf, H. & Kierdorf, U. 2009 The Akela effect—is there an evolutionary benefit from senators in mammals? *Biol. Hyp.* **2**, 213–216.

12 McAuliffe, K. & Whitehead, H. 2005 Eusociality, menopause and information in matrilineal whales. *Trends Ecol. Evol.* **20**, 650. (doi:10.1016/j.tree.2005.09.003)

13 Van Vugt, M. 2006 Evolutionary origins of leadership and followership. *Pers. Soc. Psychol. Rev.* **10**, 354–371. (doi:10.1207/s15327957pspr1004_5)

14 Grossmann, I., Na, J., Varnum, M. E. W., Park, D. C., Kitayama, S. & Nisbett, R. E. 2010 Reasoning about social conflicts improves into old age. *Proc. Natl Acad. Sci. USA* **107**, 7246–7250. (doi:10.1073/pnas.1001715107)

15 Foley, C., Pettorelli, N. & Foley, L. 2008 Severe drought and calf survival in elephants. *Biol. Lett.* **4**, 541–544. (doi:10.1098/rsbl.2008.0370)

16 Mutinda, H., Poole, J. H. & Moss, C. J. 2011 Decision-making and leadership in using the ecosystem. In *The Amboseli elephants: a long-term perspective on a long-lived mammal* (eds C. J. Moss, H. Croze & P. C. Lee), pp. 246–259. Chicago, IL: The University of Chicago Press.

17 Caro, T. 2005 *Antipredator defenses in birds and mammals*. Chicago, IL: The University of Chicago Press.

18 Moss, C. 2001 The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *J. Zool.* (*Lond.*) **255**, 145–156. (doi:10.1017/S0952836901001212)

19 Douglas-Hamilton, I. 1972 The ecology and behaviour of the African elephant: the elephants of Lake Manyara. PhD thesis, University of Oxford, Oxford, UK

20 Wittemyer, G., Douglas-Hamilton, I. & Getz, W. M. 2005 The socio-ecology of elephants: analysis of the processes creating multileveled societies. *Anim. Behav.* **69**, 1357–1371. (doi:10.1016/j.anbehav.2004.08.018)

21 Joubert, D. 2006 Hunting behaviour of lions (*Panthera leo*) on elephants (*Loxodonta africana*) in the Chobe National Park, Botswana. *Afr. J. Ecol.* **44**, 279–281. (doi:10.1111/j.1365-2028.2006.00626.x)

22 Power, R. J. & Compion, R. X. S. 2009 Lion predation on elephants in the Savuti, Chobe National Park, Botswana. *Afr. Zool.* **44**, 36–44. (doi:10.3377/004.044.0104)
23 Loveridge, A. J., Hunt, J. E., Murindagomo, F. & Macdonald, D. W. 2006 Influence of drought predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah. *J. Zool.* (*Lond.*) **270**, 523–530. (doi:10.1111/j.1469-7998.2006.00181.x)
24 Ruggiero, R. G. 1991 Opportunistic predation on elephant calves. *Afr. J. Ecol.* **29**, 86–89. (doi:10.1111/j.1365-2028.1991.tb00823.x)
25 Funston, P. J., Mills, M. G. L. & Biggs, H. C. 2001 Factors affecting the hunting success of male and female lions in the Kruger National Park. *J. Zool.* (*Lond.*) **253**, 419–431. (doi:10.1017/S0952836901000395)
26 Funston, P. J., Mills, M. G. L., Biggs, H. C. & Richardson, P. R. K. 1998 Hunting by male lions: ecological influences and socioecological implications. *Anim. Behav.* **56**, 1333–1345. (doi:10.1006/anbe.1998.0884)
27 Owen-Smith, R. N. 1992 *Megaherbivores: the influence of very large body size on ecology*. Cambridge, UK: Cambridge University Press.
28 Smuts, G. L., Robinson, G. A. & Whyte, I. J. 1980 Comparative growth of wild male and female lions (*Panthera leo*). *J. Zool.* (*Lond.*) **190**, 365–373. (doi:10.1111/j.1469-7998.1980.tb01433.x)
29 Graw, B. & Manser, M. 2007 The function of mobbing in cooperative meerkats. *Anim. Behav.* **74**, 507–517. (doi:10.1016/j.anbehav.2006.11.021)
30 Caro, T. M., Graham, C. M., Stoner, C. J. & Vargas, J. K. 2004 Adaptive significance of antipredator behaviour in artiodactyls. *Anim. Behav.* **67**, 205–228. (doi:10.1016/j.anbehav.2002.12.007)
31 Moss, C. 1988 *Elephant memories*. Chicago, IL: The University of Chicago Press.
32 Moss, C. 1996 Getting to know a population. In *Studying elephants* (ed. K. Kangwana), pp. 58–74. Nairobi, Kenya: African Wildlife Foundation.
33 McComb, K., Packer, C. & Pusey, A. 1994 Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Anim. Behav.* **47**, 379–387. (doi:10.1006/anbe.1994.1052)
34 Grinnell, J. & McComb, K. 1996 Female grouping as a defense against infanticide by males: evidence from field playback experiments on African lions. *Behav. Ecol.* **7**, 55–59. (doi:10.1093/beheco/7.1.55)
35 Burnham, K. P. & Anderson, D. R. 1998 *Model selection and inference: a practical information-theoretic approach*. New York, NY: Springer.
36 Freeman, E. W., Whyte, I. & Brown, J. 2008 Reproductive evaluation of elephants culled in Kruger National Park, South Africa between 1975 and 1995. *Afr. J. Ecol.* **47**, 192–201. (doi:10.1111/j.1365-2028.2008.00957.x)
37 Laws, R. M., Parker, I. S. C. & Johnstone, R. C. B. 1975 *Elephants and their habitats: the ecology of elephants in North Bunyoro, Uganda*. Oxford, UK: Clarendon Press.
38 Shultz, S. & Dunbar, R. I. M. 2006 Chimpanzee and felid diet composition is influenced by prey brain size. *Biol. Lett.* **2**, 505–508. (doi:10.1098/rsbl.2006.0519)
39 Bates, L., Sayialel, K. N., Njiraini, N. W., Moss, C. J., Poole, J. H. & Byrne, R. W. 2007 Elephants classify human ethnic groups by odor and garment color. *Curr. Biol.* **17**, 1938–1942. (doi:10.1016/j.cub.2007.09.060)
40 Creel, S. & Creel, N. M. 1997 Lion density and population structure in the Selous Game Reserve: evaluation of hunting quotas and off take. *Afr. J. Ecol.* **35**, 83–93. (doi:10.1111/j.1365-2028.1997.062-89062.x)
41 Packer, C., Herbst, L., Pusey, A. E., Bygott, J. D., Hanby, J. P., Cairns, S. & Borgerhoff-Mulder, M. 1988 Reproductive success of lions. In *Reproductive success* (ed. T. H. Clutton-Brock), pp. 363–383. Chicago, IL: University of Chicago Press.
42 van der Werf, M. 2008 Lions (*Panthera leo*) of Amboseli National Park: a study on lion ecology in relation to conflict with livestock owners. Master's thesis, University of Leiden, The Netherlands.
43 Pfefferle, D., West, P. M., Grinnell, J., Packer, C. & Fischer, J. 2006 Do acoustic features of lion, *Panthera leo*, roars reflect sex and male condition? *J. Acoust. Soc. Am.* **121**, 3947–3953. (doi:10.1121/1.2722507)
44 Johnstone, R. A. & Cant, M. A. 2010 The evolution of menopause in cetaceans and humans: the role of demography. *Proc. R. Soc. B* **277**, 3765–3771. (doi:10.1098/rspb.2010.0988)
45 Sukumar, R. 1992 *The Asian elephant*. Cambridge, UK: Cambridge University Press.
46 Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M. & Russel, A. F. 2004 Fitness benefits of prolonged reproductive lifespan in women. *Nature* **428**, 178–181. (doi:10.1038/nature02367)
47 Shanley, D. P., Sear, R., Mace, R. & Kirkwood, T. B. L. 2007 Testing evolutionary theories of menopause. *Proc. R. Soc. B* **274**, 2943–2949. (doi:10.1098/rspb.2007.1028)

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RESEARCH ARTICLE

Housing and Social Environments of African (*Loxodonta africana*) and Asian (*Elephas maximus*) Elephants in North American Zoos

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Abstract

We evaluated 255 African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants living in 68 North American zoos over one year to quantify housing and social variables. All parameters were quantified for the both the day and the night and comparisons were made across these time periods as well as by species and sex. To assess housing, we evaluated not only total exhibit size, but also individual animals' experiences based on the time they spent in the unique environments into which the exhibits were subdivided. Variables developed to assess housing included measurements of area as a function of time (Total Space Experience), environment type (Indoor, Outdoor, In/Out Choice) and time spent on hard and soft flooring. Over the year, Total Space Experience values ranged from 1,273 square feet to 169,692 square feet, with Day values significantly greater than Night values (p<0.001). Elephants spent an average of 55.1% of their time outdoors, 28.9% indoors, and 16% in areas with a choice between being in or out. Time spent on hard flooring substrate ranged from 0% to 66.7%, with Night values significantly greater than Day (p<0.001). Social factors included number of animals functionally housed together (Social Experience) and social group characteristics such as time spent with juveniles and in mixed-sex groups. Overall Social Experience scores ranged from 1 to 11.2 and were significantly greater during the Day than at Night (p<0.001). There were few significant social or housing differences between African (N = 138) and Asian (N = 117) species or between males (N = 54) and females (N = 201). The most notable exception was Total Space Experience, with African and male elephants having larger Total Space Experience than Asian and female elephants, respectively (P-value<0.05). The housing and social variables evaluated herein have been used in a series of subsequent epidemiological analyses relating to various elephant welfare outcomes.

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Introduction

Addressing questions regarding zoo elephant welfare is important, as significant public attention has been directed toward the housing and care of elephants in zoos. Of particular interest is an enhanced understanding of elephant housing and management as they relate to welfare outcomes. In order to determine the factors most salient to elephant welfare and inform evidence-based elephant care, elephant housing and management and their associations with elephant welfare must be systematically assessed in zoological settings.

Comprehensive animal welfare assessment relies on the collection and analysis of two distinct, yet related, types of data [1]. The first describes housing features and management practices—also known as resource-based measures, and the second requires the measurement of welfare indicators such as behavior, physical health and physiology–also known as outcome-based measures. In most cases resource-based measures must be assessed in conjunction with welfare outcomes in order to understand the animals— responses to variation in environmental parameters. This can be accomplished either through experimental means by comparing welfare outcomes of animals exposed to different housing or care conditions (i.e. [2,3,4,5]) or through epidemiological studies correlating resource-based parameters and welfare outcomes within a diverse population (i.e. [6,7,8]).

Using resource-based parameters as independent variables in an epidemiological study requires the development of measurement methods that account for significant variation in form and practice within the population. This paper focuses on the development and analysis of variables relating to housing and social aspects of elephant management in accredited zoos in North America. The dual purpose was to provide a comprehensive review of elephant housing and social management in zoos and to generate appropriate independent variables to be used in subsequent epidemiological analyses of behavioral [9,10,11] physiological [12] and health-related [13,14] welfare indicators.

Our study focused on environmental and social factors because both of these play an important role in the behavior and ecology of wild elephants [15, 16, 17, 18] and because research in many managed species demonstrates that animals' experiences of physical space and social milieu play a critical role in their welfare. For example, studies have shown that for social species, isolation, exposure to groups of unnatural size or composition, or repeated disruption of established social groups have detrimental effects on physiology behavior, and e psychological state [19, 20]. Conversely, social environments can be used to promote positive welfare in managed animals by increasing mental stimulation, promoting social learning and the expression of highly motivated and/or natural behaviors, and by buffering stress [21, 22].

The physical environment also plays an important role in the welfare of managed animals across contexts and species [23]. One key component of the physical environment is the amount of space to which an animal has access. Variation in the amount of space available to animals has been shown to affect welfare, although these effects vary. Some studies show that experimental decreases in space allowance result in negative effects such as increases in aggressive behaviors, adrenocortical secretion [3], and stereotypic behavior [4,24]. Other studies, however, have failed to demonstrate associations between smaller spaces and indicators of compromised welfare [6, 25, 26, 27]. Differences in the effect of space allowance on welfare indicators such as stereotypic behavior may be attributable to the natural history of the species such that spatial restriction plays a larger role in welfare outcomes for species with large home ranges (e.g. carnivores:[28]).

The quality of space experienced by animals is also important. For elephants, flooring and substrate composition may be particularly critical aspects of environmental quality. Hard surfaces have been associated with poor elephant foot and joint conditions including trauma to foot pads, toenails, joints and other musculoskeletal structures [29, 30, 31, 32]. Studies in cattle have shown similar trauma associated with hard surfaces [33, 34], as well as a protective effect of soft substrates [35].

To date, no studies have systematically evaluated the effects of social and housing factors on the welfare of zoo elephants, nor is there information about how species and sex contribute to variation in these factors. Given the importance of resource-based measures in developing an understanding of elephant management and facilitating welfare assessment, our study was designed to collect detailed information about the housing and social management of zoo elephants in a way that captured the variation in these factors both within zoos and across the zoo population. Subsequently, we translated these data into standardized variables suitable for descriptive and comparative analyses. A similar approach was taken in a related manuscript that to quantifies other elephant management factors for this population including enrichment, training, feeding and exercise [36].

Materials and Methods

Ethics Statement

This study was authorized by the management at each participating zoo and, where applicable, was reviewed and approved by zoo research committees. In addition the study protocol was reviewed and approved by the Zoological Society of San Diego Institutional Animal Care and Use Committee N.I.H. Assurance A3675-01; Protocol 11–203. The study was non-invasive.

Data Collection

The evaluation of housing and social resource-based parameters in multi-institutional zoo studies is typically conducted using facility-level or herd-level surveys [36, 37]. However, exploratory conversations with participating elephant care professionals at the outset of this project revealed significant variation not only between zoos, but also within zoos with respect to how individual elephants were managed spatially and socially. Within zoos, elephant managers often vary housing options and social groupings to account for time of day, time of year, herd dynamics, husbandry schedules, and individual elephant characteristics. Therefore, in order to accurately measure factors related to zoo elephants' housing and social environments across the population of elephants, we developed a data model and accompanying software interface to capture both the range in complexity between zoos and the variability at the individual elephant level within zoos.

The process for capturing these data included two integrated steps completed by each participating zoo. The first step was the zoo registration process, which captured data relating to demographics, exhibit characteristics, and social groupings (Table 1). The second step was submission of monthly Management Logs reporting housing and social time budgets for each elephant. Each zoo completed these logs for day management and for night management every month for 12 months. To account for variation and fluctuation in how day and night were defined by the zoos, the number of hours associated with day management (Day) and night management (Night) were reported by each zoo on a monthly basis. These management periods generally coincided with employee schedules (e.g., day management meant that employees were onsite), but varied within and between facilities due to seasonal and geographic differences.

Social time budgets were based on how each individual elephant's time was spent in each of the social groups of which it was a member. Social groups were defined as being comprised of elephants that shared unrestricted space during the course of normal social management. Additionally, when elephants were reported to spend time housed alone, managers were asked

Table 1. Data captured through the zoo registration process and web portal that were used as the basis for variable creation.

Data Category	Parameters
Demographics	
For Each Elephant	Name
	Date of Birth
	Species
	Sex
	Studbook Number
Exhibit	
Enclosures: defined as each individual unit of space available for housing elephants.	Area
	Exposure (Indoors / Outdoors / In/Out Choice)
	Flooring Substrate Types and Percent Coverages
Environments: defined as the ways that enclosures were used individually or in combination (by opening doors/gates to join adjacent areas) to house elephants	Included Enclosures
	Area*
	Exposure (Indoors / Outdoors / In/Out Choice)*
	Flooring Substrate Types and Percent Coverages*
Social Groupings	
Social Groups: defined as all groupings of elephants used in the course of normal management. Elephants considered to be in a social group must share unrestricted space.	Members of Group
	Time Period (when each group occurs): Day, Night or Both

*Calculated by software based on enclosure level data

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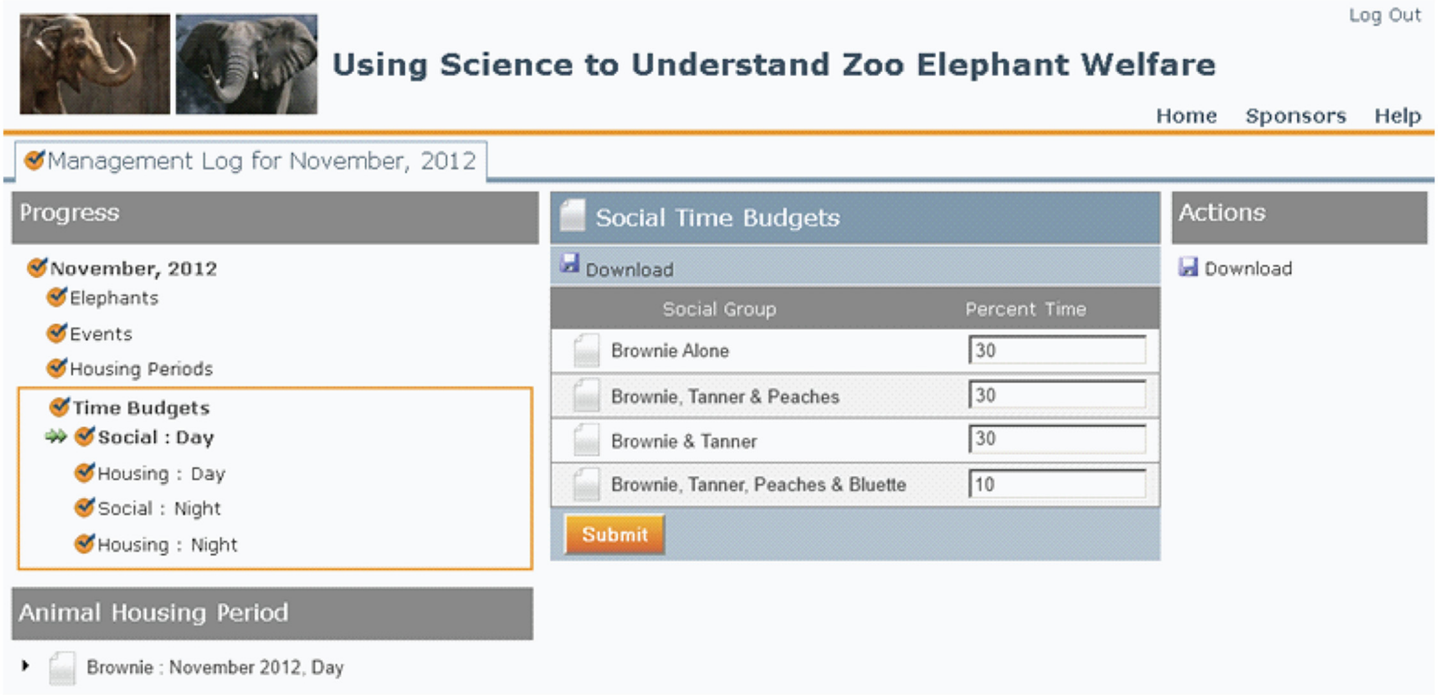
to report the percentage of time housed alone that was spent with restricted access (via a barrier) to one or more other elephants. An example of the software interface for the social time budget of an elephant is provided in Fig 1.

Housing time budgets allowed zoos to report how much time each social group spent in each of the available environments. Environments were defined as single or multiple contiguous units of space in which elephants were housed during the course of normal management. An example of the software interface for the housing time budget is provided in Fig 2.

All data were stored in a relational database using SQL server. Confidentiality of data was ensured by using randomly generated unique alpha-numeric codes for zoos and elephants. Data were exported to MS Excel (Seattle, WA) and SAS 9.3 (Cary, NC) for variable creation.

Subjects

Monthly Management Logs were completed by 68 zoos, which represented 96% of the AZA accredited elephant holding institutions in 2012. Elephant-level data were only included for analysis if the elephant was not born, did not die, and was not transferred between zoos during the period from January 1, 2012 to December 31, 2012. These criteria were met by 255 elephants, 138 of which were African (110 females and 28 males) and 117 of which were Asian (91 females and 26 males). Cases where sample sizes varied due to data availability / applicability are noted in the results.



Social Group	Percent Time
Brownie Alone	30
Brownie, Tanner & Peaches	30
Brownie & Tanner	30
Brownie, Tanner, Peaches & Bluette	10

Fig 1. Illustration of the process by which elephant managers provided social time budget information for an elephant (Brownie) that was a member of 4 social groups and spent time in each social group option during the Day during November. This interface was presented sequentially for all elephants at a zoo. When applicable, fields were auto-filled to reflect the fact that by definition time assigned to one member of a social group must apply to all members of that social group. The software also verified that the values entered summed to 100.

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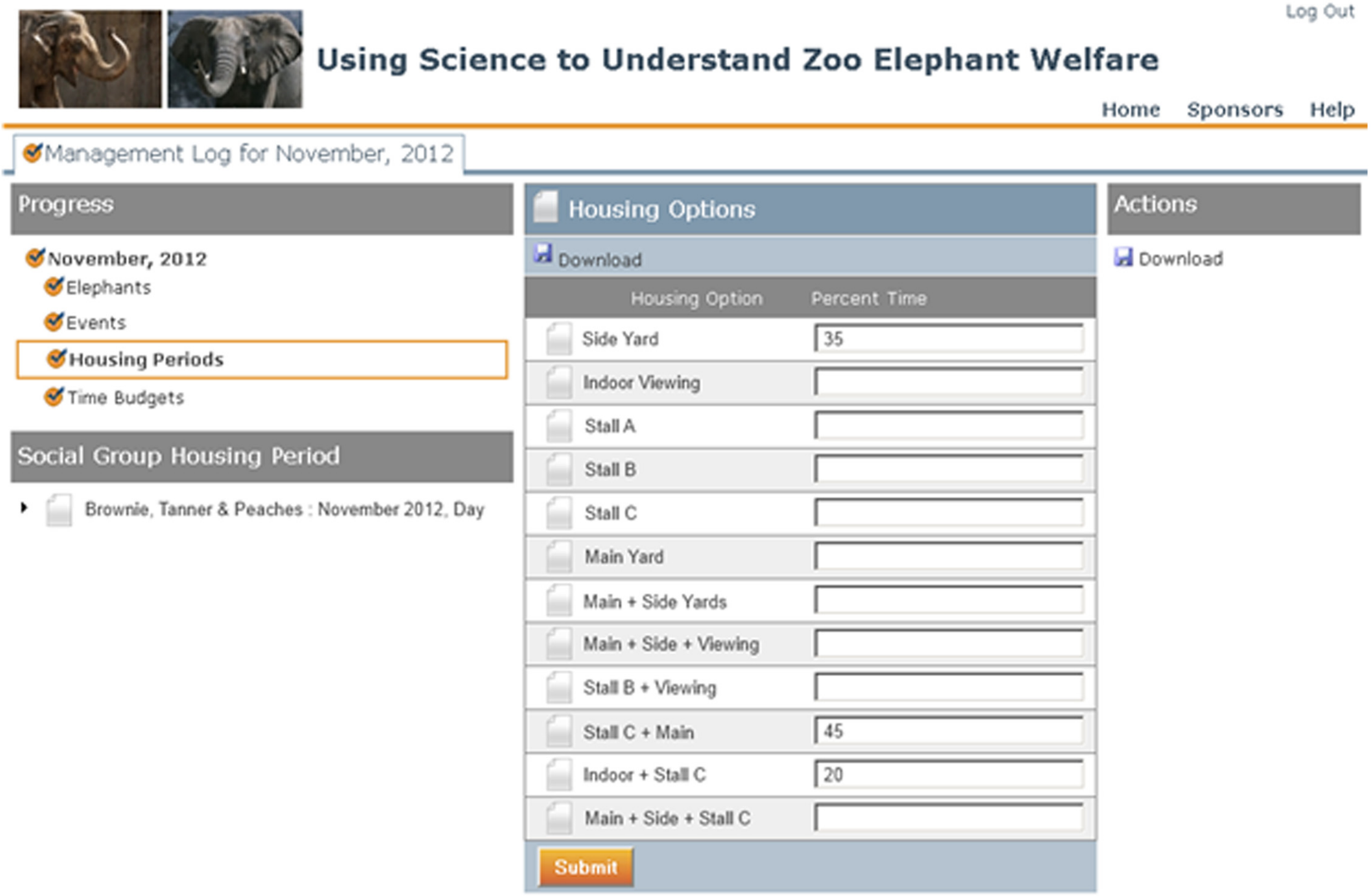
Variable Creation

While data were collected monthly, all results presented herein represent yearly averages. Descriptions of all calculated variables are presented in Table 2; the following paragraphs describe these variables in more detail.

Social. Each elephant's social situation was evaluated using several distinct variables. Herd Size was defined as the maximum number of elephants present at a zoo during the 2012 study period. Within a zoo, elephants were combined into social groups for management purposes and individual elephants spent varying amounts of time in the social groups of which they were members. Social groups were defined as groups of elephants that shared physical space without an intervening barrier, and each Social Group was comprised of a unique set of animals. Animal Contact was defined as the maximum number of unique elephants (not including itself) with which an elephant shared social groups and Social Group Contact was defined as the maximum number of unique social groups of which an elephant was a member per management period (Day, Night, and Overall) throughout the study.

The percent of time each elephant spent in each social group during each management period (Day, Night, and Overall) each month was taken from the monthly Management Logs. Social Experience (Eq 1) was calculated by taking the size of each social group in which an elephant spent time, multiplying it by the percentage of time the elephant spent in that social group and then averaging these weighted social group sizes. Social Experience was calculated per management period (Day, Night, and Overall). Relative Social Experience Change was calculated by taking the difference between Day Social Experience and Night Social Experience and dividing by the Day Social Experience. This relative value typically ranged from -1 to 1,



Housing Option	Percent Time
Side Yard	35
Indoor Viewing	
Stall A	
Stall B	
Stall C	
Main Yard	
Main + Side Yards	
Main + Side + Viewing	
Stall B + Viewing	
Stall C + Main	45
Indoor + Stall C	20
Main + Side + Stall C	

Fig 2. Illustration of the process by which elephant managers provided housing time budget information for the hypothetical social group "Brownie, Tanner and Peaches", which spent time in three environments during the Day during November. This interface was presented sequentially for all social groups and the software assigned values to all members of the social group in the database. The software also verified that the values entered summed to 100.

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with values close to zero indicating similar day and night experiences, values close to 1 indicating a larger social experience during the day, and values close to -1 indicating a larger social experience at night.

$$\mathit{Social\ Experience} = \frac{\sum_{i=1}^{n}((\mathit{percent\ time\ spent\ in\ social\ groups}\ x_i) * (\mathit{animal\ count\ in\ social\ group}\ x_i))}{\sum_{i=1}^{n}(\mathit{percent\ time\ spent\ in\ social\ group}\ x_i)} \qquad (1)$$

Social groups were classified by the presence or absence of a juvenile (defined as 7 years of age or younger), the presence of one or both sexes, and the number of elephants in the group. Elephants housed without a social partner (Social Group size of 1) were considered to be Housed Separately. An elephant was considered Housed Separately with Restricted Physical Access if it could see and/or touch another elephant but was in a physically separated environment. Percent Time in a social group was calculated by first summing the percent time spent in that social group in a given month, then averaging the monthly sums. This calculation was

Table 2. Description of variables created from the space and social information on manager's survey, indicating unit of analysis, unit of measurement, time scale for which each variable was evaluated, and calculation method.

Variable	Category	Unit of Analysis	Unit*	Time Scale	Description
Total Exhibit Size		Zoo	(ft^2)		Total area of space available to elephants at zoo
Herd Size		Zoo			Total number of elephants at zoo
Environment Count		Zoo			Total number of unique spaces into which an exhibit could be configured
Contact	Environment	Elephant		Overall, Day, Night	Maximum number of unique environments an elephant was housed in
	Animal	Elephant		Overall, Day, Night	Maximum number of unique elephants focal animal is in contact with
	Social Group	Elephant		Overall, Day, Night	Maximum number of unique social groups focal animal is part of
Space Experience					The average weighted (by percent time) size of all environments in which an elephant spent time.
	Total	Elephant	(ft^2)	Overall, Day, Night	For all environment types
	Indoor	Elephant	(ft^2)	Overall, Day, Night	For indoor environments only
	In/Out Choice	Elephant	(ft^2)	Overall, Day, Night	For environments where there is a choice of indoors or outdoors
	Outdoor	Elephant	(ft^2)	Overall, Day, Night	For outdoor environments only
Space Experience by Elephant		Elephant	(ft^2)	Overall	The area of all environments in which an elephant spent time, divided by the number of elephants sharing each environment, weighted by the percent time spent in each environment and averaged.
Relative Space Experience Change		Elephant			(Total Day Space Experience—Total Night Space Experience)/(Total Day Space Experience)
Proportion Space Experienced		Elephant	%		Proportion of Total Overall Space Experience to Total Exhibit Size
Social Experience		Elephant		Overall, Day, Night	The average weighted (by percent time) size of all social groups in which an elephant spent time.
Relative Social Experience Change		Elephant			(Total Day Social Experience—Total Night Social Experience)/(Total Day Social Experience)
Proportion Social Experienced		Elephant	%		Proportion of Overall Social Experience to Herd Size
Percent Time					Sum of monthly percent time spent in category, averaged over time period
	Indoor	Elephant	%	Overall, Day, Night	Time spent in indoor environments
	In/Out Choice	Elephant	%	Overall, Day, Night	Time spent in environments with an indoor/outdoor choice
	Outdoor	Elephant	%	Overall, Day, Night	Time spent in outdoor environments
	Soft Substrate	Elephant	%	Overall, Day, Night	Time spent in environment with 100% grass, sand, or rubber substrate
	Hard Substrate	Elephant	%	Overall, Day, Night	Time spent in environment with 100% concrete or stone aggregate substrate
	Dirt Substrate	Elephant	%	Overall, Day, Night	Time spent in environment with 100% dirt substrate
	Juveniles (<7 years old)	Elephant	%	Overall, Day, Night	Time spent in social groups where an elephant 7 years or younger was present
	Mixed Sex Groups	Elephant	%	Overall, Day, Night	Time spent in social groups where both males and females were present
	Housed Separately	Elephant	%	Overall, Day, Night	Time spent housed alone (Social group of 1)
	Housed Separately with Restricted Physical Access	Elephant	%	Overall, Day, Night	Percentage of elephant's time Housed Separately with contact through a barrier.

*Area based variables are presented as ft^2 for consistency with companion papers. Metric equivalents are available in (S1 Table).

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performed per social group type (with Juveniles, with Mixed Sex, Housed Separately, and Housed Separately with Restricted Physical Access) and per housing period (Day, Night, and Overall).

Housing. Ten separate housing variables were calculated. Total Exhibit Size was defined as the total area (square feet) of space available to elephants within a zoo. Exhibits are comprised of multiple units of space (Enclosures), and Environments are the unique ways in which

Enclosures are used singly or in combination to house elephants. The total number of Environments available at each zoo was tabulated as Environment Count, and the maximum number of unique environments that each elephant spent time in during the 12 month study period was calculated as Environment Contact.

Environments were classified as being indoors, outdoors, or comprised of both indoor and outdoor areas (In/Out Choice). The percent of time each elephant spent in each Environment during the Day and Night for each month was calculated by multiplying the percent time the elephant spent in a given Social Group by the percent time the Social Group spent in each Environment. Using this information, several elephant level space variables were created. Space Experience (Eq 2) was calculated by taking the size of each environment in which an elephant spent time, multiplying it by the percentage of time the elephant spent in that environment and then averaging these weighted environment sizes.

Space Experience was calculated for all environment types combined (Total), and for each of the three environment types separately (Indoor, Outdoor, and In/Out Choice). Space Experience for each of these was calculated for Day, Night and Overall. So, for example, the Night Outdoor Space Experience describes the average size of the outdoor environments the elephant spent time in at night, weighted by the amount of time spent in each outdoor environment at night. Throughout the rest of the manuscript, similar differentiations will be presented using a "per X" designation, e.g. Space Experience was calculated per environment type (Total, Indoor, Outdoor, and In/Out Choice) and per housing period (Day, Night, and Overall).

$$\mathit{Space\ Experience} = \frac{\sum_{i=1}^{n}((\mathit{percent\ time\ spent\ in\ environment}\ x_i) * (\mathit{environment}\ x_i\ \mathit{size}))}{\sum_{i=1}^{n}(\mathit{percent\ time\ spent\ in\ environment}\ x_i)} \quad (2)$$

Space Experience by Elephant was calculated much as the Total Space Experience variable was calculated, except that environment area was divided by the total number of elephants using the space at that time. This allowed for Space Experience to reflect elephant density within environments. Relative Space Experience Change was calculated by taking the difference between the Day Total Space Experience and the Night Total Space Experience and dividing by the Day Total Space Experience. This relative value typically ranged from -1 to 1, with values closer to zero indicating similar Day and Night Space Experiences, values closer to 1 indicating a larger Day Space Experience, and values closer to -1 indicating a larger Night Space Experience.

Percent Time in an environment type was calculated by first summing the percent time spent in each environment for a given month, then averaging the monthly sums. This calculation was performed for each individual environment type (Indoor, Outdoor, and In/Out Choice) and per housing period (Day, Night, and Overall).

Flooring. Seven classes of flooring substrate were defined: grass, sand, rubber padding, dirt, stone aggregate, concrete, and other. We categorized the types of substrates into hard surface (concrete and stone aggregate), soft surface (grass, sand, and rubber padding), and dirt. However, our data collection methods allowed us to detect the fact that many environments were comprised of multiple flooring substrates, including both hard and soft. We had information regarding the percent coverage of each type of substrate within an environment, but not the configuration. Furthermore, we also did not have information regarding what portion of the environments were used by an elephant, just that an elephant had access to the substrate. We were therefore not able to determine either the contiguous coverage area or the time elephants spent on each of the different substrate types in mixed-substrate environments. We therefore focused the analysis on substrate categories where we knew the environment consisted of 100% coverage of hard substrate, 100% coverage of soft substrate, or 100% coverage of dirt. This is a conservative approach, as time spent in environments with substrate coverage that was large, but less than 100%, was not captured in this analysis. Environments with 100% coverage of dirt substrate were classified as a separate category because we were informed that dirt can be either soft or hard depending on how it is managed; however, we had not collected sufficient information to make this distinction within our dataset. Percent Time on a substrate was calculated by first summing the percent time spent in environments with 100% coverage of that substrate for a given month, then averaging the monthly sums. This calculation was performed per substrate type (Soft, Hard, and Dirt) and per housing period (Day, Night, and Overall).

Statistical Analyses

Descriptive statistics, including the range, mean, and standard deviation, were calculated for all variables. Most variables were determined to be non-normally distributed, so non-parametric tests were used for population comparisons. Matched pairs for day and night housing were compared using the Wilcoxon Signed Rank Test. The variables were also assessed for species and sex differences. Means and standard deviations were calculated for variables and the Mann-Whitney U (Wilcoxon Rank Sum) Test was used to determine differences attributable to species or sex. Total Exhibit Space and Total Overall Space Experience were compared using the Wilcoxon Signed Rank Test for matched pairs. Proportion Space Experienced was determined by comparing the proportion of an elephant's Space Experience to the Total Exhibit Size, where 100% would indicate that an elephant's Space Experience matched the Total Exhibit Size at that zoo. Herd Size and Overall Social Experience were compared using the Wilcoxon Signed Rank Test for matched pairs. Proportion Social Experienced was calculated as the proportion of Social Experience to Herd Size. Statistical analyses were conducted using SAS software, version 9.3 (SAS Institute, Inc., Cary, NC), and a *P*-value of <0.05 was considered statistically significant.

Results

Twenty-three housing and social variables were created (Table 2). As many variables use hours per day and night management periods as a basis for calculation, the population range for night lengths and distribution of elephants with respect to night length are shown in Fig 3. Night length varied monthly, with an average across all months of 12.5 hours. Data for one winter (January) and one summer (July) month are presented for comparison. The modal Night length for both January and July was 14 hours, with a range among all elephants of 10–18 hours in January and 8–18 hours in July.

Table 3 lists the arithmetic mean, standard error, and range for each variable for Day, Night, and Overall management periods. Comparing the elephants' Day and Night experiences revealed several significant differences. Day values were greater for both Total Space Experience (Day = 38, 980.4 ft^2; Night = 22,098.3 ft^2) and Outdoor Space Experience (Day = 44,515.2 ft^2; Night = 26,636.4 ft^2). However, Indoor Space Experience was greater during the Night, and elephants spent a higher percentage of their time indoors at Night than during the Day (43.4% compared to 14.3%). Social Experience was greater during the Day (3.1) than at Night (2.4), and elephants spent more time at Night (35.1%) housed separately than during the Day (18.3%). The relative space and social experience change between Night and Day is shown in Fig 4. For most elephants, both space and social experiences were greater during the Day than at Night.

Of the 68 zoos assessed in this study, 45.5% (31/68) of zoos housed Asian elephants only, and 48.5% (33/68) housed African elephants only. Four zoos housed both African and Asian elephants. With respect to sex, 54.4% (36/68) of zoos housed female elephants only, and 45.5% (31/68) of zoos housed both males and females. Only one zoo housed male elephants only, and

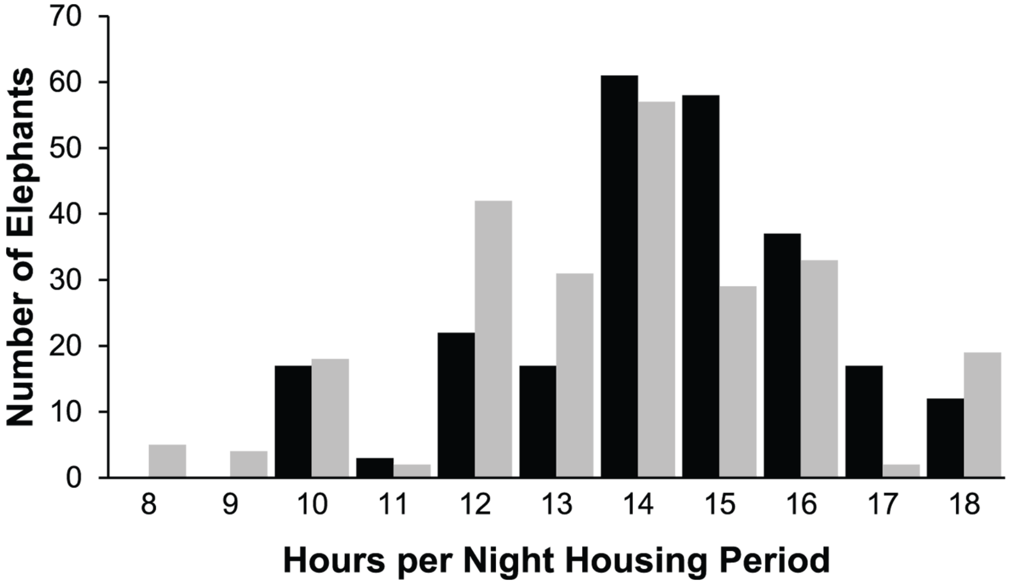

Fig 3. The number of elephants with various Night lengths. Black bars indicate January, grey bars indicate July.

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had three males. As seen in Table 4, the vast majority of measures did not differ due to either sex or species: only four of the 23 measures differed significantly between African and Asian elephants and only three of the 23 measures differed significantly between males and females. In terms of species differences, Africans had a larger Total Space Experience and spent time in more unique environments (Environment Contact) than Asians. Similarly, Overall Outdoor Space Experience was significantly greater for African elephants: African elephants experienced 52,703.3 ft^2 compared to the Asian elephant experience of 29,382.2 ft^2.

In terms of sex differences, males had a larger Overall Total Space Experience on average than females, particularly with regard to spaces that provided a choice between indoors and outdoors (Table 4). On average, males had an Overall In/Out Choice Space Experience of 25,330.7 ft^2 compared to 13,570.1 ft^2 for females. Additionally, females had a greater amount of Relative Social Experience Change than males (0.17 and 0.11, respectively). This indicates that while both males and females spent more time with other animals during the day than at night, females' social group size decreased by more at night than the males' social group size.

Comparative analysis did not detect any sex or species differences in time spent in environments with 100% coverage of hard substrates, 100% coverage of soft substrates, or 100% dirt (Table 4). Elephants spent, on average, 10.2% of their time in environments with 100% coverage of hard substrates and 10.6% in environments with 100% coverage of soft substrates. Time spent in environments with 100% coverage of either hard or soft substrate was greater during the Night than during the Day (Table 3), which indicates that elephants are more likely to be housed in single-substrate environments during the Night than during the Day.

To demonstrate the distribution of results for percentage-based variables across the population, Fig 5 presents histograms of the number of elephants that experienced between 0 and 100% time (in 10% intervals) for a number of variables. Some of these variables had bimodal distributions at the low and high ends of the scale, such as Percent Time In/Out choice, Percent Time Housed Separately, or Percent Time with Juveniles. Other measures, such as Percent Time on Hard Surfaces, showed a decrease in frequency as percent time increased. Additionally, the patterns varied between Overall and Day and Night experiences.

Table 3. Housing, flooring, and social variables for the population (Overall, Day, Night) showing means, standard errors, and ranges. Day and Night values were compared using the Wilcoxon Signed Rank Test.

		Overall				Day				Night				Day to Night Comparison	
Variable	**N**	**Mean**	**SEM**	**Min**	**Max**	**Mean**	**SEM**	**Min**	**Max**	**Mean**	**SEM**	**Min**	**Max**	***P*-value**	
Housing															
Total Exhibit Size (ft^2)	68	76767.1	5872.1	7728.5	347007.7	-	-	-	-	-	-	-	-	-	
Environment Count	68	12.5	1.2	2.0	62.0	-	-	-	-	-	-	-	-	-	
Environment Contact	252	9.4	0.4	2.0	46.0	6.7	0.3	1.0	35.0	6.2	0.3	1.0	33.0	0.054	
Space Experience Total (ft^2)	252	30253.0	2003.4	1273.4	169691.8	38980.4	2446.6	1184.0	159031.2	22098.3	1981.5	444.6	209573.1	<0.001	*
Space Experience by elephant (ft^2)	252	11136.3	731.5	328.5	100842.9	13749.8	838.1	375.7	86257.6	8771.0	738.6	242.2	120820.5	<0.001	*
Relative Space Experience Change	252	0.37	0.03	-1.20	0.99	-	-	-	-	-	-	-	-	-	
Proportion Space Experienced (%)	252	34.8	1.3	5.3	96.1	-	-	-	-	-	-	-			
Space Experience Indoor (ft^2)	252	1393.9	89.3	0.0	8603.6	1176.5	92.2	0.0	9767.2	1391.8	84.1	0.0	7288.2	0.001	*
Space Experience In/Out Choice (ft^2)	252	16089.9	1730.2	0.0	156374.7	8778.0	1,215.5	0.0	135880.2	16015.6	1800.3	0.0	181067.1	<0.001	*
Space Experience Outdoor (ft^2)	252	42203.1	2429.8	790.1	194368.1	44515.2	2,592.2	790.1	179026.3	26636.4	2554.4	0.0	287140.0	<0.001	*
Time Indoor (%)	252	28.9	1.4	0.0	81.0	14.3	1.2	0.0	79.0	43.4	2.1	0.0	100.0	<0.001	*
Time In/Out Choice (%)	252	16.0	1.3	0.0	89.8	8.5	1.1	0.0	89.6	23.4	1.9	0.0	100.0	<0.001	*
Time Outdoor (%)	252	55.1	1.6	1.3	100.0	77.1	1.6	2.7	100.0	33.2	2.1	0.0	100.0	<0.001	*
Flooring															
Time on Soft Substrate (%)	252	10.6	0.9	0.0	58.3	6.6	0.7	0.0	38.8	11.0	1.1	0.0	66.7	<0.001	*
Time on Hard Substrate (%)	252	10.2	0.8	0.0	66.7	4.8	0.5	0.0	27.1	15.0	1.3	0.0	66.7	<0.001	*
Time on Dirt Substrate (%)	252	0.8	0.3	0.0	43.9	0.7	0.3	0.0	40.3	0.9	0.4	0.0	50.7	0.0352	*
Social															
Herd Size	68	3.8	0.1	1.0	13.0	-	-	-	-	-	-	-	-	-	
Animal Contact	252	2.7	0.2	0.0	11.0	2.7	0.2	0.0	11.0	1.9	0.2	0.0	11.0	<0.001	*
Social Group Contact	252	3.9	0.3	1.0	30.0	3.1	0.2	1.0	18.0	2.5	0.2	1.0	21.0	<0.001	*
Social Experience	252	2.7	0.1	1.0	11.2	3.1	0.2	1.0	12.7	2.4	0.1	1.0	10.6	<0.001	*
Relative Social Experience Change	252	0.16	0.02	-1.04	0.90	-	-	-	-	-	-	-	-	-	
Proportion Social Experienced (%)	252	60.0	1.7	5.3	100.0	-	-	-	-	-	-	-			
Time with Juveniles (<7 years old) (%)	252	21.1	2.3	0.0	100.0	22.6	2.4	0.0	100.0	19.7	2.3	0.0	100.0	0.178	
Time with Mixed Sex Groups (%)	252	20.3	2.2	0.0	100.0	23.8	1.5	0.0	100.0	16.9	2.2	0.0	100.0	<0.001	*
Time Housed Separately (%)	252	26.6	2.2	0.0	100.0	18.3	1.2	0.0	100.0	35.1	2.7	0.0	100.0	<0.001	*
Time Housed Separately with Restricted Physical Access (%)	71	37.2	3.0	0.0	100.0	24.2	2.0	0.0	100.0	52.3	2.6	0.0	100.0	<0.001	*

* Indicates *P*-value<0.05

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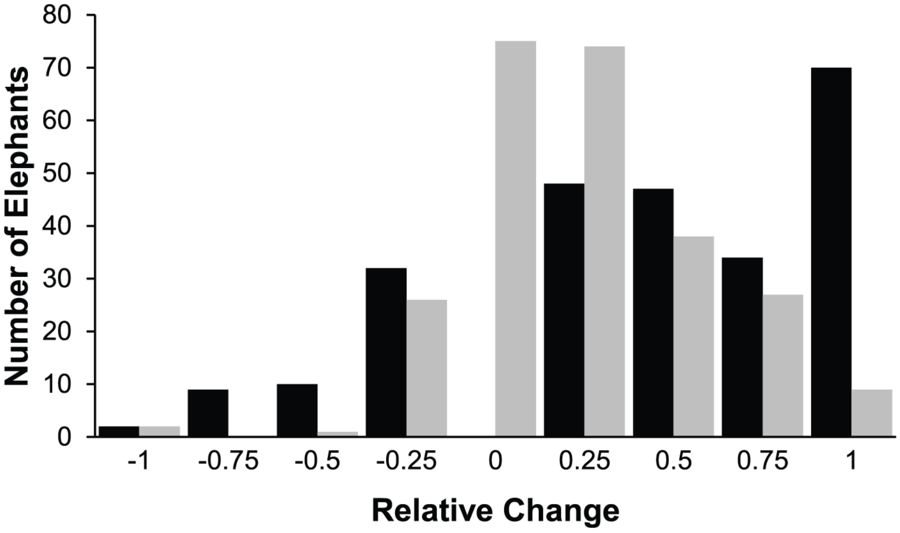

Fig 4. The number of elephants with particular amounts of relative space and social change from Day to Night. Black bars indicate relative space experience change and grey bars indicate relative social experience change. Values close to zero indicate no day to night change, values close to 1 indicate greater experience in the day and values close to -1 indicate larger experience at night.

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To illustrate the population-level variation for the Space Experience variables, Fig 6 presents histograms illustrating each elephant's Overall Space Experience for Indoor, Outdoor, Indoor/Outdoor Choice, and Total. It should be noted that the number of elephants represented in the Indoor and Indoor/Outdoor Choice figures are smaller than those in the Total or Outdoor figures due to the fact that some elephants spent no time in Indoor or Indoor/Outdoor Choice environments.

Overall Total Space Experience of an elephant did not closely correlate to the Total Exhibit Size of the zoo in which it was housed. The Wilcoxon Signed Rank test found that these two metrics of space generated significantly different (*P*-value$<$0.001) rankings. This difference can be readily explained by examining Proportion Space Experienced, as shown in Fig 7. The Overall Total Space Experience represented 75% or more of the Total Exhibit Size for only 11 elephants from 5 zoos, and two of those elephants were from the zoo with the smallest Total Exhibit Size. In contrast, the Overall Total Space Experience of 16 elephants from 11 zoos was less than 10% of the Total Exhibit Size for their respective zoos. On average, the Overall Total Space Experience to Total Exhibit Size ratio was 34.7%.

Similarly, the Overall Social Experience of an elephant did not correlate with Herd Size. The Wilcoxon Signed Rank test found that these two metrics provided significantly different (*P*-value$<$0.001) rankings, as illustrated in Fig 8. Herd Size ranged from 1 to 13 animals and an elephant's Overall Social Experience ranged from 1 (alone) to 11.23. On average an elephant's Overall Social Experience consisted of 60% of the herd, and at minimum 8% of the herd. Thirty-three elephants at 15 zoos had an Overall Social Experience score equal to the Herd Size and 10 elephants at three zoos had an overall Social Experience that equaled 95% of the Herd size.

Discussion

The results presented in this paper allow for a detailed and thorough understanding of how elephants in accredited North American zoos experienced their physical and social environments over the course of a full year. The range of variables presented reflects the complexity of

Table 4. Housing, flooring, and social variables (Overall) by species and sex including means and standard errors. Comparisons between African and Asian elephants, and male and female elephants, were made using the Mann-Whitney U (Wilcoxon Rank Sum) test.

	Species								Sex							
	African			Asian					Male			Female				
Variable	N	Mean	SEM	N	Mean	SEM	*P*-value		N	Mean	SEM	N	Mean	SEM	*P*-value	
Housing																
Total Exhibit Size (ft^2)	136	113,648.5	8,105.9	114	97,341.2	8,467.6	0.042	*	52	115,547.2	14,352.6	198	103,760.8	6,393.6	0.663	
Environment Contact	135	9.9	0.5	117	8.9	0.7	0.009	*	54	10.0	0.8	198	9.2	0.5	0.098	
Space Experience (ft^2)	135	39,338.8	3,345.1	117	19,264.2	1,327.1	<0.001	*	54	40,584.2	5,636.6	198	27,136.9	1,980.4	0.027	*
Space Experience by Elephant (ft^2)	135	12,374.5	1,192.4	117	9,707.5	752.3	0.162		54	18,848.3	2,638.2	198	9,033.1	502.3	0.162	
Relative Space Experience Change	135	0.40	0.04	115	0.33	0.04	0.361		54	0.36	0.06	198	0.37	0.03	0.630	
Proportion Space Experienced (%)																
Space Experience Indoor (ft^2)	135	1,285.2	101.1	117	1,500.5	138.7	0.518		54	1,520.9	183.4	198	1,347.6	94.9	0.436	
Space Experience In/Out Choice (ft^2)	135	19,113.5	2,727.5	117	12,602.4	1,959.7	0.726		54	25,330.7	5,332.1	198	13,570.1	1,618.0	0.042	*
Space Experience Outdoor (ft^2)	135	52,703.3	3,887.7	117	29,382.2	2,160.9	<0.001	*	54	52,293.2	6,590.5	198	3,9034.2	2,475.9	0.092	
Time Indoor (%)	135	27.0	2.0	117	31.1	2.1	0.162		54	24.3	3.1	198	30.2	1.6	0.079	
Time In/Out Choice (%)	135	16.0	1.7	117	15.9	2.1	0.620		54	17.4	2.8	198	15.6	1.5	0.202	
Time Outdoor (%)	135	57.0	2.2	117	53.0	2.4	0.206		54	58.2	3.4	198	54.3	1.8	0.325	
Flooring																
Time on Soft Substrate (%)	135	10.4	1.6	117	10.8	1.1	0.306		54	12.0	1.9	198	10.2	1.0	0.375	
Time on Hard Substrate (%)	135	10.6	1.1	117	9.7	1.2	0.253		54	8.1	1.5	198	10.7	1.0	0.189	
Time on Dirt (%)	135	1.4	0.6	117	0.2	0.1	0.085		54	1.2	0.9	198	0.8	0.3	0.507	
Social																
Herd Size	136	5.3	0.3	116	4.9	0.3	0.195		54	4.9	0.4	198	5.2	0.2	0.582	
Animal Contact	136	2.7	0.2	116	2.7	0.2	0.734		54	2.4	0.4	198	2.8	0.2	0.066	
Social Group Contact	136	3.9	0.4	116	3.9	0.5	0.443		54	3.8	0.8	198	3.9	0.4	0.126	
Social Experience	136	2.7	0.2	116	2.7	0.2	0.338		54	2.7	0.3	198	2.7	0.1	0.477	
Relative Social Experience Change	136	0.15	0.02	116	0.16	0.03	0.622		54	0.11	0.03	198	0.17	0.02	0.034	*
Proportion Social Experienced (%)																
Time with Juveniles (<7 years old) (%)	136	20.6	3.1	116	21.8	3.5	0.656		54	17.9	5.0	198	22.0	2.6	0.342	
Time with Mixed Sex Groups (%)	136	21.1	3.0	116	19.4	3.4	0.770		54	20.5	4.9	198	20.3	2.5	0.888	
Time Housed Separately (%)	136	24.2	2.8	116	29.4	3.4	0.616		54	29.3	5.6	198	25.8	2.4	0.948	
Time Socially Separated with Restricted Physical Access (%)	71	31.8	3.6	57	43.8	5.0	0.124		24	35.2	7.4	104	37.6	3.4	0.812	

* Indicates *P*-value<0.05

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elephant management and underscores the need to develop comprehensive standardized methods of translating this complexity into data suitable for use in comparative analyses and in the assessment of elephant welfare.

At its simplest, the social life of a zoo elephant can be characterized by enumerating the size of the herd at the zoo at which it lives. However, modern elephant management rarely follows a model where all the elephants at a facility spend all of their time together as a single herd. In fact, elephants are managed in social groups of varying sizes and compositions, and individual elephants can be members of multiple social groups (population range: 1–30 unique social groups per elephant) with which they spend varying amounts of time depending on management schedules, elephant characteristics, or other factors. Given this approach to social management, it becomes clear that the simplest social variable, herd size, is not necessarily adequate to explain the social life of a specific individual. Animal Contact, the next simplest variable we created, improves upon herd size in that it transitions to using the individual elephant as the unit of analysis, but provides only a count of the unique elephants with which that individual shares unrestricted space. Social Group Contact is a more complex variable that is also calculated at the elephant level, but in addition incorporates the factor of groupings to account for the fact that elephants experience diversity in their social group membership. Finally, Social Experience accounts for the factor of time in elephant social management by weighing the size of each social group experienced by the amount of time each elephant spends in each group. The fact that Social Experience integrates the number of elephants in each social grouping with the element of time makes it the most robust approach to standardizing the quantification of complex managed social milieus developed to date.

In addition to quantifying an elephant's social experience with respect to number of conspecifics, we calculated additional social variables such as percent time housed with juveniles, in a mixed sex group, separately, or separately with restricted physical access to conspecifics. Wild elephant herds typically include calves and juveniles. Allomothering,which is the caretaking of the offspring of herdmates, is prevalent and believed to provide pre-pubescent and/or nulliparous females with valuable mothering experiences and skills [38, 39]. Thus, the presence of calves and juveniles within a captive herd may have important ramifications for the successful rearing of offspring for first-time mothers. In addition, in many species juveniles are known to engage in more play than adults [40], and their presence in an elephant herd is hypothesized to add to the dynamic nature of group interactions in a way that supports normal behavioral expression [9]. In our population, 45 of the 226 adult elephants (36/181 females and 9/45 males) had the opportunity to spend time with juveniles. The mean time spent with juveniles by these elephants was 65.68%. Thus, while about two-thirds of the social time budget of these elephants was spent in social groupings that included juveniles, the opportunity for social interaction with young elephants was only available to 20% of the adult elephants in the population.

Quantifying an elephant's physical environment with respect to space requires standardization of complex management models that vary both within and between zoological settings. Elephant management rarely involves the housing of elephants in a single defined area, but rather involves shifting individuals or groups between a variety of spaces of differing sizes and features. In fact, elephants in the study population spent time in an average of 9.4 different environments in the course of regular management (population range: 2–46). To account for this practice, we looked at space allocation using multiple variables, ranging from the simplest zoo-level variable (Total Exhibit Size) to the most complex variable that accounted for different amounts of time spent in environments of differing sizes (Space Experience). In addition, housing variables were calculated to quantify both Space Experience and Percent Time in different types of environments (Indoor, Outdoor, In/Out Choice) and for different time periods (Day, Night, Overall). This yielded a variety of specific variables, each of which characterized space

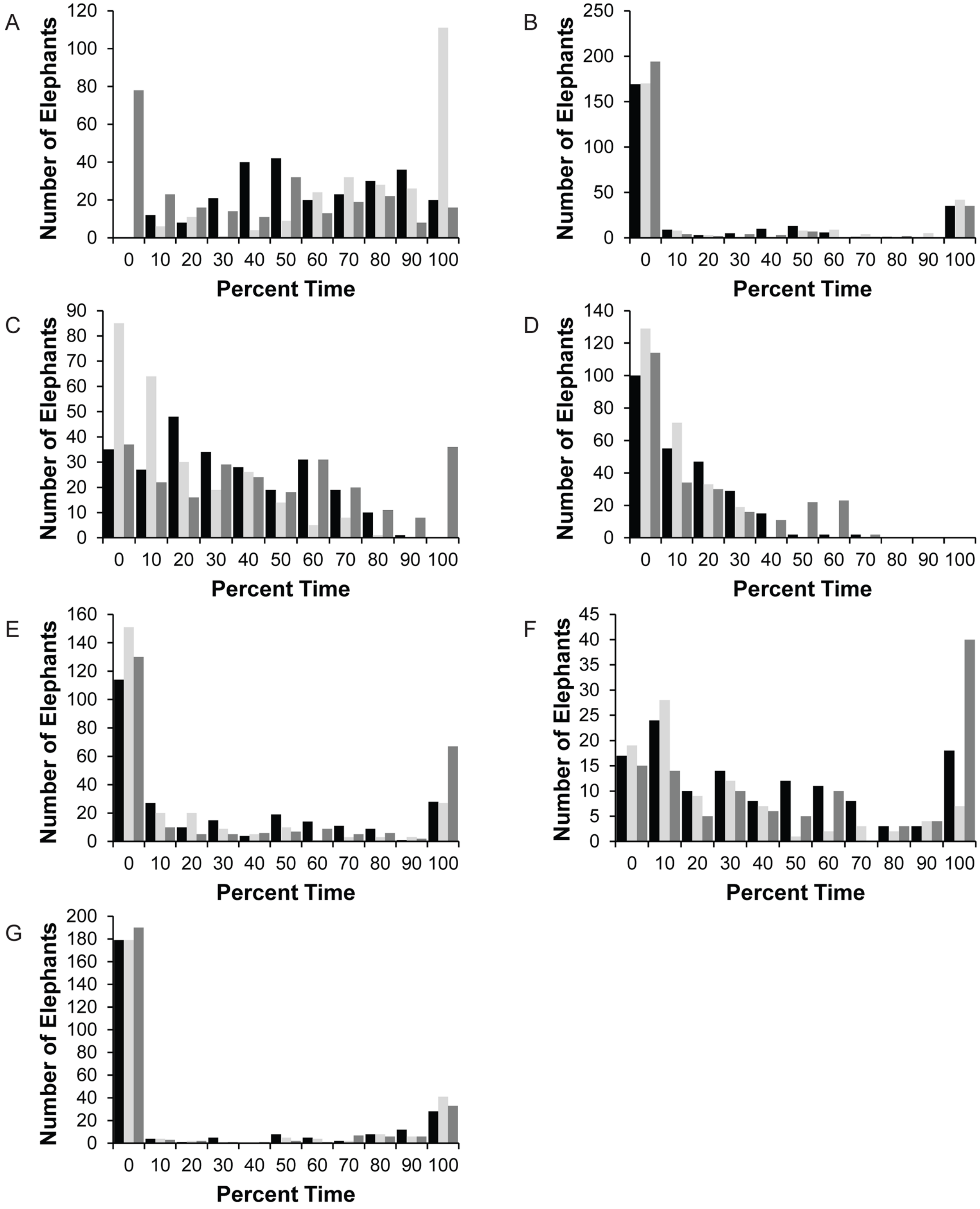

Fig 5. Frequency of number of elephants experiencing percentages of time for selected space and social measures. (A) Outdoors; (B) In/Out Choice; (C) Indoors; (D) On Hard Surfaces; (E) Housed Separately; (F) With Restricted Physical Access; and (G) With Juveniles (<7 years old). Bins include ranges of no experience (0%), 1–10, 11–20, 21–30, 31–40, 41–50, 51–60, 61–70, 71–80, 81–90, and 91–100% time. Dark gray bars indicate Overall experience, light gray bars indicate Daytime experience, and black bars indicate Nighttime experience.

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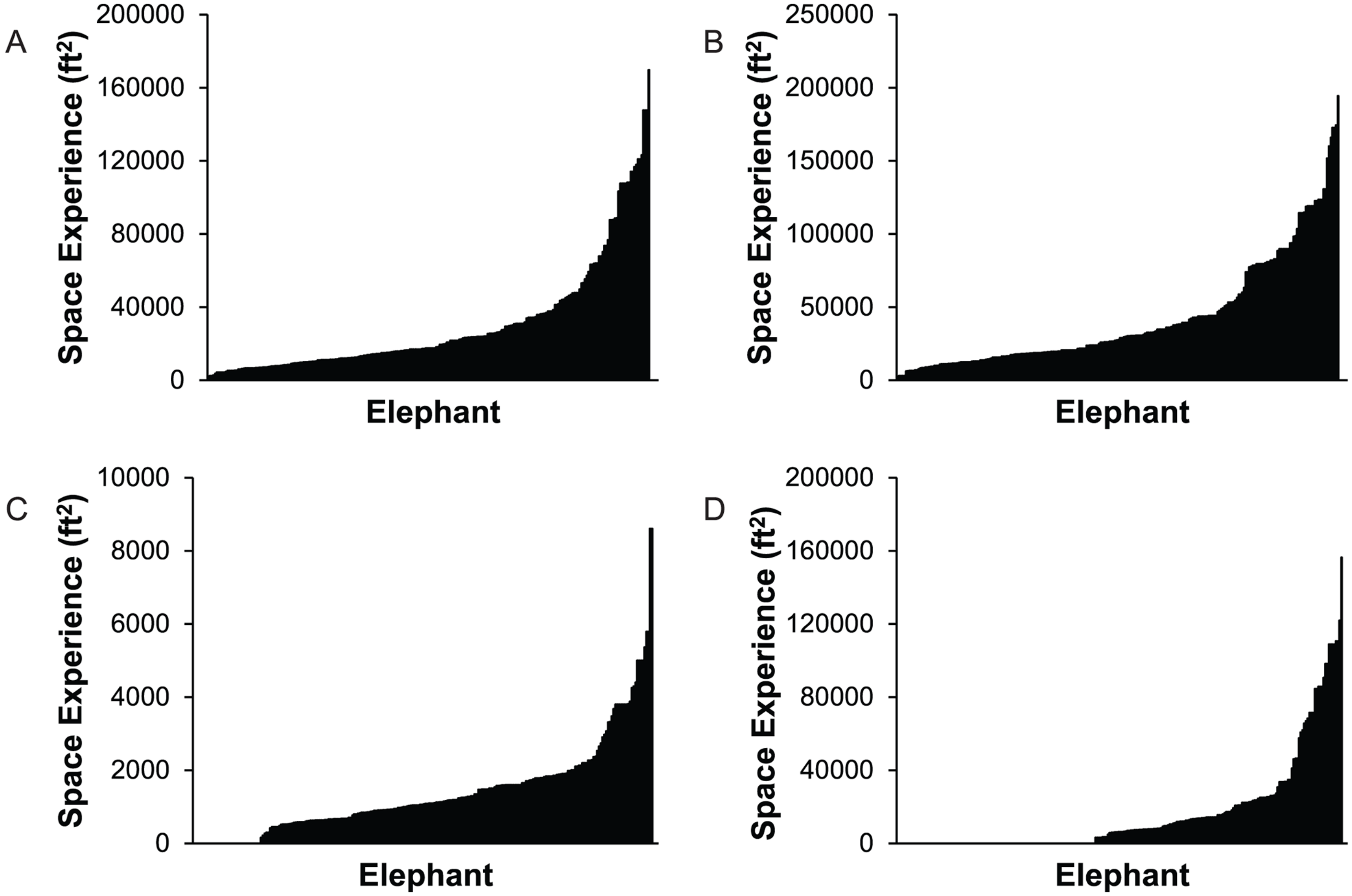

Fig 6. Overall Space Experience for every elephant in the study population A) Total Overall Space Experience where Space Experience is averaged over both day and night periods and includes Indoor, Outdoor, and Environments with In/Out Choice; B) Overall Space Experience Outdoor; C) Overall Space Experience Indoor; D) Overall Space Experience In/Out Choice.

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by accounting for relevant characteristics of the physical environment. Knowledge of these aspects of elephant housing are important given that, in other species, positive associations have been found between improvements in behavioral and/or physiological indicators of welfare and housing animals outdoors[41, 42, 43,44] or in environments that provide indoor/outdoor choice [45,46,47,48].

The Proportion Space and Social Experienced analysis was conducted to reveal how each individual elephant's experience of physical and social resources correlated with the total resources available at the zoo. Mean proportion experienced was 34.7% for spatial resources (Fig 7). While we do not know if it is logistically possible to achieve Space Experience scores that are 100% of Total Exhibit size (due to the layout of each exhibit), it is clear that there is opportunity to more efficiently utilize spatial resources by offering access to multiple contiguous enclosures at the same time. For social resources, the mean proportion experienced was 60%. While there could be many factors contributing to spatial and social resources not being fully utilized, our data indicate that these rates are being driven mainly by practices associated with Night management. The Relative Space Experience Change and Relative Social Experience Change variables (Fig 4) demonstrate that 199/252 elephants in the population had a restriction in Space Experience and 148/252 had a restriction in Social Experience when moving from

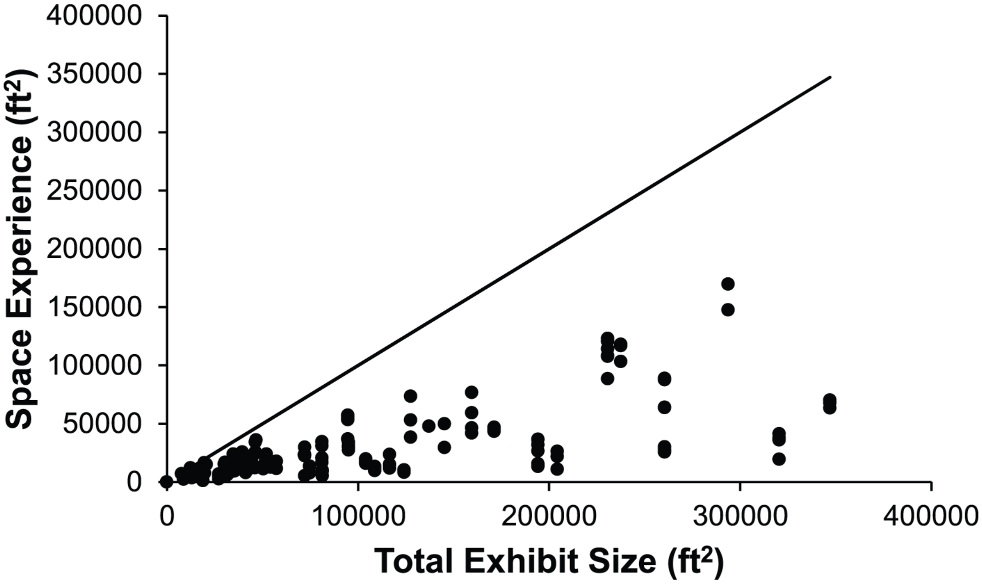

Fig 7. Proportion Space Experienced. Each elephant's Overall Total Space Experience compared to the Total Exhibit Size at its zoo. The solid line represents the relationship that would exist if the elephants experienced 100% of the Total Exhibit space.

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Day management to Night management. Across the population, Relative Change in Social Experience represents a decrease of 1.2 animals and the Relative Change in Space Experience represents a decrease of 22897.2 ft^2 from Day to Night. This trend in management is particularly notable given the fact that the Night management period was reported as ranging from 8–18 hours depending on the season with a modal value of 14 hours in both the summer and

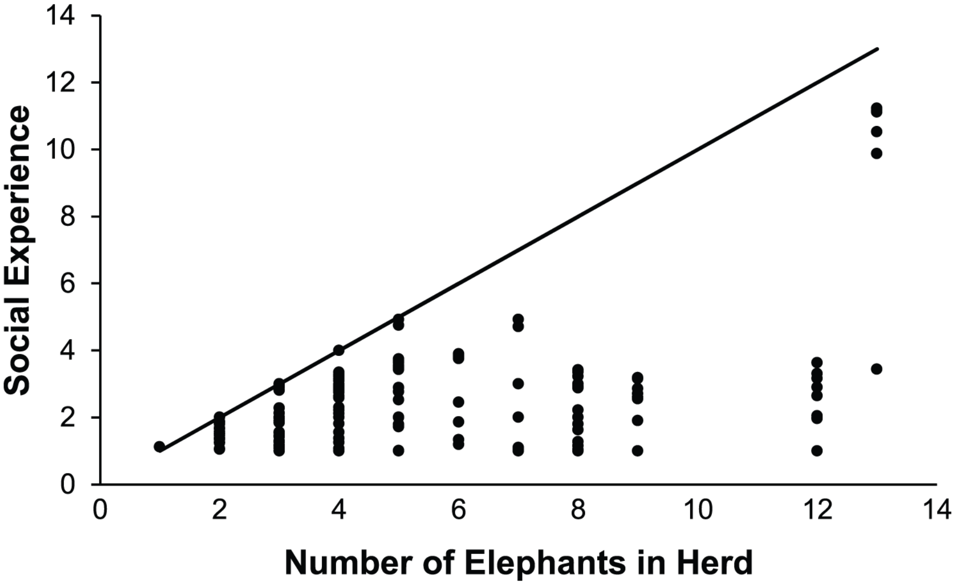

Fig 8. Proportion Social Experienced. Each elephant's Overall Social Experience is compared to number of elephants in the Herd at its zoo. The solid line represents the relationship that would exist if the elephants spent all their time as a full Herd.

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winter (Fig 3), and given that Night Social Experience was found to be significant predictor of nighttime stereotypy performance in a related study [9].

Exposure to hard substrates has been hypothesized to be associated with the prevalence of foot and musculoskeletal problems in elephants [29] and decreases in foot health and recumbent resting behavior in cattle [28, 33, 49]. Our analysis provided a conservative estimate of time spent on hard surfaces due to the fact that we were only able to capture time spent in environments with 100% coverage of either hard or soft substrates. However, the variability in substrate exposure across the population was sufficient to test for associations between exposure to hard or soft substrates and behavioral and health-related indicators of welfare in related studies [10, 11,13].

While the study population as a whole displayed a wide range of variation in many of the housing and social variables, only a few significant differences were found between the two species (Asian / African) and by sex, indicating that dissimilarities in elephant management practice do not occur consistently along species or sex lines. For the species comparisons, the most notable differences were in Space Experience. The mean Overall Total Space Experience for African elephants was 39,338.8 ft^2, which is more than twice that of Asian elephants where the mean value was 19,264.2 ft^2. The data suggest that the difference in Space Experience between the two species is driven by differences in the area of outdoor space available in exhibits, as Overall Outdoor Space Experience was also significantly greater for African elephants. Space Experience also diverged between the sexes. Both Overall Total Space Experience and Overall In/Out Choice Space Experience were significantly higher for males. The management of male elephants generally requires larger and more flexible housing resources; and these results indicate that these resources are being used such that males spend more time in larger, outdoor environments than females.

Our analyses demonstrated that the zoo-level factors Herd Size and Total Exhibit Size were not correlated with the individual-level Social Experience or Space Experience scores. This indicates that, because of the complex ways in which elephants are managed, zoo level factors are not a proxy for individual elephant experience. This is a particularly relevant finding to animal welfare assessment, because welfare outcomes such as behavior and physiology are sensitive to differences in physical and social milieu and associations could be masked if zoo-level, rather than individual-level independent variables are used. In fact, when variables presented in this paper were tested in multi-variable predictive models for a range of welfare indicators, those that were calculated at the zoo or herd level were never significant factors, whereas many of the individual elephant-level variables were significantly associated with elephant welfare outcomes (see: [9,10,11,12,13,14]).

Conclusion

Resource based measures that describe housing and management practices are necessary to provide a comprehensive assessment of the welfare of managed animals. We have described the development of such variables created as part of an epidemiological study assessing the welfare of elephants in North American zoos [50]. We found that although there was variability in how elephants are housed in terms of space, flooring, and social groups, these differences were rarely associated with the species or sex of the elephants. In addition, for both spatial and social measures, individual and zoo based variables were not correlated. These results, combined with the finding that Day and Night management varied with respect to key housing and social factors, highlight the need for individual-based variables that represent both operating and non-operating zoo hours to adequately represent animals' experiences. These can then be utilized as standardized variables for assessing resource based measures and their associations with welfare indicators both within and across institutions. This approach may be applicable to any zoo-housed animal, but is particularly relevant to those species that are managed dynamically.

Supporting Information

S1 Table. Metric equivalents for Space Experience variables.
(XLSX)

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Author Contributions

Conceived and designed the experiments: CLM JNH JAM MBS. Performed the experiments: CLM JHN MBS. Analyzed the data: JNH CLM MBS. Contributed reagents/materials/analysis tools: CLM JNH. Wrote the paper: CLM JNH JAM MBS.

References

1. Butterworth A, Mench JA, Wielebnowski N. Practical strategies to assess (and improve) welfare. In: Appleby MC, Mench JA, Olsson IAS, Hughes BO, editors. Animal Welfare. 2nd ed. Cambridge: CABI Publishing; 2011. pp. 200–214.
2. DeVries TJ, von Keyserlingk MAG, Weary DM. Effect of feeding space on the inter-cow distance, aggression, and feeding behaviour of free-stall housed lactating dairy cows. J Dairy Sci. 2004; 87: 1432–143. PMID: 15290991
3. Li C, Jiang Z, Tang S, Zeng Y. Influence of enclosure size and animal density on fecal cortisol concentration and aggression in Père David's deer stags. Gen Comp Endocrinol. 2007; 151:202–209. PMID: 17324429
4. Brummer SP, Gese EM, Shivik JA. The effect of enclosure type on the behavior and heart rate of captive coyotes. Appl Anim Behav Sci. 2010; 125:171–180.
5. Valuska AJ, Mench JA. Size does matter: The effect of enclosure size on aggression and affiliation between female New Zealand white rabbits during mixing. Appl Anim Behav Sci. 2013; 149:72–76.
6. Shepherdson D, Lewis KD, Carlstead K, Bauman J, Perrin N. Individual and environmental factors associated with stereotypic behavior and fecal glucocorticoid metabolite levels in zoo housed polar bears. Appl Anim Behav Sci. 2013; 147:268–277.
7. Garner JP, Kiess AS, Mench JA, Newberry RC, Hester PY. The effect of cage and house design on egg production and egg weight of White Leghorn hens: An epidemiological study. Poult Sci. 2012; 9:1522–1535.
8. Hockenhull J, Creighton E. Management practices associated with owner-reported stable-related and handling behaviour problems in UK leisure horses. Appl Anim Behav Sci. 2014; 155:49–55.
9. Greco BJ, Meehan CL, Hogan JN, Leighty KA, Mellen J, Mason GJ, et al. The days and nights of zoo elephants: using epidemiology to better understand stereotypic behavior of African elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) in North American zoos. PLoS ONE 2016. doi: pone.0144276.
10. Holdgate MR, Meehan CL, Hogan JN, Miller LJ, Soltis J. Walking behavior of zoo elephants: associations between GPS-measured daily walking distances and environmental factors, social factors and welfare indicators. PLoS ONE 2016. doi: pone.0150331.
11. Holdgate MR, Meehan CL, Hogan JN, Miller L, Rushen J, de Passillé AM, et al. Recumbence behavior in zoo elephants: determination of patterns and frequency of recumbent rest and associated environmental and social factors. PLoS ONE 2016. doi: pone.0153301.
12. Brown JL, Paris S, Prado-Oviedo NA, Meehan CL, Hogan JN, Morfeld K, et al. Reproductive health assessment of female elephants in North American zoos and association of husbandry practices with reproductive dysfunction in African elephants (Loxodonta africana). PLoS ONE 2016. doi: pone.0145673.
13. Miller MA, Hogan JN, Meehan CL. Housing and demographic risk factors impacting foot and musculoskeletal health in African elephants (Loxodonta africana) and Asian elephants (Elephas maximus) in North American zoos. PLoS ONE 2016. doi: pone.0155223.
14. Morfeld KA, Meehan CL, Hogan JN, Brown JL. Assessment of body condition in African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants in North American zoos and management practices associated with high body condition scores. PLoS ONE 2016. doi: pone.0155146.
15. Fernando P, Lande R. Molecular genetic and behavioral analysis of social organization in the Asian elephant (*Elephas maximus*). Behav Ecol Sociobiol. 2000; 48: 84–91.
16. Archie EA, Morrison TA, Fole CAH, Moss CJ, Alberts SC. Dominance rank relationships among wild female African elephants, Loxodonta africana. Anim Behav. 2006a; 71: 117–127.
17. Thomas B, Holland JD, Minot EO. Elephant (*Loxodonta africana*) Home Ranges in Sabi Sand Reserve and Kruger National Park: A Five-Year Satellite Tracking Study. PLoS ONE. 2008; 3(12): e3902. doi: 10.1371/journal.pone.0003902 PMID: 19065264
18. de Silva S, Rangeewa A, Kryazhimskiy S. The dynamics of social networks among female Asian elephants. BMC Ecology. 2011; 11:17. doi: 10.1186/1472-6785-11-17 PMID: 21794147
19. Olson IAS, Westlund K. More than numbers matter: the effect of social factors on behaviour and welfare of laboratory rodents and non-human primates. Appl Anim Behav Sci. 2007; 103:229–254.
20. Price EE, Stoinski TS. Group size: determinants in the wild and implications for the captive housing of wild mammals in zoos. Appl Anim Behav Sci. 2007; 103: 255–264.
21. Galindo F, Newberry RC, Mendl M. Social conditions. In: Appleby MC, Mench JA, Olsson IAS, Hughes BO, editors. Animal Welfare. 2nd ed. Cambridge: CABI Publishing; 2011. pp. 228–24.

22. Rault JL. Friends with benefits: social support and its relevance for farm animal welfare. Appl Anim Behav Sci. 2012; 136: 1–14.
23. Nielsen BL, Appleby MC, Waran NK. Physical conditions. In: Appleby MC, Mench JA, Olsson IAS, Hughes BO, editors. Animal Welfare. 2nd ed. Cambridge: CABI Publishing; 2011. pp. 215–227
24. Hogan ES, Houpt KA, Sweeney K. The effect of enclosure size on social interactions and daily activity patterns of the captive Asiatic wild horse (*Equus przewalskii*). Appl Anim Behav Sci. 1988; 21: 147–168.
25. Wiedenmayer C. Effect of cage size on the ontogeny of stereotyped behaviour in gerbils. Appl Anim Behav Sci. 1996; 47: 225–233.
26. Kaufman BM, Pouliot AL, Tiefenbacher S, Novak MA. Short and long-term effects of a substantial change in cage size on individually housed, adult male rhesus monkeys (*Macaca mulatta*). Appl Anim Behav Sci. 2004; 88: 319–330.
27. Hansen SW, Malmkvist J, Palme R, Damgaard BM. Do double cages and access to occupational materials improve the welfare of farmed mink? Anim Welf. 2007; 16: 63–76.
28. Clubb R, Mason G. Animal Welfare: Captivity effects on wide-ranging carnivores. Nature. 2003; 425: 473–474. PMID: 14523435
29. Fowler ME. An overview of foot conditions in Asian and African elephants. In: Csuti B, Sargent EL, Bechert US, editors. The Elephant's Foot: Prevention and Care of Foot Conditions in Captive Asian and African Elephants. Ames: John Wiley & Sons; 2001a. pp. 3–7.
30. Fowler ME. Foot disorders. In: Fowler ME, Mikota SK, editors. Biology, Medicine, and Surgery of Elephants. Ames: Blackwell Publishing; 2006. pp. 217–261.
31. West G. Musculoskeletal system. In: Fowler ME, Mikota SK, editors. Biology, Medicine, and Surgery of Elephants. Ames: Blackwell Publishing; 2006. pp. 263–271.
32. Harris M, Sherwin C, Harris S (University of Bristol). The welfare, housing and husbandry of elephants in UK zoos. Final Report. London: Department of Food, the Environment and Rural Affairs; 2008. DEFRA Science and Research Project WC05007.
33. Barker ZE, Amory JR, Wright JL, Mason SA, Blowey RW, Green LE. Risk factors for increased rates of sole ulcers, white line disease, and digital dermatitis in dairy cattle from twenty-seven farms in England and Wales. J Dairy Sci. 2009; 92: 1971–1978. doi: 10.3168/jds.2008-1590 PMID: 19389954
34. Frankena K., Somers JGCJ, Schouten WGP, van Stek JV, Metz JHM, Stassen EN, et al. The effect of digital lesions and floor type on locomotion score in Dutch dairy cows. Prev Vet Med. 2009; 88: 150–157. doi: 10.1016/j.prevetmed.2008.08.004 PMID: 18842310
35. Haufe HC, Gygax L, Wechsler B, Stauffacher M, Friedli K. Influence of floor surface and access to pasture on claw health in dairy cows kept in cubicle housing systems. Prev Vet Med. 2012; 105: 85–92. doi: 10.1016/j.prevetmed.2012.01.016 PMID: 22326044
36. Greco BJ, Meehan CL, Miller LJ, Shepherdson DJ, Morfeld KA, Andrews J, et al. Elephant management in North American zoos: environmental enrichment, feeding, exercise, and training. PLoS ONE 2016. doi: pone.0152490.
37. Lewis KD, Shepherdson DJ, Owens TM, Keele M. A survey of elephant husbandry and foot health in North American zoos. Zoo Biol. 2010; 29: 221–236. doi: 10.1002/zoo.20291 PMID: 20014111
38. Fuller G, Kuhar CW, Dennis PM, Lukas KE. A Survey of Husbandry Practices for Lorisid Primates in North American Zoos and Related Facilities. Zoo Biol. 2013; 32: 88–100. doi: 10.1002/zoo.21049 PMID: 23161761
39. Gadgil M, Nair PV. Observations on the social behaviour of free ranging groups of tame Asiatic elephant (*Elephas maximus* Linn). Proc Ind Acad Sci (Anim Sci). 1984; 93:225–233.
40. Lee PC. Allomothering among African elephant. Anim Behav. 1987; 35: 278–291.
41. Fagen R. Animal play behavior. New York, NY: Oxford University Press; 1981.
42. Johnsen PF, Johannesson T, Sandøe P. Assessment of farm animal welfare at herd level: many goals, many methods. Acta Agr Scand A-Anim Sci Suppl. 2001; 30: 26–33.
43. Fontenot MB, Wilkes MN, Lynch CS. Effects of outdoor housing on self-injurious and stereotypic behavior in adult male rhesus macaques (*Macaca mulatta*). J Am Assoc Lab Anim. 2006; 45: 35–43
44. Nakamura K, Tanaka T, Nishida K, Uetake K. Behavioral indexes of piglet welfare: comparison of indoor and outdoor housing systems. Anim Sci J. 2011; 82: 161–168. doi: 10.1111/j.1740-0929.2010.00806.x PMID: 21269375
45. Schumann K, Guenther A, Jewgenow K, Trillmich F. Animal housing and welfare: effects of housing conditions on body weight and cortisol in a medium-sized rodent (*Cavia aperea*). J Appl Anim Welf Sci. 2014; 17: 111–124. doi: 10.1080/10888705.2014.884407 PMID: 24665951

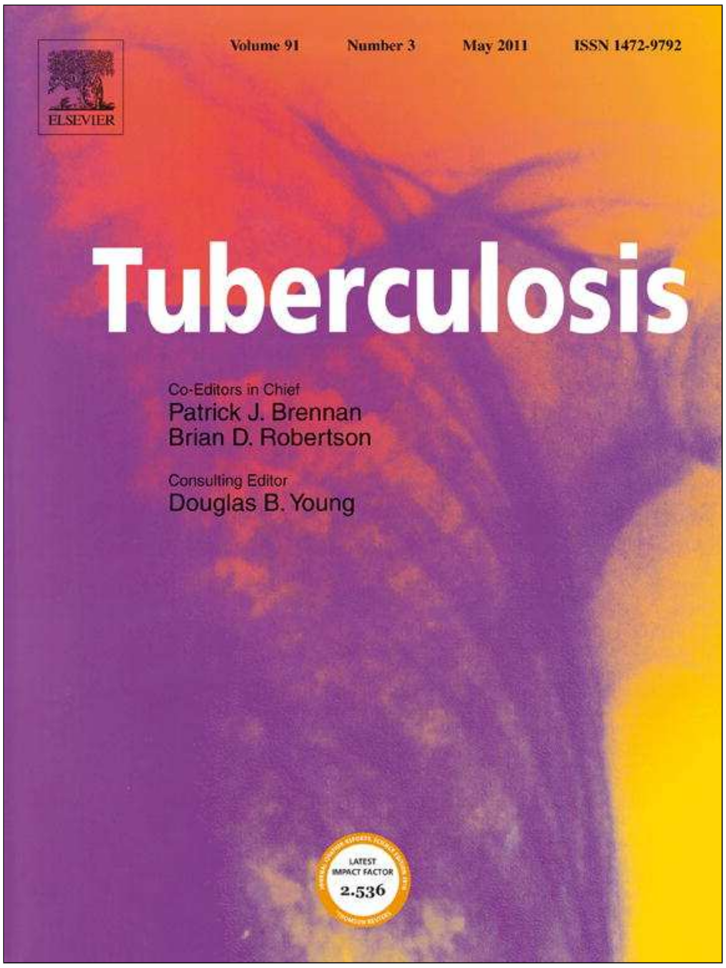
46. Owen MA, Swaisgood RR, Czekala NM, Lindburg DG. Enclosure choice and well-being in giant pandas: Is it all about control? Zoo Biol. 2005; 24: 475–48.

47. Ross SR. Issues of choice and control in the behaviour of a pair of captive polar bears (*Ursus maritimus*). Behav Processes. 2006; 3: 117–120.

48. Kurtycz LM, Wagner KE, Ross SR. The Choice to Access Outdoor Areas Affects the Behavior of Great Apes. J Appl Anim Welf Sci. 2014; 17: 185–197. doi: 10.1080/10888705.2014.896213 PMID: 24673476

49. Haley DB, de Passillé AM, Rushen J. Assessing cow comfort: Effects of two floor types and two tie stall designs on the behaviour of lactating dairy cows. Appl Anim Behav Sci. 2001; 71: 105–117. PMID: 11179563

50. Carlstead K, Mench JA, Meehan C, Brown JL. An epidemiological approach to welfare research in zoos: the Elephant Welfare Project. J Appl Anim Welf Sci. 2012; 16: 319–37.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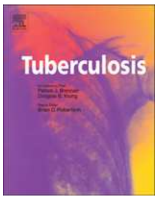

REVIEW

Tuberculosis at the human–animal interface: An emerging disease of elephants

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SUMMARY

Over the past 15 years, cases of infection with organisms of the *Mycobacterium tuberculosis* complex have been diagnosed among captive elephants in the United States and worldwide. Outbreak investigations have documented that among staff employed at facilities housing infected animals, skin test conversion to purified protein derivative have been documented. Clonal spread among animals in close contact and even inter-species spread between elephant and human has been documented. Detection of actively infected animals relies on samples obtained by trunk wash. Diagnosis has been augmented by the development of a multi-antigen serologic assay with excellent specificity and sensitivity. Treatment regimens are still in development with efficacy largely unknown due to a paucity of both premortem follow-up and necropsy data of treated animals. The epidemiology, diagnosis and treatment of tuberculosis in elephants require additional careful study of clinical data.

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1. Introduction

Over the past 2 decades, tuberculosis (TB) has seen a resurgence initially associated with the epidemic of human immunodeficiency virus (HIV) infection and more recently with the emergence of multi-drug resistant (MDR) and extremely drug resistant (XDR) strains. Surprisingly overlooked in the fight against TB is the potential for transmission at the human–animal interface.[1] This interface includes not only domestic livestock such as cattle and buffalo but also non-human primates, elephants, and other species that interact with people in zoos, circuses, temples, and tourist facilities around the world and that represent potential reservoirs of both drug-susceptible and resistant strains of TB. In fact, the isolation of MDR-TB from an elephant in the United States (U.S.)[27] highlights what was heretofore a theoretical concern in the nation's population of approximately 450 elephants.

While elephants are maintained in many zoos and circuses worldwide, Asia in particular hosts a large population of captive elephants including 3400–3600 in India alone.[2] Reports from India, Sri Lanka, and other Asian countries indicate that TB is not an unusual finding on post-mortem examination in captive elephants.[3,4] Moreover, unofficial reports from Asia and the U.S. indicate that some elephants with apparent active disease have been treated with short courses using single anti-mycobacterial drug regimens at doses that would be considered ineffective to achieve therapeutic serum levels creating the potential for drug resistance.

The pathogenesis of human TB has been studied for many centuries with the introduction of drug treatment in the 1940's. In contrast, TB in elephants has been studied for only 14 years with limited, poorly funded research and reluctance to publish and/or share data.

While inter-species transmission of TB between elephants and humans has been described,[1] and public health evaluations have documented a risk for human exposure from infected elephants,[1,5,6] the risk to animal handlers or to the general public of acquiring TB from non-humans is incompletely understood.

2. History and current status of tuberculosis in elephants

Descriptions of a disease in elephants resembling TB were reported by Ayurvedic physicians in Asia over 2000 years ago.[7,8] Based on characteristic skeletal lesions a TB pandemic has been implicated as a causative factor in the extinction of the mastodon (*Mammut americanum*).[9] Although case reports appeared in the 1800s[10] and the early 1900s,[11] TB "emerged" in elephants in 1996 with the death of two circus elephants.[12] Notably, two cases from this herd were reported in 1983[13] and 1994.[12]

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TB was subsequently identified in five additional elephant herds[12] and prompted a collaborative effort by the United States Department of Agriculture (USDA), the American Association of Zoo Veterinarians (AAZV), zoos, circuses, and experts representing the veterinary and human healthcare communities to develop the Guidelines for the Control of Tuberculosis in Elephants that were first published in 1997. The Guidelines, which recommend diagnostic methods and treatment protocols, were revised in 2000, 2003, 2008, and 2010[14] as new information became available.

Between 1994 and November 2010, TB was confirmed by culture in 50 U.S. elephants. *Mycobacterium tuberculosis* was isolated from 46 Asian elephants (*Elephas maximus*) and 3 African elephants (*Loxodonta africana*) and *Mycobacterium bovis* from 1 African elephant. Thirty-one cases were diagnosed antemortem and 19 post-mortem, most lacking clinical signs consistent with TB.[14] Among the current population of 246 Asian elephants in the U.S. the approximate prevalence is 18% versus 2% among the 204 African elephants. As culture has poor sensitivity, the true prevalence may be higher. *Mycobacterium avium* and a variety of non-tuberculous mycobacteria are frequent isolates[15] but have not been associated with pathology with the exception of two cases of *Mycobacterium szulgai* in African elephants.[16]

Epidemiologic and outbreak investigations of TB in elephants in the U.S. is challenged by movement of elephants between facilities and changes in ownership. Additionally, reluctance of private owners to provide information regarding heritage and movements and privacy concerns relating to human caretakers complicates contact tracing.

Evaluation of elephants for TB worldwide has also begun. In Sweden TB was confirmed by culture in 5 elephants post-mortem.[17,18] Other European countries have initiated testing campaigns, although prevalence rates have not yet been reported. Surveillance in Asia began in 2006 when Elephant Care International (www.elephantcare.org), initiated a surveillance program in Nepal. Of 211 elephants screened (90% of the known captive population), greater than 20% were seroreactive (Mikota, unpublished). A survey conducted in India found that 15% of 387 temple, government, and privately owned elephants were seroreactive by the commercially available Elephant TB Stat-Pak® assay (ChemBio, Medford, NY) detailed below.[19] Elephants housed at religious temples, the group with the greatest human contact, had the highest rate of seroreactivity (25%) versus 12–15% in other groups.[19] And this year, 4 cases of culture confirmed disease in Thai elephants were reported.[20] The sensitivity and specificity of serodiagnosis for TB in elephants are discussed below. Culture provides a lower limit of detection but likely underestimates disease burden in this species of animal.

No formal studies to delineate the exposure risks for elephants have been performed. An unproven supposition is that index infections occur due to prolonged close contact with an infected human. Transmission between elephants with close contact has been documented by molecular typing.[12,15]

3. Clinical disease and diagnosis in elephants

TB in elephants may present as a chronic wasting disease with weight loss, exercise intolerance, and occasionally coughing or abnormal discharges. Frequently, clinical signs are lacking until the disease is quite advanced.[12] *M. tuberculosis* has been isolated pre-mortem from respiratory secretions, feces, and vaginal discharges. On post-mortem, some elephants have significant abscess formation and casseation of the lungs, thoracic and abdominal lymph nodes, and liver. Other cases have been diagnosed incidentally at necropsy by identification and culture of small, focal granulomas.[11,12] Chest radiographs are impossible in adult elephants and the intradermal tuberculin test has proven to be unreliable as a screening test.[12,17] Culture has served as the “gold-standard” for diagnosis. Nucleic acid amplification to detect mycobacterial DNA in primary specimens obtained by trunk wash has comparable diagnostic capability as for humans.[15] The problem of PCR inhibitors due to contamination with organic material and soil may be minimized by use of modifications using common laboratory and commercially available specimen decontamination systems.[21]

The trunk wash has been devised to collect samples from elephants for culture. Sterile saline is instilled into the trunk, the trunk is elevated, and the sample is collected into a sterile plastic bag as the elephant forcibly exhales.[22,23] The behaviors necessary for the trunk wash require training and can be dangerous in certain elephants. If the elephant fails to forcibly exhale, only the distal trunk is sampled rather than the respiratory tract. Bacterial and fungal sample contamination is common because elephants use their trunk for a variety of functions. Moreover, elephants shed organisms intermittently as exemplified by the Swedish experience where only 7 of 189 trunk wash samples collected from five infected elephants yielded *M. tuberculosis*.[18] Similar results were experienced by investigators in Thailand where only 2 of 60 trunk wash cultures were positive in four infected elephants.[20]

Other techniques including an experimental ELISA assay[24] and a formerly commercially available Blood TB Test[12] that combines serologic detection and lymphocyte transformation in response to purified protein derivative (PPD)-A derived from *M. tuberculosis* and PPD-B derived from *M. bovis*[25] have been studied.[26] A commercial assay based on serologic detection of pooled *M. tuberculosis* complex antigens as a screening assay (TB Rapid Test or ElephantTB STAT PAK® assay, ChemBio Inc., Medford, NY) with a confirmatory antigen-specific multi-antigen print immunoassay (MAPIA®, ChemBio) has been shown to be accurate and reproducible for elephants.[27,28] The Stat Pak® assay is licensed by the United States Department of Agriculture (USDA) as a screening test of TB in elephants. The sensitivity and specificity of the STAT PAK® to diagnose *M. tuberculosis* complex infection is 100% and 95%, respectively.[29] Sequential application of the confirmatory assay, increases the accuracy to approximately 100%.[27,29] This assay has identified infected elephants 8 years prior to diagnosis by culture[18,27] and was useful as a screening tool for outbreaks in Sweden and in Thailand.[17,18,20] Thus, the assay may have utility to detect latent infection. Moreover, the finding that treatment of culture-positive elephants yielded a decline in antigenic reactivity suggested that the assay may have utility to monitor therapy.[27]

4. Treatment

Treatment recommendations were modeled on regimens from the American Thoracic Society with the assumption that drug acceptance may be erratic, pharmacokinetics could differ for elephants, and that disease might be more difficult to eradicate in elephants. At the time that the first treatment protocols were published in 1997, these issues were still unresolved. Whereas there was consensus regarding the treatment of animals that were actively shedding tubercle bacilli, the same was not the case for exposed elephants. Further, a key untested assumption was that treatment was curative.

Elephants with active disease receive 3 drugs for 2 months followed by 2 drugs for 10 months. Isoniazid (INH) and rifampin (RIF) were considered the 2 key drugs with either pyrazinamide (PZA) or ethambutol (EMB) as the third drug. A 12-month treatment course was chosen due to uncertainties regarding the extent of disease and treatment requirements in elephants. Efficacy was determined by ascertainment of serum drug levels. Due to concerns for toxicity, targets were set as the lower of the human therapeutic ranges.[30] Because oral dosing was poorly tolerated, rectal administration was explored.

Pharmacokinetic trials were conducted to determine optimal dosing regimens and routes. Since dosing was conducted as part of actual treatment regimens, pharmacokinetic (PK) data was analyzed from composite dosing trials. The results of PK studies in elephants was published for four of the primary anti-tuberculous drugs INH, RIF, EMB, and PZA.[31–34] Additionally, single dose trials were performed in bongo antelope for amikacin (AMK), INH and EMB[35] that provides comparative data for another large mammal, albeit a ruminant with different gastrointestinal and drug absorption physiology. Prior PK studies from bongo antelope suggested that dosing anti-tuberculous drugs obeys allometric scaling, a zoologic concept that the dose divided by the log-mass of the animal is a constant for select drugs.[36] However, data from elephants suggests linear scaling of dosing is more appropriate. INH, PZA, and EMB were well absorbed rectally with the maximal serum concentration (Cmax), area under the curve (AUC), and elimination parameters similar to that for oral dosing[31,32,34] whereas RIF was absorbed poorly via the rectum[33] presumably due to its higher lipophilic nature. Moreover, PK data in elephants indicated absorption and elimination characteristics similar to humans. Recent unpublished studies have demonstrated that INH absorption via the rectum may actually be as rapid as 7.5–15 min (Maslow and Mikota unpublished data). While prior publications reported Cmax at 1 or 2 h, these times represented the first blood draw.

Other considerations that may affect PK studies and dose relationships relate to vehicles used to administer drug to elephants and to the necessity of obtaining specimens in the field. INH when provided as a suspension is particularly volatile in food especially in acidic vehicles such as colas or other foods with a low pH.[37] Additionally, INH quickly degenerates after blood draw necessitating samples be maintained on ice and then rapidly processed and frozen.

5. Drug resistance

There have been two elephants reported with drug resistant TB.[27] One elephant was diagnosed with pan-susceptible infection from positive cultures obtained via trunk wash and from vaginal discharge. Despite 10 months of two drug treatment with INH and PZA administered rectally followed by an additional 10 months of three-drug treatment with INH, PZA, and RIF the animal developed recurrent culture positive vaginal discharge with MDR-TB a year after treatment was completed ([27] and G Dumonceaux, personal communication). The second animal is stated to have developed recurrent pulmonary infection with a RIF-resistant strain following a treatment course with INH and PZA, i.e. there was no documented exposure to RIF.

The efficacy of treatment is unknown. Although treated animals are required to undergo quarterly trunk-wash evaluations, there is no central repository for results. Also there is limited post-mortem data with no requirement for reporting. As noted above, the observation that treated animals manifest loss of seroreactivity to a combined antigen panel[27] may be useful.

Recurrent infection has been documented in at least 4 cases. Two cases were cited above; a third case has also been published.[27] A fourth case of recurrent infection occurred in an animal that had achieved target serum levels with 2 drugs.[12] The latter case was considered to arise from a peri-bronchial lymph node that eroded into the respiratory tree; re-treatment was apparently successful without second recurrence. In contrast, for some herds that achieved subtherapeutic levels, attack rates of recurrent infection in other herd members have approached 50% (S Mikota, unpublished data). Fortunately, the latter have developed recurrent infection with susceptible strains.

6. Zoonotic implications

Elephants can spray many feet and often place their trunks inside the mouths of other elephants presenting risks for both zoonotic and animal-to-animal transmission. Michalak et al. reported on the investigation of the animal handlers at a facility with three known active cases.[1] Of 22 animal handlers tested, 11 had reactions to intradermal PPD from *M. tuberculosis*; 3 were PPD converters, including one individual without direct involvement in elephant care. The other 8 reactive individuals had either unknown prior PPD status or were previously PPD-positive. One elephant handler had a chest radiograph suggestive of active tuberculosis and sputum was culture positive for *M. tuberculosis* that had an IS6100 restriction fragment length polymorphism (RFLP) pattern matching the elephants and confirming inter-species transmission of infection. And while the route of infection was presumed to be elephant to human, the index case was not known.

A subsequent paper reported on an outbreak investigation at the Los Angeles Zoo following the identification of *M. tuberculosis* in 2 Asian elephants, 3 Rocky Mountain goats, and a black rhinoceros.[6] IS6110 RFLP typing demonstrated clonal spread of infection. Of 307 individuals screened by skin testing, 55 (18%) were reactive at baseline and 15 (5%) demonstrated PPD conversion for whom risk for conversion included elephant training, attendees at the first elephant necropsy, and groundskeepers. A third outbreak investigation was conducted of employees at an elephant refuge following the identification of active infection in an elephant.[38] Nine employees demonstrated PPD conversion including 8 of 13 quarantine area workers of whom 3 were administrators who did not have direct elephant contact.[38]

A fourth outbreak investigation involved the potential for transmission of *M. bovis* in captivity, albeit not in elephants. Necropsy of a rhinoceros, with unsuspected *M. bovis* infection resulted in multiple PPD conversions[39] and resulted in the infection of non-human primates housed near the rhino barn and was the likely source of infection in a bongo antelope diagnosed years later.[35] Zoonotic transmission of *M. bovis* is well described among abattoir workers and was a cause of gastrointestinal TB from ingestion of infected milk or meat. Deer and wild animals such as badgers[40] continue as a reservoir of under-appreciated infection.

7. Conclusion

Tuberculosis in elephants and other wildlife poses the potential for animal and human disease. Collaborative efforts began in 1996 among regulatory bodies, animal and human medical providers, and the zoological and circus communities to identify sources of infection, develop and evaluate potential diagnostic tests, and share treatment information. These efforts represent a beginning to understand this disease in animals beyond commercially used hoofstock. Without a concerted effort among the diverse stakeholders, TB will continue to affect exotic animals posing the risk for morbidity and death for endangered species and potential risks for dissemination of resistant strains between animals and to people.

To attain the goal of TB eradication sharing of treatment outcomes and protocols is needed. Secondly to enable this to happen is to guarantee that privacy concerns are addressed to protect facilities from backlash that would derail efforts to collect epidemiologic data and thus analyze population results. Only when treatment decisions can be based on fact rather than anecdotal experience can veterinary care move forward and the public health be promoted.

Disclaimer

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References

1. Michalak K, Austin C, Diesel S, Bacon JM, Zimmerman P, Maslow JN. *Mycobacterium tuberculosis* infection as a zoonotic disease: transmission between humans and elephants. *Emerg Infect Dis* 1998;**4**:283–7.
2. Elephant database. http://www.elephant.se/country.php?name=india; [accessed 8.02.11].
3. Cheeran J, Nair N. *Techniques & procedure for post-mortem of elephants*. URL:. New Delhi, India: Project Elephant and Central Zoo Authority, Ministry of Environment and Forests http://cheerans.com/files/postmortem.pdf; 2003.
4. Dangolla A, Silva I. The status and veterinary problems in captive elephants in Sri Lanka. http://www.aserc.org/index.php?option=com_content&task=view&id=37; [accessed 8 02 11].
5. Murphree R, Warkentin J, Dunn J, Schaffner W, Jones T. Outbreak of *Mycobacterium tuberculosis* infection among employees of an elephant refuge. In: 2010 National tuberculosis conference; June 22–24 2010.
6. Oh JY, Kim KS, Jeong YW, Cho JW, Park JC, Lee JC. Human exposure following *Mycobacterium tuberculosis* infection of multiple animal species in a metropolitan zoo. *Emerg Infect Dis* 2002;**8**(11):1290–3.
7. Iyer AK. Veterinary science in India, ancient and modern with special reference to tuberculosis. *Agric Livest India* 1937;**7**:718–24.
8. McGaughey CA. Diseases of elephants: part III. *Ceylon Vet J* 1961;**9**:94–8.
9. Rothschild B, Laub R. Hyperdisease in the late Pleistocene: validation of an early 20th century hypothesis. *Naturwissenschaften* 2006;**93**:557–64.
10. Garrod AH. Report on the Indian elephant which died in the society's gardens on July 7th, 1875. *Proc Zool Soc Lond* 1875;**1875**:542.
11. Mikota S. Tuberculosis in elephants. In: Fowler M, Miller R, editors. *Zoo and wild animal medicine, current therapy*. 6th ed. St. Louis, MO: Saunders/Elsevier; 2008. p. 355–68.
12. Mikota SK, Peddie L, Peddie J, Isaza R, Dunker F, West G, et al. Epidemiology and diagnosis of *Mycobacterium tuberculosis* in captive Asian elephants (*Elephas maximus*). *J Zoo Wildl Med* 2001;**32**:1–16.
13. Saunders G. Pulmonary *Mycobacterium tuberculosis* infection in a circus elephant. *J Am Vet Med Assoc* 1983;**183**:1311–2.
14. Miller M. Update on elephant tuberculosis guidelines; report of the scientific subcommittee for tuberculosis in elephants. In: Meeting of the United States Animal Health Association (USAHA). Minneapolis, MN; 2010.
15. Payeur JB, Jarnagin JL, Marquardt JG, Whipple DL. Mycobacterial isolations in captive elephants in the United States. *Ann N Y Acad Sci* 2002;**969**:256–8.
16. Lacasse C, Terio K, Kinsel MJ, Farina LL, Travis DA, Greenwald R, et al. Two cases of atypical mycobacteriosis caused by *Mycobacterium szulgai* associated with mortality in captive African elephants (*Loxodonta africana*). *J Zoo Wildl Med* 2007;**38**(1):101–7.
17. Lewerin SS, Olsson S-L, Eld K, Roken B, Ghebremichael S, Koivula T, et al. Outbreak of *Mycobacterium tuberculosis* infection among captive Asian elephants in a Swedish zoo. *Vet Rec* 2005;**156**:171–5.
18. Moller T, Roken B, Petersson L, Vitaud C, Lyashchenko K. Preliminary results of a new serological test for detection of TB-infection (*Mycobacterium tuberculosis*) in elephants (*Elaphas maximus* and *Loxodonta africanum*) Swedish case studies. *Verh ber Erkg Zootiere* 2005;**42**:173–81.
19. Abraham D, Cheeran JV, Sukumar R, Mikota SK, Rao S, Ganguly A, et al., 20 June 2008. (Project Elephant, Ministry of Environment and Forests, Government of India, Parayavaran Bahvan, CGO Complex, Lodhi Road). Health assessment of captive Asian elephants in India with special reference to tuberculosis.
20. Angkawanish T, Wajjwalku W, Sirimalaisuwan A, Mahasawangkul S, Kaewsakhorn T, Boonsri K, et al. *Mycobacterium tuberculosis* infection in domesticated Asian elephants, Thailand. *Emerg Infect Dis* 2010;**16**:1949–51.
21. Kay M, Linke L, Triantis J, Salman M, Larsen R. Evaluation of DNA extraction techniques for detecting *Mycobacterium tuberculosis*-complex organisms in Asian elephant trunk washes. *J Clin Microbiol*; 2011 [epub ahead of print].
22. Abraham D, Davis J. Revised trunk wash collection procedure for captive elephants in a range country setting. *Gajah* 2008;**28**:53–4.
23. Isaza R, Ketz C. A trunk wash technique for the diagnosis of tuberculosis in elephants. *Verh ber Erkg Zootiere* 1999;**29**:121–4.
24. Larsen RS, Salman MD, Mikota SK, Isaza R, Montali RJ, Triantis J. Evaluation of a multiple-antigen enzyme-linked immunosorbent assay (ELISA) for detection of *Mycobacterium tuberculosis* in captive elephants. *J Zoo Wildl Med* 2000;**31**:291–302.
25. Griffin J, Buchan G. Aetiology, pathogenesis and diagnosis of *Mycobacterium bovis* in deer. *Vet Microbiol* 1994;**40**:193–205.
26. Mikota SK, Maslow JN. Theoretical and technical aspects of diagnostic techniques for mammalian tuberculosis. In: Baer CK, editor. *Annual conference of the American association of zoo veterinarians*; 1997. p. 162–5. Houston, TX.
27. Lyashchenko KP, Greenwald R, Esfandiari J, Olsen JH, Ball R, Dumonceaux G, et al. Tuberculosis in elephants: antibody responses to defined antigens of *Mycobacterium tuberculosis*, potential for early diagnosis, and monitoring of treatment. *Clin Vaccine Immunol* 2006;**13**(7):722–32.
28. Lyashchenko KP, Singh M, Colangeli R, Gennaro ML. A multi-antigen print immunoassay for the development of serological diagnosis of infectious diseases. *J Immunol Methods* 2000;**242**:91–100.
29. Greenwald R, Lyashchenko O, Esfandiari J, Miller M, Mikota S, Olsen JH, et al. Highly accurate antibody assays for early and rapid detection of tuberculosis in African and Asian elephants. *Clin Vaccine Immunol* 2009;**16**(5):605–12.
30. Peloquin CA. Therapeutic drug monitoring in the treatment of tuberculosis. *Drugs* 2002;**62**(15):2169–83.
31. Maslow JN, Mikota SK, Zhu M, Isaza R, Peddie LR, Dunker F, et al. Pharmacokinetics of isoniazid (INH) in the treatment of *Mycobacterium tuberculosis* among Asian and African elephants (*Elephas maximus* and *Loxodonta africana*). *J Vet Pharmacol Ther* 2005;**28**:21–8.
32. Maslow JN, Mikota SK, Zhu M, Riddle H, Peloquin CA. Pharmacokinetics of ethambutol (EMB) in the treatment of *Mycobacterium tuberculosis* in Elephants. *J Vet Pharmacol Ther* 2005;**28**:321–3.
33. Peloquin CA, Maslow JN, Mikota SK, Forrest A, Dunker F, Isaza R, et al. Dose selection and pharmacokinetics of rifampin in elephants for the treatment of tuberculosis. *J Vet Pharmacol Ther* 2006;**29**:581–5.
34. Zhu M, Maslow JN, Mikota SK, Isaza R, Dunker F, Riddle H, et al. Population pharmacokinetics of pyrazinamide in elephants. *J Vet Pharmacol Ther* 2005;**28**:403–9.
35. Auclair B, Mikota SK, Peloquin CA, Aguilar R, Maslow JN. Population pharmacokinetics of antituberculous drugs and treatment of *Mycobacterium bovis* infection in bongo antelope (*Tragelaphus eurycerus isaaci*). *J Zoo Wildl Med* 2002;**33**(3):193–203.
36. Hunter R, Isaza R. Concepts and issues with interspecies scaling in zoological pharmacology. *J Zoo Wildl Med* 2008;**39**(4):517–26.
37. Peloquin CA, Durbin D, Childs J, Sterling T, Weiner M. Stability of antituberculosis drugs mixed in food. *Clin Infect Dis* 2007;**45**:521.
38. Murphree R, Warkentin J, Dunn J, Schaffner W, Jones T. Tuberculosis outbreak at Elephant refuge, Tennessee, USA, 2009. *Emerg Infect Dis*; 2011 March [Epub ahead of print].
39. Dalovisio JR, Stetter M, Mikota-Wells S. Rhinoceros' Rhinorrhea: cause of an outbreak of infection due to airborne *Mycobacterium bovis* in zookeepers. *Clin Infect Dis* 1992;**15**:598–600.
40. Gallagher J, Clifton-Hadley R. Tuberculosis in badgers; a review of the disease and its significance for other animals. *Res Vet Sci*. 2000;**69**:203–17.

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Tuberculosis in Elephants in North America

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Within the past 4 years, tuberculosis (TB) has emerged as a disease of concern in elephants. The population of elephants in North America is declining [Wiese, 1997], and transmissible diseases such as TB may exacerbate this trend. Guidelines for the Control of Tuberculosis in Elephants, which require the screening of all elephants for TB, were instituted in 1997 [USDA, 1997; 2000]. Between August 1996 and May 2000, *Mycobacterium tuberculosis* was isolated from 18 of 539 elephants in North America, indicating an estimated prevalence of 3.3%. Isolation of the TB organism by culture is the currently recommended test to establish a diagnosis of TB; however, culture requires 8 weeks. Further research is essential to validate other diagnostic tests and treatment protocols. Zoo Biol 19:393–403, 2000. © 2000 Wiley-Liss, Inc.

Key words: *Loxodonta africana; Elephas maximus;* tuberculosis; bacterial disease

INTRODUCTION

Tuberculosis (TB) was first described in elephants more than 2,000 years ago by ancient Ayurvedic physicians in Ceylon [Iyer, 1937; McGaughey, 1961]. In recent times, a case in London [Garrod, 1875] was followed by sporadic reports throughout the twentieth century [Narayanan, 1925; Baldrey, 1930; Gutter, 1981; Saunders, 1983; Chandrasekharan, et al., 1995]. Although it is thought that elephants are susceptible to *Mycobacterium bovis* [Dannenberg, 1978; Schmidt, 1986], *Mycobacterium tuberculosis* (*M. tuberculosis*) has been identified as the causative agent in all cases in which bacteria have been isolated. To date, most reported cases of TB have occurred in captive Asian elephants (*Elephas maximus*). Two suspected cases in Af-

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rican elephants (*Loxodonta africana*) in Uganda and Israel were not confirmed by culture [Woodford, 1982; Gorovitz, 1962]. *M. tuberculosis* was isolated from an African elephant in France [Urbain, 1938]. In a retrospective medical study of 379 elephants in North American zoos, eight elephants died of TB between 1908 and 1994 [Mikota et al., 1994]. It is likely that this figure would have been higher had privately owned elephants been included in the survey.

RECENT CASES (1996–2000)

Between August 1996 and June 2000, samples from 539 elephants were submitted to the National Veterinary Services Laboratory (NVSL, Ames, IA) for mycobacterial culture [J. Payeur, personal communication]. Seventeen elephants from eight herds in Illinois, California, Arkansas, Missouri, and Florida were diagnosed with TB. At the time of diagnosis, three elephants resided in American Zoo and Aquarium Association accredited zoos and 14 in private facilities. There had been known previous contact between elephants in five of the herds. Three elephants demonstrated clinical signs that could be caused by TB. *M. tuberculosis* was isolated from 12 elephants pre-mortem and five elephants post-mortem. Restriction fragment length polymorphism was performed on *M. tuberculosis* isolates from 11 elephants. Five distinct *M. tuberculosis* strains were identified by this analysis [D.L. Whipple, 1997; personal communication].

Based on the 539 elephants in the NVSL database and the 532 elephants identified by the North American Regional Studbook keepers [M. Keele and D. Olson, personal communication], the prevalence of TB in elephants in North America is estimated to be 3.3%.

CLINICAL SIGNS

Confirmed cases of TB in elephants have typically been identified on post-mortem examination as ante-mortem signs are frequently absent. Chronic weight loss, anorexia. and weakness may occur [McGaughey, 1961; Gutter, 1981; Saunders, 1983], and dyspnea and coughing are sometimes observed [Seneviratna et al., 1966; Pinto et al., 1973]. Exercise intolerance is most likely to be observed in working animals [K.U. Mar, personal communication]. In Ceylon, ancient Ayurvedic elephant physicians regarded ventral edema as a sign of incurable lung disease [Pinto et al., 1973]. More recently, ventral edema has been observed in some TB-infected elephants; however, it may have been caused by concurrent congestive heart failure, anemia, or other medical conditions [Seneviratna et al., 1966; Pinto et al., 1973].

DIAGNOSIS

Several techniques have been used to diagnose mammalian TB. Methods such as culture, acid fast smears, fluorescent smears, and nucleic acid amplification techniques directly detect the bacterial organism. Indirect methods such as serological assays, the gamma-interferon test (GIT), and the intra-dermal tuberculin test detect antigen-antibody or cellular reactivity to mycobacterial antigen [Mikota and Maslow, 1997].

In humans and domestic animals, the intra-dermal tuberculin skin test is the primary screening method to detect infection with *M. tuberculosis* or *M. bovis*. The intra-dermal tuberculin test is the official ante-mortem test in cattle, bison, and deer and is incorporated into the U.S. Department of Agriculture (USDA) eradication guidelines [Essey and Davis, 1997; USDA, 1994; 1999]. The blood TB test (BTB), enzyme-linked immunosorbent assay (ELISA), and GIT have been used to diagnose TB infection in a limited number of species [Griffin and Cross, 1989; Rothel et al., 1992; Gaborick et al., 1996]. These indirect methods have not been validated in most non-domestic species nor have they been uniformly administered or consistently interpreted [Montali and Hirschel, 1990]. The limitations of applying such diagnostic tests to non-domestic species have been discussed [Hietala and Gardner, 1999].

Intra-dermal tuberculin testing is used in conjunction with slaughter surveillance to control TB in domestic cattle [Thompson et al., 1998]. Obviously, this method should not be applied to species such as the elephant. The current gold standard for the ante-mortem diagnosis of *M. tuberculosis* infection in elephants is mycobacterial culture of respiratory secretions obtained by trunk "wash" [USDA, 1997; 2000]. Elephants must be conditioned to permit the trunk wash procedure, which consists of the instillation of 60 mL of sterile saline into one or both nostrils, application of a 1-gal plastic bag over the end of the trunk, elevation of the trunk to distribute the saline, and collection of a forcibly exhaled sample into the bag [Isaza and Ketz, 1999]. Because the TB organism can be shed intermittently, three samples are collected on separate days.

To date, intra-dermal and serologic tests have frequently shown poor correlation with mycobacterial culture results in elephants [Montali et al., 1998]. One elephant that died from disseminated pulmonary *M. tuberculosis* infection had negative results when tested with human and bovine purified protein derivative (BPPD) tuberculins [Saunders, 1983]. Furthermore, four of five *M. tuberculosis* culture-positive elephants diagnosed since 1996 have demonstrated negative intra-dermal tuberculin responses to BPPD or balanced tuberculins. Eight of 30 *M. tuberculosis* culture-negative elephants had suspect tuberculin responses [Mikota, 1999].

Nucleic acid amplification techniques (NAAT) such as PCR detect mycobacteria by amplification of DNA or RNA [de Wit et al., 1990; Clarridge et al., 1993; Liébana et al., 1995; Roberts et al., 1996]. Advantages of NAAT include rapid turnaround time (hours) and the capability of detecting low numbers of organisms. These techniques have been reported to have high specificity for *M. tuberculosis complex* organisms (*M. tuberculosis, M. bovis, M. africanum, M. microti*), but mycobacterial species cannot be differentiated. Since both live and dead organisms are detected, NAAT is of limited value in monitoring response to therapy.

There are at present two amplification assays that are approved by the U.S. Food and Drug Administration for commercial use in human clinical and public health laboratories: the Amplicor MTB PCR (Roche Molecular Systems, Branchburg, NJ) and the Amplified *M. tuberculosis* Direct Test (MTD) (Gen-Probe, San Diego, CA). These assays have demonstrated specificities of ≥95%, but they have been less sensitive than culture for diagnosis of *M. tuberculosis* infection in humans [Dalovisio et al., 1996]. Validation has not yet been reported in elephants. Between August 1996 and August 1999, the NVSL performed the MTD on 612 elephant samples. The MTD correctly diagnosed six of nine culture-positive samples and 559 of 581 culture-negative samples. Results of 23 samples were inconclusive [J. Payeur, personal communication]. Using culture as the gold standard, the MTD demonstrated a sensitivity of 66.6% and a specificity of 96.2%. Validation of this test is still needed, and, at this time, the MTD and other NAATs are considered ancillary tests for detecting TB in elephants.

Serologic testing for TB has been performed using ELISA techniques with a non-species–specific protein A that is labeled with horseradish peroxidase. Early investigation of this technique in a herd of five elephants, which included one culture-positive animal, was described by Thoen and colleagues [1980]. The antigens used were heat-killed cells of *M. bovis,* BPPD, and purified protein derivative of *M. avium* (APPD). Two tuberculin-test positive elephants showed substantial seroreactivity to heat-killed *M. bovis* and BPPD, whereas two of three tuberculin-test negative animals showed seroreactivity only to heat-killed *M. bovis.*

Between 1997 and 1998, during the evaluation of a herd of four culture-negative elephants, it was proposed that tuberculin exposure may influence serologic and BTB analysis [Montali et al., 1998]. The antigens used in this serologic investigation were BPPD, *M. tuberculosis* culture filtrate protein, *M. avium* culture filtrate protein, APPD, and a lipoarabinomannan antigen (LAM) derived from *M. tuberculosis*. Elephants showed minimal to zero reactivity to these antigens before intra-dermal tuberculin injection, but dramatic increases in seroreactivity after injection. Elephants are constantly exposed to saprophytic *Mycobacterium* species and can be colonized by non-tuberculous mycobacteria (as well as *M. avium*) due to their behavior of bathing and dusting using their trunks. These organisms do not appear to cause clinical disease, but it has been hypothesized that such exposure accounts for these seemingly non-specific reactions to mycobacterial antigens [Montali et al., 1998].

Recently, a multiple-antigen ELISA was evaluated for its ability to detect *M . tuberculosis* infection in captive elephants [Larsen et al., 2000]. Serum samples were collected from 32 Asian and 15 African elephants, and a panel of six antigens was used to determine seroreactivity. The antigens included *M. bovis* culture filtrate (CF), PPD, *M. bovis* modified protein 70, two LAM antigens from strains of *M. tuberculosis*, and APPD. Discriminant analysis was used to determine the linear combination of antigens that accurately predicted the true infection status of the most animals, and the resulting classification functions were used to calculate the percentage of animals that were correctly classified. Of 47 elephants, seven of the Asians were infected (culture-positive); 25 Asians and 15 Africans were considered non-infected (culture-negative). Criteria for elephants designated as non-infected were: 1) trunk washes within 4 months of serum sampling that were negative for mycobacterial culture of *M. tuberculosis* or *M. bovis*; 2) no contact with elephants or other animals that had been diagnosed with *M. tuberculosis* of *M. bovis* within the past 5 years; 3) no intra-dermal tuberculin testing within the 6 months before sampling; and 4) no travel outside the institution in the previous 5 years. The specificity and sensitivity of the multiple-antigen ELISA, with 95% confidence intervals, were 100% (91.9–100%) and 100% (54.4–00%), respectively. The limitations inherent to this study suggest that much additional research is needed regarding the use of this ELISA; however, the results also indicate that this multiple-antigen ELISA may be a good screening test for elephants [Larsen et al., 2000].

PATHOLOGIC FINDINGS

The major pathology in elephants infected with *M. tuberculosis* infections occurs primarily in the lungs and thoracic lymph nodes with lesser involvement of extra-thoracic sites [Seneviratna et al., 1966; Pinto et al., 1973, Gutter 1981; Saunders 1983; Michalak et al., 1998; R.J. Montali, unpublished observations, 1999]. As in other animals, tubercular lesions in elephants appear to vary with the staging of the disease. In the less extensive cases, firm granulomatous nodules, sometimes with caseous foci, are noted in the bronchial lymph nodes and pulmonary tissue. Elephants with extensive involvement of both lungs (≥66%) usually die with severe caseo-calcareous and cavitating lesions. These often result in large pulmonary abscesses from which *M. tuberculosis* and opportunistic bacteria such as *Pseudomonas aeruginosa* have been isolated. Tenacious, mucopurulent, bronchial plugs are also common in advanced TB; bronchial and other thoracic lymph nodes are markedly enlarged and usually show a proliferative response with less caseation than the pulmonary lesions.

The pathologic descriptions “caseous” and “mucopurulent” are based on post-mortem observations of the lungs and upper respiratory tract. At post-mortem, the severity of the disease is determined and a time frame ascribed. Active, early lesions, which conceivably can occur within weeks to months, are usually localized and limited in size and scope. Advanced lesions may involve major portions of one or both lung lobes and become mineralized over a period of months to years. Both, however, may have areas that are caseous or mucopurulent.

Characteristic histologic findings include epithelioid granulomas with some giant cell formation in the earlier lymph node and pulmonary lesions and extensive caseous and pyogranulomatous pneumonia in the advanced forms. Though sparse, acid-fast bacilli are more easily found in central areas of caseation in the lungs but are typically rare in the lymph nodes.

Bronchial and tracheal tuberculous plaques and caseous and mucopurulent exudate in the nasal passages have been noted in both the early and late stages of TB, suggesting that the shedding of mycobacteria may occur at any stage of the disease. Less extensive tuberculous lesions were observed in the mesenteric lymph nodes, liver, kidneys, adrenals, and spleen in some of the more advanced cases. These lesions suggest that in disseminated cases shedding may occur by routes other than the respiratory system.

TREATMENT

There is little information in the literature regarding treatment of elephants for TB. In one report, an Asian elephant was treated prophylactically with isoniazid (INH) after a suspect intradermal tuberculin test [Devine et al., 1983]. Another suspected case of TB was treated with streptomycin administered intramuscularly on alternate days for 4 weeks [Chandrasekharan et al., 1995]. Current treatment protocols have been extrapolated from human treatment regimens [American Thoracic Society, 1994] and are still under investigation for efficacy in elephants.

Anti-TB drugs recently used in elephants includes INH, pyrazinamide (PZA), rifampin (RIF), and ethambutol (ETH). These drugs have been administered to elephants in food, by direct oral administration, and rectally. Oral delivery has been challenging, as many elephants refuse oral medications. Direct oral administration can be achieved in some elephants by conditioning the animals to accept a bite block and oral syringe [L. Peddie and J. Peddie, personal communication]. For other elephants, rectal drug administration techniques (including suppositories) have been developed.

Blood levels of INH, consistent with human therapeutic values, can be achieved in elephants by direct oral or rectal administration. Blood levels of RIF can be achieved orally, but not rectally [Dunker and Rudovsky, 1998]. PZA appears to be absorbed by either route [S.K. Mikota, unpublished data]. When anti-TB drugs are administered in food, blood levels are variable and this route of administration is not recommended. Anti-TB drug doses for individual elephants should be determined by measuring blood-level response. Elephants should be weighed before and throughout treatment.

The current recommended treatment for known infected elephants consists of INH and RIF daily for 2 months, then every other day for 10 months. A third drug, such as PZA, is given daily for the first 2 months of treatment. As a starting dose, INH can be given orally or rectally at a dose of 2.5–5.0 mg/kg. Although humans typically achieve a blood level of 3–5 µg/mL of INH at 2 hours [C.A. Peloquin, personal communication], some elephants became ill when their blood levels were in this range. An INH blood level of 1–2 µg/mL is recommended for elephants.

RIF can be initiated orally at a dose of 7.5–10.0 mg/kg orally. Human 2-hour blood levels for this drug are 8–24 µg/mL. PZA can be initiated at a dose of 25–35 mg/kg orally or rectally. Human 2-hour levels for PZA are 20–60 µg/mL. Supplementation with vitamin B6 (pyridoxine) at a daily dose of 1 mg/kg is recommended to prevent possible peripheral neuropathy, a condition that has been associated with INH therapy in humans [Goldman and Braman, 1972].

Side effects of treatment may include anorexia, lethargy, and colitis. Leukopenia was observed in one elephant receiving INH and RIF; the condition resolved after treatment was temporarily stopped and dosages adjusted [L. Peddie and J. Peddie, personal communication]. Elevations of liver enzymes have been observed in association with INH toxicity in humans and elephants.

Of 11 living *M. tuberculosis* culture-positive elephants, six are currently receiving anti-TB drugs including one elephant that is undergoing a second course of treatment. Five elephants that completed treatment in December 1997, June 1998, December 1998, October 1999, and April 2000, are presently culture negative. All culture-positive elephants ceased shedding organisms shortly after treatment was initiated and remained culture-negative during the treatment period.

GUIDELINES FOR THE CONTROL OF TB IN ELEPHANTS

In 1996, in response to the TB-related deaths of two privately owned elephants, an Elephant Tuberculosis Advisory Panel was formed. This panel, which was composed of USDA and zoo veterinarians, cooperated with the National Tuberculosis Working Group for Zoo and Wildlife Species to develop *Guidelines for the Control of Tuberculosis in Elephants* [USDA, 1997; 2000; www.aphis.usda.gov/ac/acindex.html]. These guidelines specify criteria for the testing, surveillance, and treatment of elephants for TB. In January 1998 and January 2000, they were distributed by the Animal Care Division of the USDA Animal Plant Health Inspection Service (USDA-APHIS) to all licensed elephant exhibitors regulated by the Animal Welfare Act. The guidelines require annual testing (three trunk cultures) of all elephants and strongly recommend submission of samples for ancillary diagnostic tests.

According to the guidelines, elephants are placed in one of four groups based on culture results and exposure history. Group A elephants have negative culture results and no known exposure to a culture-positive animal in the previous 5 years. These animals are cultured annually and have no travel restrictions while they remain culture negative for *M. tuberculosis.* Culture-negative elephants exposed to a culture-positive animal 1–5 years previously (group B) are cultured quarterly and have no travel restrictions. Culture-negative elephants exposed to a culture-positive animal within the previous 12 months (group C) may be monitored by culture (three-sample method), every other month for 1 year, with no travel permitted or, alternatively, may be treated, with travel permitted after 2 months if cultures remain negative. Culture-positive elephants (group D) are not permitted to travel until at least 6 months of treatment have been completed and two negative cultures have been demonstrated. Figure 1 illustrates the sequence of events for each of the four groups.

A thorough post-mortem examination should be performed on all elephants that die or are euthanized. Lungs and lymph should be closely examined for evidence of TB. Cultures for TB should be submitted on all elephants even if gross lesions are absent. A necropsy protocol for elephants may be accessed at the above website.

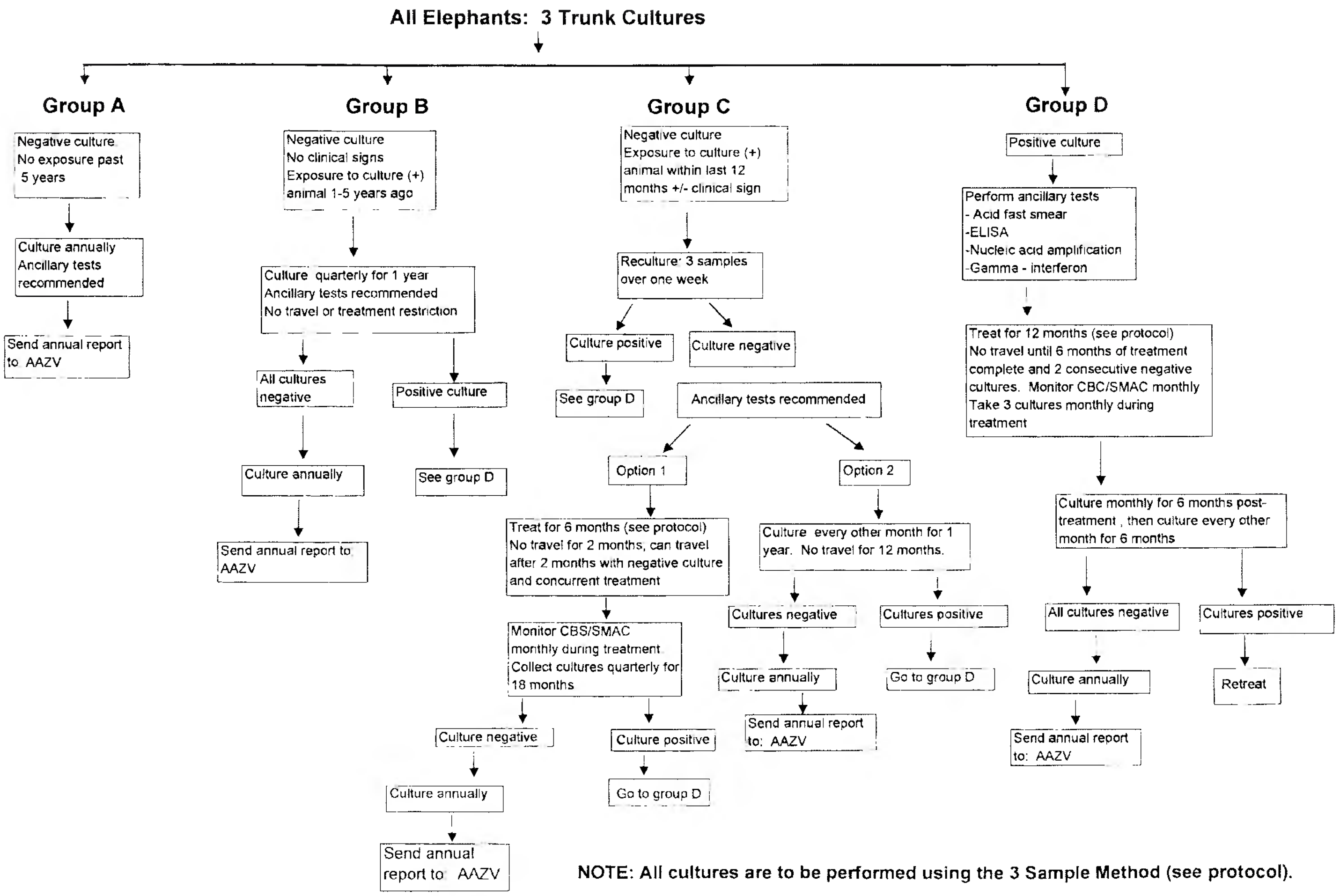
IMPLICATIONS FOR HUMAN HEALTH

After the diagnosis of TB in the Illinois herd, all personnel were tuberculin tested by the Illinois Department of Health. Of 22 handlers, 11 were tuberculin test positive. Eight of the 11 were positive on the initial test, indicating the possibility of prior exposure; three individuals converted during the investigation. One handler had culture-positive TB. The isolate from this individual matched that of the Illinois elephants [Michalak et al., 1998]. The original source of infection (for both elephants and humans) is unknown.

The apparent low incidence of TB in African elephants and the absence of reports of TB in free-ranging elephants suggest that this is primarily a disease of humans and that elephants are accidental hosts. Nonetheless, *M. tuberculosis* can be transmitted between elephants and humans and must be considered zoonotic [Maslow, 1997; Michalak et al., 1998]. Humans are most likely to contract TB when they have prolonged contact with infected individuals. It is likely that this is also the case with elephants, suggesting that handlers with close, daily contact with infected animals are at greatest risk. Elephant handlers and other personnel in contact with elephants should be tested for TB annually following established human testing protocols. All new employees should be tested before contact with elephants and anyone with active TB should not have contact with elephants. Some zoos have developed elephant/people interaction protocols to limit direct visitor contact with elephants, a practice that should be encouraged [Montali, 1999].

RESEARCH ISSUES

The ante-mortem diagnosis of TB in elephants continues to be problematic. Although identification of *M. tuberculosis* definitively establishes the presence of infection, failure to isolate the organism does not rule out infection. Mycobacteria are slow-growing organisms and culture typically requires 8 weeks. Clearly, better



NOTE: All cultures are to be performed using the 3 Sample Method (see protocol).

Fig. 1. Elephant management groups for TB surveillance [from USDA, 2000]. (For protocol, see Guidelines for the Control of Tuberculosis in Elephants [USDA, 2000] www.aphis.usda.gov/ac/acindex.html).

diagnostic tests are needed. Preliminary ELISA results are promising, but many more samples (both culture positive and negative) must be analyzed before this test (or any other serologic test) can be validated. Institutions holding elephants are strongly encouraged to submit samples for ancillary diagnostic tests so that valuable research data may be collected.

Although there is optimism that infected elephants in the North American population have been successfully treated, only long-term monitoring will confirm this. Pharmacokinetic studies are needed to further evaluate anti-TB drugs and to validate therapeutic protocols. It is essential that elephants that undergo treatment be observed for possible side effects. Blood levels of anti-TB drugs must be documented and correlated with treatment outcome.

Information on the pathophysiology and staging of TB in elephants is needed. A necropsy should be performed on all elephants that die and a thorough search for TB lesions should be conducted, even if the disease is not suspected. The elephant necropsy protocol (available on the USDA website) outlines appropriate samples to submit for laboratory evaluation. In cases of euthanasia, a diagnostic workup for TB (including ancillary tests as outlined in the guidelines) should be performed premortem so that results can be correlated with postmortem findings.

A reporting mechanism has been established whereby annual culture and ancillary test results are submitted to the American Association of Zoo Veterinarians for tabulation. Compliance has been poor for this critically needed information. We encourage the cooperation of the zoo community to comply with this reporting mechanism so that we may further our understanding of TB in elephants.

CONCLUSIONS

1. Reported cases of TB in elephants have been caused by *M. tuberculosis* (the agent of human TB). Although TB has been reported more frequently in Asian elephants, it is unknown whether there is a true species predilection.
2. Isolation of *M. avium* and non-tuberculous mycobacteria from elephant trunk wash samples is common, but these organisms have not been associated with clinical disease.
3. Isolation of *M. tuberculosis* is currently the only definitive test to diagnose TB in elephants, although ancillary tests such as NAAT and ELISA may be useful.
4. The intra-dermal tuberculin test is unreliable for diagnosing TB in elephants.
5. It is possible to deliver dosages of anti-TB drugs that achieve blood levels consistent with therapeutic levels in humans; however, the long-term efficacy of current treatment protocols remains to be documented.
6. Shedding of TB organisms generally ceases when elephants receive adequate levels of anti-TB drugs.
7. Transmission of TB between an elephant and a human has been reported. Handlers in close daily contact with infected elephants are at greatest risk.
8. Elephants may be at risk of contracting TB from infected humans. Handlers should undergo periodic TB screening to minimize risks to elephant health.
9. Complete post-mortem examination should be performed on all elephants that die. A thorough search for TB lesions should be conducted even if TB is not suspected.
10. Zoos are encouraged to establish protocols for elephant-visitor interactions.

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REFERENCES

American Thoracic Society. 1994. Treatment of tuberculosis and tuberculosis infection in adults and children. Am J Respir Crit Care Med 149:359–74.

Baldrey FSH. 1930. Tuberculosis in an elephant. J R Army Vet Corps 1:252.

Chandrasekharan K, Radhakrishnan K, Cheeran JV, Muraleedharan Nair KN, Prabhakaran T. 1995. Review of the incidence, etiology and control of common diseases of Asian elephants with special reference to Kerala. A week with elephants. Proceedings of the International Seminar on the Conservation of the Asian Elephant (June 1993). Bombay Natural History Society, Bombay: Oxford University Press. p 439–49.

Clarridge JE, Shawar RM, Shinnick TM, Plikaytis BB. 1993. Large-scale use of polymerase chain reaction for detection of *Mycobacterium tuberculosis* in a routine mycobacteriology laboratory. J Clin Microbiol 31:2049–56.

Dalovisio JR, Montenegro-James S, Kemmerly SA, Genre CF, Chambers R, Greer D, Pankey GA, Failla DM, Haydel KG, Hutchinson L, Lindley MF, Nunez BM, Praba A, Eisenach KD, Copper ES. 1996. Comparison of the amplified *Mycobacterium tuberculosis* (MTB) direct test, Amplicor MTB PCR, and IS6110-PCR for detection of MTB in respiratory specimens. Clin Infect Dis 23:1099–106.

Dannenberg AM. 1978. Pathogenesis of tuberculosis in man and animals: protection of personnel against tuberculosis. In: Montali RJ, editor. Mycobacterial infections of zoo animals. Washington, DC: Smithsonian Institution Press. p 65–75.

de Wit D, Steyn L, Shoemaker S, Sogin M. 1990. Direct detection of *Mycobacterium tuberculosis* in clinical specimens by DNA amplification. J Clin Microbiol 28:2437–41.

Devine JE, Boever WJ, Miller E. 1983. Isoniazid therapy in an Asiatic elephant (*Elephas maximus*). J Zoo Anim Med 14:130–3.

Dunker F, Rudovsky M. 1998. Management and treatment of a *Mycobacterium tuberculosis* positive elephant at the San Francisco Zoo. Proceedings of the American Association of Zoo Veterinarians and the American Association of Wildlife Veterinarians Joint Conference. Omaha, NE. p 122–3.

Essey MA, Davis JP. 1997. Status of the national cooperative state-federal bovine tuberculosis eradication program fiscal year 1997. Proceedings of the One Hundred and First Annual Meeting of the United States Animal Health Association. Louisville, KY. p 561–81.

Gaborick CM, Salman MD, Ellis RP, Triantis J. 1996. Evaluation of a five-antigen ELISA for diagnosis of tuberculosis in cattle and Cervidae. J Am Vet Med Assoc 209:962–6.

Garrod AH. 1875. Report on the Indian elephant which died in the society's gardens on July 7, 1875. Proceedings Zoological Society of London. p 542.

Goldman AL, Braman MAJ.1972. Isoniazid: A review with emphasis on adverse effects. Chest 62:71–7.

Gorovitz C. 1962. Tuberculosis in an African Elephant. Nord Vet Med 14:351–2.

Griffin JF, Cross JP. 1989. Diagnosis of tuberculosis in New Zealand farmed deer: an evaluation of intradermal skin testing and laboratory techniques. Irish Vet J 42:101–7.

Gutter A. 1981. *Mycobacterium tuberculosis* in an Asian elephant. Proceedings of the American Association of Zoo Veterinarians. Seattle, WA. p 105–6.

Hietala SK, Gardner IA. 1999. Validity of using diagnostic tests that are approved for use in domestic animals for nondomestic species. In: Fowler, ME, editor. Zoo and wild animal medicine, 4th ed. Philadelphia: WB Saunders. p 55–8.

Isaza R, Ketz CJ. 1999. A trunk wash technique for the diagnosis of tuberculosis in elephants. Verhandlungsbericht des Internationalen Symposiums uber die Erkrankungen der Zootiere, Vienna. p 121–4.

Iyer AK. 1937. Veterinary science in India, ancient and modern with special reference to tuberculosis. Ag Lvstk India 7:718–24.

Larsen RS, Salman MD, Mikota SK, Isaza R, Montali RJ, Triantis J. Evaluation of a multiple-antigen enzyme-linked immunosorbent assay for detection of *Mycobacterium tuberculosis* in captive elephants. J Zoo Wild Med (in press).

Liébana E, Aranaz A, Mateos A, Vilafranca M, Gomez-Mampaso E, Tercero JC, Alemany J, Suarez G, Domingo M, Domingez L. 1995. Simple and rapid detection of *Mycobacterium tuberculosis* complex organisms in bovine tissue samples by PCR. J Clin Microbiol 33:33–6.

Maslow J. 1997. Tuberculosis and other mycobacteria as zoonoses. Proceedings of the American Association of Zoo Veterinarians, Houston, TX. p 110–4.

McGaughey CA. 1961. Diseases of elephants. part III. Ceylon Vet J 9:94–8.

Michalak K, Austin C, Diesel S, Bacon JM, Zimmerman P, Maslow JN. 1998. *Mycobacterium tuberculosis* infection as a zoonotic disease: transmission between humans and elephants. Emerg Infect Dis 4:283–7.

Mikota SK, Sargent EL, and Ranglack GS. 1994. Medical management of the elephant. Bloomfield, MI: Indira Publishing House. 298 p.

Mikota SK, Maslow J. 1997. Theoretical and technical aspects of diagnostic techniques for mammalian tuberculosis. Proceedings of the American Association of Zoo Veterinarians. Houston, TX. p 162–6.

Mikota S. 1999. A review of diseases of the elephant. Verhandlungsbericht des Internationalen Symposiums uber die Erkrankungen der Zootiere, Vienna. p 1–5.

Mikota SK, Peddie L, Peddie J, Isaza R, Dunker F, West G, Lindsay W, Larsen RS, Salman MD, Chatterjee D, Payeur J, Whipple D, Thoen C, Davis DS, Montali RJ, Maslow J. Epidemiology and diagnosis of *Mycobacterium tuberculosis* in six groups of elephants. J Zoo Wild Med (in press).

Montali RJ, Hirschel PG. 1990. Survey of tuberculin testing practices at zoos. Proceedings of the American Association of ZooVeterinarians. South Padre Island, TX. p 105–9.

Montali RJ, Spelman LH, Cambre RC, Chatterjee D, Mikota SK. 1998. Factors influencing interpretation of indirect testing methods for tuberculosis in elephants. Proceedings of the American Association of Zoo Veterinarians and the American Association of Wildlife Veterinarians. Omaha, NE. p 109–12.

Montali RJ. Important aspects of zoonotic diseases in zoo and wildlife species. 1999. Verhandlungsbericht des Internationalen Symposiums uber die Erkrankungen der Zootiere, Vienna. p 149–55.

Narayanan RS. 1925. A case of tuberculosis in an elephant. J Comp Pathol 38:96–7.

Pinto MRM, Jainudeen MR, Panabokke RG. 1973. Tuberculosis in a domesticated Asiatic elephant, *Elephas maximus*. Vet Rec 93:662–4.

Rothel JS, Jones SL, Corner LA, Cox JC, Wood PR. 1992. The gamma-interferon assay for diagnosis of bovine tuberculosis in cattle: conditions affecting the production of gamma-interferon in whole blood. Aust Vet J 69:1–4.

Roberts GD, Böttger EC, Stockman L. 1996. Methods for the rapid identification of mycobacterial species. Clin Mycobact 16:603–15.

Saunders G. 1983. Pulmonary *Mycobacterium tuberculosis* infection in a circus elephant. J Am Vet Med Assoc 183:1311–2.

Schmidt MJ. 1986. Elephants. In: Fowler, ME, editor. Zoo and wild animal medicine, 2nd ed. Philadelphia: W.B. Saunders. p 883–923.

Seneviratna P, de S Wettimuny SG, Seneviratna D. 1966. Fatal tuberculosis in an elephant. Vet Med Small Anim Clin 60:129–32.

Thoen CO, Mills K, Hopkins MP. 1980. Enzyme-linked protein A: an enzyme-linked immunosorbent assay reagent for detecting antibodies in tuberculous exotic animals. Am J Vet Res 41:833–5.

Urbain A. 1938. L'infection tuberculeuse spontanee chez les mammiferes sauvages en captivite. Ann Inst Pasteur 61:705–30.

United States Department of Agriculture, Animal and Plant Health Inspection Service 91-45-005. 1994. Tuberculosis eradication in Cervidae uniform methods and rules, effective May 15, 1994. Washington, DC.

United States Department of Agriculture, Animal and Plant Health Inspection Service, Animal Care. 1997. Guidelines for the control of tuberculosis in elephants.

United States Department of Agriculture, Animal and Plant Health Inspection Service, 91-45-011. 1999. Bovine tuberculosis eradication uniform methods and rules, January 22, 1999. Washington, DC.

United States Department of Agriculture, Animal and Plant Health Inspection Service, Animal Care. 2000. Guidelines for the Control of Tuberculosis in Elephants. www. aphis.usda.gov/ac/acindex.html

Wiese R. 1997. Demographic analysis of the Asian elephant population in North America. Proceedings of the Elephant Managers Association Workshop. 18:57.

Whipple DL. 1997. Molecular epidemiology of tuberculosis in wild white-tailed deer in Michigan and elephants. Proceeding One Hundred and First Annual Meeting of the United States Animal Health Association. p 543–6.

Woodford MH. 1982. Tuberculosis in wildlife in the Ruwenzori National Park, Uganda (part II). Trop Anim Health Prod 14:155–60.

RESEARCH ARTICLE

Housing and Demographic Risk Factors Impacting Foot and Musculoskeletal Health in African Elephants [*Loxodonta africana*] and Asian Elephants [*Elephas maximus*] in North American Zoos

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Abstract

For more than three decades, foot and musculoskeletal conditions have been documented among both Asian [*Elephas maximus*] and African [*Loxodonta africana]* elephants in zoos. Although environmental factors have been hypothesized to play a contributing role in the development of foot and musculoskeletal pathology, there is a paucity of evidence-based research assessing risk. We investigated the associations between foot and musculoskeletal health conditions with demographic characteristics, space, flooring, exercise, enrichment, and body condition for elephants housed in North American zoos during 2012. Clinical examinations and medical records were used to assess health indicators and provide scores to quantitate conditions. Using multivariable regression models, associations were found between foot health and age [*P* value = 0.076; Odds Ratio = 1.018], time spent on hard substrates [*P* value = 0.022; Odds Ratio = 1.014], space experienced during the night [*P* value = 0.041; Odds Ratio = 1.008], and percent of time spent in indoor/outdoor exhibits during the day [*P* value < 0.001; Odds Ratio = 1.003]. Similarly, the main risk factors for musculoskeletal disorders included time on hard substrate [*P* value = 0.002; Odds Ratio = 1.050] and space experienced in indoor/outdoor exhibits [*P* value = 0.039; Odds Ratio = 1.037]. These results suggest that facility and management changes that decrease time spent on hard substrates will improve elephant welfare through better foot and musculoskeletal health.

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Competing Interests: CM and JH are employed by AWARE Institute. AWARE Institute is a commercial entity founded by CM in 2014 and provides animal welfare assessment, research and education services to zoos and aquariums. These interests do not alter the authors' adherence to all the PLOS ONE policies on sharing data and materials, as detailed online in the guide for authors.

Introduction

Foot and musculoskeletal []conditions are among the most commonly reported health issues affecting African and Asian elephants under human care, and have been challenging veterinary issues for zoo elephants for nearly a century [1, 2]. In 1994, Mikota et al. published an extensive review of medical records from 69 North American zoos and concluded that over the course of the 84 years for which documentation was available, an average of 50% of the elephants experienced foot pathology and 64% experienced musculoskeletal abnormalities [other than those affecting the feet] [3]. More recently, 33% of zoos surveyed reported at least one foot abnormality, 36% reported at least one case of arthritis, and 18% reported at least one case of lameness in their elephant populations within the previous year [4].

Foot and musculoskeletal health conditions of concern in elephants are pododermatitis, toenail cracks and overgrowth, onychia [inflammation/infection of the toenail bed], sole overgrowth and abscesses, osteomyelitis of the phalanges, degenerative joint disease, osteoarthritis, trauma, and soft tissue strains, although this is not an inclusive list [5,6,7]. Elephant feet and limbs may be predisposed to some of these conditions due to their unique anatomy and pressures experienced due to large body mass [8]. Bones of the feet are oriented so that just the tips of the phalanges come into contact with the substrate via the associated nails [8]. In addition a cartilaginous rod extends caudally to support the large cushion in the heel which distributes forces across the foot [9]. Studies have shown that increased foot pressures are associated with larger body mass, and that elephants carry more than 60% of their weight in the forelimbs [10]. Limb bones in normal elephants have little angulation, and therefore, forces are transmitted in line with the axis of the leg through the joints [3]. The long life of these species may lead to repeated force to the structures of the foot and limbs, potentially leading to health concerns.

Since health is an important indicator of animal welfare [11], there is considerable interest in developing a better understanding of the risk factors that contribute to poor foot and musculoskeletal health so that targeted prevention and intervention strategies may be applied. Clinical experiences suggest that lack of exercise, limited space, standing on hard substrates, environmental factors that increase contact of feet with excrement, urine, and moisture, and obesity are potential contributors to foot and musculoskeletal pathology [5,6,7]. However, there is a paucity of literature that scientifically investigates the association of these factors with foot and musculoskeletal disorders in elephants. The goals of this study were to 1) ascertain the current status of foot and musculoskeletal health of elephants housed at zoos accredited by the Association of Zoos and Aquariums (AZA) in North America; 2) investigate the associations of demographic, environmental, and management factors with foot and musculoskeletal problems; and 3) support evidence-based recommendations for interventions to prevent pathology and improve the foot and musculoskeletal health of zoo elephants.

Materials and Methods

Ethics Statement

This study was authorized by the management at each participating zoo and, where applicable, was reviewed and approved by zoo research committees. In addition the study protocol was reviewed and approved by the Zoological Society of San Diego Institutional Animal Care and Use Committee N.I.H. Assurance A3675-01; Protocol 11–203. The study was non-invasive.

Study Population

Elephants selected for this study were present in AZA accredited zoos in 2012. Additionally, elephants selected for study were not born, did not die, and were not transferred between zoos within the 2012 study year. Data were sourced from medical records and physical exams for each elephant completed by veterinarians at each participating zoo.

Musculoskeletal Assessment

Zoo-based veterinarians performed a visual/tactile examination of each individual elephant using a checklist to record the presence or absence of abnormalities in the musculoskeletal system of the limbs (shoulders, elbows, carpi, hips, stifles, tarsi) (S1 Template). Occurrences of abnormalities such as swelling, heat, or angular deformities that reflected musculoskeletal pathology were documented. Due to the elephant's anatomy, visual and tactile examination is less effective for detecting abnormalities in the more proximal joints, such as the shoulders and hips. Therefore veterinarians also evaluated each animal for evidence of stiffness, lameness, abnormal weight bearing, or mechanical limitations in the range of motion of the limb joints as an additional indicator of musculoskeletal problems.

The project veterinarian reviewed all physical examination results and assigned each elephant a musculoskeletal (MS) score based on the following system: a MS score of 0 indicated no gait change, limb deformity, joint heat or swelling on the physical exam. A score of 1 indicated one joint/limb had heat, swelling, or mild lameness/gait change; a score of 2 indicated one joint/limb exhibited heat or swelling with associated lameness or stiffness; and a score of 3 indicated two or more joints or limbs with heat, swelling or joint deformity associated with lameness or other gait deficiencies. The severity of abnormalities was not assessed since these could not be reliably standardized between the different veterinarians performing the examinations.

Foot Assessment

Zoo-based veterinarians evaluated each elephant's external pedal tissue structures (foot pad, interdigital space, cuticle, toenail) and recorded the presence or absence of abnormalities (but not severity) on each foot (S1). Toenails were examined for any cracks, defects, or horn growth abnormalities. In addition, veterinarians recorded any cracks, ulcerations, bruises, fissures, abscesses, or horn growth/sole abnormalities on the foot pads and in the interdigital spaces. Osteo-articular pathologies of the feet were not assessed during this portion of the examination and results of radiographs were not included since the majority of elephants did not have concurrent imaging at the time of these evaluations.

Foot data from the physical examinations were reviewed by the project veterinarian and each elephant was assigned a score based on the following system: each of three locations (toenail, pad, or interdigital space) on a foot were assessed for the presence of an abnormality, and each location on each foot with an abnormality was scored as 1, such that each foot could have a maximum score of 3, with each elephant having a maximum score of 12.

In order to determine the subset of the elephant population that could potentially be affected by chronic or recurrent foot problems, we requested the complete 2011 veterinary records of each elephant included in the study. Where veterinary records were obtained and complete for the calendar year, the project veterinarian assessed each record for notes where the attending veterinarian had described problems or treatment pertaining to the elephant's feet. We were interested in evaluating chronic or recurrent (described as "possibly persistent" in the remainder of the text) foot problems, however due to the level of detail provided in the 2011 records, we were not able to determine the severity of lesions nor whether the abnormalities reported in the physical examination were the same exact location as those observed in 2011. As such, the population of interest for further risk factor analyses included elephants with a completed physical examination in 2012 who also had a record of one or more foot abnormalities in 2011. In this case, elephants with “possible persistent” foot problems had one or more foot problems in both 2011 and 2012, but the exact nature and location of those problems could not be confirmed to be the same.

Independent Variables

We selected independent variables based on hypotheses regarding their potential association with foot and MS scores. Definitions for the variables selected for testing in this study are described in Table 1. Details on the collection and calculation of independent variables are presented in [12–16], but a few novel variables warrant further description.

We were interested in quantifying the amount of space available to each elephant. Because many zoo elephants are shifted between different environments that comprise an exhibit for varying amounts of time each day, a new variable was calculated to capture the experience of the elephants as a factor of both the size of their different environments and the amount of time they are housed in each space. This Space Experience variable [12] was calculated by first taking the size [m^2] of each environment in which an elephant spent time and then multiplying it by the percentage of time the elephant spent in that environment. These weighted

Table 1. Description of variables used in analysis of musculoskeletal and possible persistent foot score analysis of African and Asian elephants.

Variable	Unit of Analysis	Unit	Time Scale	Description	Ref
Age	Elephant			Age of elephant (years)	[14]
Sex	Elephant			Male or Female	[14]
Species	Elephant			African (*Loxodonta africana*) or Asian (*Elephas maximus*)	[14]
Origin	Elephant			Captive or wild born	[14]
Environment Contact	Elephant		Overall, Day, Night	Maximum number of unique environments an elephant was housed in	[12]
Space Experience				The average weighted (by percent time) size of all environments in which an elephant spent time	[12]
Total	Elephant	[m^2]	Overall, Day, Night	For all environment types	[12]
Indoor	Elephant	[m^2]	Overall, Day, Night	For indoor environments only	[12]
In/Out Choice	Elephant	[m^2]	Overall, Day, Night	For environments where there is a choice of indoors or outdoors	[12]
Outdoor	Elephant	[m^2]	Overall, Day, Night	For outdoor environments only	[12]
Percent Time				Sum of monthly percent time spent in category, averaged over time period	[12]
Indoor	Elephant	%	Overall, Day, Night	Time spent in indoor environments	[12]
In/Out Choice	Elephant	%	Overall, Day, Night	Time spent in environments with an indoor/outdoor choice	[12]
Outdoor	Elephant	%	Overall, Day, Night	Time spent in outdoor environments	[12]
Soft Substrate	Elephant	%	Overall, Day, Night	Time spent in environment with 100% grass, sand, or rubber substrate	[12]
Hard Substrate	Elephant	%	Overall, Day, Night	Time spent in environment with 100% concrete or stone aggregate substrate	[12]
Body Condition Score	Elephant			Score based on body condition, ranging from 1–5 with an ideal score of 3	[15]
Musculoskeletal Physical Exam Score	Elephant			Score of 0–3 indicating range of motion or joint abnormalities based on physical exam	
Foot Physical Exam Score	Elephant			Score of 0–12 indicating abnormalities on nails, pads, and interdigital space on any foot based on physical exam	
Mean Daily Walking Distance	Elephant			Average distance [km] that an elephant walks per day	[16]
Exercise Week	Elephant			Number of reported hours spent exercising animals each week, where 0 indicates less than 1 hour of staff-directed exercise per week and 7 indicates >14 hours of staff directed exercise per week	[13]
Exercise Diversity	Zoo			Diversity index score of exercises conducted at zoo	[13]
Enrichment Diversity	Zoo			Diversity index score of enrichment activities conducted at zoo	[13]

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environment sizes were then averaged to calculate a representative value for each elephant. The Space Experience variables were adjusted to a value of "per 500 ft^2" to aid in interpretation of Beta values.

To calculate our environment type and flooring substrate variables, we first defined each space in which elephants spent time as indoors, outdoors or mixed based on detailed facility surveys [12]. Mixed environments were areas where elephants had a choice to move freely between indoor and outdoor spaces. We then defined multiple classes of flooring substrate: grass, sand, rubber padding, stone aggregate, concrete and categorized the types of substrates into hard surface (concrete and stone aggregate), soft surface (grass, sand, and rubber padding) and determined the percent coverage for each substrate type for each environment. We wanted to calculate the time that elephants spent in contact with each substrate type so to confirm this we determined which environments were comprised of 100% hard and 100% soft substrate and calculated the percent time each elephant spent in environments that met this criteria from detailed housing time budgets [12]

Statistical Analysis

The MS score, foot score, and co-localization frequencies were calculated. Co-localization was defined as more than one type of abnormality per foot. Sex and species differences were assessed using Chi-Square analysis. We calculated descriptive statistics for the mean percent coverage of hard and soft flooring surfaces for each environment type (indoors, outdoors, and mixed), and Chi-Square analysis was used to determine if there were any associations between the environment type (indoors, outdoors, and mixed) and the frequency of 100% coverage of hard or soft surfaces.

Predictive models for MS and foot scores were fitted using generalized estimating equations (GEE), which allowed for repeated measurement and clustering of individual animals within zoos. Multinomial logistic regression was used for MS scores, with a reference level of zero, or "no joint problems". For foot scores, the score mean equaled the variance, supporting the use of log-linear Poisson regression models. Residual over-dispersion was accounted for by allowing a multiplicative over-dispersion factor, specified as the deviance scale. Multivariable regression models were built by assessing individual predictors and manually conducting forward stepwise selection based on quasi-likelihood under the independence model criterion (QIC) values and parameter estimates of explanatory variables. Models exhibiting multi-collinearity, as defined by a variance inflation factor (VIF) of greater than 10 and a Condition Index (CI) of greater than 30, were not considered for further analysis. Age, sex, species, and origin were assessed as potential confounders to the models. An independent correlation structure was specified. Statistical analyses were conducted using SAS software, version 9.3 [PROC GENMOD, with options REPEATED, CORR = IND, DIST = [MULT or POISSON], LINK = [CLOGIT or LOG]; SAS Institute, Inc., Cary, NC], and a P value of < 0.05 was considered statistically significant.

Results

Musculoskeletal Health

Within the study population of 255 elephants, 198 had complete musculoskeletal health data. The majority of elephants, 74.7% (148 / 198), did not have any reported musculoskeletal abnormalities. Table 2 shows the frequency of MS scores within the study population. There were no significant statistical differences between the MS scores based on sex (P value = 0.070) or species (P value = 0.488).

Table 2. Frequency of MS scores among African and Asian elephants during 2012 Physical Exam.

	Species		Sex		
MSScore	**African***	**Asian***	**Male****	**Female****	**Total**
0	76	72	33	115	148
1	13	15	1	27	28
2	9	11	2	18	20
3	0	2	0	2	2
Total	98	100	36	162	198

*No significant statistical difference between species (*P* value = 0.4879)

**No significant statistical difference between sexes (*P* value = 0.0704)

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The results of univariate modeling of space and substrate variables on MS scores are presented in Table 3, and were used to guide development of the multivariable model. Descriptive statistics detailing the variables included in the multi-variable regression model are shown in Table 4. In the multivariable multinomial logistic predictive model, the combination of time on hard substrate, Space Experience in environments that included both indoor and outdoor areas, and the interaction of Space Experience In/Out Choice with age had the most effect on odds of increased MS scores (Table 5). The odds ratio for percent time spent on hard surfaces was 1.050. An example of how this odds ratio associates time on hard substrates with MS scores is illustrated using population-level descriptive statistics for time on hard substrates. Elephants that spend 4 hours per 24 hour period on hard substrates (population 3rd quartile) are 68% more likely to have a MS score of 2 (versus 1) than are elephants which spend 2.5 hours per 24 hour period on hard substrates (population mean). Space Experience for areas with a choice of indoors or outdoors is associated with a 3.7% increase in odds of a higher MS score. However, this effect is attenuated by age, such that for each year an elephant ages, the effect of Space Experience In/Out Choice on MS score decreases by 0.1%.

Foot Health

Within the study population of 255 elephants, 215 had physical examinations completed for foot health. Of these, 32.6% (70 / 215) had no noted foot abnormalities at the time of examination, and for those that did, 88.3% (128 / 145) had foot scores of between 1 and 4 (maximum score of 12). Table 6 details the frequency of foot scores within the population. There was no difference in foot scores by species (P value > 0.05).

Of the 145 animals with recorded abnormalities, 92.4% (134 / 145) elephants had abnormalities of the nails, 13.1% (19 / 145) had abnormalities on their pads, and 22.8% (33 / 145) had abnormalities in their interdigital space. Fig 1 shows the distribution of feet per elephant where abnormalities were present. Co-localization, the occurrence of abnormalities in combination (two or three locations per foot), was present in 13.0% (28 / 215) of the population, as seen in Fig 2.

One hundred sixty-three elephants had complete 2011 veterinary records and a physical exam conducted in 2012. Sixty-four of those 163 elephants had at least one foot abnormality in their 2011 records, and therefore met the criteria for the analysis of possible persistent foot (PPF) abnormalities. Table 6 lists the foot score frequencies for the full population (2012), and for those with PPF scores (2012 score if abnormality listed in 2011). Of those elephants meeting the criteria for PPF scores, 79.7% (51 / 64) had at least one foot abnormality reported in the 2012 physical exam, suggesting potential chronicity or recurrence. The majority of these elephants had abnormalities of the toenails (73.4%; 47 / 64), while 10.9% (7 / 64) had abnormalities on pads and 20.3% (13 / 64) had abnormalities in the interdigital space. There were no

Table 3. Univariate assessment of musculoskeletal (MS) scores in African and Asian elephants using multinomial logistic regression. OR: Odds Ratio; *: *P* value < 0.05; ^ P value < 0.15 significance threshold for model building. Hypothesis: + Increase odds of having increased MS score;—Decrease odds of having increased MS score; 0 Neutral relationship on MS score.

				Overall				Day				Night			
Hypothesis	**Variable**	**Reference**	**N**	**Beta**	**OR**	***P* value**		**Beta**	**OR**	***P* value**		**Beta**	**OR**	***P* value**	
+	Age		198	-0.076	0.927	<0.001	*								
0	Sex	ref = Male	36												
		Female	162	-1.472	0.229	0.017	*								
0	Species	ref = African	98												
		Asian	100	-0.317	0.729	0.327									
0	Origin	ref = Wild	143												
		Captive	55	2.142	8.516	<0.001	*								
-	Environment Contact		196	0.011	1.011	0.602		0.009	1.009	0.718		0.014	1.014	0.601	
-	Space Experience		196	0.0004	1.000	0.889		0.0001	1.000	0.935		-0.0002	1.000	0.921	
+	Space Experience Indoors		196	0.076	1.078	0.216		0.131	1.140	0.043	*	0.055	1.057	0.351	
-	Space Experience Outdoors		196	0.001	1.001	0.794		0.001	1.001	0.689		0.0001	1.000	0.957	
-	Space Experience In/Out Choice		196	0.007	1.007	0.094	^	0.009	1.009	0.125		0.006	1.006	0.137	^
+	Percent Time Indoors		196	0.012	1.012	0.050	*	0.016	1.016	0.056	^	0.007	1.007	0.121	
-	Percent Time Outdoors		196	-0.009	0.991	0.133	^	-0.009	0.991	0.155		-0.005	0.995	0.225	
-	Percent Time In/Out Choice		196	-0.0003	1.000	0.964		0.004	1.004	0.670		-0.002	0.999	0.756	
+	Time on Hard Substrate		196	0.045	1.046	0.002	*	0.053	1.055	0.018	^	0.023	1.023	0.024	*
-	Time on Soft Substrate		196	-0.006	0.994	0.513		-0.010	0.990	0.473		-0.011	0.989	0.134	^
+	Foot Physical Exam Score		183	-0.149	0.862	0.038	*								
-	Mean Daily Walking Distance		47	0.341	1.407	0.063	^								
-	Enrichment Diversity		181	0.327	1.386	0.648									
-	Exercise Diversity		173	-0.406	0.666	0.143	^								
-	Exercise Week	ref = 1	33												
		2	80	-0.389	0.678	0.285									
		3	0												
		4	14	-0.429	0.651	0.417									
		5	27	0.396	1.486	0.550									
		6	4	-0.838	0.433	0.406									
		7	15	-0.153	0.858	0.753									
+	Body Condition Score	1	2	-3.171	0.042	0.155									
		2	6	-1.458	0.233	0.032	*								
		ref = 3	47												
		4	68	-0.276	0.759	0.560									
		5	68	-0.434	0.648	0.311									

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Table 4. Descriptive statistics for variables retained in final multi-variable regression model for the population with MS scores.

	Musculoskeletal Population		
Variable	**N**	**Mean**	**Std Dev**
Age	198	31.5	13.5
Space Experience In/Out Choice (per 500 ft^2)	196	26.7	47.5
Percent Time on Hard Substrate	196	10.3	11.9

doi:10.1371/journal.pone.0155223.t004

Table 5. Multivariable assessment of MS scores using multinomial logistic regression.

Variable	Beta	Odds Ratio	*P* value
Intercept 1 (Score 0 vs. Score 1)	0.506		0.029
Intercept 2 (Score 0 vs. Score 2)	1.557		< 0.001
Intercept 3 (Score 0 vs. Score 3)	4.089		< 0.001
Time on Hard Substrate	0.049	1.050	0.002
Space Experience In/Out Choice (per 500 ft^2)	0.036	1.037	0.039
Age*Space Experience In/Out Choice (per 500 ft^2)	-0.001	0.999	0.045

doi:10.1371/journal.pone.0155223.t005

significant statistical differences between the PPF scores based on sex (*P* value = 0.820) or species (*P* value = 0.527).

Since chronic or recurrent foot issues have been postulated to be related to husbandry/management conditions, univariate modeling of the foot scores from the 64 elephants in the PPF sub-population was performed and results presented in Table 7. These findings were used to guide development of the multivariable model. Descriptive statistics detailing the variables retained in the final multi-variable model are shown in Table 8. The multivariable Poisson predictive model found that the combination of time on hard substrate, percent of time spent during the day with a choice of indoors or outdoors, and Space Experience at night (11) had the greatest effect on risk of possible persistent foot scores (Table 9). The risk ratio for percent time spent on hard surfaces was 1.014 (Fig 3). An example of how this risk ratio associates time on hard substrates with foot scores is illustrated using the population-level descriptive statistics for time on hard substrates. Elephants that spend 3 hours per 24 hour period on hard substrate (population mean) are 18% more likely to have a foot score of 6, while those spending 5 hours per 24 hour period (population 3rd quartile) are 32% more likely to have a foot score of 7. We found a smaller

Table 6. Frequency of elephants per foot score for the Foot Physical Exam and for Possible Persistent Foot (PPF) scores. The Foot Physical Exam was conducted in 2012. Possible Persistent Foot (PPF) scores were defined by an elephant's 2012 physical exam score only for elephants that had existing 2011 veterinary records showing foot abnormalities in 2011.

	Foot Physical Exam	Foot Physical Exam: Possible Persistent				
			Species		Sex	
Score	All Elephants	All Elephants	African*	Asian*	Male**	Female**
0	70	13	6	7	1	12
1	33	12	7	5	1	11
2	39	14	9	5	1	13
3	23	9	5	4	1	8
4	33	9	2	7	2	7
5	3	3	1	2	1	2
6	5	1	1	0	0	1
7	4	3	1	2	0	3
8	4	0	0	0	0	0
9	0	0	0	0	0	0
10	0	0	0	0	0	0
11	0	0	0	0	0	0
12	1	0	0	0	0	0
Total	215	64	32	32	7	57

*No significant statistical difference between species (*P* value = 0.5271]

**No significant statistical difference between sex (*P* value = 0.8198]

doi:10.1371/journal.pone.0155223.t006

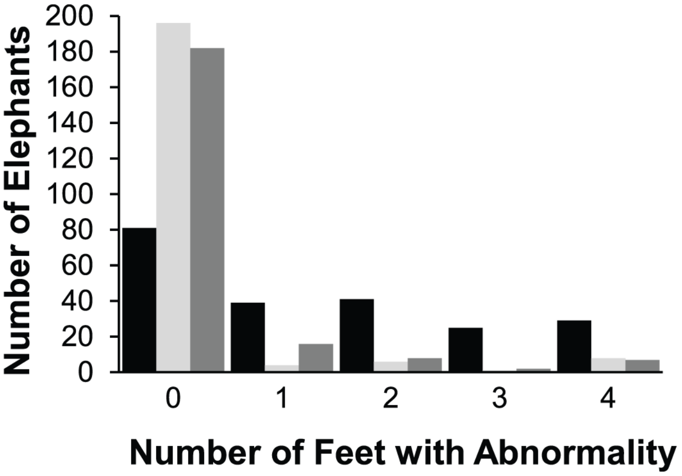

Fig 1. Frequency of elephants with multiple foot abnormalities separated by location of abnormality. Black indicates nail, grey indicates pad, and hashed pattern indicates interdigital space.

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effect on foot score when elephants spent time in environments where there was a choice of being indoors or outdoors during the day; there was a 0.8% increase in risk of increased foot score for each incremental increase in percent time increase in these mixed indoor/outdoor environments. In addition, Space Experience at night is associated with a 0.3% increase in risk in foot score. Age is included in the model as a confounder of nighttime Space Experience.

Flooring and Environment Associations

We further analyzed the flooring substrate coverage data to better understand the potential associations between environment types (indoors, outdoors and mixed) with flooring surfaces.

Table 10 shows the descriptive statistics for average percent coverage of hard flooring surfaces (concrete and stone aggregate) and soft flooring surfaces (grass, sand, and rubber padding) in different environment types (indoor, mixed, and outdoor). This analysis demonstrates that the average coverage of hard and soft surfaces did not differ between indoor, outdoor and mixed environments. While many environments had multiple substrate types, our modeling

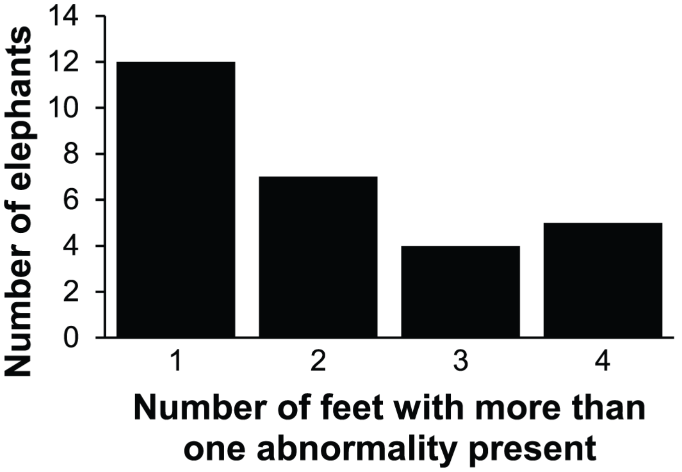

Fig 2. Frequency of elephants with co-localization of foot abnormalities.

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Table 7. Univariate assessment of possible persistent foot scores for African and Asian elephants using Poisson regression. RR: Risk Ratio; nd: no data, *: *P* value < 0.05; ^ P value <0.15 significance threshold for model building. Hypothesis: + Increase risk of having increased PPF score;—Decrease risk of having increased PPF score; 0 Neutral relationship on PPF score.

				Overall				Day				Night			
Hypothesis	**Variable**	**Reference**	**N**	**Beta**	**RR**	***P* value**		**Beta**	**RR**	***P* value**		**Beta**	**RR**	***P* value**	
+	Age		64	0.014	1.014	0.168									
0	Sex	ref = Male	7												
		Female	57	-0.205	0.814	0.405									
0	Species	ref = African	32												
		Asian	32	0.180	1.197	0.437									
0	Origin	ref = Wild	52												
		Captive	12	-0.102	0.903	0.663									
-	Environment Contact		64	-0.010	0.990	0.571		-0.007	0.993	0.704		-0.006	0.995	0.776	
-	Space Experience		64	-0.001	0.999	0.827		-0.002	0.998	0.452		0.002	1.002	0.007	*
+	Space Experience Indoors		64	-0.097	0.907	0.035	*	-0.045	0.956	0.267		-0.091	0.913	0.038	*
-	Space Experience Outdoors		64	-0.001	0.999	0.693		-0.002	0.998	0.397		0.001	1.001	0.144	^
-	Space Experience In/Out Choice		64	0.002	1.002	0.093	^	0.002	1.002	0.113	^	0.002	1.002	0.047	*
+	Percent Time Indoors		64	-0.004	0.996	0.413		-0.004	0.996	0.548		-0.003	0.997	0.436	
-	Percent Time Outdoors		64	-0.002	0.998	0.752		-0.003	0.997	0.525		-0.0002	1.000	0.964	
-	Percent Time In/Out Choice		64	0.006	1.006	0.211		0.009	1.009	0.037	*	0.003	1.003	0.414	
+	Time on Hard Substrate		64	0.009	1.009	0.091	^	0.017	1.018	0.180		0.006	1.006	0.122	^
-	Time on Soft Substrate		64	-0.012	0.988	0.220		-0.009	0.416	0.416		-0.010	0.990	0.205	
+	Musculoskeletal Score	ref = 0	40												
		1	12	0.219	1.244	0.445									
		2	5	0.470	1.600	0.009	*								
		3	1	0.981	2.667	<0.001	*								
-	Mean Daily Walking Distance		51	0.027	1.027	0.754									
-	Exercise Diversity		59	0.464	1.591	0.081	^								
-	Enrichment Diversity		62	-1.471	0.230	0.045	*								
-	Exercise Week	ref = 1	6												
		2	27	0.818	2.267	0.234									
		3	0												
		4	6	0.876	2.400	0.233									
		5	14	1.099	3.000	0.111									
		6	3	1.386	4.000	0.085	^								
		7	4	1.629	5.100	0.024	*								
-	Body Condition Score	1	2	nd											
		2	0	nd											
		ref = 3	16												
		4	20	-0.128	0.880	0.630									
		5	25	-0.110	0.896	0.654									

doi:10.1371/journal.pone.0155223.t007

Table 8. Descriptive statistics for variables which were retained in the multi-variable regression model for the possible persistent foot score subpopulation.

	Possible Persistent Foot Population		
Variable	**N**	**Mean**	**Std Dev**
Age	64	36.1	10.8
Space Experience, Night (per 500 ft^2]	64	36.6	64.2
Percent Time In/Out Choice, Day	64	9.7	17.3
Percent Time on Hard Substrate	64	12.7	15.5

doi:10.1371/journal.pone.0155223.t008

Table 9. Multivariable assessment of possible persistent foot scores using Poisson regression.

Variable	Beta	Risk Ratio	*P* value
Intercept	-0.252		0.624
Time on Hard Substrate	0.014	1.014	0.022
Percent Time In/Out Choice, Day	0.008	1.008	0.041
Space Experience (per 500 ft^2], Night	0.003	1.003	< 0.001
Age	0.018	1.018	0.076

doi:10.1371/journal.pone.0155223.t009

process only included environments that had 100% coverage of hard or soft substrate. Table 11 details the cross-tabulation of unique environments included in the study between flooring substrate (100% hard surface and 100% soft surface) with environment type (indoor, mixed, and outdoor). No statistical association of environment type by 100% substrate coverage was found (X^2 (2, N = 443) = 3.36, *P* value = 0.186).

Discussion

A number of factors such as age, housing conditions and management practices have been suggested as risk factors for foot and musculoskeletal pathologies in elephants under managed care, but to date no studies have tested these associations with robust sample sizes and clinical assessments collected by veterinarians on individual elephants. For example, Fowler [5] proposes that lack of exercise, limited space, standing on hard substrates, environmental factors that increase contact of feet with excrement, and moisture, and obesity are important contributing factors to elephant foot and musculoskeletal health problems (based on clinical observations], while Lewis et al. [4] used regression modeling to demonstrate that age predicted likelihood of arthritis (based on surveys without accompanying clinical assessments]. In this study, clinical assessments of musculoskeletal and pedal external tissue conditions were paired with individual elephant data describing demographic, housing, flooring, exercise, enrichment, body condition and other variables to determine associations and to provide potential insights into facility and management changes that could improve health and welfare.

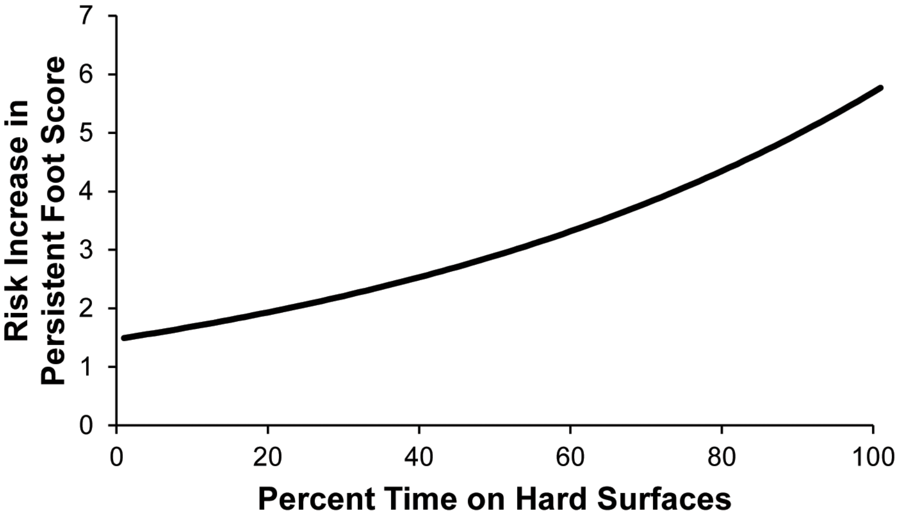

Fig 3. Risk increase for possible persistent foot scores by percent time on hard surfaces for an elephant 25 years old, where Percent Time In/Out Choice during the day and Space Experience at night are kept to average (8.52% and 22097.91 ft^2, respectively].

doi:10.1371/journal.pone.0155223.g003

Table 10. Average percent coverage of hard surfaces (concrete and stone aggregate) and soft surfaces (grass, sand, and rubber padding) in Indoors, Mixed, and Outdoor Environments. Range for all combinations was 0–100% coverage.

		Hard Surface		Soft Surface	
Environment Type	**N**	**Mean**	**SEM**	**Mean**	**SEM**
Indoors	382	39.20%	2.68%	43.30%	1.19%
Mixed	239	34.20%	2.76%	47.50%	2.79%
Outdoors	227	35.00%	2.84%	49.70%	2.84%

doi:10.1371/journal.pone.0155223.t010

When musculoskeletal health was evaluated via physical examination, the majority (74.5%; 148 / 198) of elephants had no observable movement or clinical abnormalities (i.e., swelling, heat, or deformity] of their limbs. Twenty-two animals (11.1%; 22 / 198) had problems with stiffness, gait, or limitations in movement in addition to one or more detectable musculoskeletal abnormalities (swelling, heat or deformity], suggesting more significant pathology. However it is important to note that visual and tactile examination is limited as a technique for detecting musculoskeletal abnormalities compared to the clinical use of radiography or thermography. As such, the prevalence of joint abnormalities found in this study may be underestimated due to the fact that we did not employ more sensitive diagnostic techniques.

Although there were no statistical differences between frequencies of musculoskeletal abnormalities in African and Asian elephants in this study, the only two elephants with multiple musculoskeletal abnormalities were Asian. This finding differs from previous studies in which musculoskeletal abnormalities were statistically more frequently in Asian elephants [3, 17]. Further, in the Lewis et al. study [4], most of the variance attributed to species differences was explained by the fact that the Asian elephants significantly older than the African elephants, however we did not find a similar positive association between age and MS scores in our study.

With respect to foot abnormalities, we found that approximately two-thirds of elephants in the current study had recorded nail, pad, or interdigital space abnormalities. Toenail problems, specifically onychitis (inflammation/infection of the nail bed] have been previously reported as the most common zoo elephant foot pathology [3]. In our population, toenail abnormalities including cracks, defects, inflammation, and horn growth abnormalities comprised 72.7% of all reported foot issues. These findings support those of a recent study in which the highest pressure measured in elephant feet occurred at the distal ends of the lateral toes which make contact through the toenails, suggesting a biomechanical link to foot pathologies (8). In addition, as elephants grow larger and older, their gait changes so that more pressure is initially placed on the cranial aspect of the foot. Over time, these repeated concussive forces may lead to development of abnormalities. Our data suggest that increased age did have an effect on risk of persistent foot abnormalities. Conformation, individual weight-bearing patterns, or musculoskeletal issues (i.e., arthritis] may also predispose to pedal aberrations [5, 7]. To support this premise, 13% of elephants in our study had concurrent abnormalities of several areas on a single foot, which

Table 11. Environment type (indoor, mixed, outdoor) frequency by 100% substrate coverage of hard (concrete and stone aggregate) or soft (grass, sand, and rubber padding) surfaces.

	Flooring Surface		
Environment Type	**Hard**	**Soft**	**Total**
Indoor	122	80	202
Mixed	64	62	126
Outdoor	61	54	115
Total	247	196	443

doi:10.1371/journal.pone.0155223.t011

suggests more extensive pathology. Twelve of the 28 elephants with multiple foot abnormalities had only one foot affected while 7 elephants had two feet affected and 5 individuals displayed multiple abnormalities on all 4 feet. Coexisting abnormalities on multiple feet suggest the inclusion of other influencing factors, such as environmental conditions, management practices (including participation of elephant for routine foot care), or changes in overall health status [7]. Thus, our data suggest that despite improvements in preventive foot care in AZA facilities [4], foot pathology remains a health concern for elephants housed in North American zoos.

In order to determine persistence of foot abnormalities in our study population, historical medical records (calendar year 2011] from 163 elephants were matched with findings of the 2012 physical exam. Of the 64 animals with recorded foot issues during 2011, the majority (79.7%; 51 / 64] had one or more recorded abnormalities on examination in 2012, suggesting chronic or recurring pedal pathology.

Our results demonstrate that one of the main housing risk factors for increased foot and musculoskeletal abnormalities was time spent on hard surfaces. Studies in cattle have shown that hard surfaces in alleys and walk-ways contribute to an increased incidence of claw lesions and lameness [18, 19], whereas cattle that have access to pasture (natural substrate] have lower levels of foot abnormalities [20]. In zoo settings, the prevalence of chronic foot disease in greater one-horned rhinoceros (*Rhinoceros unicornis*) was found to be 22.2%, and the authors speculated that trauma from concrete and lack of access to ponds and wallows were contributing factors [21]. Clinical case studies with elephants show that standing or walking on hard substrates such as concrete or stone can lead to trauma of foot pads, toenails, joints, and other musculoskeletal structures resulting in cracks, abscesses, bruises, strains, and degenerative joint disease [5, 7, 17]. Indeed, the final multi-variable models revealed a significant relationship between time on hard substrate and both foot and MS scores such that just a 10% increase in time on hard surfaces was associated with increased risk of both foot and musculoskeletal abnormalities. Since our objective was to measure the amount of time the elephants spent in contact with different substrate types, we therefore focused the analysis on substrate categories where we knew the environment consisted of 100% coverage of hard substrate or 100% coverage of soft substrate. This is a conservative approach, as time spent in environments with substrate coverage that was large, but less than 100%, was not captured in this analysis [12]. Despite these limitations, our methods for estimating exposure to hard and soft surfaces proved sufficient for detecting associations with both foot and musculoskeletal problems. Our findings support the supposition that there is a link between foot pathology and regional peak pressures in the elephant's foot [8]. Since foot pressure would be expected to increase with firmer surfaces, this may explain the observations that associate foot problems and hard substrate [5, 7].

Both foot and musculoskeletal scores were also associated with variables that described elephants' access to exhibit spaces made up of both indoor and outdoor areas. For foot health, the variable included in the final model described the percent time the elephants spent in mixed indoor/outdoor spaces and the MS scores model included Space Experience In/Out Choice, which is a measure of the size of the mixed indoor/outdoor spaces weighted by the amount of time the elephant spent in those spaces [12]. Although we hypothesized that mixed exhibits would encourage more walking, which would promote better foot (through normal wear] and musculoskeletal health (through exercise] and thereby be associated with decreased scores, the opposite relationship between time spent in mixed exhibits and both foot and MS scores was found. For example, an incremental increase of 10% time in mixed exhibit space increased the risk of foot abnormalities by 8.3%, and there was a 3.7% incremental increase in risk for musculoskeletal abnormalities in elephants that experienced increased indoor/outdoor exhibit Space Experience, although this was attenuated with age. One possible explanation for these finding could be that when elephants spend more time in mixed exhibits, they are more likely to be on hard surfaces. However, our assessment of substrate type by environment type indicated that mixed indoor/outdoor environments are not more likely to have 100% coverage of hard substrate, and we found that mixed environments had the same average percent coverage of hard and soft substrates as indoor or outdoor environments. Since our assessment of flooring did not capture time spent in environments with less than 100% substrate coverage, we cannot completely rule out substrate exposure as the underlying reason for the effects that mixed indoor/outdoor environments had in our models, but our investigation of the potential associations between substrate and environment type indicates that there is likely another explanation for these correlations. For example, it is possible that when elephants have the opportunity to move between indoor and outdoor areas, they are exposed to fluctuations in temperature or humidity that could impact musculoskeletal or pedal health, or that, movement between different types of spaces could be associated with more frequent contact with environmental features (gates, thresholds) that could lead to trauma to pedal and other limb structures. Given that time spent in mixed indoor/outdoor exhibits is associated with a decreased risk of performing stereotypic behavior [22], further investigation into underlying contributors to the association between mixed environments and foot/musculoskeletal health is warranted.

We also investigated the association between space and foot and MS scores with the hypothesis that increased space would improve foot and MS scores via increased locomotion. However, this supposition was not supported in the multi-variable analyses. In fact, an incremental increase in 500 square feet of space available at night led to a 0.3% increased risk of higher foot scores. We are unclear as to why this relationship was found in the model, but further research including observational studies of elephants at night could potentially reveal behavioral differences associated with larger spaces that could help explain this result. Age was a significant risk factor for foot problems. For example, a ten year increase in age led to a 19.5% increase in probability of foot abnormalities. Degenerative processes of the musculoskeletal system have been found to be age-related in a variety of species. For example, age has been previously identified as a contributor to increases in the likelihood of foot pathology and diagnosis of arthritis in zoo elephants [7]. In dairy cattle, age-related increases in locomotive abnormalities have been reported [23], and age was also strongly associated with risk of cranial cruciate ligament rupture in dogs that have had a previous episode [24].

Significant morbidity can result from chronic pododermatitis and degenerative joint disease in elephants [2,25–26]. Foot abscesses may progress to pedal osteomyelitis, which requires intensive management and may lead to euthanasia in unresolved cases [7]. Chronic joint pathology may lead to limited range-of-motion and lameness, which reflects declining welfare for the individual [2]. One of the logistical constraints in this study was the inability to evaluate the severity of individual foot and musculoskeletal abnormalities. Since physical exams and medical record entries were performed by the attending veterinarian at each facility rather than a consistent set of observers for all facilities, measures of foot and musculoskeletal health were limited to the presence or absence of abnormalities rather than a quantitative evaluation of severity. Future studies of this nature may endeavor to include assessments of severity to further develop our understanding of foot and musculoskeletal conditions in zoo elephants.

The conclusion that more time spent on hard surfaces is associated with increased trauma to pedal and musculoskeletal structures resulting in pathology is supported by cases in the literature as well as the results of our multivariable analyses [1, 2, 3, 8, 25]. Space Experience at night and in mixed exhibits also appear to be factors that need further investigation. The identified associations between risk of developing foot and musculoskeletal health issues and environmental conditions in elephants in North American zoos provide focused areas for recommendations and further research. The results indicate that foot and musculoskeletal health continue to be a concern for elephants housed in North American zoos. Prevention is fundamental through identifying and minimizing risk factors that contribute to these health conditions. The evidence indicates that facility and management changes which decrease time spent on hard substrates are likely to lead to improvements in foot and musculoskeletal health and overall welfare.

Supporting Information

S1 Template. Using Science To Understand Zoo Elephant Welfare Study Physical Exam Foot and Musculoskeletal Assessment.
(PDF)

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Author Contributions

Conceived and designed the experiments: MAM CLM JNH. Performed the experiments: MAM CLM JNH. Analyzed the data: JNH. Contributed reagents/materials/analysis tools: MAM CLM JNH. Wrote the paper: MAM CLM JNH.

References

1. Houck R. Veterinary care of performing elephants. In: Fowler ME, Miller RE, editors. Zoo, and Wild Animal Medicine Current Therapy. St. Louis, MO: Saunders; 1993. p. 453–4.
2. Schwammer HM. Elephant husbandry and foot care at the Schonbrunner Tiergarten, Vienna. In: Csuti B, Sargent EL, Bechert US, editors. The Elephant's Foot: Prevention and Care of Foot Conditions in Captive Asian and African Elephants. Ames, IA: John Wiley & Sons; 2001. p. 69–71.
3. Mikota SK, Sargent EL, Ranglack G. Medical Management of the Elephant. Ithaca, NY: Indira Publishing House; 1994.
4. Lewis KD, Shepherdson DJ, Owens TM, Keele M. A survey of elephant husbandry and foot health in North American zoos. Zoo Biology. 2010; 29(2):221–36. doi: 10.1002/zoo.20291 PMID: 20014111
5. Fowler ME. An overview of foot conditions in Asian and African elephants. In: Csuti B, Sargent EL, Bechert US, editors. The Elephant's Foot: Prevention and Care of Foot Conditions in Captive Asian and African Elephants. Ames, IA: John Wiley & Sons; 2001. p. 3–7.
6. West G. Musculoskeletal system. In: Fowler ME, Mikota S, editors. Biology, Medicine, and Surgery of Elephants. Ames, IA: John Wiley & Sons; 2006. p. 263–70.
7. Fowler ME. Foot disorders. In: Fowler ME, Mikota S, editors. Biology, Medicine, and Surgery of Elephants. Ames, IA: John Wiley & Sons; 2006. p. 271–90.
8. Panagiotopoulou O, Pataky TC, Hill Z, Hutchinson JR. Statistical parametric mapping of the regional distribution and ontogenetic scaling of foot pressures during walking in Asian elephants (*Elephas maximus*). The Journal of Experimental Biology. 2012; 215(9):1584–93.
9. Weissengruber G, Egger G, Hutchinson J, Groenewald HB, Elsässer L, Famini D, et al. The structure of the cushions in the feet of African elephants (*Loxodonta africana*). Journal of Anatomy. 2006; 209 (6):781–92. PMID: 17118065
10. Alexander R McN, Maloiy GMO, Hunter B, Jayes AS, Nturibi J. Mechanical stresses in fast locomotion of buffalo (Syncerus caffer) and elephant (Loxodonta africana). Journal of Zoology, 1979; 189: 135–144.
11. Veasey J. Concepts in the care and welfare of captive elephants. International Zoo Yearbook. 2006; 40 (1): 63–79.
12. Meehan CL, Hogan JN, Bonaparte-Saller M, Mench JA. Housing and social environments of African (Loxodonta africana) and Asian (Elephas maximus) elephants in North American zoos. PLoS ONE 2016. doi: pone.0146703.
13. Greco BJ, Meehan CL, Miller LJ, Shepherdson DJ, Morfeld KA, Andrews J, Baker AM, Carlstead K, Mench JA. Elephant management in North American zoological facilities: environmental enrichment, feeding, exercise, and training. PLoS ONE 2016. doi:pone.0152490.
14. Prado-Oviedo NA, Bonaparte-Saller MK, Malloy EJ, Meehan CL, Mench JA, Carlstead K. et al. Evaluation of demographics and social life events of Asian (Elephas maximus) and African elephants (Loxodonta africana) in North American zoos. PloS One 2016. doi: pone.0154750.
15. Morfeld KA, Meehan CL, Hogan JN, Brown JL. Asseessment of body condition in African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants in North American zoos and management practices associated with high body condition scores. PLoS ONE 2016. doi: pone.0155146.
16. Holdgate MR, Meehan CL, Hogan JN, Miller LJ, Soltis J. Walking behavior of zoo elephants: associations between GPS-measured daily walking distances and environmental factors, social factors and welfare indicators. PLoS ONE 2016. doi: pone.0150331.
17. Luikart KA, Stover SM. Chronic sole ulcerations associated with degenerative bone disease in two Asian elephants (*Elephas maximus*). Journal of Zoo and Wildlife Medicine. 2005; 36(4):684–8. PMID: 17312727
18. Barker Z, Amory J, Wright J, Mason S, Blowey R, Green LE. Risk factors for increased rates of sole ulcers, white line disease, and digital dermatitis in dairy cattle from twenty-seven farms in England and Wales. Journal of Dairy Science. 2009; 92(5):1971–8. doi: 10.3168/jds.2008-1590 PMID: 19389954
19. Frankena K, Somers J, Schouten W, Van Stek J, Metz J, Stassen E, et al. The effect of digital lesions and floor type on locomotion score in Dutch dairy cows. Preventive Veterinary Medicine. 2009; 88 (2):150–7. doi: 10.1016/j.prevetmed.2008.08.004 PMID: 18842310
20. Haufe HC, Gygax L, Wechsler B, Stauffacher M, Friedli K. Influence of floor surface and access to pasture on claw health in dairy cows kept in cubicle housing systems. Preventive Veterinary Medicine. 2012; 105(1):85–92.
21. von Houwald F, Flach E. Prevalence of chronic foot disease in captive greater one-horned rhinoceros (*Rhinoceros unicornis*). EAZWV Sci Meet. 1998; 2:323–7.
22. Greco BJ, Meehan CL, Hogan JN, Leighty KA, Mellen J, Mason GJ, Mench JA. The days and nights of zoo elephants: using epidemiology to better understand stereotypic behavior of African elephants

(*Loxodonta africana*) and Asian elephants (*Elephas maximus*) in North American zoos. PLoS ONE 2016. doi: pone.0144276.

23. duPlessis I. Foot health in housed cattle: a review. SA-Anim Sci. 2007; 8:11–7.
24. Little JP, Bleedorn JA, Sutherland BJ, Sullivan R, Kalscheur VL, Ramaker MA, et al. Arthroscopic assessment of stifle synovitis in dogs with cranial cruciate ligament rupture. PloS One. 2014; 9(6): e97329. doi: 10.1371/journal.pone.0097329 PMID: 24892866
25. Gage LJ, Fowler ME, Pascoe JR, Blasko D. Surgical removal of infected phalanges from an Asian elephant (*Elephas maximus*). Journal of Zoo and Wildlife Medicine. 1997; 28(2):208–11. PMID: 9279413
26. Spelman L, Yates R, Anikis P, Galuppo L. Regional digital intravenous perfusion in an African elephant (*Loxodonta africana*). Annual Conference-American Association of Zoo Veterinarians. 2000:388–90.

Demographic Side Effects of Selective Hunting in Ungulates and Carnivores

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Review

Demographic Side Effects of Selective Hunting in Ungulates and Carnivores

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Abstract: *Selective harvesting regimes are often implemented because age and sex classes contribute differently to population dynamics and hunters show preferences associated with body size and trophy value. We reviewed the literature on how such cropping regimes affect the demography of the remaining population (here termed* demographic side effects *). First, we examined the implications of removing a large proportion of a specific age or sex class. Such harvesting strategies often bias the population sex ratio toward females and reduce the mean age of males, which may consequently delay birth dates, reduce birth synchrony, delay body mass development, and alter offspring sex ratios. Second, we reviewed the side effects associated with the selective removal of relatively few specific individuals, often large trophy males. Such selective harvesting can destabilize social structures and the dominance hierarchy and may cause loss of social knowledge, sexually selected infanticide, habitat changes among reproductive females, and changes in offspring sex ratio. A common feature of many of the reported mechanisms is that they ultimately depress recruitment and in some extreme cases even cause total reproductive collapse. These effects could act additively and destabilize the dynamics of populations, thus having a stronger effect on population growth rate than first anticipated. Although more experimental than observational studies reported demographic side effects, we argue that this may reflect the quite subtle mechanisms involved, which are unlikely to be detected in observational studies without rigorous monitoring regimes. We call for more detailed studies of hunted populations with marked individuals that address how the expression of these effects varies across mating systems, habitats, and with population density. Theoretical models investigating how strongly these effects influence population growth rates are also required.*

Keywords: big game, population dynamics, selective harvesting, trophy hunting, wildlife exploitation, wildlife management

Efectos Demográficos Secundarios de la Cacería Selectiva en Ungulados y Carnívoros

Resumen: *Los regimenes de cosecha selectiva a menudo son implementados porque las clases de edad y sexo contribuyen distintamente a la dinámica de la población y los cazadores muestran preferencias asociadas con el tamaño corporal y el valor como trofeo. Revisamos la literatura sobre los efectos de esos regimenes de cosecha sobre la demografía del resto de la población (denominados aquí* efectos demográficos secundarios*). Primero, examinamos las implicaciones de la remoción de la mayor parte de una clase específica de edad o sexo. Tales estrategias de cosecha a menudo sesgan la proporción de sexos de la población hacia hembras y reducen la edad promedio de los machos, lo que consecuentemente puede retardar fechas de nacimiento, reducir la sincronía de nacimientos, retardar el desarrollo de la masa corporal y alterar la proporción de sexos de las crías. Segundo, revisamos los efectos secundarios asociados con la remoción selectiva de relativamente pocos individuos específicos, a menudo machos grandes. Tal cosecha selectiva puede desestabilizar las estructuras sociales y la jerarquía de dominancia y puede provocar la pérdida de conocimiento social, infanticidio seleccionado sexualmente, cambios de hábitat entre hembras reproductivas y cambios en la proporción de sexos de las crías. Una característica común de muchos de los mecanismos reportados es que, a fin de cuentas, deprimen el*

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reclutamiento y en algunos casos extremos causan un colapso reproductivo total. Estos efectos pueden actuar aditivamente y desestabilizar la dinámica de las poblaciones, por lo que tienen un mayor efecto que el esperado sobre la tasa de crecimiento poblacional. Aunque estudios más experimentales que de observación reportaron efectos demográficos secundarios, argumentamos que esto puede reflejar los sutiles mecanismos implicados, que pueden no ser detectados en estudios de observación sin regimenes de monitoreo rigurosos. Hacemos un llamado para la realización de estudios más detallados de poblaciones cazadas utilizando individuos marcados para abordar la variación de esos efectos en sistemas de apareamiento, hábitats y densidades poblacionales diferentes. También se requieren modelos teóricos que investiguen el impacto de estos efectos sobre las tasas de crecimiento poblacional.

Palabras Clave: caza deportiva, caza mayor, cosecha selectiva, dinámica poblacional, explotación de vida silvestre, gestión de vida silvestre

Introduction

One of the central aspects of conservation biology is the relationship between human exploitation and the conservation of exploited resources. Throughout the world terrestrial mammals are hunted for sport, subsistence, and to control population size (Festa-Bianchet 2003). Hunting thus provides a significant source of meat and income in rural communities and beyond. Nevertheless, there are numerous examples of populations being overharvested, and subsistence hunting may be one of the most urgent current threats to the persistence of species in tropical ecosystems (Robinson & Bennett 2000; Milner-Gulland & Bennett 2003). Over 30% (250 species) of mammals currently listed as endangered on the World Conservation Union (IUCN) Red List are threatened by overexploitation (Baillie et al. 2004). Of these, larger mammal species, especially ungulates and carnivores, are particularly targeted (Baillie et al. 2004; Fig. 1).

Although subsistence hunting may take a random sample of a population, in many other instances—particularly associated with sport hunting of ungulates and carnivores—economic demands, ecological knowledge, and hunter preferences have led to the implementation of selective harvesting regimes (e.g., Ginsberg & Milner-Gulland 1994; Solberg et al. 1999). Here the offtake is focused around predetermined sex and/or age classes or specific individuals. Such selective hunting will, in addition to the obvious direct effects of reducing the population size, also affect the demography of populations by altering age and sex structures (Ginsberg & Milner-Gulland 1994) and potentially disrupting social systems (Swenson et al. 1997). Although such effects have received far less attention than direct overharvesting, they are potentially equally undesirable (Festa-Bianchet 2003) and occur even when the overall offtake is not regarded as excessively high.

We sought to synthesize the current knowledge on how selective harvesting regimes affect the performance of populations. We considered the effects of hunting a large proportion of a selected sex and/or age class of the population, so affecting the age and sex structure of the remaining population and hunting specific individuals for trophies, so disturbing social structures and dominance hierarchies. We included recreational or sport hunting for meat and trophies, and poaching and population control where specific individuals or sex/age classes are targeted. We focused on ungulates and carnivores because, with the exception of a vast literature on size-selective exploitation of fish stocks and its consequences (see e.g., Law 2001), these are the groups for which most information regarding selective harvesting is available.

Consequences of Perturbing the Population Age and Sex Structure

Many mammalian populations are strongly structured by age and sex. Because survival rates typically differ among age and sex classes (Gaillard et al. 1998), populations of equal size but differing structures will have different temporal dynamics (Coulson et al. 2001) and will respond differently to stochastic environmental variation (Cameron & Benton 2004). Consequently, by perturbing population sex and age structure, selective harvesting affects population dynamics (Festa-Bianchet 2003).

Theoretically, the most productive populations are those with a female-biased sex ratio (Caughley 1977). Male-biased harvesting regimes have therefore been widely applied to ungulates in North America (McCullough 2001; Stalling et al. 2002), Scandinavia (Langvatn & Loison 1999; Sæther et al. 2004*b*), and in wildlife cropping schemes in Africa (Ginsberg & Milner-Gulland 1994). Even though a more balanced or slightly female-biased harvest is taken in many European countries (Milner et al. 2006), harvested ungulate populations invariably have mortality patterns that deviate significantly from those in unhunted populations (Ginsberg & Milner-Gulland 1994; Langvatn & Loison 1999). In particular, mortality rates of prime-aged adults, especially males, are considerably higher than in unhunted populations.

Male-biased harvesting regimes have led to severely biased sex ratios; for example, there are 0.05 adult males

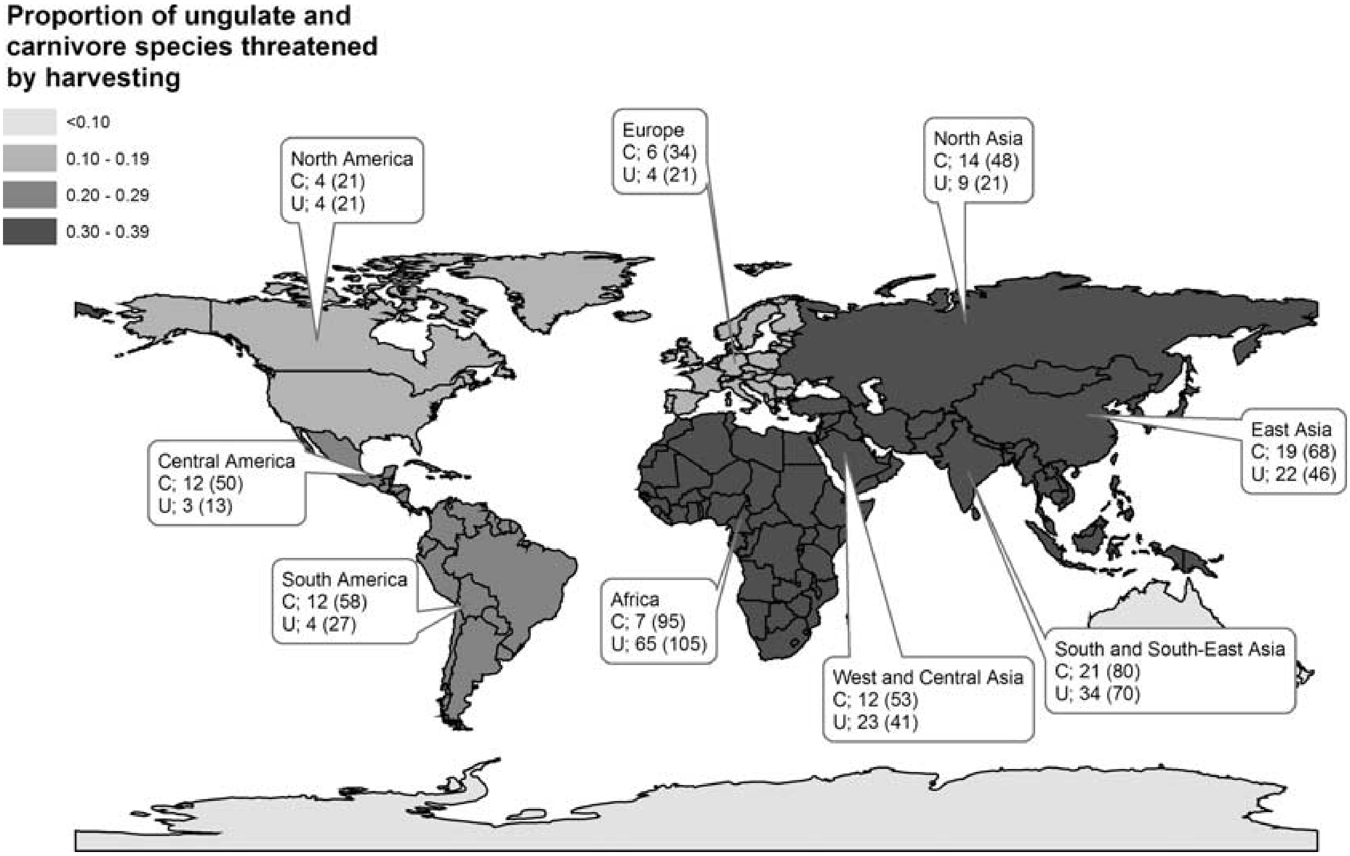

Figure 1. The number of ungulate (U) and carnivore (C) species registered as threatened (all threat categories) at least partly due to harvesting (IUCN 2004) relative to the total number (in parentheses) of ungulate and carnivore species evaluated in each region. Shading represents the approximate proportion of ungulate and carnivore species threatened. There are substantial differences among the regions with the highest proportion of threatened species (0.37) occurring in south and southeast Asia and west and central Asia.

per female in populations of both North American elk (if not provided, scientific names are in Table 1 or 2) (Noyes et al. 1996) and the central Asian saiga antelope (Milner-Gulland et al. 2003). In addition, the often high harvesting pressure on mature males for trophies results in harvested populations with lower average ages of males and fewer old males than unhunted populations (Langvatn & Loison 1999; Laurian et al. 2000; Apollonio et al. 2003). For example, 70% of all males in a Norwegian moose population are harvested by 3 years of age (Solberg et al. 1999).

In the following we discuss how sex- and age-specific hunting affects various demographic processes. We do not discuss genetic and evolutionary effects in detail because they have been reviewed recently (Harris et al. 2002; Festa-Bianchet 2003).

Effects on Reproduction

Although selective harvesting of males leads to female-biased adult sex ratios, this does not necessarily lead to a reduction in fecundity rate because most harvested game species have polygynous mating systems in which a single mature male is capable of inseminating many females (Ginsberg & Milner-Gulland 1994; Mysterud et al. 2002; but see Greene et al. 1998 for monogamous species). Consequently in many cases, recruitment rates are resilient to skewed sex ratios (Table 1) and may even increase because of higher proportion of females in the adult population (Solberg et al. 2000). But there may nonetheless be a sex-ratio threshold below which fecundity collapses. Indeed, if the offtake is strongly male-biased, population crashes due to reduced fecundity can occur at lower overall offtake rates than if a random harvest is taken (Ginsberg & Milner-Gulland 1994). This has been observed in saiga antelope at a ratio of between 0.025 and 0.009 males per female (Milner-Gulland et al. 2003), caribou (*Rangifer tarandus*) at a sex ratio of 0.08 (Bergerud 1974), elk populations with a sex ratio of 0.04 (Freddy 1987), and elephants with a sex ratio of 0.013 (Dobson & Poole 1998). In moose, even moderately, female-biased sex ratios (0.25–0.70) can affect the fecundity of primiparous females, although the fecundity of older females seems to be unaffected (Solberg et al. 2002).

Table 1. Demographic consequences of a selective-harvesting regime that creates a female-biased adult sex ratio and/or a young average age of males.

	Effect of harvesting		*Demographic consequence*[a]							
Species	*♀-biased sex ratio*	*reduced ♂age*	*fecundity rate*	*breeding/ birth date*	*birth synchrony*	*offspring sex ratio*	*offspring 1) survival 2) weight*	*young ♂ 1) survival 2) weight*	*adult ♀ condition*	*Reference*
Moose (*Alces alces*)	X		+							Solberg et al. 1999
	X		−[b]							Solberg et al. 2002
		X				<♂				Sæther et al. 2004
	X		0	−[c]	−		2) −	2) 0		Sæther et al. 2003
		X	0	−	0		2) −	2) 0		Sæther et al. 2003
	X							2) −		Garel et al. 2006
	X	X	0	0	0					Laurian et al. 2000
	X		0				2) −[d]			Taquet et al. 1999
	X		0							Courtois & Lamontagne 1999
Elk (*Cervus elaphus*)	X		−							Freddy 1987
		X	−[e]	−	−				0	Noyes et al. 1996
		X								Squibb 1985
	X		−							White et al. 2001
	X	X	0							Bender & Miller 1999
Red deer (*Cervus elaphus*)	X	X	0							Langvatn & Loison 1999
Fallow deer (*Dama dama*)		X		−	+					Komers et al. 1999
Mule deer (*Odocoileus hemionus*)	X		−							White et al. 2001
White-tailed deer (*Odocoileus virginianus*)		X	0	+[b]		<♂[e]				Ozoga & Verme 1985
Bighorn sheep (*Ovis canadensis*)		X	0	0			1) 0	1) 0	0	Singer & Zeigenfuss 2002
		X	0	0	0					Shackleton 1991
		X						1) −		Jorgenson et al. 1997
Dall sheep (*Ovis dalli*)		X	0					1) 0		Murphy et al.1990
		X	0	−				1) −		Singer & Zeigenfuss 2002
		X						1) −		Heimer et al. 1984
Caribou (*Rangifer tarandus*)	X		−							Bergerud 1974
Reindeer (*Rangifer tarandus*)	X		0	−	0		2) 0			Holand et al. 2003
		X	0	−	0		2) 0			Holand et al. 2003
	(X)[f]	(X)[f]			−	<♂[g]	2) −			Holand et al. 2006
	X							2) −[h]		Mysterud et al. 2003
Saiga antelope (*Saiga tatarica*)	X		−							Milner-Gulland et al. 2003

[a] *Key: 0, no effect; +, positive effect; −, negative effect.*

[b] *Primiparous females only, no effect in adult females.*

[c] *Skewed adult sex ratio had significantly stronger effect on calving date than young-male age structure.*

[d] *Offspring size measured by length of hind foot not body weight.*

[e] *Nonsignificant trend.*

[f] *A group of the females were inhibited from mating during their first cycle, thus conceiving in the second cycle. Simulates skewed sex ratio and/or male age structure.*

[g] *Sex ratio of calves conceived in second estrus.*

[h] *Increased weight loss during the rut.*

Many populations with low male-to-female ratios also tend to have a low mean male age, which may be a contributing factor to lower fecundity (Solberg et al. 2002). Nevertheless, even though it has been suggested that subadults show immature courtship behavior, are socially disruptive, and prolong the mating season (Squibb 1985; Shackleton 1991; Singer & Zeigenfuss 2002; Stalling et al. 2002), young males are nonetheless capable of achieving paternities successfully (Stevenson & Bancroft 1995; Hogg & Forbes 1997). It is less clear whether they are able to inseminate as many females as old males (Ginsberg & Milner-Gulland 1994). Overall, there is little clear evidence that a reduction in male age affects fecundity rate per se (Table 1). Rather, the literature points toward changes in parturition dates, birth synchrony, and offspring sex ratio with a reduction in male age.

Selective harvesting may also have indirect effects on recruitment through its influence on the mean age of adult females. For example, in an Norwegian moose population in which selective harvesting protects adult females, the resulting increase in average female age led to an increase in both calving rate and twinning rate (Solberg et al. 1999). In other situations, such as game ranching, cropping results in a general reduction in average female age and thus in an increased reproductive rate due to the absence of senescent individuals (Ginsberg & Milner-Gulland 1994).

Effects on Timing and Synchrony of Birth

Timing and synchrony of birth have important implications for demography because of their effects on offspring body weights and survival. Greater birth synchrony leads to higher survival in species with heavy predation of neonates (Sinclair et al. 2000), whereas late-born individuals often have lower survival (Clutton-Brock et al. 1987; Festa-Bianchet 1988) or delayed body mass development (Sæther et al. 2003; Nilsen et al. 2004; Holand et al. 2006). In female ungulates this may lead to a delay in onset of reproduction (Langvatn et al. 1996).

In both reindeer and moose calving is earlier when the adult sex ratio is even rather than female-biased (Holand et al. 2003, Sæther et al. 2003). In addition, timing of calving in moose can be delayed when the male population is restricted to yearlings (Sæther et al. 2003). Similarly, birth dates in fallow deer (Komers et al. 1999), timing of the rut in elk (Noyes et al. 1996), and median date of accepted mounts in Dall sheep (Singer & Zeigenfuss 2002) are all significantly earlier in groups or populations with mature males than when only young males are present, although other studies have shown no such effects (Table 1). Birth synchrony was greater in a moose population with an even sex ratio compared with a population in which the sex ratio was experimentally manipulated toward females (Sæther et al. 2003), whereas birth dates are more synchronous with increasing male age in elk (Noyes et al. 1996) but less synchronous in fallow deer (Komers et al. 1999). By contrast, no effects of male age on rutting behavior or the timing of the birth season were found in bighorn sheep (Shackleton 1991) or in a hunted moose population (Laurian et al. 2000).

Effects on Offspring Sex Ratio

In dimorphic and polygynous species birth size is more strongly correlated with fitness in males than in females (Kruuk et al. 1999). The Trivers-Willard model (Trivers & Willard 1973) predicts that mothers in good condition should therefore produce male offspring because this yields the highest fitness return (Sheldon & West 2004). Nevertheless, other factors such as male quality and timing of breeding may also influence natal sex ratio. For example, if females hesitate to mate with young males and thus conceive late, the model predicts that fitness would be maximized by producing females because late-born offspring generally have lower birth and autumn weights (Holand et al. 2006).

In an experimental study of a Norwegian moose population, a change in male age structure toward younger males led to a reduction in the proportion of male calves born (Sæther et al. 2004*b*), whereas manipulation of the adult sex ratio had no effect. Similarly, Holand et al. (2006) showed that reindeer conceived in the first estrus are more likely to be male, whereas second-estrus offspring are more likely to be female. They argue that a skewed sex ratio and young male age structure could result in fewer adult females conceiving during the first cycle due to their hesitation to mate with young males. A trend toward more male offspring being sired by older males than by yearling males has also been observed in white-tailed deer (Ozoga & Verme 1985).

Effects on Survival

Participation in rutting activities is energetically costly, and, consequently, winter survival rates of participating males are typically lower than for other individuals (Geist 1971; Stevenson & Bancroft 1995; Jorgenson et al. 1997). Subordinate males may engage in high-risk alternative mating tactics (Hogg & Forbes 1997) and may invest more heavily in reproductive activities when there is either an abundance of females relative to males or a paucity of prime-age males (Squibb 1985; Singer & Zeigenfuss 2002; Mysterud et al. 2003). One might therefore predict that young males will be more involved in the rut and suffer higher winter mortality rates in areas where heavy hunting of mature males occurs (Geist 1971; Murphy et al. 1990). Evidence for the so-called depressed survival hypothesis, however, is equivocal (Singer & Zeigenfuss 2002; Table 1). No effect is seen in Dall sheep populations in which young rams show adult mating behavior in the absence of mature males (Murphy et al. 1990) or in lightly hunted populations of desert bighorn sheep and bighorn sheep (Singer & Zeigenfuss 2002). Higher mortality rates have been detected only among young rams in a heavily hunted Dall sheep population (Singer & Zeigenfuss 2002).

Where selective hunting leads to high adult mortality, populations tend to have a high proportion of juveniles and yearlings. Because overwinter survival of these classes is variable from year to year (Gaillard et al. 1998), such populations are more sensitive to winter mortality in harsh years than unhunted populations, leading to greater population variability (Cameron & Benton 2004; Gordon et al. 2004).

Effects on Body Weights

Another cost to young males participating in the rut is reduced body growth as resources are diverted to reproduction (Stearns 1992). In populations with few mature males, one might expect increased energy expenditure of young males participating in mating behavior to lead to greater weight loss during the rut. This is observed in male reindeer (Mysterud et al. 2003) and moose (Solberg & Sæther 1994; Garel et al. 2006). However, Sæther et al. (2003) found no such effect when mature male moose were removed from a population, although they found an indirect negative effect on calf body weight the following winter due to delayed parturition dates. Similarly, lower birth and autumn body weights occur in second-estrus offspring in moose (Schwartz & Becker 1994) and reindeer (Holand et al. 2003, 2006). Low mass at birth has implications for other life-history traits such as survival, age and body size at maturity, and lifetime reproductive success (Kruuk et al. 1999).

As a result of expending more energy in avoidance behavior, female fallow deer in an enclosure with only young males lost significantly more body weight than females enclosed with only mature males (Komers et al. 1999). Female white-tailed deer in a low-density hunted population significantly increased their daily movement and home range size in peak and late rut, apparently in response to low availability of adult males (Labisky & Fritzen 1998). By contrast, Singer and Zeigenfuss (2002) found no compelling evidence for any negative effects on ewe energetics of increased harassment of ewes by young rams in hunted mountain sheep populations.

Consequences of Removing a Few Targeted Individuals

Trophy hunting typically targets the largest males or those with impressive ornaments but is generally restricted to relatively few individuals. Nonetheless, a high proportion of individuals that qualify as trophy individuals may be removed each year (Coltman et al. 2003). Species subject to trophy hunting include large carnivores and large horn-, tusk-, or antler-bearing herbivores. Trophy hunting is usually associated with a considerable fee, making it an important tool for wildlife management and conservation programs, particularly in developing countries, where it offers potential benefits for rural economies (Festa-Bianchet 2003). Within Europe and North America, there is also considerable interest in the trophy hunting of some relatively common ungulate species that, are also hunted for meat or population control (Festa-Bianchet 2003; Milner et al. 2006).

In many mammals the largest individuals are also the oldest and, as such, play an important role in leading social groups that benefit from their greater experience. Nevertheless, these are often the same individuals that are typically targeted by trophy hunters because of their size. For example, in elephants, tusk size is related to age, and hunters or poachers focus their efforts on individuals with the largest tusks, including matriarchs (Dobson & Poole 1998). Older matriarchs have social discrimination abilities that are superior to those of young matriarchs, so enabling them to make more appropriate responses during encounters with other elephant groups (McComb et al. 2001). These factors and a greater knowledge of the distribution of resources may result in higher per capita reproductive success for female groups led by older individuals. Consequently, if groups rely on older members for their store of social knowledge, then whole populations may be affected by the removal of a few key individuals (McComb et al. 2001).

Among lions, the absence of males within a pride enables hyenas to drive females and subadults off their kills under certain circumstances, constituting a constant energy drain by forcing them to hunt more frequently (Cooper 1991). In populations where adult males are scarce, due, for example, to trophy hunting, cleptoparasitism by hyenas is likely to increase.

In most species managers assume that sport hunting for trophy males only reduces the overall population size when the rate of male removal is so high that not all females are impregnated. In many cases it is thought that sport hunting of males may even have a positive effect on population growth through compensatory density dependence (McLellan 2005; but see also Miller 1990). In monogamous species and species in which males provide parental care, however selective removal of even a modest number of adult males is predicted to have a stronger impact on population growth than random removals (Greene et al. 1998).

Effects on Juvenile Survival

Removal of trophy individuals, especially dominant males, can have far-reaching effects where male replacement is associated with infanticide. Sexually selected infanticide (SSI) can occur when a male gains increased mating success by killing dependent young he has not sired himself (Swenson 2003). By killing unrelated offspring a mature

Table 2. Demographic consequences of selective removal of a few specific individuals from a population.

	Effect of harvesting		*Demographic consequence*^{a}				
Species	*removal dominant♂*	*removal dominant ♀*	*fecundity rate*	*offspring sex ratio*	*offspring survival*	*adult ♀ condition*	*Reference*
Plains zebra (*Equus burchelli*)	X		–			–	Hack et al. 2002
Feral horses (*Equus caballus*)	X		–				Berger 1983
Shackleford Banks horses (*Equus caballus*)	X		–			–	Rubenstein 1986
Elephants (*Loxodonta africana*)	X		–				Dobson & Poole 1998
		X	–				McComb et al. 2001
Lion (*Panthera leo*)	X				–		Pusey & Packer 1994
	X			>♂			Smuts 1978
	X			>♂			Creel & Creel 1997
Brown bear (*Ursus arctos*)	X				–		Swenson et al. 1997
	X				0		Miller et al. 2003
	X		–				Wielgus & Bunnell 2000
	X		–^{b}		(–)^{b}		Stringham 1983
	X		–^{b}		(–)^{b}		McCullough 1981
	X				0		McLellan 2005

[a] *Key: 0, no effect; +, positive effect; –, negative effect.*

[b] *Reduced cub recruitment when adult males were removed, but effects on fecundity rate and offspring survival not distinguished.*

male can reduce the interbirth period and sire the next litter. Furthermore, because males tend to roam over larger areas than females (Nilsen et al. 2005), the turnover of one male can affect several females. For example, in root voles (*Microtus oeconomus*), high male turnover rates severely hamper population growth (Andreassen & Gundersen 2006). Male infanticide occurs primarily in primates, terrestrial carnivores, and some rodents.

Among bears, older males may limit the immigration of younger males (Rogers 1987). Therefore, increasing the mortality rate of old males can result in a higher immigration rate of younger, potentially infanticidal, males (Table 2). In Scandinavian brown bears survival rates of cubs are depressed in areas with high adult-male hunting offtake (juvenile survival 0.98 vs. 0.72 in unhunted and hunted populations, respectively; Swenson et al. 1997). A considerable body of evidence points toward infanticide as the cause of this (Swenson et al. 1997; Swenson 2003). In North American brown bear populations the evidence for SSI due to male turnover is still controversial (McCullough 1981; Stringham 1983; Wielgus & Bunnell 2000; Miller et al. 2003; McLellan 2005). Nevertheless, cases of SSI are extremely difficult to document in the field, and recent studies strongly support the SSI model and the adaptive value of SSI for male brown bears (Bellemain et al. 2006). In hunted black bear (*Ursus americanus*) populations with high male turnover rates, SSI is thought to cause high intraspecific juvenile mortality (LeCount 1987).

Sexually selected infanticide is also well documented in lions (Pusey & Packer 1994), and because trophy hunting is expected to increase the rate of male takeovers, excessive trophy hunting could limit recruitment through the negative effects of infanticide on cub survival (Whitman et al. 2004). Although trophy hunting increases the risk of population extinction, quite extensive trophy hunting could be sustained as long as only old males are targeted (Whitman et al. 2004).

Rare cases of SSI have been documented in some herbivore species (captive red deer: Bartos & Madlafousek 1994; hippopotamus [*Hippapotamus amphibious*]: Lewison 1998; captive plains zebra [*Equus burchelli*]: Pluhacek & Bartos 2005). Although the evidence is somewhat circumstantial, this suggests that similar effects could arise in ungulates under some conditions where trophy hunting for adult males takes place.

Effects on Reproduction

In situations where SSI is not documented the removal of a few adult males may nonetheless have an impact on demography through other mechanisms. For example, when comparing two North American grizzly bear populations, Wielgus and Bunnell (2000) found that reproductive rates were suppressed in the hunted compared with the unhunted population (Table 2). These differences were caused by mature females avoiding food-rich areas inhabited by potentially infanticidal immigrant males (sexual segregation), forcing them to use suboptimal habitats (Wielgus & Bunnell 2000). Subsequent modeling exercises show that this has a strong negative effect on the population growth rate and thus increases the risk of population extinction (Wielgus et al. 2001).

Equids often show highly developed multilevel social organization. Harem-forming feral horses and plains zebras are vulnerable to social instability and a high turnover of harem males (Hack et al. 2002). The selective removal of harem stallions can lead to increased stress levels, reduced grazing time, and loss of body condition in females subject to harassment from intruding males, resulting in induced abortion (Berger 1983) and lower female reproductive success (Rubenstein 1986). Male takeovers in feral horses led to abortion due to forced copulation in 80% of females <6 months pregnant and due to other stress factors in a further 10% (Berger 1983). Females were subsequently reinseminated by new males resulting in a reduced interbirth interval and genetic investment of rival males.

As with the selective hunting of specific age and sex classes, the selective removal of individuals could also affect other birth characteristics. For example, lion populations in which males are hunted, rear a higher proportion of male than female cubs (Smuts 1978; Creel & Creel 1997). According to the sex-allocation theory (Charnov 1982), this could compensate for a high turnover of adult males (Packer & Pusey 1987) but reduces the number of lions that can be sustainably harvested before the availability of females becomes limiting (Greene et al. 1998).

Synthesis and Conclusions

Our review shows that when selective harvesting perturbs the sex or age structure in such a way that the mating system is disrupted, the fecundity and survival of certain sectors of the population and the offspring sex ratio may all be affected. The removal of even a few targeted individuals could have similar consequences. Nevertheless, the evidence for the occurrence of such unintended demographic side effects is somewhat equivocal (Tables 1 & 2), being more common in experimental than observational studies. We believe this arises because such effects are often subtle, indirect, and sometimes involve time lags (Fig. 2). Changes such as shifts in calving date or offspring sex ratio are difficult to detect without detailed monitoring programs, and there is currently a lack of long-term studies of marked individuals in hunted populations (Festa-Bianchet 2003). This limits our understanding of how and when these demographic effects are expressed

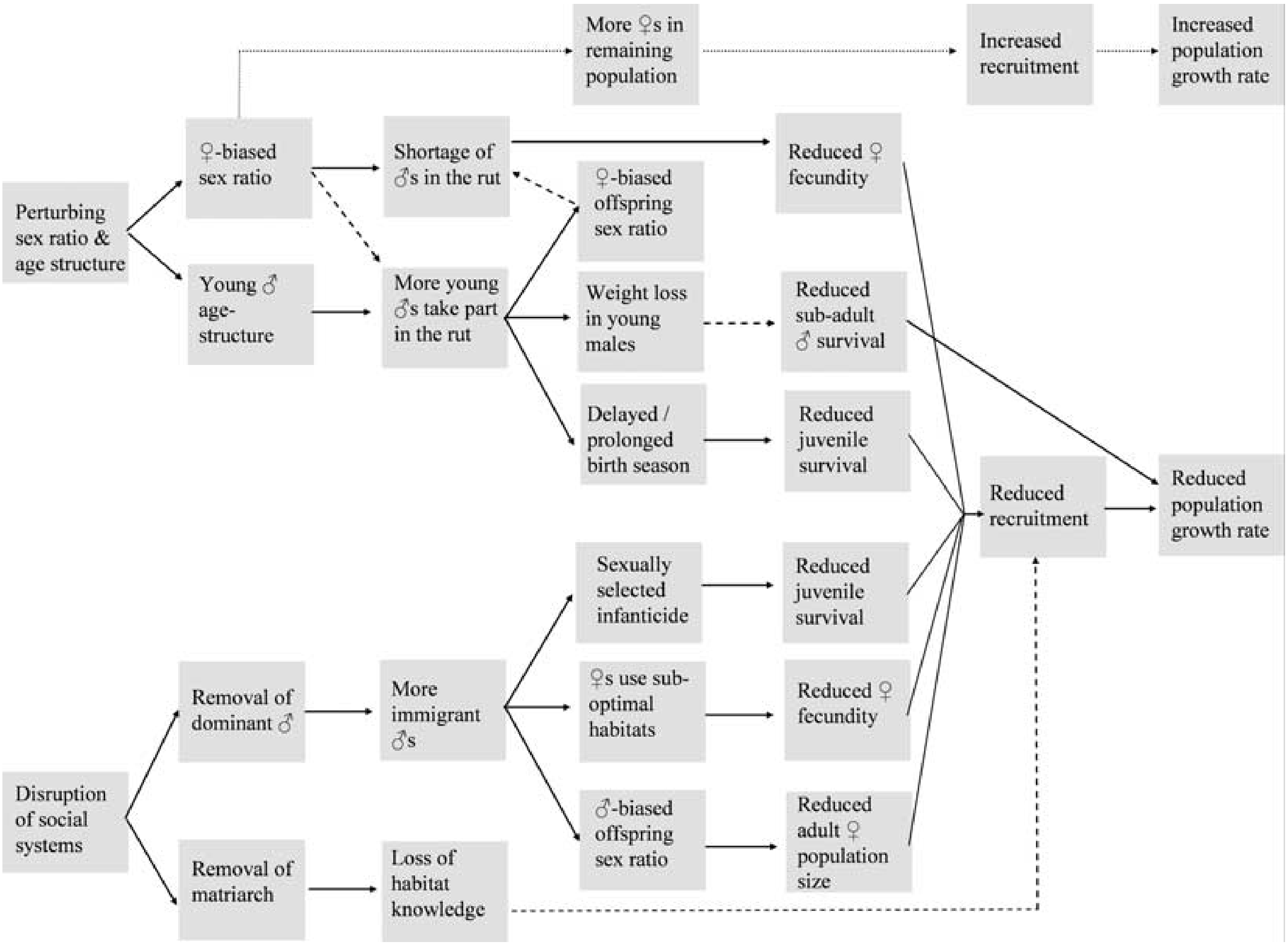

Figure 2. Schematic model of some of the processes and indirect pathways by which selective harvesting may affect population growth rate. Solid lines are mechanisms and effects that are well documented, and dashed lines indicate effects that are less well documented. The dotted lines indicate the path by which selective harvesting can increase population growth rate.

across different mating systems, habitat types, and population densities.

Many of the processes triggered by selective harvesting indirectly reduce the recruitment of new individuals, thereby potentially reducing the population growth rate (Fig. 2). Recruitment is depressed because females hesitate to mate with young males (e.g., Holand et al. 2006), ovulation is delayed in the absence of stimulation from mature males (e.g., McComb 1987; Komers et al. 1999), or, more rarely, there are insufficient males for all females to be mated (e.g., Milner-Gulland et al. 2003). Conception rates can be limited by spatial (Mysterud et al. 2002) and social (Greene et al. 1998) factors influencing access to mates and by a physical limit to the number of females each male can inseminate (Ginsberg & Milner-Gulland 1994). Although there are clearly differences between monogamous and polygynous mating systems in the ratio of adult males to females necessary for all females to be mated, within polygynous species differences in female group size (solitary individuals, small social groups, or large harems) and male mating behavior (e.g., tending, lekking, or harem holding) also influence access to mates. In addition, mate access may vary within species because group size differs with habitat type (Hewison et al. 1998). Extrapolation of adult sex ratios from domestic populations is not advisable. Generally, daily sperm production, sperm density, and absolute sperm numbers are directly related to testes size (Møller 1989), and most domestic animals have large testes for their body weight (Ginsberg & Milner-Gulland 1994). Under intense competition between males, sperm depletion can occur before the end of the rut, even in species with relatively large testes (Preston et al. 2001).

Although the mechanisms by which selective harvesting could affect population demography are relatively well documented (Fig. 2), the extent to which they affect population growth is still poorly understood (e.g., Wielgus et al. 2001; Whitman et al. 2004). Because the sensitivity of population growth rate to recruitment is generally lower than its sensitivity to adult female survival (Gaillard et al. 2000), demographic side effects that depress recruitment may not have as strong an effect on population growth rate as the direct harvesting of adult females. Nevertheless, because many of these effects are likely to act additively (Fig. 2), they may nonetheless reduce the population growth rate more than first anticipated. Although good estimates are lacking for many parameters, conceptual models would be helpful in suggesting when demographic side effects might start to limit population growth and in guiding empirical data collection.

The occurrence of demographic side effects of selective harvesting has implications for the performance of population viability analyses (PVA). In many of the most commonly used PVA software programs there is an implicit assumption that sex does not matter as long as the number of adult males is ≥ 1 (Brook et al. 2000). Nevertheless, estimated extinction probabilities are affected by both population sex ratio and mating system (Ginsberg & Milner-Gulland 1994; Sæther et al. 2004*a*). In addition, for small populations, demographic stochasticity in the sex ratio could have a direct negative effect on mean population growth rate (Sæther et al. 2004*a*). If the abundance of one sex is particularly low, chance events could result in that sex being limiting in certain years. This would be especially important in small, harvested populations and in more abundant populations when the sex ratio is close to the threshold where these effects become important.

Selective harvesting regimes can have destabilizing effects on populations. The young age structure of harvested populations results in less-stable dynamics due to high stochasticity in juvenile survival (e.g., Gordon et al. 2004). Furthermore, if late-born offspring enter the winter with lower body weights (e.g., Holand et al. 2006), they are more likely to be affected by random climatic variation (Festa-Bianchet 1988), which, together with reduced birth synchrony, could result in large interannual fluctuations in juvenile survival. In addition, in species with SSI, the effect of male removal on population growth rate is hard to predict because it depends on the number of offspring killed by immigrant males. In a Scandinavian bear population Swenson et al. (1997) estimated that the removal of one male was equivalent to the removal of 0.5–1.0 females, depending on the extent to which the immigrant male killed the cubs in the area. In such situations harvesting juveniles and females will have more predictable effects.

In response to the demographic side effects discussed here and the evolutionary consequences of selective harvesting (Harris et al. 2002; Festa-Bianchet 2003), wildlife managers are advised to implement harvesting regimes that mimic natural mortality patterns more closely. Because natural mortality is typically higher among juveniles and old individuals (Gaillard et al.1998), these groups should be targeted (Ginsberg & Milner-Gulland 1994), although this may conflict with economic considerations in some areas (Festa-Bianchet 2003; Milner et al. 2006). Applying a minimum age threshold is a possibility for trophy males if a reliable assessment of age can be made independently from trophy phenotype, which may be well developed at a young age in high-quality males (Whitman et al. 2004). An additional approach would be to consider the timing of the harvest. Currently many temperate ungulates are hunted during the breeding season. If the harvest is delayed until after the rut, older males have the opportunity to breed and could be harvested at the time of year when their reproductive value is lowest (Kokko et al. 2001). In lions the optimal time for hunting a pride male would be as his cubs become independent (Whitman et al. 2004). In this way, and by following natural pride take over intervals, infanticide can be minimized.

We are now starting to understand the mechanisms by which undesirable side effects of selective hunting occur, but much less is known about when they occur and the extent to which they affect population growth. To be able to make firmer predictions about the effects on population growth and viability, both large-scale empirical manipulations of harvesting regimes and theoretical studies, including simulation modeling, are urgently needed. Because most of the effects discussed here operate through recruitment, monitoring recruitment and juvenile sex ratios should be standard routines for managers, in addition to assessment of total population size. In addition, stronger emphasis should be put on the timing of the harvest. Until the importance of the mechanisms triggered by selective harvesting discussed here are more clearly understood, we urge managers to be cautious in their use of nonrandom harvesting strategies.

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Literature Cited

Andreassen, H. P., and G. Gundersen. 2006. Male turnover reduces population growth: an enclosure experiment on voles. Ecology **87:**88-94.

Apollonio, M., B. Bassano, and A. Mustoni. 2003. Behavioral aspects of conservation and management in European mammals. Pages 157-170 in M. Festa-Bianchet and M. Apollonio, editors. Animal behavior and wildlife conservation. Island Press, Washington, D.C.

Baillie, J. E. M., C. Hilton-Taylor, and S. N. Stuart. 2004. 2004 IUCN red list of threatened species. A global species assessment. World Conservation Union, Gland, Switzerland, and Cambridge, United Kingdom.

Bartos, L., and J. Madlafousek. 1994. Infanticide in a seasonal breeder—the case of red deer. Animal Behaviour **47:**217-219.

Bellemain, E., J. E. Swenson, and P. Taberlet. 2006. Mating strategy in relation to sexually selected infanticide in a nonsocial carnivore: the brown bear. Ethology **112:**238-246.

Bender, L., and P. J. Miller. 1999. Effects of elk harvest strategy on bull demographics and herd composition. Wildlife Society Bulletin **27:**1032-1037

Berger, J. 1983. Induced abortion and social factors in wild horses. Nature **303:**59-61.

Bergerud, A. T. 1974. Rutting behaviour of the Newfoundland caribou. Pages 395-435 in V. Geist and F. Walther, editors. The behaviour of ungulates and its relation to management. World Conservation Union, Morges, Switzerland.

Brook, B. W., M. A. Burgman, and R. Frankham. 2000. Differences and congruencies between PVA packages: the importance of sex ratio for predictions of extinction risk. Conservation Ecology **4:** http://www.ecologyandsociety.org/vol4/iss1/art6/.

Cameron, T. C., and T. G. Benton. 2004. Stage-structured harvesting and its effects: an empirical investigation using soil mites. Journal of Animal Ecology **73:**996-1006.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, Chichester, United Kingdom.

Charnov, E. 1982. The theory of sex allocation. Princeton University Press, Princeton, New Jersey.

Clutton-Brock, T. H., M. Major, S. D. Albon, and F. E. Guinness. 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. Journal of Animal Ecology **56:**53-67.

Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. Nature **426:**655-658.

Cooper, S. M. 1991. Optimal hunting group-size—the need for lions to defend their kills against loss to spotted hyaenas. African Journal of Ecology **29:**130-136.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science **292:**1528-1531.

Courtois, R., and G. Lamontagne. 1999. The protection of cows: its impacts on moose hunting and moose populations. Alces **35:**11-29.

Creel, S., and N. M. Creel. 1997. Lion density and population structure in the Selous Game Reserve: evaluation of hunting quotas and offtake. African Journal of Ecology **35:**83-93.

Dobson, A., and J. Poole. 1998. Conspecific aggregation and conservation biology. Pages 193-208 in T. Caro, editor. Behavioural ecology and conservation biology. Oxford University Press, Oxford, United Kingdom.

Festa-Bianchet, M. 1988. Birthdate and survival in bighorn lambs (*Ovis canadensis*). Journal of Zoology **214:**653-661.

Festa-Bianchet, M. 2003. Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. Pages 191-210 in M. Festa-Bianchet and M. Apollonio, editors. Animal behavior and wildlife conservation. Island Press, Washington, D.C.

Freddy, D. J. 1987. The White River elk herd: a perspective 1960-85. Wildlife technical publication. Colorado Division of Wildlife, Fort Collins.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution **13:**58-63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics **31:**367-93.

Garel, M., E. J. Solberg, B. E. Sæther, I. Herfindal, and K. A. Hogda. 2006. The length of growing season and adult sex ratio affect sexual size dimorphism in moose. Ecology **87:**745-758.

Geist, V. 1971. Mountain Sheep, a study in behavior and evolution. University of Chicago Press, Chicago.

Ginsberg, J. R., and E. J. Milner-Gulland. 1994. Sex-biased harvesting and population-dynamics in ungulates—implications for conservation and sustainable use. Conservation Biology **8:**157-166.

Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology **41:**1021-1031.

Greene, C., J. Umbanhowar, M. Mangel, and T. Caro. 1998. Animal breeding systems, hunter selectivity and consumptive use in wildlife conservation. Pages 271-305 in T. Caro, editor. Behavioural ecology and conservation biology. Oxford University Press, Oxford, United Kingdom.

Hack, M. A., R. East, and D. I. Rubenstein. 2002. Status and Action Plan for the Plains Zebra (*Equus burchellii*). Pages 43-60 in P. D. Moehlman, editor. Equids: zebras, asses and horses. World Conservation Union (IUCN) Species Survival Commission Equid Specialist Group, IUCN, Gland, Switzerland.

Harris, R. B., W. A. Wall, and F. W. Allendorf. 2002. Genetic consequences of hunting: what do we know and what should we do? Wildlife Society Bulletin **30:**634-643.

Heimer, W. E., S. M. Watson and T. C. Smith. 1984. Excess ram mortality in a heavily hunted Dall sheep population. Symposium Northern Wild Sheep & Goat Council **4:**425-432.

Hewison, A. J. M., J.-P. Vincent, and D. Reby. 1998. Social organisation of European roe deer. Pages 189-219 in R. Andersen, P. Duncan, and J. D. C. Linnell, editors. The European roe deer: the biology of success. Scandinavian University Press, Oslo.

Hogg, J. T., and S. H. Forbes. 1997. Mating in bighorn sheep: frequent male reproduction via a high-risk "unconventional" tactic. Behavioral Ecology and Sociobiology **41:**33–48.

Holand, Ø., K. H. Roed, A. Mysterud, J. Kumpula, M. Nieminen, and M. E. Smith. 2003. The effect of sex ratio and male age structure on reindeer calving. Journal of Wildlife Management **67:**25–33.

Holand, Ø., A. Mysterud, K. H. Røed, T. Coulson, H. Gjøstein, R. B. Weladji, and M. Nieminen. 2006. Adaptive adjustment of offspring sex ratio and maternal reproductive effort in an iteroparous mammal. Proceedings of the Royal Society B **273:**293–299.

IUCN (World Conservation Union). 2004. 2004 IUCN Red List of threatened species. IUCN, Gland, Switzerland. Available from http://www.iucnredlist.org (accessed February 2006).

Jorgenson, J. T., M. Festa-Bianchet, J.-M. Gaillard, and W. D. Wishart. 1997. Effects of age, sex, disease, and density on survival of Bighorn sheep. Ecology **78:**1019–1032.

Komers, P., B. Birgersson, and K. Ekvall. 1999. Timing of estrus in fallow deer is adjusted to the age of available mates. The American Naturalist **153:**431–436.

Kokko, H., J. Lindström, and E. Ranta 2001. Life histories and sustainable harvesting. Pages 301–322 in J. D. Reynolds, G. M. Mace, K. H. Redford, and J. G. Robinson, editors. Conservation of exploited species. Cambridge University Press, Cambridge, United Kingdom.

Kruuk, L. E. B., T. H. Clutton-Brock, K. E. Rose, and F. E. Guinness. 1999. Early determinants of lifetime reproductive success differ between the sexes in red deer. Proceedings of the Royal Society B **266:**1655–1661.

Labisky, R. F., and D. E. Fritzen. 1998. Spatial mobility of breeding female white-tailed deer in a low-density population. Journal of Wildlife Management **62:**1329–1334.

Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology, and variation in age at first reproduction in a temperate herbivore. Journal of Animal Ecology **65:**653–670.

Langvatn, R., and A. Loison. 1999. Consequences of harvesting on age structure, sex ratio, and population dynamics of red deer *Cervus elaphus* in central Norway. Wildlife Biology **5:**213–223.

Laurian, C., J. P. Ouellet, R. Courtois, L. Breton, and S. St-Onge. 2000. Effects of intensive harvesting on moose reproduction. Journal of Applied Ecology **37:**515–531.

Law, R. 2001. Phenotypic and genetic changes due to selective exploitation. Pages 323–342 in J. D. Reynolds, G. M. Mace, K. H. Redford, and J. G. Robinson, editors. Conservation of exploited species. Cambridge University Press, Cambridge, United Kingdom.

LeCount, A. L. 1987. Causes of black bear cub mortality. International Conference on Bear Research and Mangement **7:**75–82.

Lewison, R. 1998. Infanticide in the hippopotamus: evidence for polygynous ungulates. Ethology, Ecology & Evolution **10:**277–286.

McComb, K. 1987. Roaring by red deer stags advances the date of oestrus in hinds. Nature **330:**648–649.

McComb, K., C. Moss, S. M. Durant, L. Baker, and S. Sayialel. 2001. Matriarchs as repositories of social knowledge in African elephants. Science **292:**491–494.

McCullough, D. R. 1981. Population dynamics of the Yellowstone grizzly bear. Pages 173–196 in C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. John Wiley & Sons, New York.

McCullough, D. R. 2001. Male harvest in relation to female removals in a black-tailed deer population. Journal of Wildlife Management **65:**46–58.

McLellan, B. N. 2005. Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. Ursus **16:**141–156.

Miller, S. D. 1990. Impact of increased bear hunting on survivorship of young bears. Wildlife Society Bulletin **18:**462–467.

Miller, S. D., R. A. Sellers, and J. A. Keay. 2003. Effects of hunting on brown bear cub survival and litter size in Alaska. Ursus **14:**130–152.

Milner, J. M., C. Bonenfant, A. Mysterud, J.-M. Gaillard, S. Csányi, and N. C. Stenseth 2006. Temporal and spatial development of red deer harvesting in Europe—biological and cultural factors. Journal of Applied Ecology **43:**721–734.

Milner-Gulland, E. J., and E. L. Bennett. 2003. Wild meat: the bigger picture. Trends in Ecology & Evolution **18:**351–357.

Milner-Gulland, E. J., O. M. Bukreevea, T. Coulson, A. A. Lushchekina, M. V. Kholodova, A. B. Bekenov, and I. A. Grachev. 2003. Reproductive collapse in saiga antelope harems. Nature **422:**135.

Møller, A. P. 1989. Ejaculate quality, testes size and sperm competition in primates. Journal of Human Evolution **17:**479–488.

Murphy, E. C., F. J. Singer, and L. Nichols. 1990. Effects of hunting on survival and productivity of Dall sheep. Journal of Wildlife Management **54:**284–290.

Mysterud, A., T. Coulson, and N. C. Stenseth. 2002. The role of males in the dynamics of ungulate populations. Journal of Animal Ecology **71:**907–915.

Mysterud, A., O. Holand, K. H. Roed, H. Gjostein, J. Kumpula, and M. Nieminen. 2003. Effects of age, density and sex ratio on reproductive effort in male reindeer (*Rangifer tarandus*). Journal of Zoology **261:**341–344.

Nilsen, E. B., J. D. C. Linnell, and R. Andersen. 2004. Individual access to preferred habitat affects fitness components in female roe deer *Capreolus capreolus*. Journal of Animal Ecology **73:**44–50.

Nilsen, E. B., I. Herfindal, and J. D. C. Linnell. 2005. Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? Écoscience **12:**68–75.

Noyes, J. H., B. K. Johnson, L. D. Bryant, S. L. Findholt, and J. W. Thomas. 1996. Effects of bull age on conception dates and pregnancy rates of cow elk. Journal of Wildlife Management **60:**508–517.

Ozoga, J. J., and L. J. Verme. 1985. Comparative breeding behavior and performance of yearling vs. prime-age white-tailed bucks. Journal of Wildlife Management **49:**364–372.

Packer, C., and A. E. Pusey. 1987. Intrasexual cooperation and the sex ratio in African lions. The American Naturalist **130:**636–642.

Pluhacek, J., and L. Bartos. 2005. Further evidence for male infanticide and feticide in captive plains zebra, *Equus burchelli*. Folia Zoologica **54:**258–262.

Preston, B. T., I. R. Stevenson, J. M. Pemberton, and K. Wilson. 2001. Dominant rams lose out by sperm depletion. Nature **409:**681–682.

Pusey, A. E., and C. Packer. 1994. Infanticide in lions: consequences and counterstrategies. Pages 277–299 in S. Parmigiani, and F. S. vom Saal, editors. Infanticide & parental care. Harwood Academic, London.

Robinson, J. R., and E. L. Bennett 2000. Hunting for sustainability in tropical forests. Columbia University Press, New York.

Rogers, L. L. 1987. Effects of food-supply and kinship on social behavior, movements, and population growth of black bears in Northeastern Minnesota. Wildlife Monographs **97:**1–72.

Rubenstein, D. I. 1986. Ecology and sociality in Horses and Zebras. Pages 282–302 in D. I. Rubenstein and R. W. Wrangham, editors. Ecological aspects of social evolution. Princeton University Press, Princeton, New Jersey.

Sæther, B.-E., E. J. Solberg, and M. Heim. 2003. Effects of altering sex ratio structure on the demography of an isolated moose population. Journal of Wildlife Management **67:**455–466.

Sæther, B. E., S. Engen, R. Lande, A. P. Moller, S. Bensch, D. Hasselquist, J. Beier, and B. Leisler. 2004*a*. Time to extinction in relation to mating system and type of density regulation in populations with two sexes. Journal of Animal Ecology **73:**925–934.

Sæther, B.-E., E. J. Solberg, M. Heim, J. E. Stacy, K. S. Jakobsen, and R. Olstad. 2004*b*. Offspring sex ratio in moose *Alces alces* in relation to paternal age: an experiment. Wildlife Biology **10:**51–57.

Schwartz, C. C., and E. F. Becker. 1994. Growth of moose calves conceived during the first versus second estrus. Alces **30:**91–100.

Shackleton, D. M. 1991. Social maturation and productivity in bighorn sheep: are young males incompetent? Applied Animal Behaviour Science **29:**173–184.

Sheldon, B. C. and S. A. West. 2004. Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. The American Naturalist **163:**40–54.

Sinclair, A. R. E., S. A. R. Mduma, and P. Arcese. 2000. What determines phenology and synchrony of ungulate breeding in Serengeti? Ecology **81:**2100–2111.

Singer, F. J., and L. C. Zeigenfuss. 2002. Influence of trophy hunting and horn size on mating behavior and survivorship of mountain sheep. Journal of Mammalogy **83:**682–698.

Smuts, G. L. 1978. Effects of population reduction on the travels and reproduction of lions in Kruger National Park. Carnivore **1:**61–72.

Solberg, E. J., and B.-E. Sæther. 1994. Male traits as life-history variables: annual variation in body mass and antler size in moose (*Alces alces*). Journal of Mammalogy **75:**1069–1079.

Solberg, E. J., B.-E. Sæther, O. Strand, and A. Loison. 1999. Dynamics of a harvested moose population in a variable environment. Journal of Animal Ecology **68:**186–204.

Solberg, E. J., A. Loison, B.-E. Sæther, and O. Strand. 2000. Age-specific harvest mortality in a Norwegian moose *Alces alces* population. Wildlife Biology **6:**41–52.

Solberg, E. J., A. Loison, T. H. Ringsby, B.-E. Sæther, and M. Heim. 2002. Biased adult sex ratio can affect fecundity in primiparous moose *Alces alces*. Wildlife Biology **8:**117–128.

Squibb, R. C. 1985. Mating success of yearling and older bull elk. Journal of Wildlife Management **49:**744–750.

Stalling, D. H., G. J. Wolfe, and D. K. Crockett. 2002. Regulating the hunt. Pages 749–791 in D. E. Toweill and J. W. Thomas, editors. North American elk. Ecology and management. Smithonian Institution Press, Washington, D.C.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, United Kingdom.

Stevenson, I. R., and D. R. Bancroft. 1995. Fluctuating trade-offs favour precocial maturity in male Soay sheep. Proceedings of the Royal Society B **262:**267–275.

Stringham, S. F. 1983. Roles of adult males in grizzly bear populations. International Conference on Bear Research and Mangement **5:**140–151.

Swenson, J. E. 2003. Implications of sexually selected infanticide for the hunting of large carnivores. Pages 171–189 in M. Festa-Bianchet and M. Apollonio, editors. Animal behavior and wildlife conservation. Island Press, Washington, D.C.

Swenson, J. E., F. Sandegren, A. Söderberg, A. Bjärvall, R. Franzén, and P. Wabakken. 1997. Infanticide caused by hunting of male bears. Nature **386:**450–451.

Taquet, M., J.-P. Ouellet, R. Courtois, and C. Laurian. 1999. Does unbalanced sex ratio in adult moose affect calf size in the fall? Alces **35:**203–211.

Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science **179:**90–92.

White, G. C., D. J. Freddy, R. B. Gill, and J. H. Ellenberger. 2001 Effect of adult sex ratio on mule deer and elk productivity in Colorado. Journal of Wildlife Management **65:**543–551.

Whitman, K., A. M. Starfield, H. S. Quadling, and C. Packer. 2004. Sustainable trophy hunting of African lions. Nature **428:**175–178.

Wielgus, R. B., and F. L. Bunnell. 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. Biological Conservation **93:**145–154.

Wielgus, R. B., F. Sarrazin, R. Ferriere, and J. Clobert. 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. Biological Conservation **98:**293–303.

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Neo-colonialism and greed: Africans' views on trophy hunting in social media

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ABSTRACT

Existing studies on the trophy hunting controversy in recent years have largely represented the anti-hunting views of the Western public, while overlooking the opinions of African people. This study taps into Africans' social media narratives to illuminate the racially, politically, and historically charged context in which trophy hunting occurs in Africa. Data were collected from the Facebook pages of three major social media players with a predominantly African followership, namely, BBC News Africa, News24.com, and NewsDay-Zimbabwe. The dominant pattern was resentment towards what was viewed as the neo-colonial character of trophy hunting, in the way it privileges Western elites in accessing Africa's wildlife resources. However, the West's passionate criticism of violence against animals was viewed by participants as overblown, and as evidence of their (Westerners') higher regard for animals than for African people. Interestingly, trophy hunting was not objectionable from an animal rights perspective, but as a consequence of its complex historical and postcolonial associations. In addition, criticism was directed at African politicians who were perceived as allowing wildlife exploitation to satisfy their own greed. In this instance, far from tourism being a facilitator of intercultural understanding and peace, it appears to reproduce images and wounds of a colonial past.

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Introduction

The last few years have seen sustained academic and public debate on trophy hunting, sparked by the much publicized shooting of Cecil-the-lion in July 2015 by an American tourist. However, most of the focus in scholarly works has been on the largely anti-hunting views of the Western public—the views of Africans who are much more connected to the hunting context have been overlooked. To address this gap, this study taps into social media to understand the ways in which Africans' responses to the trophy hunting controversy diverge from those of the anti-hunting Western public.

The lack of scholarly interest in Afro-based environmental views is noted by Chibvongodze (2016), who sees it as arising from the long colonial history in which indigenous people were denied recognition as effective ecological agents who were able to manage their natural resources sustainably. As a result, their views are either ignored or trivialised. Garland (2008) similarly notes that Western wildlife scientists and advocates working in Africa, although not all, are often

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ignorant of local worldviews, and frequently lament locals being corrupt, "in it for the money", or lacking the skills required to carry out conservation work.

More pointedly, with respect to the trophy hunting debate, Macdonald et al. (2017, p. 251) write

> … views widely held in the wealthy West are often at odds with views within lion range countries, where lions often impose severe costs (including man-eating) on the people who live alongside them. Who has the right to make decisions about trophy hunting? How should the weight of opinions held on lion hunting in countries without lions, such as the USA (which has a thriving domestic hunting market), be ranked against the opinions held in African countries where lions occur (and where the financial consequences of a cessation of trophy hunting might bite hardest)?

Indeed, much of the opposition to trophy hunting comes from people who are far removed from the issues, with very little or no African experience (Angula et al., 2018). Thus, Angula et al. (2018) assert that the opinions held in Africa should not be overridden by those of people living in the developed West, as they (Westerners) do not have to bear the direct consequences of wildlife policy changes. For Batavia et al. (2018) top-down decisions by Western policymakers to enforce a ban on trophy hunting in communities where trophy hunting as a form of wildlife tourism has local support is not a sustainable pathway. Thus, for long-term sustainability of wildlife tourism in Africa to be possible, and for a more balanced and complete body of knowledge in that respect, it is important to consider the socio-cultural meanings and implications of trophy hunting, taking into account the views of local communities and broader stakeholders (Nordbø, Turdumambetov, & Gulcan, 2018). It is within this epistemic argument that this study is located. The social media methodology provided convenient access to a much larger sampling frame for African participants than is possible with interviews and other traditional techniques. Furthermore, by using already existing Facebook User Generated Content, the data could be gathered with minimal researcher bias.

Literature review

Trophy hunting in Africa: recent debates and developments

There is an extensive body of research on trophy hunting in Africa stretching over decades (Baker, 1997; Humavindu & Barnes, 2003; Lindsey, Roulet, & Romanach, 2007; Lindsey, Alexander, Frank, Mathieson, & Romanach, 2006; Lindsey et al., 2013; Lindsey, Frank, Alexander, Mathieson, & Romanach, 2007). However, most of these studies focus on the economic contribution of trophy hunting, and its contested link with conservation (Creel et al., 2016; Crosmary, Côté, & Fritz, 2015; Lindsey et al., 2006; Vora, 2018). In a large body of the conservation literature, as Batavia et al. (2018) note, trophy hunting has largely been tolerated and even supported. This is perhaps partially motivated by a desire to appear to be driven by reason and evidence, rather than emotion and hype (Nelson, Bruskotter, Vucetich, & Chapron, 2016). For instance Di Minin, Leader-Williams, and Bradshaw (2016) argue that banning trophy hunting would exacerbate biodiversity loss.

Over the last few years, however, especially following the shooting of Cecil in Zimbabwe, there has also been particular scholarly and public interest in the moral tenability of trophy hunting, with strong critiques of the consequentialist arguments typically used by hunters to justify their "sport" (Nelson et al., 2016). Within the consequentialist argument, trophy hunting's capacity to generate funds and other benefits such as food and employment for local communities are emphasised (Di Minin et al., 2016; Mbaiwa, 2018). Since "Cecilgate", the industry has seen increased negative publicity and opposition (Batavia et al., 2018; Crosmary et al., 2015; Macdonald, Jacobsen, Burnham, Johnson, & Loveridge, 2016).

In reference to the moral debates, Batavia et al. (2018) assert that trophy hunting is morally indefensible, because compelling evidence shows that the animals typically hunted for trophies have intelligence, emotion, and sociality. In addition, they argue, in trophy hunting, the animals are debased, commoditized and "relegated to the sphere of mere things when they are turned into souvenirs, oddities, and collectibles" (Batavia et al., 2018, p. 3). This sentiment is echoed in other recent studies (Lindsey, Balme, Funston, Henschel, & Hunter, 2016; Macdonald, Jacobsen, et al., 2016; Nelson et al., 2016). Trophy hunting has also been described as an ongoing re-enactment of Western colonialist history, wherein the hunting of wildlife is viewed as symbolically representing the conquering and subjugation of "subhuman" indigenous peoples (Batavia et al., 2018; see also Kalof & Fitzgerald, 2003; Mullin, 1999). Thus recent debates have sought to demonstrate that the trophy hunting controversy is not only about whether the practice supports or impedes conservation agendas, but also about the welfare of animals, and its more complex historical associations (Batavia et al., 2018; Nelson et al., 2016). As a result of the ethical concerns around trophy hunting, Bouché et al. (2016) note that there is continued pressure on Western countries to ban lion imports, and indeed countries such as Australia and France have instituted bans (Bouché et al., 2016). A number of airlines have also responded with transportation bans (Bouché et al., 2016).

Bauer et al. (2017) argue that under these circumstances, new approaches to wildlife conservation are needed. The challenge is that in many hunting areas, there are very few, if any, alternatives to trophy hunting which would maintain wildlife habitat and be economically viable (Macdonald et al., 2017). Lindsey et al. (2016) argue that there is an urgent need to find alternative funding streams to reduce the reliance of African countries on trophy hunting, while at the same time cautioning against short term moves to preclude hunting, before such alternatives are in place. In a response to Batavia et al. (2018), Dickman et al. (2019, p. 1) similarly advocate "a 'journey' rather than a 'jump' to end hunting, in the interests of limiting unintended consequences".

Traditional African views on wildlife

As noted, very little consideration has been given in existing literature to Africans' worldviews in relation to trophy hunting. Extant studies on the subject may be described as largely etic, that is, as privileging the outsider's gaze. However, a number of studies have examined the concept of Ubuntu (Chibvongodze, 2016; Forster, 2010; Murove, 2004), which underpinned traditional African views of and relationships with nature, including wildlife.

Ubuntu is a word from the Southern African family of languages (Ndebele, Swati,/Swazi, Xhosa, and Zulu), and, as Outwater, Abrahams, and Campbell (2005) note, Ubuntu is not easily translatable; it represents not a thing, but a philosophy and way of life that is the foundation of many African societies, with complex cultural connotations. Ubuntu combines the values of "humaneness", "caring and sharing", or "being in harmony with all of creation". It may also be understood as meaning "I am because we are" (Andreasson, 2010). As Du Plessis (2001) argues, understanding "interconnectedness" as encapsulated by the cultural concept of Ubuntu offers insight into an African concept of sustainability that can inform the Western sustainability model and make it relevant to Africa. Regarding the perspective of this article, Ubuntu can be viewed as providing a reconceptualization of the trophy hunting debate—in Ubuntu philosophy, the wellbeing of all humanity and of all nature takes precedence, before the rights of the individual (trophy hunter). Thus while a tourist might have a permit to hunt and shoot an animal, if the community and the environment suffer, it is considered that the principles of Ubuntu have been violated. It could also be argued that the consequentialist justification of sacrificing individual animals for the greater conservation good of populations and species would not be compatible with Ubuntu either. Ubuntu, being grounded in an attitude of caring and compassion, does not excuse gratuitous violence towards individual animals. In traditional African society, animals were killed if they posed danger (for example, to crops or to humans), or for survival (that is, for meat). There is however still work to be done on the finer interpretations of Ubuntu, as Lutz (2009) notes.

Chibvongodze (2016, p. 159) argues that African indigenous knowledge systems "utilise cultural beliefs and norms embedded in taboos, totems and proverbs to promote human tolerance towards plants, animals, mountains and rivers." He draws a contrast between Western philosophies on environmental conservation, which promote an individualistic moral obligation to conserve animals, with African philosophy which encourages a collective sense of responsibility to conservation, by meshing animal identities with clan names to create a sense of human/animal similitudes, thereby encouraging a communal commitment to conservation of animals (Chibvongodze, 2016; Galaty, 2014). Ubuntu signifies that the "wholeness of an African can only be complete when the human-spiritual-nature tripartite is achieved" (Chibvongodze, 2016, p. 158).

However, with the advent of colonialism, the role of Ubuntu in African communities was usurped by Western approaches to conservation, as indigenous people were systematically alienated from their natural environment (Akama, 1996; Akama, Maingi, & Camargo, 2011; Chibvongodze, 2016). When colonial conservation methods were introduced, nature was appropriated through fenced game parks, transforming native hunters into poachers, trespassers, and criminals (Chibvongodze, 2016; MacKenzie, 1997). Colonialism challenged the African philosophy that views humans and nature as an inseparable, singular entity—while Ubuntu attests to humans and nature as equals, Western anthropocentricism mandated humans as primary and central in the order of things (Chibvongodze, 2016; Steiner, 2010). Whereas historically Western philosophy viewed nature only as a means to an end, African philosophy depicted it as an end in itself (Chibvongodze, 2016; Murphy, 2018).

On a broader level, however, the role and merits of Ubuntu for modern African society remain a point of considerable contention. The 'incompatibility school of thought' (see Mwipikeni, 2018), on one hand, views Ubuntu as incompatible with contemporary African society's socio-political system. Matolino and Kwindingwi (2013, p. 202) point out, in their work titled "the end of ubuntu", that traditional worldviews such as Ubuntu only work well for "undifferentiated, small and tight-knit communities that are relatively undeveloped". Referring in particular to the South African case, they question whether Ubuntu can be made to fit in contemporary, highly diverse African societies that espouse ideas such as tolerance, cosmopolitanism, and democracy. The Ubuntu narrative, they assert "hardly addresses the increasingly globalised and sophisticated outlook" of modern African communities (p. 2015).

Koenane and Olatunji (2017), on the other hand, hold a starkly different view, arguing that Ubuntu remains competitive as a moral theory, and that it "will ultimately prove to be a desirable ethic which could contribute positively towards developing moral character in the contemporary socio-political environment in parts of Africa" (p. 263). In a similar manner, Metz (2014) finds Ubuntu a compelling philosophy that merits pride on behalf of sub-Saharans; one that can be refined and exported to international audiences. Other scholars argue that Ubuntu would need to be re-invented in order to suit modern African society (Chimakonam, 2016). Modern African society can therefore be described as characterized by a tension between a modern, globalized outlook, and the traditional Ubuntu ethos, each with its own set of virtues and challenges. One of the objectives of this study is to examine whether or in what ways African social media users express opinions of trophy hunting reminiscent of traditional Ubuntu views.

Method

Overview of the grounded theory approach

Given the many complex questions and research gaps around how trophy hunting is viewed from an African perspective, as shown by the review of existing knowledge, a grounded theory approach was adopted to allow the findings to emerge without confining them to a predetermined theoretical lens. Grounded theory is particularly useful where a relevant theory does not exist or in areas where little is already known (Charmaz, 2014). The present study meets these two criteria. Furthermore, it would be counter-intuitive to impose an existing (Western) theoretical framework on a study which seeks to foreground a non-Western perspective.

Grounded theory systematically gathers and analyses data to identify key constructs relating to a particular phenomenon (Charmaz, 2014; Glaser & Strauss, 2017). The process involves three steps: coding and theorising; memoing and theorising; and, integrating, refining and writing up theories (Charmaz, 2014).

The grounded theory approach possesses three major strengths, which enhance the rigour and richness of this study:

i. *Ecological validity*: The emergent constructs in a grounded theory study are context-specific, detailed, and tightly connected to the data (Charmaz, 2014; Corbin & Strauss, 1990; Glaser & Strauss, 2017).
ii. *Novelty:* Grounded theories have the potential to offer fresh and innovative perspectives on a phenomenon because they are not tied to any pre-existing theory.
iii. *Parsimony:* Grounded theories unpack complex phenomena in ways that help us to understand our social world.

The study's rigour is further enhanced through thick description. The goal of thick description is to create verisimilitude, so that the reader is transported into a setting or situation (Creswell and Miller, 2000). In this instance, the quoted narratives are lengthier than is often the case in similar qualitative studies, to allow a more comprehensive representation of the posters' views to emerge.

In addition, the study combines data from three different Facebook pages, to maximise the diversity of perspectives on the investigated phenomenon. This triangulated approach created a richer, robust data set that captured African users' meanings more rigorously.

Data strategy

An online data strategy presented the best opportunity to tap into naturally occurring exchanges, or User-Generated Content (see Lu & Stepchenkova, 2014; Mkono & Holder, 2019), on the topic of trophy hunting, generated free from researcher bias. Facebook was chosen as the data source due to its ubiquity among Africans living in Africa and in the Diaspora. The pages of news channels that focus on African coverage were identified as the most strategic platforms for collecting data, because of their large African followership. Three Facebook pages were selected for that purpose, namely, BBC News Africa, News24.com (South African news), and NewsDay-Zimbabwe. These pages may be located via a simple search on Facebook.

Descriptions of the three pages are provided in Table 1, showing the numbers of followers, example stories on trophy hunting, and the total number of comments analysed. Relevant posts within the selected pages were then identified through keyword searches using the terms "Cecil the lion", "trophy hunting", and "Walter Palmer". The iterative data search continued until no new relevant insights were emerging from new results, that is, when data saturation was attained. A total of 1,070 posts were collated and analysed.

As the data were already available in the public domain, no consent was sought from individual participants. However, no identifying information about participants was collected or included in the presentation of findings.

Data analysis

The data were subjected to the constant comparative method of grounded theory (Boeije, 2002; Kolb, 2012). The first step was open-coding, which began with reading through and close

Table 1. Data sources.

Data Source (Facebook page)	Description (as of June 6, 2018)	Example stories (list not exhaustive)	Total comments analysed = 1070
BBC News Africa	4,015,939 followers	*Xanda: Son of Cecil the 'lion killed by hunter' in Zimbabwe* Posted July 1, 2017 *What Cecil the lion means to Zimbabwe* Posted July 31, 2015 *US lion killer 'sorry for disruption'* Posted July 30, 2015	519
News24.com	6,447,689 followers	*Foreign hunter accused of killing Zim's famous lion* Posted July 28, 2015 *10 consequences of banning trophy hunting in SA* Posted August 6, 2015	333
NewsDay-Zimbabwe	730,960 followers	*Zimbabwean pair appear in court over Cecil the lion killing* Posted July 29, 2015 *Do you know Cecil the lion? Watch what some Zimbabweans answered.* Posted July 31, 2015	218

examination of the collated social media posts. Proceeding sentence by sentence, sections of the narratives which addressed the research focus (that is, Africans' views on trophy hunting and the controversy around it) were identified and given labels, or codes. This was followed by axial coding, which identified similar codes and grouped them into core categories.

The second step, memoing and theorising, involved writing running notes on each of the identified categories, in order to delve into the latent meanings in data more deeply. The notes served as an interpretive tool and audit trail that connected the researcher's interpretations with the data. The iterative process of coding, memoing and theorising continued until no new insights were emerging.

In the third and final integrative phase of analysis, which is also termed selective coding (Corbin & Strauss, 1990; Glaser & Strauss, 2017), the goal was to identify the central story line by establishing the relationships between the themes and synthesising them in the context of existing literature, but without necessarily seeking to fit the findings within a particular theoretical lens.

Limitations of social media analysis

Notwithstanding its many merits, the present social media analysis is subject to two particular limitations, which must be noted. First, the data by default exclude Africans who are not active on social media. This is significant to mention given the internet penetration in Africa of less than 40%. Secondly, social media analysis is subject to the sensationalisation and bias by the news media, in the reporting of stories. This may in turn influence the strength and direction of responses among social media users. However, this limitation is moderated by social media users' access to other information sources online and offline.

Findings

Five initial core categories were identified from the data, illuminating how African Facebook users viewed trophy hunting and the controversy around it, namely, (i) Western elites exploiting African resources; (ii) 'Cecil the lion' as 'Cecil John Rhodes'; (iii) Animals valued more than humans; (iv) Lions as a threat to human life; and (v) The politics of greed (see Table 2). Further interrogation of the categories revealed overlaps between them, on some patterns. On that basis, the categories were collapsed and reorganised into three themes, which were labelled to capture the essence of the data.

Table 2. Summary of data patterns and example posts.

Recurrent patterns	Example Facebook posts
Western elites exploiting African resources	Why paying in Las Vagas, USA. Africa needs money from its resources to develop. Why not paying here in Africa? Thats colonial mentality.
	Hunting in Africa while licenses are bought in Las Vegas? What the f**k is going on? If u want to kill my lion come get the license from me here in Africa!!!!
	They're mining our minerals and exporting it to Europe, America and etc, now killing our untamed animals, what is our leaders doing?
	These are terrorists. These terrorists should be treated as murderous, we are really trying to save our nature, and they come all the way from America to kill our beautiful animals, in the name of trophy hunters. … If I see you, I'll shoot you with an arrow. Useless pink nose.
	White people: "How can they kill such precious animals"
	Also white people: "We're a group of trophy hunters. I killed 16 lions boet" smh
'Cecil the lion' as 'Cecil John Rhodes'	That's wat i hv been wondering my Zim neighbours, takin pride in naming our heritage after the oppressors, why wasn't the lion named Farai?
	I'm relieved that Cecil the lion died. He was named after Cecil John Rhodes and this is testament to the death of the spirit of Cecil Rhodes in Zim. It's a mystery how both of them were linked to Oxford.
	All this puff & huff for nothing, what about thousands of innocent Zimbabweans killed during the satanic Gukurahundi. Its just a meer animal named after a colonial remnant, Cecil John Rhodes.
Animals valued more than humans	When a person is killed by a lion u smile no action taken, but a lion killed u run to arrest a person
	whats is so important about a 13yr old lion we got kids dying or pple starving and having no jobs and excess to proper healthcare but all you think of is a lion …
	So what he kılled a lıon note a humen so nothıng wrong wıth that Why others pay to hunt ın the park so whats the dıfference??????
	Rubbish, what's is it about this Lion? This is just wild animal. BBC please give us a better news
	Many Heroes and heroens dies in Africa were not praise like this Lion what was important in the animal does its value more than human beings created in Gods likenes and image or it was the god for Zimbabweans to worship? If it was an idol then iam sorry
	But what is it about these animals on BBC CNN et al? One time 47 people died in a road accident one day—I never saw it on BBC The other time 39 burnt beyond recognition in another accident—it was never breaking news. No drugs in hospitals—it's never told on the elite TV channels. Why why why ?
	How many people did that same lion killed.it's life lions kill people and people kill lions.get over it
	Oooh Man! Ooh brothers and sisters in Africa. Wild life?
	What are wildlife, when millions of African are dying and no African ountry could stand up and says no, enough?
	People are dying in neighbouring countries and home countries and they see it as normal. You want people who have not lost their senses join you in your ranting about a missing or dead WILD LIFE? What about the humans?
	Crazy world!
	People of nawadays value animals more than human beings and that's too bad … We are imitating the western world and that is not encouraging …
	People shedding more tears for Cecil, what of Dzamara
	… those beast are now devouring humans babies, of recent is a poor 10 year girl who was devoured by those beast as she went to toilet. So sad . It's better the lions be killed than lions killing humans!
	Why is the world paying more attention to that animal? Is that lion better or have more value than the hundred Isis is killing now are day? Or what about the school girls in Nigeria the conflict in Congo, insecurity and suffering of African migraines in some countries like Spain Greece etc. I think this are some of the issues people should place values on
Lions as a threat to human life	How many people did that same lion killed. it's life lions kill people and people kill lions.get over it
	These lions are, plenty in the Hwange national park busy eating people.'s domesticated animals in that area get one rename it,Cecil then,n stop mourning abt this dead lion afterall the proceeds frm that tourism business is not, benefitting the locals there

(*continued*)

Table 2. Continued.

Recurrent patterns	Example Facebook posts
	Some few months ago, a lion killed people in South Africa, nothing was done to it. I don't think killing a lion is a violation of any God-given commandment.
	We should be thankful that the people living in the area have one less man Hunter to worry about while they go about their lives.
The politics of greed	*In SA we have a rubbish practiced by white people called sport hunting. One wonders as to how can killing an animal be a sport. Their habit of giving fancy names to foolish acts is really disgusting. Savages!*
	Now I see why Mugabe dislikes these species. Kill all animals there and leave our animals alone.
	Thats the only problem i find in these moroons, they come to Africa to plunder our resources with their stupid dollars
	Too bad the question is do Africa value wild animals nature the answer is not, money first that matters more for black man
Outlier/minority opinions	*This is not just a lion. It was the biggest tourist attraction at Hwange. If you can't respect wildlife you won't respect your fellow man period! Animals think feel and have as much right to the planet as you do!*
	Whatever happened Cecil the lion has gone as thousands of other lions have been massacred. Mr. Walter is angry because of inconveniences or backlashes for him and his family after killing Cecil the lion, but he didn't think of Cecil's family!
	Cecil was not just an ordinary animal he was the most adorable lion possibly in the world.
	Without hunters there would be no game left in Africa. Hunters are the reasen the Sabel is back fron the indaingerd list ext ext. Catle use to be wild man made them tame for food.

The dominant pattern was resentment towards what was viewed as the neo-colonial character of trophy hunting, in the way it privileges Western elites in accessing Africa's wildlife resources. However, the Western public's passionate criticism of violence against animals (especially in the case of Cecilgate) was viewed as overblown and as evidence of their (Westerners') higher regard for animals than for African people. Thus, trophy hunting was not objectionable from an animal rights perspective, but as a consequence of its complex historical and postcolonial associations. It is notable too that in these narratives that the focus was neither on the animals that are shot by hunters, nor on the supposed benefits of trophy hunting for conservation. In particular, the consequentialist argument [the assertion that trophy hunting offers the only viable funding model for conservation in Africa (Nelson et al., 2016)] was conspicuously absent from the posts. Rather, among African users, trophy hunting was judged on its political and historical associations, that is, on the human actors, and their bases of power. In addition, criticism was directed at African politicians for allowing an exploitative form of consumptive tourism to occur, in order to satisfy their greed for money.

In the next sections the three key themes which emerged from the categories are discussed, namely (i) trophy hunting as neo-colonialist; (ii) animals valued more than humans; and (iii) the politics of greed. It should be noted that the Facebook quotes are not edited for typographical and grammatical errors, to preserve their raw authenticity.

Trophy hunting as neo-colonialist

Trophy hunting was viewed by the majority of African participants (70%) as neo-colonialist in the way it appears to exclusively give rich Westerners power over the majestic megafauna of Africa, through an activity from which Africans are economically excluded—[Walter Palmer paid over USD50,000 in fees for the Cecil hunt, for example (Pearce, 2018)]. The colonial histories of Africa and the postcolonial imbalances of power and wealth thus informed the way in which Africans constructed meanings about trophy hunting as a form of touristic consumption. One poster, expressing disapproval for Westerners' extraction of Africa's wildlife resources, wrote:

> They imported all the African exotic animals to their countries and have kept them in the Zoos for their locals to see instead of traveling to Africa.in other words they want to kill the tourism industry in Africa.these ppl colonized us and continue to harass our lives.

Another poster added, “They’re mining our minerals and exporting it to Europe, America and etc., now killing our untamed animals, what is our leaders doing?”, stressing the (perceived) failure of African leaders. Hunters were thus framed as exploitative and callous. In another post, trophy hunting was juxtaposed with what the poster characterised as other forms of Western domination and exploitation:

> When Somalis put out in small boats, and hold Western freight ships for ransom, the Somalis are labeled "pirates". But, how do we label foreign fishermen who poach sea life off the Horn of Africa, and dump toxic chemicals in the African waters. Trophy hunting is nothing new, just the most recent form of Western Colonialism

Under the new forms of Western colonialism which the poster alludes to, or neo-colonialism, developed countries are seen to exercise subtle forms of domination, exploitation and control over former colonies (Akama et al., 2011; Antwi-Boateng, 2017).

The exploitation discourse was also recurrent in the critique of the structural design of the hunting industry, which determines who profits financially from the activity. Here, posters criticised the purchasing of hunting licenses overseas: “Why paying in Las Vagas, USA. Africa needs money from its resources to develop. Why not paying here in Africa? Thats colonial mentality.” Another poster echoed the sentiment: “Hunting in Africa while licenses are bought in Las Vegas? What the f**k is going on? If u want to kill my lion come get the license from me here in Africa!!!!”.

The objections raised resonate with the concept of “distributive (in)justice” (Lamont, 2017)—a concern over whether monetary gains from the tourism system wholly flow back to Africa and to local communities there, who are considered the true owners and custodians of the wildlife resources (see also Dickman, Packer, Johnson, & Macdonald, 2018; Rylance & Spenceley, 2017). Indeed, trophy hunting has always raised questions around how benefits are allocated (Lindsey et al., 2006; Lindsey et al., 2007). Where distributive justice is not delivered, tourism is complicit in the articulation and perpetuation of unequal territorial and cultural relations; it becomes, as a result, a locus of “contradictions, juxtapositions and intersections”, as D’Hauteserre (2004, p. 238) puts it. The configuration of the tourism industry in the trophy hunting scenario where some of the revenues accrue to overseas agents (for example in the form of booking/license commissions) re-enacts economic imbalances of the colonial past (Garland, 2008).

Other posters criticised the abandonment of indigenous African models of wildlife management, founded on Ubuntu philosophy, in favour of Western approaches. Within this critique, Western models were branded as responsible for the conservation crises that Africa faces:

> In the not too distant past African people had a healthy respect for the natural world and were more careful about hunting. Now most African people have had at least 150 years of being told all of the old ways were backward, sub-intelligent, and proof of our lack of civilisation. Having been forced off the land and out of the old systems of land use and frailties—old understandings of society and the animal world so many are disconnected to those old ways, no longer valuing animals and helping careless people hunt them all to extinction.

The poster here echoes Chibvongodze’s (2016) assertion that with the advent of colonialism and the effects of globalisation under the neo-liberal project, the intimate relationship Africans had with nature has been undermined. Chibvongodze argues that in the pre-colonial era, guided by Ubuntu, African societies strove to co-exist and co-relate with animals and the environment in a respectful, and non-exploitative manner. Nature was not a commodity to be consumed for a price, nor was conservation dependent on the tourist dollar. The poster however goes further and acknowledges the shortcomings of the indigenous approaches: “The past of course wan’t perfect but the old ideals of Kingship, man and nature were way better than the broken confused understandings people have been left with", while still dismissing the West's quest for "'civilising us' so we take money from anyone no matter how uncaring for killing just about any animal anywhere!". Nonetheless, the yearning for the pre-colonial past yet again demonstrates a dissatisfaction with a system that legitimises trophy hunting as necessary for conservation, perpetuating in the process the domination of the "rich white man".

Animals valued more than humans

A significant number of African posters (about 80%) also criticised the Western community, particularly in reference to Cecilgate (Lindsey et al., 2016), for championing the animal rights cause, while, in their view (the posters'), completely overlooking the suffering of African people. In short, the participants felt that Westerners cared more for animals than for African people, which, to them, undermined the West's moral authority—the West, for all its noble adulation and veneration of wildlife, seemed to care very little about the people who live in proximity to that wildlife:

> kids die everyday here in africa because of hunger but all you care about more are these "majestic" animals, i hear so much noise about these animals but hardly ever hear people protesting against poverty, what is wrong with this planet
>
> whats is so important about a 13yr old lion we got kids dying or pple starving and having no jobs and excess to proper healthcare but all you think of is a lion …

Notably, these criticisms expressed frustration with what was perceived as the misanthropic views of Western publics, which show undue moral concern for nonhuman animals while failing to demonstrate proper moral concern for human beings. One poster dismisses the animal rights sentiment of the Western public as un-African: "People of nawadays value animals more than human beings and that's too bad … We are imitating the western world and that is not encouraging … ". We observe here an instance where, as Akama et al. (2011) notes, neo- and post-colonisations result in hegemonic struggles as locals negotiate, resist and reject external influences and values.

Similarly, another poster commented, "Concentrate more on pple' well being than these animals. Cecil for that matter. Animals has become more important than pple? Hallelujah". It is interesting to note here also how the advent of colonialism has resulted in a sharper distinction between humans and nature, whereas traditionally, human and wildlife domains were intricately interconnected. The poster also took issue with the Westerners' response especially because the lion was named "Cecil", a name which, for many Africans, brings to mind the British imperialist Cecil Rhodes. This association was raised by many other posters, for example:

> I was curious about that too. Cecil Rhodes and Rhodesia came to my mind. Why would any Africa nation, and in particular Zimbabwe, name its favorite lion after its murderering oppressor Cecil Rhodes? Could the name Cecil be the reason behind this Lion being sacrificed. Maybe in their minds they were killing Cecil Rhodes and any reminders of Cecil Rhodes.
>
> That's wat i hv been wondering my Zim neighbours, takin pride in naming our heritage after the oppressors, why wasn't the lion named Farai?

Another poster cheekily observed that both Cecil Rhodes and Cecil-the-lion were linked to Oxford University (referring to Cecil the lion being studied by WildCRU, the Conservation Research Unit at Oxford University): "I'm relieved that Cecil the lion died. He was named after Cecil John … It's a mystery how both of them were linked to Oxford." Of course, the Oxford link is only coincidental, but the colonial associations are, in the mind of the poster, deliberate.

The posters also queried the "icon" status accorded to Cecil by many in the West in the aftermath of the lion's shooting, citing the many incidences of man-eating by lions. Again, by not focusing on the loss of African lives to wild animals, Westerners had failed to match their compassion for animals with compassion for African people:

> And when did an animal become an icon? I think we have to come out of this so called crazy love for animals. By the time we start to care for animal as if its human then something is wrong. Some few months ago, a lion killed people in South Africa, nothing was done to it. I don't think killing a lion is a violation of any God-given commandment.

Another poster added: "We should be thankful that the people living in the area have one less man Hunter to worry about while they go about their lives". Although the issue of human-wildlife conflict has been thoroughly investigated in a number of studies (see, for example, Graham, Douglas-Hamilton, Adams, & Lee, 2009; Macdonald et al., 2017), from the posters' perspective, Westerners fail to appreciate the social cost of co-existing with wildlife for African communities. Understanding this reality helps illuminate, at least in part, why attitudes towards wildlife are vastly different between Westerners and locals (for an expanded discussion on this point, see Mkono, 2018).

The politics of greed

Criticism was not only directed at Westerners, but also at African politicians and leaders who were characterised as greedy and lacking a moral compass. Posters (60%) felt that white elites were able to take advantage of the economic desperation of Africa and its money-hungry politicians: "Corruption! The true cancer of Africa. No vision with a lack of leadership produces such results. Who's hands did this idiot grease?".

Another poster viewed African countries as faced with the difficult dilemma of choosing between the preservation of nature, or monetary gain, concluding that the latter prevails:

> The dichotomy of poor African states that rely on ecotourism is precisely this … what's more important, the preservation of nature (lions, rhinos, elephants) or self preservation? Clearly the latter seems to tip the scale unfortunately its at the cost of nature … .the lure of the elusive dollar is simply too great to ignore. Its a real sad state of affairs.

Trophy hunting was therefore the product of complicity between white men and greedy African leaders: "These are shameless white men, who believe that since they can give our stupid greedy leaders a few dollars to buy sausages for their kids, that they can boss around Africa doing as they wish. And that we the idiots will run to chew on the carcases with tears of appreciation in our eyes!". Greed violates the principles of Ubuntu, which places the needs of the community above the needs of the individual (Chibvongodze, 2016; Nussbaum, 2003). It is un-African. Again, the issue of distributive justice is brought to the fore, as posters felt that only the political elites and their families were enjoying the economic proceeds from the trophy hunting industry. For some countries, it is not clear from existing research what proportion of trophy hunting fees are actually channelled to conservation or to benefit local communities in Africa. Under Zimbabwe's Communal Areas Management Programme for Indigenous Resources (CAMPFIRE), communities should get some 80% of wildlife revenues and should be able to use them as they desire (Lindsey et al., 2007). Frost and Bond (2008) report, for example, that between 1989 and 2001, CAMPFIRE generated more than US$20 million of transfers to the participating communities, 89% of which came from trophy hunting. However, as Lindsey et al. (2007) note, corruption is endemic in all levels of the trophy hunting industry including politicians who are bribed to favour certain operators when granting hunting concessions.

The strong associations with race ("shameless white men") are again telling of the role of colonial histories and the neo-colonial present in the way Africans perceive trophy hunting. Trophy hunting therefore is shown to be divisive in a manner which is particularly unhelpful for achieving racial harmony in postcolonies. Whereas tourism recreation has been lauded in other contexts as fostering liminal experiences within which people of different backgrounds are able to transcend their differences, this analysis of trophy hunting by Western tourists at least suggests that it engenders an atmosphere of strife and even racial hatred.

Outlier views

For completeness, it is important to note that there were a number of other outlier or minority views which largely echoed the criticisms raised by the Western public. These included questioning the machoistic motivations of hunters: “What kind of a human being feels that they are real man after trophy hunting and killing an animal that cant even fight back”. Several other posters also expressed indignation over Walter Palmer’s acquittal by the Zimbabwean government: “A statue!!!!!??? Instead bringing Walter James Palmer to prison … To save other lions like Jericho. You are building Cecil a statue … instead of giving him justice … ”. A few posters stressed the intrinsic value of animals, and their revenue generating capacity: “This is not just a lion … If you can’t respect wildlife you won’t respect your fellow man period! Animals think feel and have as much right to the planet as you do!”, and “It’s so embarrassing how Zimbabweans don’t know the importance of wildlife, hear people say ’what’s so special about the lion we want bread and butter issues’ … Cecil was not just an ordinary animal he was the most adorable lion possibly in the world. … It’s a big blow to tourism which in turn a blow to that bread and butter you so desperately need”. Space limitations do not allow for a detailed analysis of these outlier views. They are however discussed in other recent studies (Lindsey et al., 2016; Macdonald, Jacobsen, et al., 2016; Nelson et al., 2016).

Discussion

The moral quandaries surrounding trophy hunting in recent years have typically been debated in reference to the violence towards animals, and in terms of the links between the activity and wildlife conservation (Baker, 1997; Coltman et al., 2003; Lindsey et al., 2006; Macdonald, Jacobsen, et al., 2016; Nelson et al., 2016; Packer et al., 2011; Vora, 2018). However, in the findings presented, trophy hunting is understood and critiqued through a very different lens—the colonial histories of Africa and the associated neo-colonial distribution of power, money and access to resources in the present day. In addition, the moral authority of the West’s recent anti-hunting campaign is also undermined on account of its (perceived) lack of compassion for African people. As such, among Africans, trophy hunting was a domain of political and cultural associations that transcend the conservation debate. Thus trophy hunting was interrogated as a racially divisive activity that, rather than helping to heal the wounds of the colonial past, aggravates them. This is particularly apparent in the view of the Cecil movement as proof that Westerners cared more for African animals than for African people. It is also evident in the interpretation of the name Cecil as associated with the imperialist Cecil Rhodes. To progress towards healing, as Garland (2008) argues, it is necessary to confront the colonial nature of the conservation model in Africa. Furthermore, it is important to recognise that sustainable conservation in Africa hinges on the long-term support of African publics at all levels.

It has however long been established that, through its approach to developing country destinations, tourism often perpetuates colonial forms of interaction (D’Hauteserre, 2004). Tourism in Africa reinforces and is indeed embedded in postcolonial relationships (Hall & Tucker, 2004). Akama et al. (2011) argues that forms of tourism that evolved during the colonial era interpellate into tourism structures in the postcolonial to perpetuate economic, political, and socio-cultural domination, stirring in the process local struggle and resistance.

For the African participants, trophy hunting re-enacts the past when settlers in the colonial era could hunt recreationally in national parks, while subsistence hunting by indigenous people was banned and officially classified as poaching (Akama et al., 2011). In postcolonial times, what constitutes hunting versus poaching is also a racially drawn demarcation, as the "pastime" of trophy hunting can only be afforded almost exclusively by rich white foreigners. Garland (2008) suggests in this connection that it is important for Western biologists and conservationists to educate themselves about the complexities of African culture and history in ways they have not previously done. They must accept that their social responsibilities extend beyond a few outreach programs in the rural villages adjacent to protected areas in Africa, and assume responsibility for the role they play in shaping the world's imagination of both African animals and African human beings. It should also be noted, however, regarding the economic exclusion of locals from trophy hunting, that the same can be said about other forms of tourism which require significant discretionary income.

It is also clear that African leaders need to involve their citizens in crafting and defending their wildlife conservation policies. The image of the industry would benefit from greater transparency and accountability of all actors in relation to their use of trophy hunting revenues. Failing that, trophy hunting would continue to be associated with greed and immorality. In the long run, it is imperative that African governments strive to meaningfully empower communities to fully own, manage, and profit from wildlife resources.

Furthermore, although Ubuntu's role in traditional African society has largely been rendered redundant under the Western conservation models, there remains an opportunity for more culturally inclusive models. As Akama et al. (2011) argue, current Western models are problematic because they are grounded in a colonial legacy that serves to exclude indigenous approaches. Conservation should be more firmly anchored in the service of African communities, and in their traditional ways of being. By evoking the values of Ubuntu, conservation in Africa might have a greater chance of success by creating a stronger sense of cultural sensitivity and inclusion. But, of course, whatever the merits of Ubuntu are, it would be unrealistic and naive to expect African countries to revert *wholly* to traditional management approaches. Some sort of hybrid model would be more feasible and pragmatic.

To bridge the gaps between Western and African views on wildlife conservation, Garland (2008) suggests that conservation education campaigns run by Western NGOs and zoological parks need to broaden their message, contextualizing it within discussions of the histories and legal statuses of the habitats in question, and of the issues of poverty and rural development that shape these habitats' positions within the surrounding African societies. Garland (2008) further urges that influential representational channels such as the National Geographic Society (NGS), the Wildlife Conservation Society (WCS), the African Wildlife Foundation (AWF), the World Wide Fund for Nature (WWF), and the Frankfurt Zoological Society (FZS) must emphasise the ownership of wildlife resources by African nations and the crucial dependence of conservation efforts on the goodwill and labour of African people.

Conclusion

The article reveals strong links between the perception of trophy hunting and the colonial histories of Africa. Trophy hunting was viewed by African participants as a political and physical enclave in which the precious wildlife resources of Africa were plundered by rich Westerners, with the complicity of greedy African leaders. Far from tourism being a facilitator of intercultural understanding and peace, it appears in this instance to reproduce images and wounds of a colonial past.

The findings point to the need for a more reflexive Western thought on conservation which takes into account the less audible voices and of alternative cultural lenses. As Garland (2008) urges, it is important to reconfigure conservationist discourses so that they become an vector for educating Western publics about the challenges that African people face, and about the legacies of colonialism and marginalization on the continent, not just for African landscapes and game populations, but for African people as well. Thus, it is important to continue to interrogate the ways in which tourism may deliberately and also unwittingly serve to neo-colonise. In that respect, tourism studies would benefit from more applications of neo-colonialist frames of analysis which reassert the ongoing nature of colonial power imbalances and cultural domination.

By investigating wildlife tourism practices using alternative lenses such as Ubuntu, a more diverse body of knowledge would emerge. Ubuntu in particular has been described as the gift that Africa will give to the world (Bolden, & Kirk, 2009; Forster, 2010), by making whole what is socially, culturally, and spiritually kept separate; by bridging rather than recreating Other boundaries of division (Andreasson, 2010; Seedat, Baw, & Ratele, 2010). The contribution that Ubuntu can make to sustainable tourism lies in its premise that nature is not just a resource to be exploited for human advancement. The challenge then is to find ways of integrating it with existing frameworks, cognisant of the evolving nature of modern African societies operating in an outward-looking, global geopolitical environment.

However, while it is useful to examine alternative cultural lenses for human-nature relationships, it is important to remain conscious of the nuances in worldviews among different African societies and individuals. Only by appreciating the vastly different lived experiences of African peoples in relation to wildlife will the West engage meaningfully with conservation in Africa. It would also be interesting to investigate, in future research, whether non-consumptive forms of tourism evoke the same reactions as those recorded here.

From a sustainability perspective, it is crucial to continue to interrogate consumptive forms of tourism such as trophy hunting, not only in terms of their economic value, but also in relation to their moral integrity, and from the perspective of local communities. In that endeavour, Africa's leaders are likely to have more support if they find meaningful ways of engaging their citizens in wildlife policy decisions.

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References

Akama, J. S. (1996). Western environmental values and nature-based tourism in Kenya. *Tourism Management*, *17*(8), 567–574. doi:10.1016/S0261-5177(96)00077-5

Akama, J. S., Maingi, S., & Camargo, B. A. (2011). Wildlife conservation, safari tourism and the role of tourism certification in Kenya: A postcolonial critique. *Tourism Recreation Research*, *36*(3), 281–291. doi:10.1080/02508281.2011.11081673

Andreasson, S. (2010). Confronting the settler legacy: Indigenisation and transformation in South Africa and Zimbabwe. *Political Geography*, *29*, 24–433.

Angula, H. N., Stuart-Hill, G., Ward, D., Matongo, G., Diggle, R. W., & Naidoo, R. (2018). Local perceptions of trophy hunting on communal lands in Namibia. *Biological Conservation*, *218*, 26–31. doi:10.1016/j.biocon.2017.11.033

Antwi-Boateng, O. (2017). New world order neo-colonialism: A contextual comparison of contemporary China and European colonization in Africa. *Journal of Pan African Studies*, *10*(2), 177-195.

Baker, J. E. (1997). Trophy hunting as a sustainable use of wildlife resources in southern and eastern Africa. *Journal of Sustainable Tourism*, *5*(4), 306–321. doi:10.1080/09669589708667294

Batavia, C., Nelson, M. P., Darimont, C. T., Paquet, P. C., Ripple, W. J., & Wallach, A. D. (2018). The elephant (head) in the room: A critical look at trophy hunting. *Conservation Letters*, *12*, e12565. doi:10.1111/conl.12565

Bauer, H., Henschel, P., Packer, C., Sillero-Zubiri, C., Chardonnet, B., Sogbohossou, E. A., … Macdonald, D. W. (2017). Lion trophy hunting in West Africa: A response to Bouché et al. *Plos One*, *12*(3), e0173691. doi:10.1371/journal.pone.0173691

Boeije, H. (2002). A purposeful approach to the constant comparative method in the analysis of qualitative interviews. *Quality and Quantity*, *36*(4), 391–409.

Bolden, R., & Kirk, P. (2009). African leadership. *International Journal of Cross Cultural Management*, *9*(1), 69–86. doi:10.1177/1470595808101156

Bouché, P., Crosmary, W., Kafando, P., Doamba, B., Kidjo, F. C., Vermeulen, C., & Chardonnet, P. (2016). Embargo on lion hunting trophies from West Africa: An effective measure or a threat to lion conservation? *PLoS One*, *11*(5), e0155763doi:10.1371/journal.pone.0155763

Charmaz, K. (2014). *Constructing grounded theory*. 2nd ed. Thousand Oaks, CA: Sage.

Chibvongodze, D. T. (2016). Ubuntu is not only about the human! An analysis of the Role of African philosophy and ethics in environment management. *Journal of Human Ecology*, *53*(2), 157–166. doi:10.1080/09709274.2016.11906968

Chimakonam, J. O. (2016). The end of Ubuntu or its beginning in Matolino-Kwindingwi-Metz debate: An exercise in conversational philosophy. *South African Journal of Philosophy*, *35*(2), 224–234. doi:10.1080/02580136.2016.1174921

Coltman, D. W., O'Donoghue, P., Jorgenson, J. T., Hogg, J. T., Strobeck, C., & Festa-Bianchet, M. (2003). Undesirable evolutionary consequences of trophy hunting. Nature, *426*(6967), 655–658. doi:10.1038/nature02177

Corbin, J. M., & Strauss, A. (1990). Grounded theory research: Procedures, canons, and evaluative criteria. *Qualitative Sociology*, *13*(1), 3–21. doi:10.1007/BF00988593

Creel, S., M'soka, J., Dröge, E., Rosenblatt, E., Becker, M. S., Matandiko, W., & Simpamba, T. (2016). Assessing the sustainability of African lion trophy hunting, with recommendations for policy. *Ecological Applications*, *26*(7), 2347–2357. doi:10.1002/eap.1377

Creswell, J. W., & Miller, D. L. (2000). Determining validityin qualitative inquiry. *Theory into Practice*, *39*(3), 124–130.

Crosmary, W. G., Côté, S., & Fritz, H. (2015). The assessment of the role of trophy hunting in wildlife conservation. *Animal Conservation*, *18*(2), 136–137. doi:10.1111/acv.12205

D'Hauteserre, A. M. (2004). Postcolonialism, colonialism, and tourism. In A. Lew, M. Hall, and A. Williams, (Eds) *A companion to tourism* (pp. 235-245). Maiden, Mass: Blackwell

Di Minin, E., Leader-Williams, N., & Bradshaw, C. J. (2016). Banning trophy hunting will exacerbate biodiversity loss. *Trends in Ecology & Evolution*, *31*(2), 99–102. doi:10.1016/j.tree.2015.12.006

Dickman, A. J., Johnson, P. J., 't Sas-Rolfes, M., Di Minin, E., Loveridge, A. J., Good, C., … Macdonald, D. W. (2019). Is there an elephant in the room? A response to Batavia et al. *Conservation Letters*, *12*(1), e12603. doi:10.1111/conl.12603

Dickman, A., Packer, C., Johnson, P. J., & Macdonald, D. W. (2018). A sideways look at conservation and consistency in tourism policy. *Conservation Biology: The Journal of the Society for Conservation Biology*, *32*(3), 744–746. doi:10.1111/cobi.13066

Forster, D. A. (2010). African relational ontology, individual identity, and Christian theology. *Theology*, *113*(874), 243–253. doi:10.1177/0040571X1011300402

Frost, P. G., & Bond, I. (2008). The CAMPFIRE programme in Zimbabwe: payments for wildlife services. *Ecological Economics*, *65*(4), 776–787. doi:10.1016/j.ecolecon.2007.09.018

Galaty, J. G. (2014). Animal spirits and mimetic affinities: The semiotics of intimacy in African human/animal identities. *Critique of Anthropology*, *34*(1), 30–47. doi:10.1177/0308275X13510189

Garland, E. (2008). The elephant in the room: Confronting the colonial character of wildlife conservation in Africa. *African Studies Review*, *51*(03), 51–74. doi:10.1353/arw.0.0095

Glaser, B. G., & Strauss, A. L. (2017). *Discovery of grounded theory: Strategies for qualitative research*. New York: Routledge.

Graham, M. D., Douglas-Hamilton, I., Adams, W. M., & Lee, P. C. (2009). The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation*, *12*(5), 445–455. doi:10.1111/j.1469-1795.2009.00272.x

Hall, M. C., & Tucker, H. (Eds.). (2004). *Tourism and postcolonialism: Contested discourses, identities and representations*. London: Routledge.

Humavindu, M. N., & Barnes, J. I. (2003). Trophy hunting in the Namibian economy: an assessment. *South African Journal of Wildlife Research*, *33*(2), 65–70.

Kalof, L., & Fitzgerald, A. (2003). Reading the trophy: Exploring the display of dead animals in hunting magazines. *Visual Studies*, *18*(2), 112–122. doi:10.1080/14725860310001631985

Koenane, M. L., & Olatunji, C.-M. P. (2017). Is it the end or just the beginning of Ubuntu? Response to Matolino and Kwindingwi in view of Metz's rebuttal. *South African Journal of Philosophy*, *36*(2), 263–277. doi:10.1080/02580136.2016.1225188

Kolb, S. M. (2012). Grounded theory and the constant comparative method: Valid research strategies for educators. *Journal of Emerging Trends in Educational Research and Policy Studies*, *3*(1), 83.

Lamont, J. (ed.) (2017). *Distributive justice*. London: Routledge.

Lindsey, P. A. (2008). Trophy hunting in Sub Saharan Africa, Economic scale and conservation significance. *Best Practices in Sustainable Hunting*, *1*, 41–47.

Lindsey, P. A., Alexander, R., Frank, L., Mathieson, A., & Romanach, S. (2006). Potential of trophy hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable. *Animal Conservation*, *9*(3), 283–291. doi:10.1111/j.1469-1795.2006.00034.x

Lindsey, P. A., Balme, G. A., Funston, P. J., Henschel, P. H., & Hunter, L. T. (2016). Life after Cecil: Channelling global outrage into funding for conservation in Africa. *Conservation Letters*, *9*(4), 296–301. doi:10.1111/conl.12224

Lindsey, P. A., Balme, G. A., Funston, P., Henschel, P., Hunter, L., Madzikanda, H., … Nyirenda, V. (2013). The trophy hunting of African lions: Scale, current management practices and factors undermining sustainability. *PLoS One*, *8*(9), e73808.

Lindsey, P. A., Frank, L., Alexander, R., Mathieson, A., & Romanach, S. (2007). Trophy hunting and conservation in Africa: Problems and one potential solution. *Conservation Biology*, *21*(3), 880–883. doi:10.1111/j.1523-1739.2006.00594.x

Lindsey, P., Roulet, P., & Romanach, S. (2007). Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation*, *134*(4), 455–469. doi:10.1016/j.biocon.2006.09.005

Lu, W., & Stepchenkova, S. (2014). User-generated content as a research mode in tourism and hospitality applications: Topics, methods, and software. *Journal of Hospitality Marketing & Management*, *24*(2), 119–154. doi:10.1080/19368623.2014.907758

Lutz, D. W. (2009). African Ubuntu philosophy and global management. *Journal of Business Ethics*, *84*(S3), 313. doi:10.1007/s10551-009-0204-z

Macdonald, D. W., Jacobsen, K. S., Burnham, D., Johnson, P. J., & Loveridge, A. J. (2016). Cecil: A moment or a movement? Analysis of media coverage of the death of a Lion, Panthera leo. *Animals*, *6*(5), 26.

Macdonald, D. W., Johnson, P. J., Loveridge, A. J., Burnham, D., & Dickman, A. J. (2016). Conservation or the moral high ground: Siding with Bentham or Kant. *Conservation Letters*, *9*(4), 307–308. doi:10.1111/conl.12254

Macdonald, D. W., Loveridge, A. J., Dickman, A., Johnson, P. J., Jacobsen, K. S., & Du Preez, B. (2017). Lions, trophy hunting and beyond: Knowledge gaps and why they matter. *Mammal Review*, *47*(4), 247–253. doi:10.1111/mam.12096

MacKenzie, J. M. (1997). *The empire of nature: Hunting, conservation and British imperialism*. Manchester: Manchester University Press.

Matolino, B., & Kwindingwi, W. (2013). The end of Ubuntu. *South African Journal of Philosophy*, *32*(2), 197–205. doi:10.1080/02580136.2013.817637

Mbaiwa, J. E. (2018). Effects of the safari hunting tourism ban on rural livelihoods and wildlife conservation in Northern Botswana. *South African Geographical Journal*, *100*(1), 41–61. doi:10.1080/03736245.2017.1299639

Metz, T. (2014). Just the beginning for Ubuntu: Reply to Matolino and Kwindingwi. *South African Journal of Philosophy*, *33*(1), 65–72. doi:10.1080/02580136.2014.892680

Mkono, M. (2018). The age of digital activism in tourism: evaluating the legacy and limitations of the Cecil anti-trophy hunting movement. *Journal of Sustainable Tourism*, *26*(9), 1608–1624. doi:10.1080/09669582.2018.1489399

Mkono, M., & Holder, A. (2019). The future of animals in tourism recreation: Social media as spaces of collective moral reflexivity. *Tourism Management Perspectives*, *29*, 1–8. doi:10.1016/j.tmp.2018.10.002

Mullin, M. H. (1999). Mirrors and windows: sociocultural studies of human-animal relationships. *Annual Review of Anthropology*, *28*(1), 201–224. doi:10.1146/annurev.anthro.28.1.201

Murove, M. F. (2004). An African commitment to ecological conservation: The Shona concepts of Ukama and Ubuntu. *Mankind Quarterly*, *45*(2), 195–215.

Murphy, R. (2018). *Rationality and nature: A sociological inquiry into a changing relationship*. London: Routledge.

Mwipikeni, P. (2018). Ubuntu and the modern society. *SouthAfrican Journal of Philosophy*, *37* , 322–334.

Nelson, M. P., Bruskotter, J. T., Vucetich, J. A., & Chapron, G. (2016). Emotions and the ethics of consequence in conservation decisions: Lessons from Cecil the Lion. *Conservation Letters*, *9*(4), 302–306. doi:10.1111/conl.12232

Nordbø, I., Turdumambetov, B., & Gulcan, B. (2018). Local opinions on trophy hunting in Kyrgyzstan. *Journal of Sustainable Tourism*, *26*(1), 68–84. doi:10.1080/09669582.2017.1319843

Nussbaum, B. (2003). African culture and Ubuntu. *Perspectives*, *17*(1), 1–12.

Outwater, A., Abrahams, N., & Campbell, J. C. (2005). Women in South Africa. *Journal of Black Studies*, *35*(4), 135–154. doi:10.1177/0021934704265915

Packer, C., Brink, H., Kissui, B., Maliti, H., Kushnir, H., & Caro, T. (2011). Effects of trophy hunting on lion and leopard populations in Tanzania. *Conservation Biology*, *25*(1), 142–153. doi:10.1111/j.1523-1739.2010.01576.x

Pearce, F. (2018). In for the kill. *New Scientist*, *237*(3160), 42–43. doi:10.1016/S0262-4079(18)30089-7

Plessis, C. D. (2001). Sustainability and sustainable construction: the African context. *Building Research & Information*, *29*(5), 374–380. doi:10.1080/09613210110063809

Rylance, A., & Spenceley, A. (2017). Reducing economic leakages from tourism: A value chain assessment of the tourism industry in Kasane, Botswana. *Development Southern Africa*, *34*(3), 295–313. doi:10.1080/0376835X.2017.1308855

Seedat, M., Baw, U., & Ratele, K. (2010). Why the wretched kill in democratic South Africa. *Social Change*, *40*(1), 15–27. doi:10.1177/004908570904000103

Steiner, G. (2010). *Anthropocentrism and its discontents: The moral status of animals in the history of western philosophy*. Pittsburgh: University of Pittsburgh Press.

Vora, A. (2018). Legal and ethical implications of using trophy hunting as a conservation tool. *Journal of International Wildlife Law & Policy*, *21*(1), 46–50. doi:10.1080/13880292.2017.1419657

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Communication

Elephants, mobility and captivity: what can these mighty and majestic animals teach us about joint health and osteoarthritis?

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Simple Summary: African and Asian elephants are the largest animals that live on land. In order to find fresh food and water they need to be highly mobile and active. Despite their huge size, African elephants are highly mobile and can walk up to 28 km per day, although they usually walk 25 km on a daily basis. Asian elephants walk up to 21 km each day and they can be active for up to 20 hours every day through walking, grazing, swimming and socializing. Mobility helps elephants maintain their joints and muscles. However, many captive-held zoo elephants are kept in small enclosures with hard surfaces (i.e. concrete, tarmac and hard backed dirt), often in very small spaces. Therefore, captive-held elephants cannot exercise freely and as much as wild-living elephants. This makes them more prone to gaining weight, getting obese, becoming lame and developing bone and joint diseases such as arthritis, especially osteoarthritis (OA). Health and welfare problems in captive-held elephant may be caused by the lack of mobility. This communication focuses on the possible link between mobility, captivity and the development of OA in elephants.

Abstract: The African bush and forest elephants, *Loxodonta Africana* and *Loxodonta cyclotis*, and the Asian elephant, *Elephas maximus*, are the largest land-dwelling animals. Elephants need to be highly mobile and active in order to find fresh food and water, and in the case of males, to locate females in estrus for breeding. Asian elephants walk up to 21 km each day and African elephants can walk up to 28 km per day. This high level of mobility in the wild is also important for maintaining an optimum musculoskeletal health. However, most zoo elephants live in restricted spaces and cold climates that require extended periods of indoor confinement are therefore unable to be as physically active. Zoo enclosures for elephants are relatively small with hard surfaces (i.e. concrete, tarmac and hard packed dirt), so they cannot exercise and are forced to stand on unnaturally hard surfaces continually. Physical inactivity in captivity makes them more prone to gaining weight and developing bone and joint diseases such as osteomyelitis, joint ankylosis and osteoarthritis (OA). Many health and welfare problems in captive elephants are likely to be caused by the lack of mobility. This perspective article focuses on the possible link between captivity, mobility, physical inactivity and the development of OA in captive elephants.

Keywords: osteoarthritis; African elephant; Asian elephant; captivity; housing; mobility

1. Introduction

Osteoarthritis (OA) is the most common form of arthritis in the world, the leading cause of disability and the primary source of societal cost in older adult humans [1]. According to the World Health Organization (WHO), OA affects millions of people worldwide [1]. Recent studies suggest that OA affects 7% of the global population, which is more than 500 million people worldwide, with women disproportionately affected by the condition [2], especially after menopause [3–5]. Although OA is primarily related to aging, it is, along with many other forms of chronic disease, also associated with a wide variety of modifiable and non-modifiable risk factors that include: overweight and obesity [6,7], sedentary behavior [8] and lack of physical exercise [9]. In addition to the primary risk factors of aging, obesity, gender, and genetics, other inciting risk factors for OA may include previous joint trauma or history of repetitive joint injuries or even the presence of metabolic syndrome and endocrine disease [10]. However, the disease is primarily biomechanical. There are biomechanical [11–13], inflammatory [14–16], metabolic [17] and nutritional [18–20] factors that have been demonstrated to play dominant roles in the initiation and progression of OA.

2. Mobility and the evolution and migration of modern *Homo sapiens*

Mobility was essential for the evolution of Homo sapiens and an essential component of the "Global Human Journey" [21,22]. Humans evolved from an ancestor that was not limited to trees or other elevated habitats. Our human ancestors were highly mobile and agile, which was essential for gathering food and finding new shelter [23]. The ability to move and migrate allowed them to colonize the entire planet and settle on every continent [24]. Now that we have colonized and dominated every corner of the globe we face a new set of challenges. The rising global burden musculoskeletal (MSK) diseases is now threatening one of the key the human qualities that allowed us to become the dominant species: mobility. The recent Global Burden of Disease (GBD) Study estimated the burden disability in 187 countries and 21 regions of the world for the years 1990, 2010 and 2013 of all MSK disorders. OA rheumatoid arthritis (RA), gout, low back pain (LBP), neck pain (NP) and all other MSK disorders combined caused 21.3% of the total years lived with disability (YLDs) globally [25,26]. MSK health is critical for human function, enabling mobility, dexterity and the ability to work and actively participate in all aspects of life [27]. Global MSK health targets should also be set to reflect maintenance of mobility, participation and physical function as key components of functional ability and performance [28].

3. What can we learn about joint health and OA from the African elephant *Loxodonta Africana* and the Asian elephant *Elephas maximus*?

Much of what we know about osteoarthritis comes from epidemiological studies [29–32], especially studies that were conducted in large cohorts such as the Framingham Study [33,34]. Many investigators have designed and conducted clinical trials to examine the effects of physical activity and inactivity on synovial joint health and OA symptoms, focusing on humans as the primary target population [35]. However, there is a great deal that we can learn from large animals. Elephants are the largest land-dwelling mammal. They have evolved a specialized foot morphology to help reduce locomotor pressures while supporting their large body mass [36]. Elephant limbs display unique morphological features which are related mainly to supporting their enormous body weight and the knee joint plays crucially important roles in weight bearing and locomotion [37]. They are not perhaps the largest land dwelling mammals that roamed the Earth; the woolly mammoth (*Mammuthus primigenius*), *Deinotherium* and *Palaeoloxodon namadicus* were the largest known mammals to walk on the planet.

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[1] https://www.who.int/medicines/areas/priority_medicines/Ch6_12Osteo.pdf

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4. Mobility

Elephants and their ancestors were designed to be highly mobile mammals, enabling them to migrate and expand their territory [38]. Wild modern elephants need to be highly mobile to find fresh food and water, and this mobility helps them survive and maintain optimal musculoskeletal health. Despite their massive size, African elephants are highly mobile and can walk up to 28 km per day, which creates exciting opportunities for research on gait and kinematics of locomotion in these animals [39]. Asian elephants walk up to 21 km each day and they can be active for up to 20 hours every day through walking, grazing, swimming and socializing. African elephants need to be mobile and find water source to rehydrate themselves. However, recent research suggests that captive elephants can only walk up to a maximum of 5 km per day [40]. Holdgate et al., who did this work have proposed that distance walked is not related to health or behavioral outcomes including foot health, joint health, body condition, although their studies do not compare captive and wild elephant populations [40].

4. Housing, Husbandry and Management

An important consideration is the overall housing, husbandry and management of captive elephants and the size of environments and enclosures in which they are kept. Captive elephants experience a number of health issues that can contribute to their overall well-being and survival and it known that housing [41]., husbandry [42] and management [43] are important for their welfare. Elephants kept in captivity should be managed by employing the best practices aimed at meeting their welfare needs (i.e. physical, physiological and psychological) to ensure healthy, sustainable populations [44].

This is an under-researched area, especially in relation to the development of lameness and OA in captive elephants. However, most zoo elephants are kept in enclosures with hard surfaces (i.e. concrete, tarmac and hard packed dirt) and small spaces and they cannot exercise as much as wild animals [45]. This raises important questions for the management of these animals, highlighting the crucially important areas of stress, obesity and poor adult survivorship among captive elephants [44,45]. Captivity makes elephants more prone to gaining weight and developing diseases such as osteomyelitis, joint ankylosis and OA.

In elephants age is the primary contributing factor in the pathogenesis of foot pathology [46] and joint diseases such as OA [47]. After age, obesity and adiposity are important risk factors for the development of OA in humans and animals [48–50]. Given that increasing age and obesity are major risk factors for the development of human OA, closer examination of captive animals is likely to contribute to a broader comparative understanding of OA development across a number of mammalian species, including elephants [29,51]. Therefore, captive elephants can teach us a great deal about the link between mobility, captivity and the development of OA associated with sedentary behavior. In fact, it could be argued that the captive elephant is a perfect large animal model for the studying the link between sedentarism, lack of mobility, osteoarthritis and the co-morbidities that are commonly associated with osteoarthritis [52]. For many decades OA was considered to be a wear and tear disease but recent research suggests that OA has important metabolic and inflammatory components [16,17,53,54].

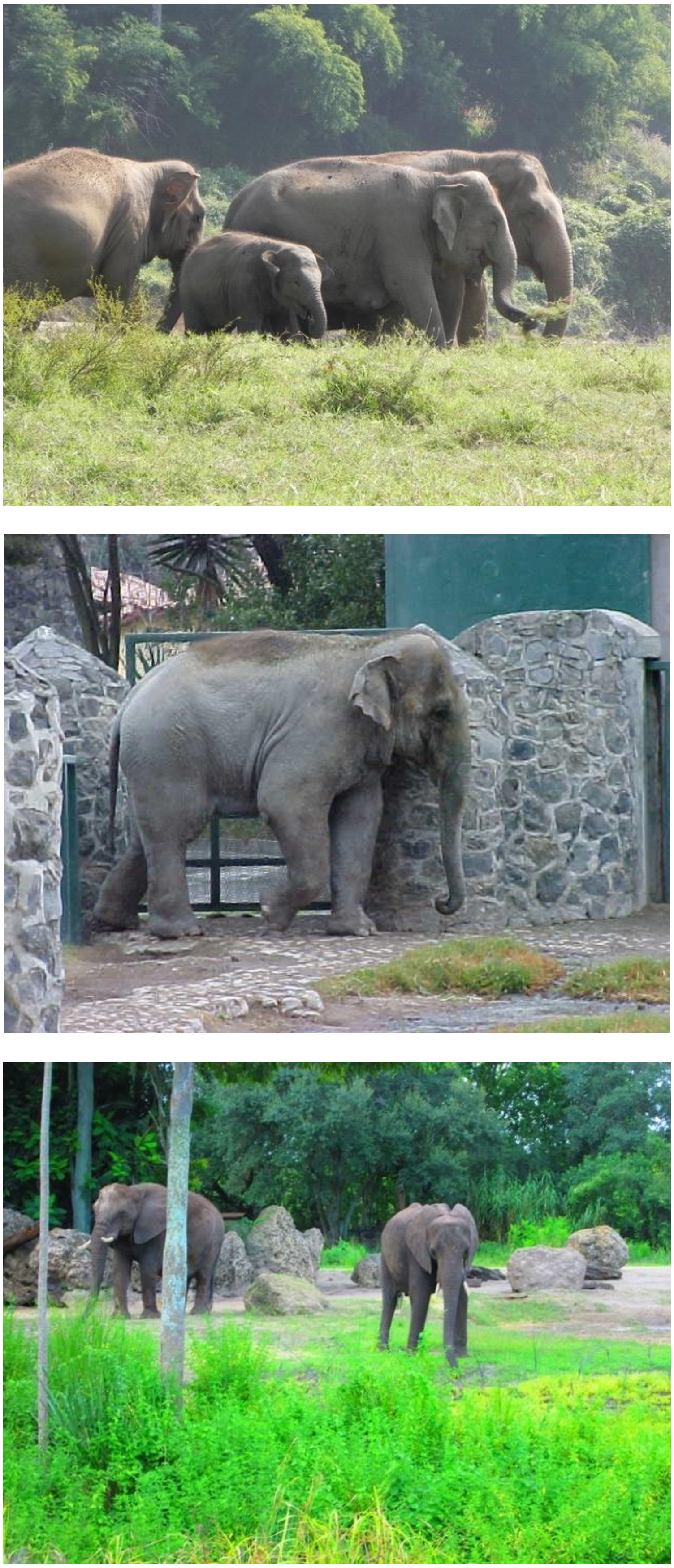

Figure 1. Asian elephants in the wild (top panel) and in captivity with limited space (middle panel). African elephants with more space in a reserve (bottom panel).

In humans obesity and lack of physical activity are major contributors to the development of OA [33]. However, there is no convincing published evidence in humans that walking and running contributes to OA [55][56]. Therefore, it is hardly surprising that captive elephants suffer from lameness and OA as they have to stand for long periods of time on hard surfaces and they are unable to exercise enough and walk the normal distances that they would in the wild every day. They cannot be active in very cold climates and in small zoo enclosures where their freedom and mobility is highly restricted. These are important ethical and welfare considerations that must be taken into account in future captivity and conservation programs.

There are currently no effective drugs and pharmacological treatments for OA [57]. Recent clinical research suggests that weight loss, physical activity and increasing muscle mass and strength are the only effective strategies for reducing pain and enhancing mobility in subjects with OA [58]. The only way to slow down the pain and progression of OA appears to be physical exercise, avoiding obesity and maintaining a healthy weight [59–62]. Non-steroidal anti-inflammatory drugs (NSAIDs) can only treat the symptoms of OA. Studies have examined the pharmacokinetics of orally administered phenylbutazone in African and Asian elephants and the evidence suggests that different treatment regimens should be used for each species, based on size and weight [63]. Similar studies have established the optimal dosage for using ketoprofen [64] and ibuprofen [65] in elephants. However, these NSAIDs can be highly toxic to the gastrointestinal tract in humans and in large animals such as horses and elephants, causing general toxicity, colitis and inhibition of mucosal barrier healing [66].

Cellular senescence is a state of irreversible growth arrest triggered by various stressors [67]. In synovial joints the process of chondrosenescence is an important contributor to OA progression [68–70]. A deeper understanding of the molecular mechanisms underlying the multi-step progression of senescence may lead to the development of new therapeutic strategies for age-related pathologies [71], such as OA. A recent systematic review of the published literature on studies of the senolytic effects of exercise and physical activity on senescent cells under various states in both human and animal models suggests that exercise has senolytic properties [72]. This may explain the beneficial impacts that patients with OA see when they exercise. Therefore, one possible and achievable strategy currently available to slow OA progression in elephants is to allow them to exercise and walk more and to look after their feet by limiting walking on unnaturally hard surfaces. It is vitally important that more exercise should be recommended for captive elephants, and hopefully this paper will contribute to the development of future guidelines and white papers to support the development of better welfare for captive animals. Zoo elephants will need to get as much space as possible (with softer surfaces) to move and exercise freely but dietary supplementation may also be necessary. There is no solid research in this area and most of the evidence is anecdotal and provided by wildlife and zoo veterinarians. Meanwhile, OA researchers are looking for new therapies for this disease in humans and non-human animal models and all the evidence from captive elephants suggests that captivity and reduced physical activity can accelerate the development of OA. Therefore, the physical activity that has been recommended for human patients with OA can also be recommended for elephants, who need it as much as we do.

5. Conclusions

Physical inactivity and sedentary behavior contribute to poor health in humans. Captivity and reduced mobility are also major contributors to poor health in captive animals, including elephants. Wild elephants are highly mobile and require the freedom and space to reach their daily activity goals, often called "lumbering". Elephants in small enclosures in zoos do not get enough exercise compared to their counterparts in the wild. Elephants in Safari parks and sanctuaries may have more freedom to move around but unless they live in reserves and national parks, they do not have enough space and opportunities for "lumbering" or "hurtling" the long distances that they were evolutionary designed for. Captive elephants have a shorter lifespan. Keeping them in captivity may protect them from poaching but the protection afforded to them presents a whole new set of health challenges, including overweight, obesity, lameness and OA. Several years ago the American Zoological Association (AZA) published research proposing that captive Asians live on average 44 years. They also claimed wild Asian elephants live about the same length of time. However, from our experience there is a problem with this claim pertaining to wild elephants. There are no long-term studies of wild Asian elephants to support such a claim. However, there is much information about captive elephants living into their 80's all over Asia. The reason the captive elephants in Asia live much longer than the captive elephants in the Western world is due to climate and management. In Asia, until very recently, captive elephants lived in the jungles and worked in the lumber industry. They did not live on hard surfaces, they were fed a natural diet, they got plenty of exercise and usually were with conspecifics. More recently, as the captive-held elephant in Asia has been brought out of the jungle and into cities for tourist entertainment, their health has suffered, disease is prevalent, and lives are shorter. In conclusion, elephants confined in small spaces without adequate exercise, living on unnaturally hard surfaces suffer from musculoskeletal disease and pain and consequently die early.

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Conflicts of Interest: C.B. is the founder of Elephant Aid International, a charitable organization dedicated to the health and welfare of elephants worldwide. https://elephantaidinternational.org. A.M. is a member of the Integrative Health Team of Elephant Aid International. https://elephantaidinternational.org/about/integrative-health-team/. The authors declare no conflicts. The funders had no role in the decision to publish this paper.

References

1. Hunter, D. J.; Bierma-Zeinstra, S. Osteoarthritis. *Lancet* **2019**, *393*, 1745–1759.
2. Hunter, D. J.; March, L.; Chew, M. Osteoarthritis in 2020 and beyond: a Lancet Commission. *Lancet* **2020**, *396*, 1711–1712.
3. Hanna, F. S.; Wluka, A. E.; Bell, R. J.; Davis, S. R.; Cicuttini, F. M. Osteoarthritis and the postmenopausal woman: Epidemiological, magnetic resonance imaging, and radiological findings. *Semin. Arthritis Rheum.* **2004**, *34*, 631–636.
4. Karsdal, M. A.; Bay-Jensen, A. C.; Henriksen, K.; Christiansen, C. The pathogenesis of osteoarthritis involves bone, cartilage and synovial inflammation: may estrogen be a magic bullet? *Menopause Int* **2012**, *18*, 139–146.
5. Stevenson, J. C. A woman's journey through the reproductive, transitional and postmenopausal periods of life: impact on cardiovascular and musculo-skeletal risk and the role of estrogen replacement. *Maturitas* **2011**, *70*, 197–205.
6. Felson, D. T. Weight and osteoarthritis. *Am. J. Clin. Nutr.* **1996**, *63*, 430S–432S.

7. Zhang, Y.; Jordan, J. M. Epidemiology of osteoarthritis. *Clin Geriatr Med* **2010**, *26*, 355–369.

8. Blüher, M. Obesity: global epidemiology and pathogenesis. *Nat. Rev. Endocrinol.* **2019**, *15*, 288–298.

9. Booth, F. W.; Roberts, C. K.; Laye, M. J. Lack of exercise is a major cause of chronic diseases. *Compr. Physiol.* **2012**, *2*, 1143–1211.

10. Felson, D. T. Risk factors for osteoarthritis: understanding joint vulnerability. *Clin. Orthop. Relat. Res.* **2004**, S16-21.

11. Englund, M. The role of biomechanics in the initiation and progression of OA of the knee. *Best Pract Res Clin Rheumatol* **2010**, *24*, 39–46.

12. Andriacchi, T. P.; Mündermann, A. The role of ambulatory mechanics in the initiation and progression of knee osteoarthritis. *Curr. Opin. Rheumatol.* **2006**, *18*, 514–518.

13. Pandy, M. G.; Andriacchi, T. P. Muscle and joint function in human locomotion. *Annu. Rev. Biomed. Eng.* **2010**, *12*, 401–433.

14. Berenbaum, F. Osteoarthritis as an inflammatory disease (osteoarthritis is not osteoarthrosis!). *Osteoarthr. Cartil.* **2013**, *21*, 16–21.

15. Berenbaum, F.; Walker, C. Osteoarthritis and inflammation: a serious disease with overlapping phenotypic patterns. *Postgrad. Med.* **2020**, *132*, 377–384.

16. Sellam, J.; Berenbaum, F. Is osteoarthritis a metabolic disease? *Joint Bone Spine* **2013**, *80*, 568–573.

17. Mobasheri, A.; Rayman, M. P.; Gualillo, O.; Sellam, J.; van der Kraan, P.; Fearon, U. The role of metabolism in the pathogenesis of osteoarthritis. *Nat. Rev. Rheumatol.* **2017**, *13*, 302–311.

18. Thomas, S.; Browne, H.; Mobasheri, A.; Rayman, M. P. What is the evidence for a role for diet and nutrition in osteoarthritis? *Rheumatology* **2018**, *57*, iv61-iv74.

19. Musumeci, G.; Mobasheri, A.; Trovato, F. M.; Szychlinska, M. A.; Imbesi, R.; Castrogiovanni, P. Post-operative rehabilitation and nutrition in osteoarthritis. [version 3; peer review: 2 approved, 1 approved with reservations]. *F1000Res.* **2014**, *3*, 116.

20. Szychlinska, M. A.; Di Rosa, M.; Castorina, A.; Mobasheri, A.; Musumeci, G. A correlation between intestinal microbiota dysbiosis and osteoarthritis. *Heliyon* **2019**, *5*, e01134.

21. Stringer, C.; McKie, R. African exodus: The origins of modern humanity. **1998**.

22. Harari, Y. N. Sapiens: A brief history of humankind. **2014**.

23. Lieberman, D. E. The story of the human body: evolution, health and disease. *Fam Med* **2016**, *48*, 822–823.

24. Bellwood, P. First migrants: ancient migration in global perspective. **2014**.

25. Smith, E.; Hoy, D. G.; Cross, M.; Vos, T.; Naghavi, M.; Buchbinder, R.; Woolf, A. D.; March, L. The global burden of other musculoskeletal disorders: estimates from the Global Burden of Disease 2010 study. *Ann. Rheum. Dis.* **2014**, *73*, 1462–1469.

26. Woolf, A. D. Global burden of osteoarthritis and musculoskeletal diseases. *BMC Musculoskelet. Disord.* **2015**, *16*.

27. Briggs, A. M.; Cross, M. J.; Hoy, D. G.; Sànchez-Riera, L.; Blyth, F. M.; Woolf, A. D.;

doi:10.20944/preprints202012.0271.v2

March, L. Musculoskeletal health conditions represent a global threat to healthy aging: A report for the 2015 world health organization world report on ageing and health. *Gerontologist* **2016**, *56 Suppl 2*, S243-55.

28. Milte, R.; Crotty, M. Musculoskeletal health, frailty and functional decline. *Best Pract Res Clin Rheumatol* **2014**, *28*, 395–410.

29. Felson, D. T. Epidemiology of hip and knee osteoarthritis. *Epidemiol Rev* **1988**, *10*, 1–28.

30. Hochberg, M. C. Epidemiology and genetics of osteoarthritis. *Curr. Opin. Rheumatol.* **1991**, *3*, 662–668.

31. Neogi, T.; Zhang, Y. Epidemiology of osteoarthritis. *Rheum Dis Clin North Am* **2013**, *39*, 1–19.

32. Johnson, V. L.; Hunter, D. J. The epidemiology of osteoarthritis. *Best Pract Res Clin Rheumatol* **2014**, *28*, 5–15.

33. Felson, D. T.; Anderson, J. J.; Naimark, A.; Walker, A. M.; Meenan, R. F. Obesity and knee osteoarthritis. The Framingham Study. *Ann. Intern. Med.* **1988**, *109*, 18–24.

34. Zhang, Y.; Niu, J.; Kelly-Hayes, M.; Chaisson, C. E.; Aliabadi, P.; Felson, D. T. Prevalence of symptomatic hand osteoarthritis and its impact on functional status among the elderly: The Framingham Study. *Am. J. Epidemiol.* **2002**, *156*, 1021–1027.

35. McAlindon, T. E.; Driban, J. B.; Henrotin, Y.; Hunter, D. J.; Jiang, G. L.; Skou, S. T.; Wang, S.; Schnitzer, T. OARSI Clinical Trials Recommendations: Design, conduct, and reporting of clinical trials for knee osteoarthritis. *Osteoarthr. Cartil.* **2015**, *23*, 747–760.

36. Panagiotopoulou, O.; Pataky, T. C.; Day, M.; Hensman, M. C.; Hensman, S.; Hutchinson, J. R.; Clemente, C. J. Foot pressure distributions during walking in African elephants (Loxodonta africana). *R. Soc. Open Sci.* **2016**, *3*, 160203.

37. Weissengruber, G. E.; Fuss, F. K.; Egger, G.; Stanek, G.; Hittmair, K. M.; Forstenpointner, G. The elephant knee joint: morphological and biomechanical considerations. *J. Anat.* **2006**, *208*, 59–72.

38. Purdon, A.; Mole, M. A.; Chase, M. J.; van Aarde, R. J. Partial migration in savanna elephant populations distributed across southern Africa. *Sci. Rep.* **2018**, *8*, 11331.

39. Chase, M. J.; Schlossberg, S.; Griffin, C. R.; Bouché, P. J. C.; Djene, S. W.; Elkan, P. W.; Ferreira, S.; Grossman, F.; Kohi, E. M.; Landen, K.; Omondi, P.; Peltier, A.; Selier, S. A. J.; Sutcliffe, R. Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ* **2016**, *4*, e2354.

40. Holdgate, M. R.; Meehan, C. L.; Hogan, J. N.; Miller, L. J.; Soltis, J.; Andrews, J.; Shepherdson, D. J. Walking Behavior of Zoo Elephants: Associations between GPS-Measured Daily Walking Distances and Environmental Factors, Social Factors, and Welfare Indicators. *PLoS One* **2016**, *11*, e0150331.

41. Edwards, K. L.; Miller, M. A.; Carlstead, K.; Brown, J. L. Relationships between housing and management factors and clinical health events in elephants in North American zoos. *PLoS One* **2019**, *14*, e0217774.

42. Lewis, K. D.; Shepherdson, D. J.; Owens, T. M.; Keele, M. A survey of elephant husbandry and foot health in North American zoos. *Zoo Biol* **2010**, *29*, 221–236.

43. Miller, M. A.; Hogan, J. N.; Meehan, C. L. Housing and Demographic Risk Factors Impacting Foot and Musculoskeletal Health in African Elephants [Loxodonta africana] and Asian Elephants [Elephas maximus] in North American Zoos. *PLoS One* **2016**, *11*, e0155223.

44. Bansiddhi, P.; Brown, J. L.; Thitaram, C. Welfare assessment and activities of captive elephants in thailand. *Animals (Basel)* **2020**, *10*.

45. Clubb, R.; Rowcliffe, M.; Lee, P.; Mar, K. U.; Moss, C.; Mason, G. J. Compromised survivorship in zoo elephants. *Science* **2008**, *322*, 1649.

46. Gage, L. J. Treatment of osteomyelitis in elephant feet. In *The Elephant's Foot*; Csuti, B.; Sargent, E. L.; Bechert, U. S., Eds.; Iowa State University Press: Ames, USA, 2000; pp. 117–118.

47. *Biology, medicine, and surgery of elephants*; Fowler, M. E.; Mikota, S. K., Eds.; Blackwell Publishing Ltd: Oxford, UK, 2006.

48. Sowers, M. R.; Karvonen-Gutierrez, C. A. The evolving role of obesity in knee osteoarthritis. *Curr. Opin. Rheumatol.* **2010**, *22*, 533–537.

49. Aspden, R. M. Obesity punches above its weight in osteoarthritis. *Nat. Rev. Rheumatol.* **2011**, *7*, 65–68.

50. Griffin, T. M.; Guilak, F. Why is obesity associated with osteoarthritis? Insights from mouse models of obesity. *Biorheology* **2008**, *45*, 387–398.

51. Loeser, R. F. Aging processes and the development of osteoarthritis. *Curr. Opin. Rheumatol.* **2013**, *25*, 108–113.

52. Chan, K. W.; Ngai, H. Y.; Ip, K. K.; Lam, K. H.; Lai, W. W. Co-morbidities of patients with knee osteoarthritis. *Hong Kong Med J* **2009**, *15*, 168–172.

53. Thijssen, E.; van Caam, A.; van der Kraan, P. M. Obesity and osteoarthritis, more than just wear and tear: pivotal roles for inflamed adipose tissue and dyslipidaemia in obesity-induced osteoarthritis. *Rheumatology* **2015**, *54*, 588–600.

54. van den Bosch, M. H. J. Inflammation in osteoarthritis: is it time to dampen the alarm(in) in this debilitating disease? *Clin. Exp. Immunol.* **2019**, *195*, 153–166.

55. Eichner, E. R. Does running cause osteoarthritis? *Phys. Sportsmed.* **1989**, *17*, 147–154.

56. Williams, P. T. Effects of running and walking on osteoarthritis and hip replacement risk. *Med. Sci. Sports Exerc.* **2013**, *45*, 1292–1297.

57. Ghouri, A.; Conaghan, P. G. Update on novel pharmacological therapies for osteoarthritis. *Ther Adv Musculoskelet Dis* **2019**, *11*, 1759720X19864492.

58. Messier, S. P.; Loeser, R. F.; Miller, G. D.; Morgan, T. M.; Rejeski, W. J.; Sevick, M. A.; Ettinger, W. H.; Pahor, M.; Williamson, J. D. Exercise and dietary weight loss in overweight and obese older adults with knee osteoarthritis: the arthritis, diet, and activity promotion trial. *Arthritis Rheum.* **2004**, *50*, 1501–1510.

59. Bennell, K.; Hinman, R. Exercise as a treatment for osteoarthritis. *Curr. Opin. Rheumatol.* **2005**, *17*, 634–640.

60. Bliddal, H.; Leeds, A. R.; Christensen, R. Osteoarthritis, obesity and weight loss: evidence, hypotheses and horizons - a scoping review. *Obes. Rev.* **2014**, *15*, 578–586.

61. Yu, S. P.; Hunter, D. J. Managing osteoarthritis. *Aust. Prescr.* **2015**, *38*, 115–119.

doi:10.20944/preprints202012.0271.v2

62. Barrow, D. R.; Abbate, L. M.; Paquette, M. R.; Driban, J. B.; Vincent, H. K.; Newman, C.; Messier, S. P.; Ambrose, K. R.; Shultz, S. P. Exercise prescription for weight management in obese adults at risk for osteoarthritis: synthesis from a systematic review. *BMC Musculoskelet. Disord.* **2019**, *20*, 610.

63. Bechert, U.; Christensen, J. M.; Nguyen, C.; Neelkant, R.; Bendas, E. Pharmacokinetics of orally administered phenylbutazone in African and Asian elephants (Loxodonta africana and Elephas maximus). *J. Zoo Wildl. Med.* **2008**, *39*, 188–200.

64. Hunter, R. P.; Isaza, R.; Koch, D. E. Oral bioavailability and pharmacokinetic characteristics of ketoprofen enantiomers after oral and intravenous administration in Asian elephants (Elephas maximus). *Am J Vet Res* **2003**, *64*, 109–114.

65. Bechert, U.; Christensen, J. M. Pharmacokinetics of orally administered ibuprofen in African and Asian elephants (Loxodonta africana and Elephas maximus). *J. Zoo Wildl. Med.* **2007**, *38*, 258–268.

66. Marshall, J. F.; Blikslager, A. T. The effect of nonsteroidal anti-inflammatory drugs on the equine intestine. *Equine Vet. J. Suppl.* **2011**, 140–144.

67. Wei, W.; Ji, S. Cellular senescence: Molecular mechanisms and pathogenicity. *J. Cell Physiol.* **2018**, *233*, 9121–9135.

68. Mobasheri, A.; Matta, C.; Zákány, R.; Musumeci, G. Chondrosenescence: definition, hallmarks and potential role in the pathogenesis of osteoarthritis. *Maturitas* **2015**, *80*, 237–244.

69. van der Kraan, P.; Matta, C.; Mobasheri, A. Age-Related Alterations in Signaling Pathways in Articular Chondrocytes: Implications for the Pathogenesis and Progression of Osteoarthritis - A Mini-Review. *Gerontology* **2017**, *63*, 29–35.

70. Batshon, G.; Elayyan, J.; Qiq, O.; Reich, E.; Ben-Aderet, L.; Kandel, L.; Haze, A.; Steinmeyer, J.; Lefebvre, V.; Zhang, H.; Elisseeff, J.; Henrotin, Y.; Mobasheri, A.; Dvir-Ginzberg, M. Serum NT/CT SIRT1 ratio reflects early osteoarthritis and chondrosenescence. *Ann. Rheum. Dis.* **2020**, *79*, 1370–1380.

71. van Deursen, J. M. The role of senescent cells in ageing. *Nature* **2014**, *509*, 439–446.

72. Chen, X.-K.; Yi, Z.-N.; Wong, G. T.-C.; Hasan, K. M. M.; Kwan, J. S.-K.; Ma, A. C.-H.; Chang, R. C.-C. Is exercise a senolytic medicine? A systematic review. *Aging Cell* **2020**, e13294.

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The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya

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Abstract

This paper presents basic demographic parameters of African elephants (*Loxodonta africana*) living in and around Amboseli National Park, Kenya. The study was conducted from 1972 to the present and results are based on the histories of 1778 individually known elephants. From 1972 to 1978, the Amboseli elephant population declined and then increased steadily from 1979 to the present. Births occurred throughout the year but over 80% occurred between November and May. Birth rate varied from year to year with a pattern of peaks and troughs at 4- to 5-year intervals. The birth sex ratio did not differ significantly from 1:1. Mean age at first birth was 14.1 years, determined from a sample of 546 known-age females. Mean birth interval ($n = 732$) was 4.5 years for 255 females. Fecundity and calf survival varied by age of the females. Mortality fluctuated from year to year. Sex-specific mortality rates were consistently higher for males than females at all ages.

Key words: age-specific fertility, birth interval, life tables, *Loxodonta africana*, mortality

INTRODUCTION

African elephants (*Loxodonta africana africana* [Blumenbach]) are long-lived mammals with a relatively long period of sexual immaturity and a slow rate of reproduction. As such they present various problems in the study of their population dynamics, most particularly the constraint of collecting longitudinal data on elephant demography. To gain a complete life history of a cohort could take over 60 years. Nevertheless, since elephants are such an important component of African ecosystems, it is widely acknowledged that an understanding of their key demographic parameters is essential for the conservation of the species and the areas in which they live. It is equally important to understand the variables of elephant life history in order to interpret most aspects of elephant behaviour and social organization. It is not surprising, therefore, that some of the earliest studies of reproduction and population dynamics of wild mammals in Africa focused on the elephant (Perry, 1953; Buss & Smith, 1966; Laws, 1966, 1969; Short 1966; Sikes, 1971). Many other studies in eastern and southern Africa followed (Hanks, 1969, 1972; Hanks & McIntosh, 1973; Laws, Parker & Johnstone, 1975; Williamson, 1976; Kerr, 1978).

These early studies of African elephant demography were based largely on carcass examinations of individuals shot as part of culling operations at a single point in time (e.g. Laws *et al.*, 1975). In a few areas, culls of elephants have been carried out on a regular basis providing cross-sectional samples at successive points in time (e.g. Hall-Martin, 1984), but obviously on different individuals. Overall population trends have been studied through regular aerial counts (Hall-Martin, 1984, 1992; Douglas-Hamilton, 1989), and from collections of lower jaws (e.g. Corfield, 1973). Age estimates and population age structures have been derived from ground and aerial surveys using a variety of methods, including measurements of shoulder height, back length, footprint length and dung bolus circumference (Croze, 1972; Leuthold, 1976; Martin, 1983; Jachmann & Bell, 1984; Lindeque, 1991; Lee & Moss, 1995), as well as assessments based on visual estimates (Poole, 1989*a*; Moss, 1990, 1996).

All the above methods rely on assumptions and projections to describe the population's history and predict its future trends (e.g. Armbruster & Lande, 1993). Only a few studies of elephants have actually followed a population in detail over time. In Addo National Park in South Africa precise population numbers have been recorded since the Park was fenced in 1931 and individual life histories have been reconstructed (Whitehouse & Hall-

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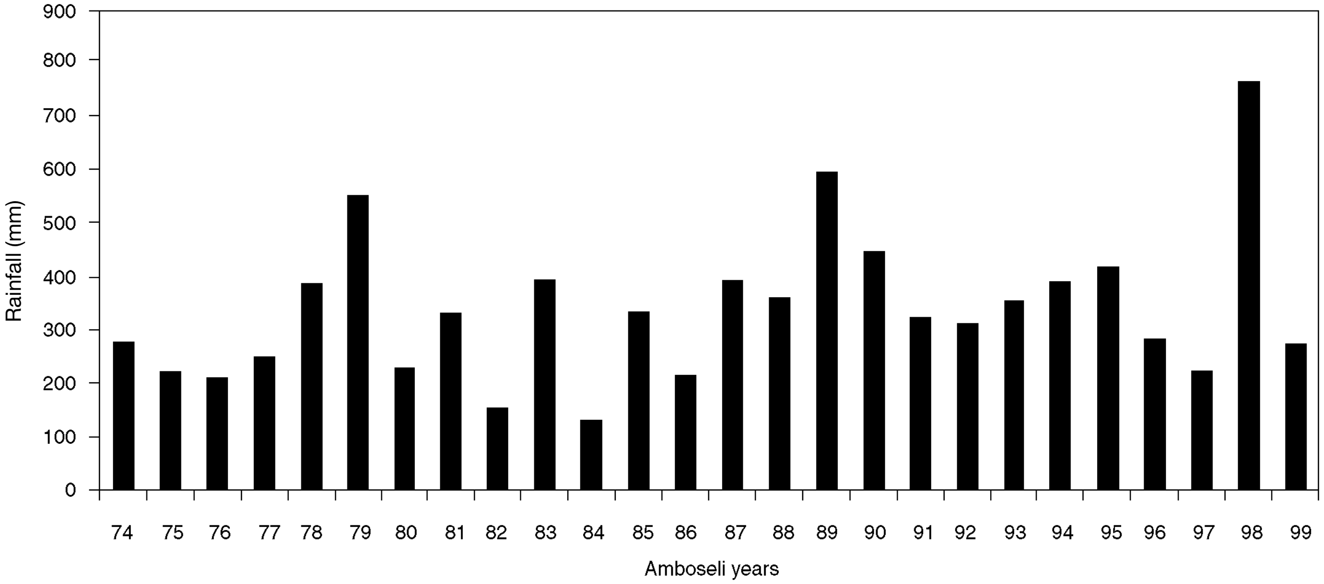

Fig. 1. Rainfall (mm) in 'Amboseli years' from 1974–1999.

Martin, 2000). In Lake Manyara National Park, Tanzania, Douglas-Hamilton (1972) studied individually known elephants for a period of 4.5 years, and subsequent workers were there for shorter periods (Weyerhaeuser, 1982), but there were long gaps between studies with loss of longitudinal data and identifications, and the study was eventually discontinued.

The Amboseli Elephant Research Project maintains the only continuous, long-term data set for an individually known, free-ranging elephant population. This paper presents the basic demographic and life-history variables found in the Amboseli population.

METHODS

Study area and animals

The study was conducted in and around Amboseli National Park in southern Kenya from September 1972 to the present, and is on-going. The Park, which was established in 1974, covers an area of 392 km^2 and the Amboseli ecosystem extends over a much wider area of approximately 3500 km^2 (Western, 1975).

The predominant habitat is semi-arid savannah (Pratt, Greenway & Gwynne, 1966) interspersed with woodlands and permanent swamps. Rain falls mainly during 2 seasons: the 'long rains' of March, April and May and the 'short rains' of November and December. Interspersed are 2 dry seasons: January, February, and most of March and then June to October. As is common in semi-arid savannahs the distribution of rainfall is unpredictable and highly variable from year to year (Fig. 1). Rainfall averages 341 mm per year (± 140, $n = 26$). The minimum annual rainfall was 136 mm and the maximum 837 mm (Amboseli Elephant Research Project records).

For the purposes of analysis 'Amboseli years' have been used rather than calendar years. The start of an Amboseli year begins with the onset of the rains and growing season on November 1 and ends on October 31, which is the end of the long dry season. For example, year '1976' covers November and December 1975 and January to October 1976.

The elephants using the Amboseli ecosystem form a relatively discrete population. Historical evidence suggests that they may once have ranged over a wider area and met elephants from adjoining populations, but since the late 1960s the population, particularly the family groups, has largely confined itself to an area of about 3000 km^2 (Western & Lindsay, 1984). The nearest elephants to the north and west are several hundred km away; to the east there is an elephant population in the Tsavo ecosystem, and animals from the 2 ecosystems may overlap in the Kimana sanctuary at the eastern edge of the Amboseli population's range. To the south there is sporadic contact between the Amboseli elephants and a small population of elephants living in the forests on Mount Kilimanjaro when the latter come down from the mountain to the Park during the wet season (Moss, 1988). There appears to be little movement of the Amboseli elephants into the montane forest (Grimshaw & Foley, 1991).

The Amboseli elephants are unusual in Africa: they have been relatively unaffected by range compression resulting from human population growth and land-use changes; they have not been heavily poached; nor have they been culled as part of a Park management programme. Although human distribution and activities influence elephant movements, and humans are an important cause of mortality, the Amboseli elephants live a comparatively 'undisturbed' existence, responding primarily to environmental conditions rather than to the effects of human development (Moss, 1988). Three reasons account for this notable exception. First, the land surrounding the National Park belongs to the Maasai people, nomadic cattle herders who have been using the ecosystem in much the same way for several hundred years (Jacobs, 1975). The National Park occupies just under 400 km^2, and the remaining area of the ecosystem (> 80%) is owned by Maasai in 4 major group ranches (Kangwana, 1993). With the exception of 2 relatively small areas there are no fences and no constraints on elephant movements. In addition, the Maasai do not hunt wild animals for consumption or trophies and have traditionally been intolerant of people coming onto their land to kill wildlife. Second, the presence of tourists in and around the National Park makes it difficult for poachers to operate without detection, and finally, the monitoring of the elephants year round by researchers is a deterrent to illegal killing.

By the end of 1999 there were 1087 living elephants in the population and 691 elephants that had been identified and which subsequently died, making a total of 1778 individuals in the data set. There were 52 family units (Moss & Poole, 1983) each made up of related cows and their calves and averaging 17.4 in number (range 3–48). Adult independent males, of which there were 183, leave their natal families at an average age of 14 years (Lee & Moss, 1999), and move singly, in loose groupings with other bulls, or in temporary association with family groups. All members of the population were individually known by means of a photographic recognition file or for young calves by their association with known mothers. Individuals were identified by features such as notches, holes, tears, bumps and vein patterns on their ears, and by tusk and body configuration (Moss, 1983, 1996).

Age determination

Births have been recorded in the Amboseli population since 1972. Assessment of newborn and young calf age (less than 3 months old) was based on body size and proportion, skin colour, motor co-ordination, presence of an umbilical cord, and by the behaviour of both the calf and the mother (Moss, 1988, 1996). In the first 3 years of the study, 1972–1975, birth dates were known ± 3 months, and from 1976 to 1999 were known, with a few exception, ± 2 weeks. Ages of animals born prior to 1972 were estimated using the following techniques:

(1) Length of hind footprint, which has a consistent relationship to growth and age (Western, Moss & Georgiadis, 1983; Lee & Moss, 1986, 1995).

(2) Tooth eruption and wear sequence, which has been a primary method of estimating ages of dead or immobilized elephants (Laws, 1966; Sikes, 1971).

(3) Tusk eruption and length, which are good age indicators for calves up to 6 years old (Moss, 1988; 1996) and tusk circumference at the lip, which is closely correlated with age throughout life (Pilgram & Western, 1986).

(4) Visual assessment of shoulder height and back length (Croze, 1972; Laws *et al.*, 1975; Douglas-Hamilton, Hillman & Moss, 1981; Lee & Moss, 1995; Moss, 1996).

(5) Photographs of recognizable Amboseli elephants taken in the 1960s and early 1970s provided additional information for making age estimates. As the study progressed and known-age individuals became older, the early photographs of estimated-age adult and young adult elephants could be compared to the known-age individuals and the age estimates adjusted (Moss, 1988).

These methods of assessing age were combined and cross-checked, especially with reference to known-age animals as individuals aged. Animals whose birth dates were unknown were aged using a combination of at least 2 of these techniques. In this way, all members of the population were assigned a birth year with a degree of accuracy code ranging from 0 (estimate) to 5 (known ± 2 weeks). Animals born from 1973 onwards were also assigned a birth month with those born from 1973 to 1975 having a birth accuracy of ± 3 months and most of those born after 1976 having an accuracy of ± 2 weeks. The birth year of those animals estimated to be born in 1970–1971 was considered accurate to ± 6 months, while the birth year of those born in 1968–1970 was considered accurate to ± 1 year. The birth year of those animals born before 1968 was estimated at ± 2.5 years; and that of those born before 1963 to ± 5 years. By December 1999 the ages of 758 living elephants were known with a birth accuracy of ± 2 weeks, representing 71% of the population, ranging from newborn calves to animals 24 years old.

For the purposes of age structure analysis, 8 age classes were created. Individuals were grouped in five 5-year classes until 25 years, and then, based on the ability to age the older animals, in one 10-year class and two 15-year classes, as follows: 0A = 0–4.99; 0B = 5–9.99; 1A = 10–14.99; 1B = 15–19.99; 2 = 20–24.99; 3 = 25–34.99; 4 = 35–49.99; 5 = 50–64.99.

Demographic data

Over the course of the study a census of each family unit was attempted at least once per month. A census consisted of the identification of all individuals present in the family on that sighting. Any new calf was noted during a census, but calves were also registered as soon as they were observed whether the family was being censused or not. As soon as a new calf was found, its age was estimated, sex noted and mother recorded. Conception dates were estimated by backdating live births by 22 months (Moss, 1983).

Dates of deaths in the Amboseli population were more difficult to pinpoint. Typically, indirect methods were used to determine mortality. Any missing animal was recorded during the monthly censuses and during routine monitoring. With a few exceptions there were no observed immigrations of females into non-natal families. If an adult female was absent and her calves were present, it was a good indication that she was dead or seriously ill. That family would then be more closely monitored. If the female was not seen for a week or more, it was assumed she was dead. If a calf less than 3 years old was missing and its mother was present, the calf was assumed to be dead. If a mother and her calf or calves were absent or a juvenile or adolescent female was missing, they were counted as dead if they were not seen with or away from their family for a month or more. Once it was decided that an individual was dead, the date of death was estimated as the midpoint between the last date the animal was seen and the date it was first recorded as missing.

Attempting to register male mortality was more problematic. Until a male calf was 7 or 8 years old he was treated in the same way as a female calf, but since males start to spend time away from their natal families as young as 8 years old (Lee & Moss, 1999), absence from the family was not necessarily an indication of death. Several months with no sightings had to pass before an adolescent male was considered dead.

Censuses were also conducted on the population of adult independent males with an attempt to find each male once a month. This goal was rarely achieved as males ranged farther than females and were often on their own or in small groups, which made them difficult to locate. An adult male was not considered dead until he had not been sighted for 1 year or more. A date of death was assigned based on the last recorded sighting but often it was only given an accuracy of ± 12 months.

Causes of death were not easily determined. Surprisingly few carcasses were found during the course of the study and the great majority of these were of adult animals. The carcasses or skeletons of calves less than 5 years old were very rarely discovered. A few animals showed signs of illness and were later found dead or they disappeared. The only positively known causes of mortality were the result of spearing by Maasai, shooting by poachers or by Park's personnel, injuries, and starvation of calves whose mothers had died. There was good circumstantial evidence for deaths due to the effects of drought, injuries incurred in fights, complications during births, predation, poisoning and old age with the wearing down of the last set of molars.

Death dates were assigned degrees of accuracy ranging from 0 (estimate) to 4 (± 1 week); and death causes were assigned the following degrees of accuracy: 0 = no cause known; 1 = suspected with some reason; 2 = good evidence; 3 = known. Only those causes of mortality that were known or were based on good circumstantial evidence were used in analyses that required finer resolution.

Analysis

Basic population trends and patterns of births and deaths are presented using total numbers. Birth rates are expressed as the number of births per Amboseli year divided by the number of females over 9 years old alive in that year, and are used here to illustrate the pattern of annual births. These rates represent contributions from the same female to different years, and are not corrected for numbers of females unavailable for conception due to pregnancy or lactation.

Fecundity was analysed as the age-specific proportions of females giving birth, and was based on hazard analyses, which tracked individual females through their reproductive careers. Age at first birth used all known-age females born into the population (*n* = 546) in a Kaplan–Meier survival analysis. Age-specific mortality was based on a standard life table survival analysis.

All statistical tests used a 2-tailed probability. Where normal distributions and variance were not assumed, non-parametric tests were used.

RESULTS

Population growth rate

The Amboseli elephant population has fluctuated in size over time (Fig. 2a). Estimates for elephant numbers in the 1960s vary from 700 to 1200 (D. Western, pers. comm.). An initial aim of this study was to determine accurate population numbers by individual registration of every living elephant. By 1978, all members of the population were known. From 1974, when most living members had been registered, population trends could be followed.

The Amboseli population declined in the 1970s due to both poaching and drought. By the end of 1978 the population had been reduced to 480 animals from a minimum population of 584 at the beginning of 1974.

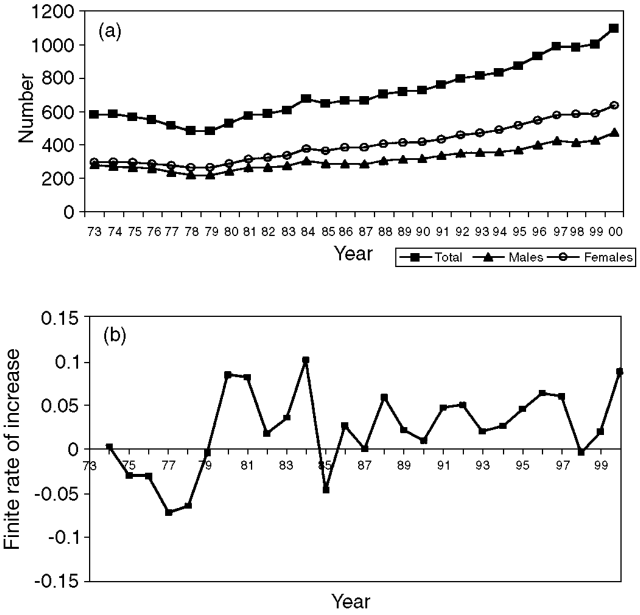

Fig. 2. Population trends for Amboseli elephants from 1972 to 1999 (a) sex-specific and total population size by year; (b) finite rate of population increase by year.

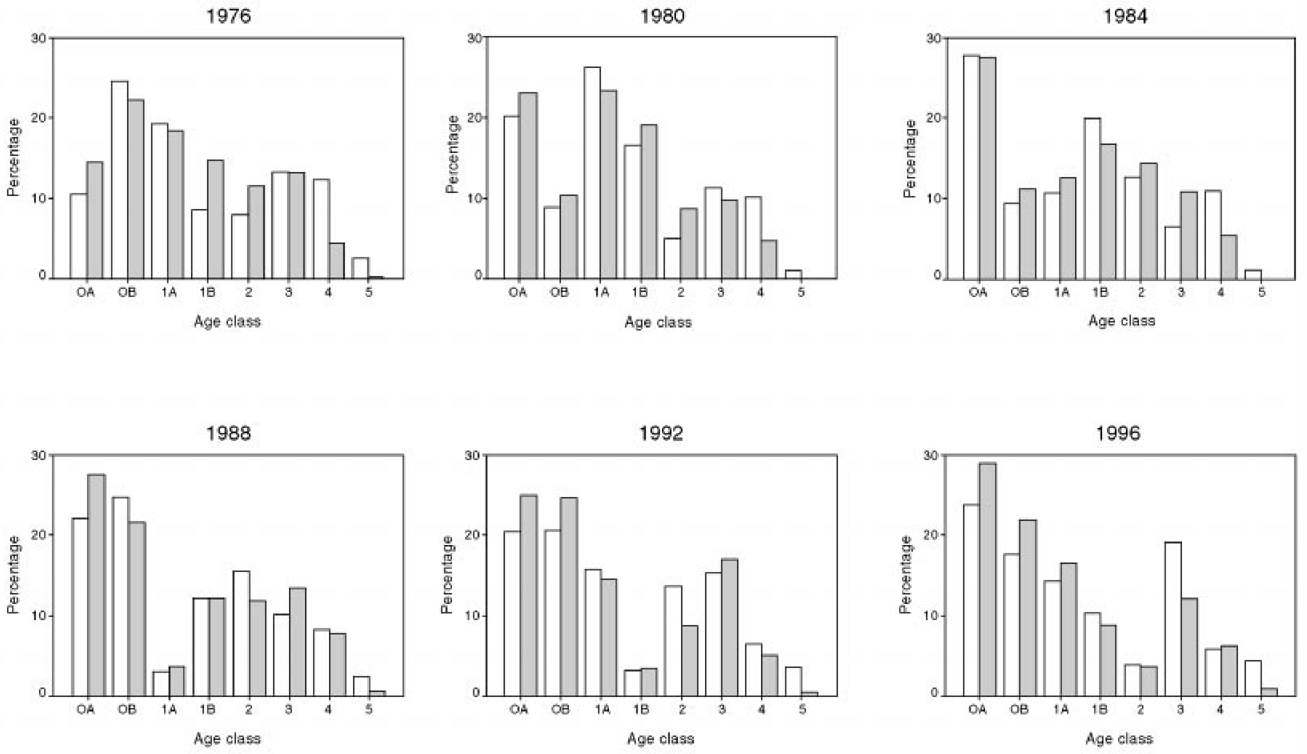

Fig. 3. Age and sex distributions for the population for 6 years illustrating changes over time. Males, solid bars; females, open bars. Age classes as noted in Methods.

The 1974 population size includes only those animals that were registered; additional individuals probably died before registration was completed in 1978. By the end of 1999 the population had grown to 1087.

The overall annual rate of population increase was 2.17% between 1974 and the end of 1999. However, from 1979, the time of recovery after the crash due to the drought, the population grew at an average annual rate of 3.75%. The maximal rate of increase was 11.28% while the maximal rate of decrease was −7.42% (Fig. 2b). There was no evidence in Amboseli of either immigration or emigration, and thus the overall increase can be attributed to a greater proportion of births over deaths since 1978.

Age structure

The age structure of the Amboseli elephant population has changed over the course of the study (Fig. 3). Early on, there were proportionally fewer calves and immature elephants and very few adult males in the older age classes. The increase in the size of the population has been matched by an increase in the proportion of immature elephants and an increase in numbers in the older male age classes (see Fig. 3). The significant gaps and pulses in the age structure reflect periods of drought when conception rates were low and calf mortality high as well as periods of poaching and sport hunting of the larger tusked individuals, particularly older males.

Age at first birth

Over the course of the study, 253 of the 546 known-age females survived to the age of 8 years and the first births for 152 of these females have been recorded. A few stillbirths and births of calves that lived less than a day may have been missed, despite additional information from a combination of oestrous records and breast development (Mutinda, 1994), and therefore the age at first birth may be slightly lower than calculated here.

A Kaplan–Meier survival analysis of age at first birth suggested that the probability of giving birth for the first time was over 50% for females aged between 14 and 15 years and the median age for the first birth was 14.1 years (95% Cl = 13.74–14.46). The mean age for first births was 13.67 (Fig. 4). The youngest known-age female at first birth was 8.9 years and the oldest was 21.6. While four females below 10 years of age have given birth, births at this age have a probability of occurrence of around 1% (0.4% for 8–9 years; 1.33% for 9–10 years). Only 25% of females had given birth by the age of 12.5 years, and only 25% remained to produce a calf by 15.3 years. There have been only 20 first births to females aged 16 years or over, and the probability of a female older than 20 years giving birth for the first time is less than 1.4%. Thus, although there is considerable individual variation in the age at first birth, most females will conceive their first calf between 11 and 13 years of age.

While females could potentially conceive as young as

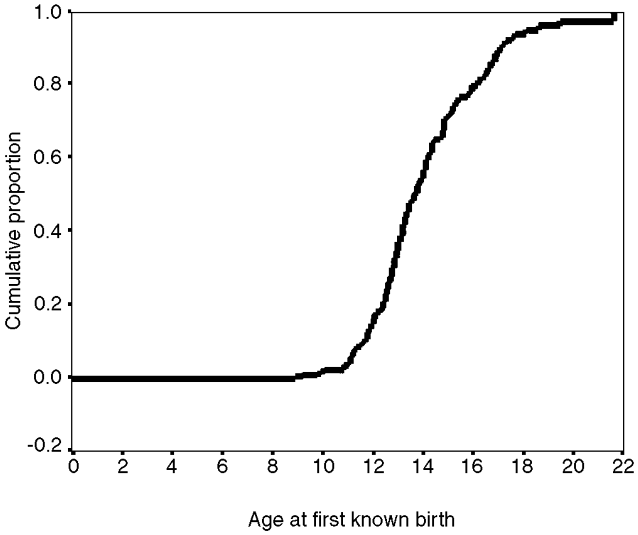

Fig. 4. Probability of first birth occurring at each age for known-age females.

7 years old in this sample, such conceptions were rare, and indeed, females who gave birth under the age of 10 years had only a 50% probability of their calf surviving the first year of life ($n = 4$). For females aged between 10 and 15 years ($n = 144$ births), calf survival in the first year increased to 76%, while for those giving birth over 15 years to either their first or second calf ($n = 70$ births), calf survival was 78.6%. After the age of 20, calf survival in the first year averaged close to 90% ($n = 411$ births).

Birth timing and sex ratio

Over the course of the study 1192 births were recorded, including one set of twins. Births were not evenly distributed within each year or between different years. Using the 1030 births of known sex with a birth date accuracy of ±2 weeks, calves could be born in each month, but 81% of births occurred between November and May (Fig. 5). There were 1162 births of calves of known sex during the study period. The sex ratio was not significantly different from 1:1 (604 females; 558 males, binomial exact $\chi^2 = 1.82$, NS) nor was there any difference in the distributions of births across months between sexes ($\chi^2 = 8.1$, df = 11, NS; Fig. 5).

The annual birth rate for females over 9 years old (potentially reproductively active females) for the period 1976–1999 revealed distinct peaks and troughs with a tendency for peaks to occur at 4- to 5-year intervals (Fig. 6). During the 1975–1976 drought, there was little reproductive activity, which resulted in extremely low birth rates in 1977 and 1978. When conditions improved after good rainfall, the females started coming into oestrus again with a resulting birth peak in 1979–1980. With a typical calving interval of 4 years (see below), the females moved into a synchronous wave pattern with birth peaks every 4 years. The additional peak in 1985 (Fig. 6) appeared to be the result of a cohort of young females reaching sexual maturity in 1983 (36% of the females who gave birth that year) and adding substantially to the birth rate.

Age-specific fecundity

Age-specific rates of reproduction were calculated for individual females giving birth during the study period using hazard analysis. These rates reflect the number of birth events per age interval as a function of the number of females who survived each interval (Fig. 7). Fecundity was relatively constant from the age of 16 to 40, and then declined slightly. The fecundity rate of the oldest females (50+ years, n of births = 46) averaged

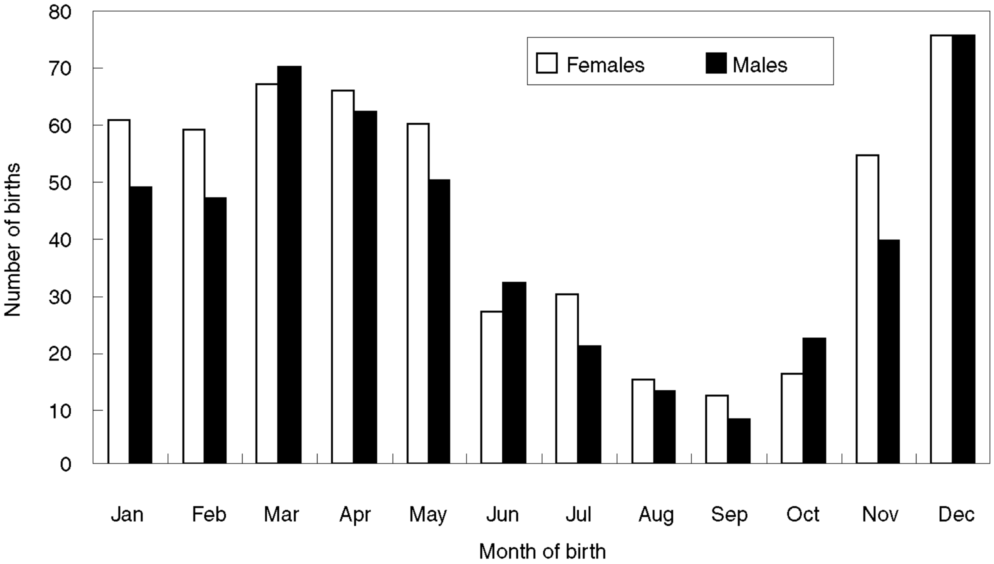

Fig. 5. Sex-specific births by month over the period of the study for calves with known birth dates ($n = 1030$).

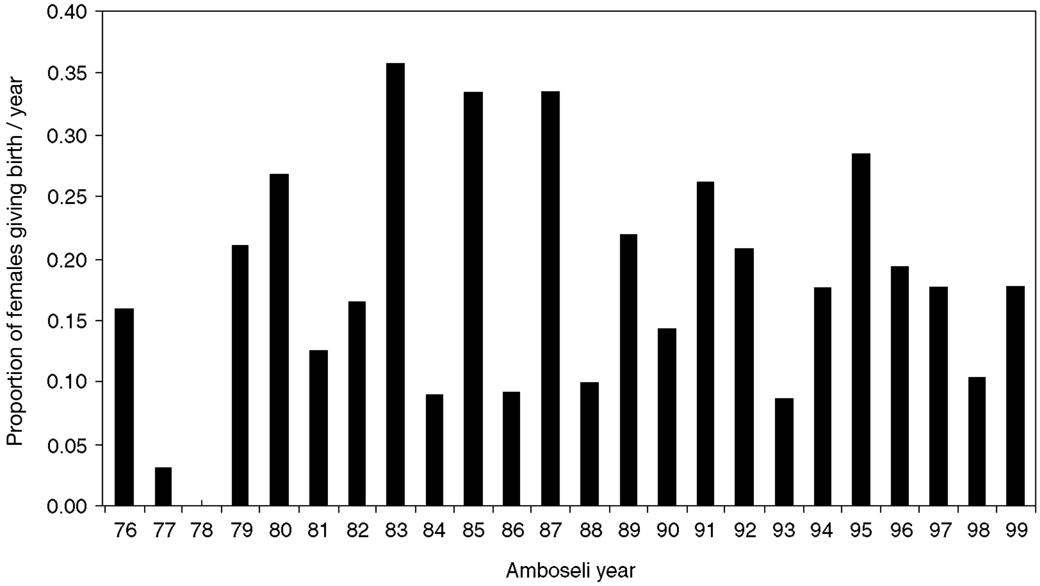

Fig. 6. The distribution of births by year, as a proportion of females > 9 years old alive in each year.

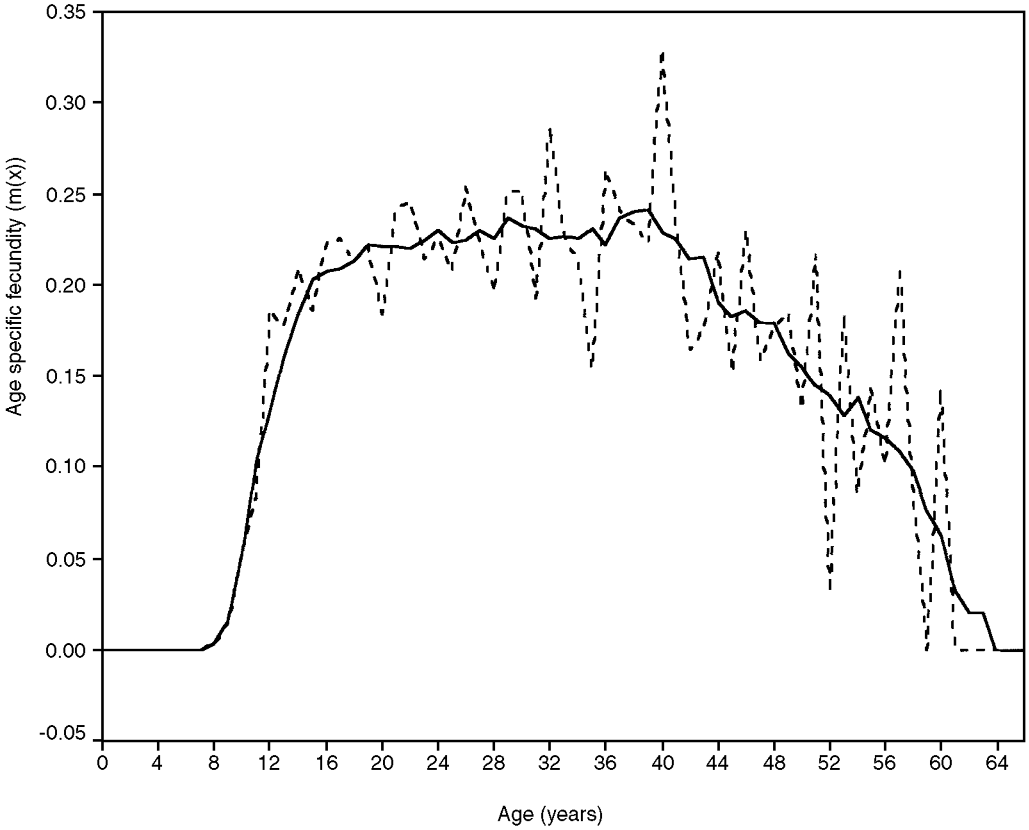

Fig. 7. Age-specific fecundity (m(x)) for female elephants. Both absolute values (dotted) and smoothed trends (solid) are shown for each age.

0.098 births/female/year while that of 40- to 50-year-old females (*n* of births = 109) averaged 0.196.

Of the 38 females in the study with well-known histories who reached 50 years old, most continued to reproduce and only nine appeared to stop breeding with 7 years or more passing since they last gave birth. There have been five births to 12 females aged over 60. For those who continued to breed, their most recent calving intervals averaged 4.75 (range = 2.75–6.9) years, compared to 4.5 years for the general population (see below).

The mean calving intervals for 255 females who gave

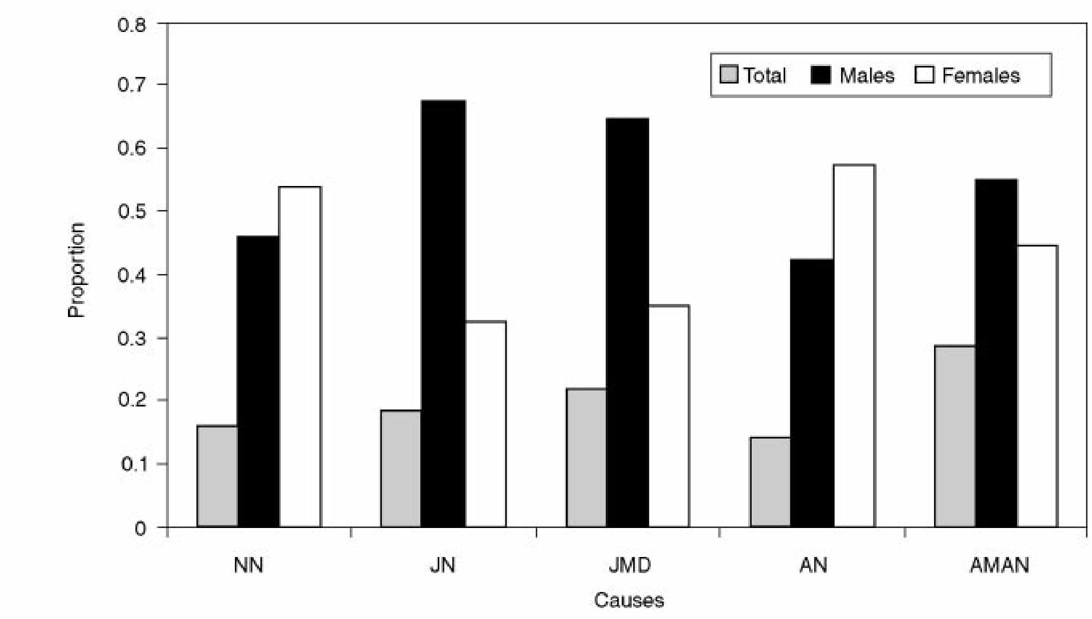

Fig. 8. Percent of total deaths ($n = 231$) attributed to different causes, and proportion of males and females within each category of death. NN, neonatal (< 1 month); JN, juvenile natural; JMD, mother died; AN, adult natural; AMAN, adult human-caused.

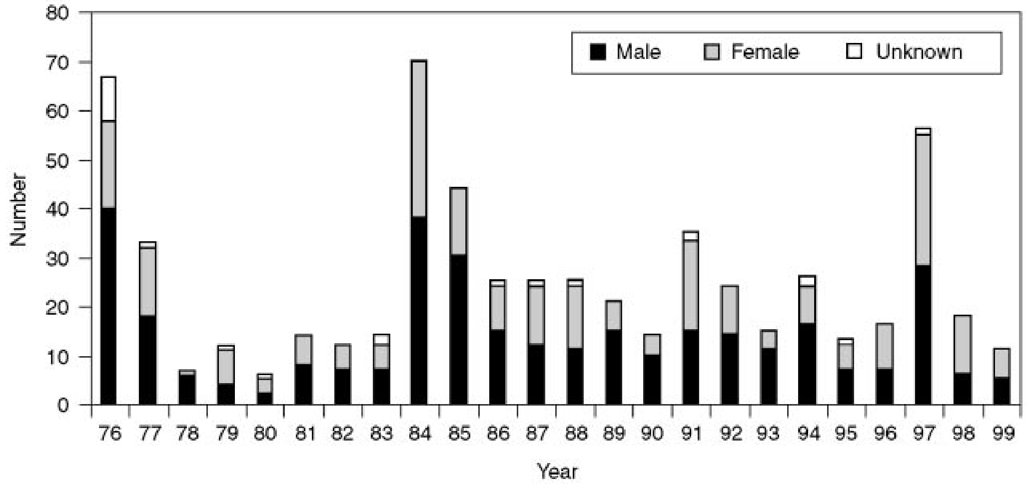

Fig. 9. The sex-specific distribution of mortality by year ($n = 691$).

birth at least twice since 1972 was 4.5 years (median = 4.2 years, $n = 732$ intervals). The modal interval was 4.0 years (range = 1.8–11.7 years) with or without the previous calf surviving. Calf survival extended birth intervals (median = 4.5 years, $n = 547$ intervals) by comparison to intervals when calves died in their first 2 years of life (median = 3.2 years, $n = 134$ intervals).

Mortality

There were 691 elephant deaths recorded from 1972 to 1999. The cause of death could be determined with accuracy for 231 individuals (Fig. 8). Natural causes accounted for most of the juvenile mortality (61%, $n = 131$), while human activities caused the majority of adult deaths (67%, $n = 100$).

The number of elephants dying per year, starting in 1976 when the majority of the population was registered, is presented in Fig. 9. Some trends are apparent in these data which reflect anthropogenic and climatic changes over the study period. A severe drought, which started in 1973, reached its culmination in 1976. That year was characterized by high calf mortality in the youngest age class (0–5 years) and high levels of spearing by the Maasai, whose livestock were in direct competition with elephants for the limited resources resulting in increased levels of contact. In addition, there was continuing poaching for ivory, particularly of older males and females. The period from 1977 to 1983 was characterized by high rainfall and low human-induced mortality, and was followed by another severe drought in 1984, accompanied by high rates of Maasai spearing, again due to competition for resources, but also to the initiation of a new warrior age set. After the 1984 drought, when 70 elephants died, there was a period of relative calm up until 1990, with a minimum of conflict between Maasai and elephants and average to higher than average rainfall. In 1991, there was a brief drought, which primarily affected young animals. From 1994 to 1997 poaching and sport hunting, in the border area between Kenya and Tanzania, of Amboseli's large bull elephants occurred and over that period nine of the males in the older age classes were killed. During the same period, Kenya Wildlife Service (KWS) policy changed, and elephants were shot by KWS staff in various conflict situations. In early 1997 there was a period of drought and once again Maasai and elephants came into conflict, with the result that some elephants were speared while others were shot by KWS. In 1998 and 1999 relations between the Maasai and KWS improved with a change in policy, and the number of elephant deaths decreased.

Age-specific mortality rates for males and females were calculated separately using a standard life table model (Fig. 10). Maximum lifespan for females was over 65 years; for males it was close to 60. Life expectancy at birth was 41 years for females and 24 years for males.

Male elephants experienced higher rates of mortality than did females over the first 10 years of life; only 75% of male calves survived to age 10 years, while 84% of female calves reached this age. Survival differences between males and females were maintained after this age. While 82% of female calves survived to the average age of first reproduction (14 years), only 39% of males survived to the age when they regularly enter musth (early 30s) and were likely to obtain significant numbers of matings (Poole & Moss, 1981; Poole, 1987, 1989*a*,*b*).

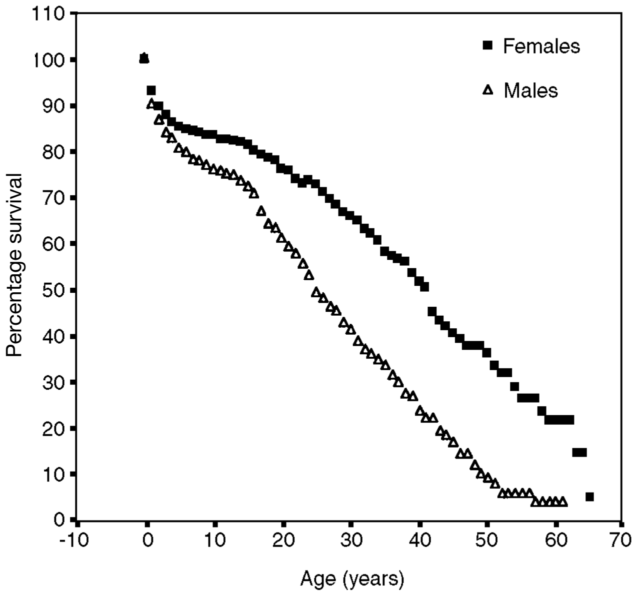

Fig. 10. Age-specific survivorship for male and female elephants.

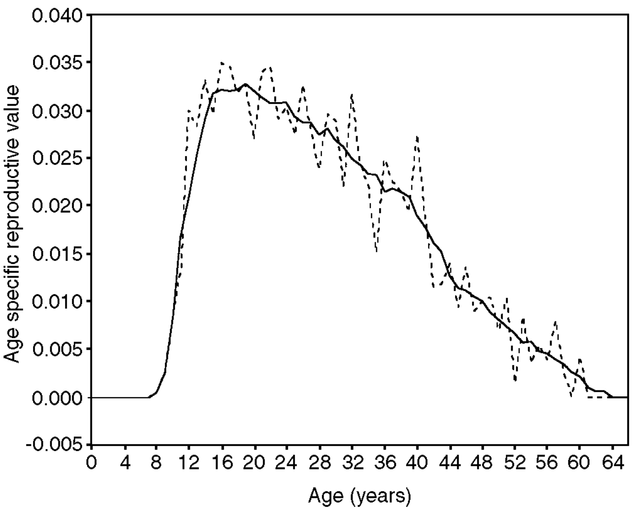

Fig. 11. Age-specific reproductive value. Both absolute values (dotted) and smoothed trends (solid) are shown.

Life-table and intrinsic growth rate

The age-specific survival and fecundity data were combined to obtain an estimate of the rate of increase for the Amboseli elephant population. Standard life table methods provide an estimate of $r = 0.0215$ for the intrinsic rate of increase and $R_0 = 2.36$ for the basic reproductive number (Birch, 1948). The generation time based on these data is 17.38 years. Age-specific reproductive value is presented in Fig. 11, suggesting that females between 12 and 30 years contributed similarly to the population increase and that their relative contribution tails off rapidly after 40 years. The average female produced just over four calves in her lifetime, each of her two female calves had a 70% chance of producing offspring; in contrast she had only a 50% chance that either of her two male calves would survive long enough to regularly enter musth and thus reproduce successfully.

DISCUSSION

Long-term studies of individually known animals in the wild are rare for both logistical and economic reasons. The Amboseli elephant population is the only population of free-ranging known individuals in Africa that has been monitored continuously for over 27 years. At the same time, it is one of the few in Africa that has not undergone disruption in terms of age or sex structure as a result of heavy poaching for ivory. There has also been no culling or cropping of the population. Thus it is reasonable to use the Amboseli population as an indicator of some typical reproductive patterns in a savannah ecosystem.

Population status, growth rate and birth rate

In the absence of heavy poaching, immigration or emigration the Amboseli population has been growing at an average rate of 2.2% per annum. The growth rate was not uniform over time and was very high (> 11%) in some years and negative in others. Given the current level of protection and available range, the population could continue to grow at a comparable rate, although many other factors, both environmental and political, could affect the population's status in the future.

Birth rate showed peaks and troughs due to the effects of drought (Moss, 1988) and a 4-year calving interval, which together tended to bring females into synchrony for conceptions and births (see also Whitehead & Mann, 2000 for cetaceans). In other elephant studies, population growth rates have been derived from counting the number of calves < 1-year-old at a given time and then using that percentage as an index of recruitment (Buss & Savidge, 1966; Laws, 1966; Calef, 1988). However, culled samples and the data presented here suggest that such instantaneous counts could merely reflect short-term patterns of 'highs' and 'lows' and thus produce misleading estimates of population growth rates. Simply using the number of calves under 1 year of age present at a single point in time does not take into account either the relatively high levels of mortality amongst the youngest age classes or variability in birth rate from year to year. In Amboseli, calf mortality was around 10% in the first year of life, and there was constant low mortality throughout the reproductively active years for females. Furthermore, in some years (see Fig. 6) less than 10% of females gave birth. Thus, instantaneous counts may reflect short-term patterns of highs or lows in reproductive rates, rather than providing an 'average' estimate of population growth rates (Laws, 1969; Hanks & McIntosh, 1973; Moss, 1988, 1994).

Mean calving interval

The mean calving interval has been considered to be the single most important parameter influencing the growth rate of an elephant population (Hanks & McIntosh, 1973). Mean calving intervals derived from culled samples from several populations in Africa ranged from 2.9 to 9.1 years (Eltringham, 1982). In high-density populations or nutritionally stressed populations, mean calving interval is relatively long, potentially slowing population growth (Laws *et al.*, 1975). In Amboseli, females can produce another calf as quickly as 22 months (one gestation length) after a birth if the first calf dies or 27 months after the birth of a surviving calf. Overall, however, females tended to produce a calf once every 4.5 years. Shorter average calving intervals have been reported in other populations with known individuals. In the Addo population (Whitehouse & Hall-Martin, 2000), mean calving intervals were 3.8 years. In general, the Amboseli results were similar to those found in other elephant populations in Africa (Eltringham, 1982).

Age of first birth

The age of sexual maturity in elephants varies in different populations across Africa (Eltringham, 1982), with the potential for a marked effect on a population's growth rate. Population modelling suggests that a delay in first parturition of even 1 year can slow growth rates (Croze, Hillman & Lang, 1981). In Amboseli, the youngest female to successfully conceive (resulting in a live birth) was 7 years old, but this was a rare event with a low probability. The median age of first conception was 12 years, which would be a more realistic age to use in modelling elephant population dynamics. While some females were able to commence reproduction relatively young, others were delayed for as much as 4 years.

I suggest that the variation in age at first reproduction observed in Amboseli is likely to be a complex function of the females' early growth and nutrition, individual variation in condition and size when close to the average age of reproduction, and the prevailing ecological and social conditions at the time (e.g. Clutton-Brock, Major & Guinness, 1985; Altmann, 1991; Reiter & Le Boeuf, 1991; Whitehead & Mann, 2000). The trade-off between starting reproduction and maintaining individual condition and growth is reflected in the observation that the calves of the youngest females had a higher probability of mortality (see also Clutton-Brock, 1984; Huber, 1987; Whitehead & Mann, 2000).

Mortality

In Amboseli, there are high rates of mortality in all age classes during years when droughts occur. Droughts not only result in inadequate nutrition, limited water, and increased energy expenditure, but also in high densities of both wildlife and Maasai cattle as they both move into the last areas with vegetation and water, increasing competition and the potential for conflict. Under these circumstances there is often a rise in spearing incidents as well as in deaths and injuries to people and cattle caused by elephants. In addition, elephants are killed as part of the Maasai culture of warriorhood. Unlike many areas in Africa, in Amboseli human-induced mortality is similar for male and female elephants, because most killing is not directed at obtaining the trophies of the much larger males, but rather it is directed at elephants in general.

It is noticeable that male mortality is higher than female mortality, especially in the first years of life, but the differential also appears to be maintained over time.

Whether this differential represents the additional costs to males of early growth (Lee & Moss, 1986), sexual dimorphism (Owen-Smith, 1993), or engaging in higher risk behaviour such as dispersal (Lee & Moss, 1999) and male–male reproductive competition (Moss & Poole, 1983, Poole, 1987, 1989*b*) has yet to be determined.

Reproductive value and life table analyses

The reproductive value curve presented here is the first such attempt for elephants. It shows a pattern similar to some other large mammals and some primates, including humans, which typically exhibit a sharp rise in reproductive value at the age of first reproduction (in elephants between 12 and 15 years) and then a gradual decline over the reproductive period (e.g. Packer, Tatar & Collins, 1998). In Amboseli, unlike Addo (e.g. Whitehouse & Hall-Martin, 2000), females are able to reproduce until the end of their lifespan, although there is a sharp drop in fecundity after 50 years with declining reproductive value from its peak at about 20 years. The elephant pattern may be of considerable interest in explorations of the evolution of reproductive senescence in other long-lived species such as whales (Marsh & Kasuya, 1986; Whitehead & Mann, 2000) and humans (Hawkes, O'Connell & Blurton-Jones, 1997; Mace, 2000).

Population models require specific, accurate population parameters. Results presented above show that for the Amboseli population, generation time was approximately 17 years, with an age at first reproduction of 14 years, a calving interval of 4.5 years, a birth sex ratio of unity and survival probabilities of 89% for females *vs.* 82% for males in the first 5 years. Age-specific fecundity, while possibly of less importance in population models, was relatively constant from 15 to 45 years at about 0.23. Maximum female lifespan was 65 years. These long-term data from Amboseli contrast with those used in some other population models (e.g. Armbruster & Lande, 1993), and should provide a basis for the development of more comprehensive models.

The African elephant faces two serious threats to its future: (1) overexploitation for its ivory and/or meat and skins; (2) loss of suitable habitat. Conservation measures may range from making decisions about saving a small remnant population to setting policy for the reduction of large expanding populations. In order to make these kinds of decisions for elephants both in and out of protected areas, it is essential to understand their basic reproductive parameters. It is hoped that these data will be of importance for future, accurate population modelling, with the aim of benefiting the long-term conservation and welfare of African elephants.

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REFERENCES

Altmann, S. A. (1991). Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. *Proc. Nat. Acad. Sci.* USA **88**: 420–423.

Armbruster, P. & Lande, R. (1993). A population viability analysis for African elephant (*Loxodonta africana*): how big should reserves be? *Cons. Biol.* **7**: 602–610.

Birch, L. C. (1948). The intrinsic rate of natural increase of an insect population. *J. Anim. Ecol.* **16**: 15–26.

Buss, I. O. & Smith, N. S. (1966). Observations on reproduction and breeding behavior of the African elephant. *J. Wildl. Mgmt*. **30**: 375–388.

Buss, I. O. & Savidge, J. M. (1966). Change in population number and reproductive rates of elephants in Uganda. *J. Wildl. Mgmt*. **30**: 791–809.

Calef, G. W. (1988). Maximum rate of increase in the African elephant. *Afr. J. Ecol*. **26**: 323–327.

Clutton-Brock, T. H. (1984). Reproductive effort and terminal investment in iteroparous animals. *Am. Nat*. **123**: 212–229.

Clutton-Brock, T. H., Major, M. & Guinness, F. E. (1985). Population regulation in male and female red deer. *J. Anim. Ecol*. **54**: 831–836.

Corfield, T. F. (1973). Elephant mortality in Tsavo National Park, Kenya. *E. Afr. Wildl. J.* **11**: 339–368.

Croze, H. (1972). A modified photogrametric technique for assessing age structures of elephant populations and its use in Kidepo National Park. *E. Afr. Wildl. J.* **10**: 91–115.

Croze, H., Hillman, A. K. K. & Lang, E. M. (1981). Elephants and their habitats: how do they tolerate each other? *Dynamics of large mammal populations*: 297–316. Fowler, C. W. & Smith, T. D. (Eds). New York: John Wiley and Sons.

Douglas-Hamilton, I. (1972). *On the ecology and behaviour of the African elephant*. PhD thesis, University of Oxford.

Douglas-Hamilton, I. (1989). Overview of status and trends of the African elephant. *The ivory trade and the future of the African elephant*. Cobb, S. (Ed.). Report for Ivory Trade Review Group. Oxford: International Development Centre.

Douglas-Hamilton, I., Hillman, A. K. K. & Moss, C. J. (1981).

Notes on vertical photography of elephants for age determination. *ILCA Monogr.* **4**: 131–142.

Eltringham, S. K. (1982). *Elephants*. Poole, Dorset: Blandford Press.

Grimshaw, J. M. & Foley, C. A. H. (1991). *Kilimanjaro elephant project, 1990*. Unpublished report, Friends of Conservation, 122 pp.

Hall-Martin, A. (1984). Conservation and management of elephants in the Kruger National Park, South Africa. *The status and conservation of Africa's elephants and rhinos*. Gland, Switzerland: IUCN.

Hall-Martin, A. (1992). Distribution and status of the African elephant, *Loxodonta africana*, in South Africa, 1652–1992. *Koedoe*, **35**(1): 65–88.

Hanks, J. (1969). Seasonal breeding of the African elephant in Zambia, *E. Afr. Wildl. J.* **7**: 167.

Hanks, J. (1972). Reproduction of the elephant (*Loxodonta africana*) in Luangwa Valley, Zambia. *J. Repro. Fert.* **30**: 13–26.

Hanks, J. & McIntosh, J. A. E. (1973). Population dynamics of the African elephant (*Loxodonta africana*). *J. Zool. (Lond.)* **169**: 29–38.

Hawkes, K., O'Connell, J. F. & Blurton-Jones, N. (1997). Hadza women's time allocation, offspring provisioning and the evolution of long postmenopausal life spans. *Cur. Anthropol.* **38**: 551–565.

Huber, H. R. (1987). Natality and weaning success in relation to age of first reproduction in northern elephant seals. *Can. J. Zool.* **65**: 1311–1316.

Jachmann, H. & Bell, R. H. V. (1984). The use of elephant droppings in assessing numbers, occupance and age structure: a refinement of the method. *Afr. J. Ecol.* **22**: 127–141.

Jacobs, A. H. (1975). Maasai pastoralism in historical perspective. *Pastoralism in Tropical Africa*: 406–425. Monod, T. (Ed.). London: Oxford University Press.

Kangwana, K. F. (1993). *Elephants and Maasai: conflict and conservation in Amboseli, Kenya*. PhD thesis, University of Cambridge.

Kerr, M. A. (1978). The reproduction of elephant in the Mana Pools National Park, Rhodesia. *Arnoldia Rhod.* **3**(29): 1–11.

Laws, R. M. (1966). Age criteria for the African elephant, Loxodonta africana. *E. Afr. Wildl. J.* **4**: 193–217.

Laws, R. M. (1969). The Tsavo Research Project. *J. Repro. Fert. Supp.* **6**: 495–531.

Laws, R. M., Parker, I. S. C. & Johnstone, R. C. B. (1975). *Elephants and their habitats*. Oxford: Clarendon Press.

Lee, P. C. & Moss, C. J. (1986). Early maternal investment in male and female African elephant calves. *Behav. Ecol. Sociobiol.* **18**: 353–361.

Lee, P. C. & Moss, C. J. (1995). Statural growth in known-age African elephants (*Loxodonta africana*). *J. Zool. (Lond.)* **236**: 29–41.

Lee, P. C. & Moss, C. J. (1999). The social context for learning and behavioural development among wild African elephants. *Mammalian social learning*: 102–125. Box, H. O. & Gibson, K. R. (Eds). Cambridge: Cambridge University Press.

Leuthold, W. (1976). Age structure of elephants in Tsavo National Park. *J. App. Ecol.* **13**: 435–444.

Lindeque, M. (1991). Age structure of the elephant population in the Etosha National Park, Namibia. *Madoqua* **18**: 27–32.

Mace, R. (2000). Evolutionary ecology of human life history. *Anim. Behav.* **59**: 1–10.

Marsh, H. & Kasuya, T. (1986). Evidence for reproductive senescence in female cetaceans. *Intl. Whaling Commission* Special Issue **8**: 57–74.

Martin, R. B. (1983). Zimbabwe completes tenth year of elephant radiotracking. *Pachyderm* **4**: 5–7.

Moss, C. J. (1983). Oestrous behaviour and female choice in the African elephant. *Behaviour* **86**(3/4): 167–96.

Moss, C. J. (1988). *Elephant memories*. New York: William Morrow.

Moss, C. J. (1990). Elephants in Tarangire. *Pachyderm* **13**: 26–30.

Moss, C. J. (1994). Some reproductive parameters in a population of African elephants, *Loxodonta africana*. *Proceedings of the second international NCRR conference*: 284–292. Bambra, C. H. (Ed.). Nairobi: Institute of Primate Research.

Moss, C. J. (1996). Getting to know a population. *Studying elephants*, African Wildlife Foundation Technical Handbook Series **7**: 58–74. Kangwana, K. (Ed.). Nairobi: AWF.

Moss, C. J. & Poole, J. H. (1983). Relationships and social structure of African elephants. *Primate social relationships: an integrated approach*: 315–325. Hinde, R. A. (Ed.). Oxford: Blackwell Scientific Publications.

Mutinda, H. S. (1994). *Assessment of reproductive status of free ranging female African elephants (**Loxodonta africana**) using non-invasive methods*. MSc thesis, University of Nairobi.

Owen-Smith, N. (1993). Comparative mortality rates of male and female kudus: the costs of sexual size dimorphism. *J. Anim. Ecol.* **62**: 428–440.

Packer, C., Tatar, M. & Collins, D. A. (1998). Reproductive cessation in female mammals. *Nature* **392**: 807–811.

Perry, J. S. (1953). The reproduction of the African elephant, *Loxodonta africana*. *Phil. Trans. Roy. Soc. Series B* **237**: 93–149.

Pilgram, T. & Western, D. (1986). Inferring the sex and age of African elephants from tusk measurements. *Biol. Conserv.* **36**: 39–52.

Poole, J. H. (1987). Rutting behaviour in African elephants: the phenomenon of musth. *Behaviour* **102**: 283–316.

Poole, J. H. (1989*a*). Announcing intent: the aggressive state of musth in African elephants. *Anim. Behav.* **37**: 140–152.

Poole, J. H. (1989*b*). Mate guarding, reproductive success and female choice in African elephants. *Anim. Behav.* **37**: 829–849.

Poole, J. H. & Moss, C. J. (1981). Musth in the African elephant, *Loxodonta africana*. *Nature* **292**: 830–31.

Pratt, D. J., Greenway, P. J. & Gwynne, M. D. (1966). A classification of East African rangeland. *J. App. Ecol.* **3**: 369–382.

Reiter, J. & Le Boeuf, B. J. (1991). Life history consequences of variation in age at primiparity in northern elephant seals. *Behav. Ecol. Sociobiol.* **28**: 153–160.

Short, R. V. (1966). Oestrous behaviour, ovulation and the formation of the corpus luteum in the African elephant, *Loxodonta africana*. *E. Afr. Wildl. J.* **4**: 56–68.

Sikes, S. K. (1971). *The natural history of the African elephant*. London: Weidenfeld & Nicholson.

Western, D. (1975). Water availability and its influence on the structure and dynamics of a savannah large mammal community. *E. Afr. Wildl. J.* **13**: 265–286.

Western, D., Moss, C. J. & Georgiadis, N. (1983). Age estimation and population age structure of elephants from footprint dimensions. *J. Wildl. Mgmt.* **47**(4): 1192–1197.

Western, D. & Lindsay, W. K. (1984). Seasonal herd dynamics of a savanna elephant population. *Afr. J. Ecol.* **22**: 229–244.

Weyerhaeuser, F. J. (1982). *On the ecology of the Lake Manyara elephants*. MSc dissertation, Yale University.

Whitehead, H. & Mann, J. (2000). Female reproductive strategies of cetaceans: life histories and calf care. *Cetacean societies: field studies of dolphins and whales*: 219–246. Mann, J., Connor, R. C., Tyack, P. L. & Whitehead, H. (Eds). Chicago: University of Chicago Press.

Whitehouse, A. M. & Hall-Martin, A. J. (2000). Elephants in Addo Elephant National Park, South Africa: reconstruction of the population's history. *Oryx* **34**: 46–55.

Williamson, B. R. (1976). Reproduction in female African elephants in the Wankie National Park, Rhodesia. *S. Afr. J. Wildl. Res.* **6**: 89–93.

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Review Paper

ECOLOGICAL, PHYSIOLOGICAL, GENETIC TRADE-OFFS AND SOCIO-ECONOMIC IMPLICATIONS OF TROPHY HUNTING AS A CONSERVATION TOOL: A NARRATIVE REVIEW

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ABSTRACT

Although the contribution of trophy hunting as a conservation tool is widely recognised, there is perpetual debate and polarization on its sustainability. This review integrates five themes mostly considered in isolation, as independent research fields in wildlife conservation: (1) trophy quality and population ecology of hunted species, (2) behavioural ecology of hunted populations and associated avoidance mechanisms, (3) physiological stress in hunted populations, (4) genetic variability and desirable traits, and (5) socio-economic imperatives in wildlife conservation. We searched for articles on search engines using specific key words and found 350 articles from which 175 were used for this review under five key themes. Population and trophy quality trends of commonly hunted species seem to be declining in some countries. Elevated hunting pressure is reported to influence the flight and foraging behaviour of wildlife thus compromising fitness of hunted species. Selective harvesting through trophy hunted is attributed to the decline in desirable phenotypic traits and increased physiological stress in most hunted species. Though it provides financial resources need for conservation in some countries, trophy hunting works well in areas where animal populations are healthy and not threatened by illegal harvesting and other disturbances. There remains much polarity on the sustainability of trophy hunting in modern-day conservation. More research need to be conducted across the five themes examined in this review for broader analytical analysis and comparison purposes. A new research agenda is needed regarding wildlife sustainable use principles and their sustainability and acceptability in modern-day conservation.

Key words: Wildlife harvesting, wildlife behaviour, landscape of fear, conservation physiology, genetic diversity, trophy hunting bans.

INTRODUCTION

Human societies have depended on the utilisation of wildlife for most of their existence (Ingold *et al*., 1991; Muboko and Murindagomo, 2014). Extractive exploitation of wildlife still remains the foundation of human survival in much of the developing world and to some extent indirectly by the developed world in various capacities (Leader-Williams and Hutton, 2005; Nasi *et al*., 2008; Ochieng *et al*., 2015). However, as a response to the overwhelming exploitation of wildlife species through hunting activities by humans in the 19th century, some mindful hunters promoted various conservation initiatives to promote the protection of the remaining wildlife populations (Adams, 2013). Accordingly, during the early 20th century, hunters played a key role in the establishment of protected areas in various countries and the subsequent institutionalisation of trophy hunting as a conservation tool using the principle of sustainable use (Mahoney, 2009; Mahoney and Jackson III, 2013), supported with proto-ecological motivations and considerations which is now known as ecological theory (Milner-Gulland *et al*., 2009; Treves, 2009).

Trophy hunting, is used to describe hunting by paying tourists, typically with the objective of selecting individuals with exceptional physical attributes (e.g., large horns, tusks, body size, mane or skull length) and usually in the company of a professional hunting guide (Lindsey *et al*., 2007c). Trophy hunting promotes the off-take of older males or individuals that would have crossed the line to post-reproductive stage (Baker, 1997; Damm, 2008). Through a quota system approach, trophy hunting, promotes sustainable off-takes by removing a fraction of natural population growth rates which arguably falls within the compensatory mortality range and has a negligible impact on overall population sizes (Cooley *et al*., 2009; Morrill, 1993). In human-dominated landscapes, humans will continue utilizing wildlife resources especially in areas where wildlife exists and thus sustainable use and incentive-driven conservation has to be at the centre of conservation initiatives (Hutton and Leader-Williams, 2003; Robinson and Bennett, 2004). Consequently, trophy hunting has been institutionalised and has evolved since the early 20th century and is currently practiced worldwide in most continents for example, America (Heffelfinger *et al*., 2013); Europe (Milner *et al*., 2006; Sharp and Wollscheid, 2009); Australia (Albrecht *et al*., 2009; Thiriet, 2009); Asia (Harris *et al*., 2013); Africa (Damm, 2008; Lindsey *et al*., 2006; Loveridge *et al*., 2006).

There is widespread recognition on the potential and significance of trophy hunting as a conservation tool (Baker, 1997; Damm, 2008; Lindsey *et al*., 2007a). Researchers acknowledge the contribution of trophy hunting towards sustainable development in biodiversity rich countries (Baldus, 2008; Fischer *et al*., 2013). More importantly, trophy hunting is considered the most profitable form of consumptive wildlife utilization, and represents a large and growing industry spreading over 23 sub-Saharan African countries (Lindsey, 2008). However, there is perpetual debate, polarisation and lack of consensus among conservation Non-Governmental Organizations, some African governments, animal rights and welfare groups over the acceptability and effectiveness of trophy hunting as a conservation tool (Loveridge *et al*., 2006; Mayaka *et al*., 2004; Sorensen, 2015). This polarisation seems to be exacerbated by a lack of reliable data on the impact of trophy hunting on wildlife species, given that most information on African trophy hunting occurs in unpublished grey literature (Lindsey *et al*., 2007c), and framing of trophy hunting issues in the mass media and social media platforms seem to be emotive and lacks parity (Gandiwa *et al*., 2014; Sorensen, 2015).

Nonetheless, at a broader scale, insufficient governance and institutional failure of regulatory authorities trophy hunting issues (Damm, 2008; Lindsey *et al*., 2007c; Palazy *et al*., 2011) may result in the population decline of hunted species and loss of some desirable traits such as the trophy size or quality (Crosmary *et al*., 2015c). Moreover, the selective nature of trophy hunting may be detrimental to the viability of harvested populations by interfering with the behaviour (de Boer *et al*., 2004; Muposhi *et al*., 2016a; Setsaas *et al*., 2007), physiological (Maréchal *et al*., 2011; Romero and Butler, 2007), genetic and evolutionary (Allendorf *et al*., 2008; Allendorf and Hard, 2009) adaptations of target species. Most of the research related to trophy hunting in mammals and its associated trade-offs is conducted in isolation hence making it difficult to promote effective adaptive management. Accordingly, this review focuses on this topical and emotive subject in modern-day conservation, to advance holistic and pragmatic policy measures in wildlife conservation in relation to sustainable utilization and development.

METHODS

A review of literature was made consulting 175 articles under the five themes outlined below on the basis of their contextual relevancy. The five themes include; (1) trophy quality and population ecology of hunted species, (2) behavioural ecology of hunted populations and associated avoidance mechanisms, (3) physiological stress in hunted populations and ecological traps, (4) genetic variability and desirable traits, and (5) socio-economic imperatives in wildlife conservation policy measures. The findings were thereafter presented in the five themes and further integrated into a conceptual framework based on the review.

RESULTS AND DISCUSSION

Trophy quality and population ecology of hunted wildlife species: Most hunters have certain expectations on the choice of individual selected, e.g., presence of animals with exceptional phenotypic traits such as large trophies (Festa-Bianchet, 2007). Accordingly, the sustainability of trophy hunting may be compromised when populations of preferred species with the desirable traits shrink in numbers and extent of occurrence (Nuzzo and Traill, 2013; Palazy *et al*., 2012). Temporal and spatial trophy quality changes may have adverse effects on the sustainability of the hunting industry (von Brandis and Reilly, 2007). Declines in trophy quality of preferred wildlife species have been reported in sub-Saharan Africa (Crosmary *et al*., 2013; Loveridge *et al*., 2009; Nuzzo and Traill, 2013; von Brandis and Reilly, 2008; Wilfred, 2012). Nonetheless, Wilfred (2012) argues that negative trends in trophy quality will certainly illicit similar trends in the economy since the trophy hunting mark*et al*igns itself with those countries producing superior trophy animals. Thus, the decrease in trophy quality may jeopardize the conservation potential of hunting areas, which would be a major concern in southern Africa where hunting zones represent over half of the total area of protected lands (von Brandis and Reilly, 2007).

Few attempts have been made in southern Africa to chronicle such trends other than those found in grey literature. As such, Loveridge *et al*. (2009) argues that it is imperative to ensure that monitoring of the population size, trends in trophy quality and hunting success in most preferred and common trophy species is done even though it may be expensive, time consuming and may require extensive expertise. Monitoring of trophy sizes offers an understanding of the short and long-term changes in populations and trophy quality parameters (e.g., horn or tusk size) of hunted species (Milner-Gulland and Rowcliffe, 2007; Wilfred, 2012). There is need to probe into whether trophy size matter for hunters or it is the overall experience these hunters rather than the ultimate traits of the target species. It is likely that with the evolution of hunters and trophy hunting as a sport, the size of the trophy may not matter due to different satisfaction needs by the hunters (Holbrook and McSwain, 1991). It is believed that with time, the total hunting experience would outweigh the need for shooting the target species (Holbrook and McSwain, 1991; Voeller, 2005), and as such the trophy quality may not matter.

Fenberg and Kaustuv (2008) outline some ecological impacts of trophy hunting in wildlife species such as: (1) changes in body size, (2) growth and survival of offspring, mortality rates, (3) reproductive investment, (4) growth size and age (size) at maturity, and (5) changes in the sex ratio of harvested populations. The effect of size-selective harvesting on the body size and phenotypic traits in wildlife species has been observed in bighorn (*Ovis canadensis*) male population due to hunting of trophy rams (Coltman *et al*., 2003). Similarly, Ginsberg and Milner-Gulland (1994) argue that harvested ungulate populations invariably have mortality patterns that deviate significantly from those in non-hunted populations.

A continual decline in the population size of wildlife species in most African countries have been reported with human activities such as trophy hunting and illegal hunting being attributed as the main causes (Ogutu *et al*., 2011; Ripple *et al*., 2015). For instance, declines in wild animal populations as a result of unsustainable exploitation have been observed in Africa, e.g., Umfurudzi Park, Zimbabwe where hunting was at one time suspended as a result of population decline (Muposhi *et al*., 2014a; Muposhi *et al*., 2014b). However, declines in species density elsewhere, have been linked to other factors other than trophy hunting, e.g., droughts (Ogutu *et al*., 2008; Ogutu and Owen-Smith, 2003), habitat change and illegal harvesting among others (Gandiwa, 2013; Muboko *et al*., 2014; Ottichilo *et al*., 2000). Nonetheless, there remain high densities of wildlife species in some hunting areas of Zimbabwe, South Africa and Botswana (Dunham, 2012; Lindsey *et al*., 2009). Similar trends where wildlife densities remained stable in southern African countries were also observed by Craigie *et al*. (2010). However, in cases where off-take rates are low and conservative and rigorously managed, trophy hunting areas maybe valuable conservation zones wildlife species (Crosmary *et al*., 2015a).

Behavioural ecology of hunted populations and associated avoidance mechanisms: Human recreation in natural areas have been observed to increase the level of disturbance to wildlife (Maréchal *et al*., 2011; Stankowich, 2008). Integrating an understanding of behaviour into wildlife conservation is becoming more important (Anthony and Blumstein, 2000). Improving the knowledge of how and to what extent the impact of anthropogenic disturbance (e.g. trophy hunting) has on the welfare and behaviour of wildlife in natural ecosystems may provide valuable information to managers and planners in conservation (Tingvold *et al*., 2013).

Trophy hunting, like predation, tends to alter wildlife behaviour by influencing the perceived risk (Muposhi *et al*., 2016a) thus shaping the landscape of fear for most wildlife species (Ciuti *et al*., 2012; Coleman and Hill, 2014; Rösner *et al*., 2014). Kilgo *et al*. (1998) observed that hunted deer evaded roads and increased nocturnal behaviour as an avoidance mechanism that has much implications on photographic tourism. Similarly, sable antelope (*Hippotragus niger*) has also been observed to avoid would be suitable habitat patches with high hunting pressure in favour of habitats areas as an avoidance strategy (Ndaimani *et al*., 2013). Instances where animals shift their habitat in response to hunting have been noted in impala (*Aepyceros melampus*) (Setsaas *et al*., 2007) and wildebeest (*Connochaetes taurinus*) (Tambling and Du Toit, 2005). This hunting aversion strategy may also come as a cost and eventually become an indirect source of stress to individuals subjected to high hunting pressure (Verdade, 1996). However, this coping strategy may result in ecological traps as individuals may prefer to use poor habitats (i.e., habitats with lower feed quality (Kilgo *et al*., 1998)) over the most suitable ones due to hunting disturbance aversion (Abrams *et al*., 2012; Battin, 2004; Robertson and Hutto, 2006).

Trophy hunting may alter the flight behaviour wildlife species in some areas depending on the intensity and frequency of the hunting (de Boer *et al*., 2004; Donadio and Buskirk, 2006). To assess the amount of perceived risk by wildlife species, several studies have used flight initiation distance (FID) as a proxy for fearfulness and anxiety as a result of human disturbances (Stankowich, 2008; Stankowich and Blumstein, 2005). Flight initiation distance is the distance at which an animal begins to flee from an approaching test-person, who in this case is perceived as a predation threat (Setsaas *et al*., 2007). To maximise the chances of survival in the wild, individuals do vary the distance at which they begin to flight from an approaching disturbance or threat (Tarakini *et al*., 2014). However, most of the studies on FID have explored the influence of environmental, predatory or prey condition-based factors (Stankowich and Blumstein, 2005). By influencing flight decisions of hunted wildlife species, trophy hunting is therefore thought to shape the landscape of fear in many human-mediated ecosystems (Muposhi *et al*., 2016a; Rösner *et al*., 2014). Here we consider the landscape of fear to represent the relative levels of ‘predation’ risk as peaks and valleys that reflect the level of fear a certain trophy species experiences in different parts of its habitat

(Laundré *et al*., 2010). There is a general realization that our understanding of the relationship between trophy hunting and behaviour is limited (de Boer *et al*., 2004). Incorporating behavioural studies in the development of management plans is therefore important in conservation especially under closed environments or areas with poor dispersal options for wildlife species. We present a model showing the different factors that may shape the landscape of fear in a human-mediated ecosystem where trophy hunting is practiced (Figure 1).

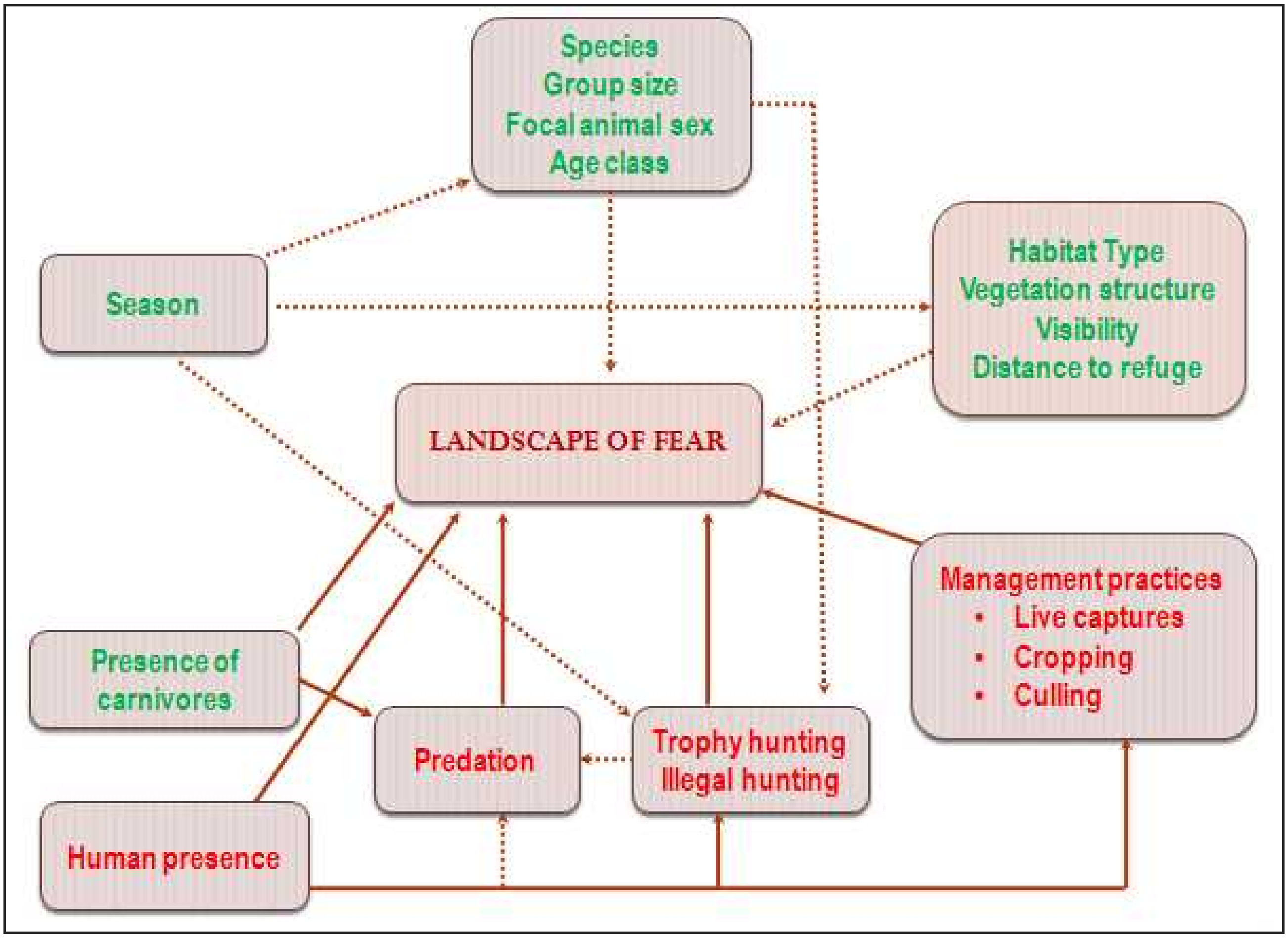

Figure 1. Conceptual model showing factors that may shape the landscape of fear in wildlife occurring in human-mediated ecosystems. Solid arrows show direct relationships whereas dotted arrows indicate indirect relationships.

Physiological stress in hunted populations and ecological traps: Concern has been raised over human activities in conservation areas, that may impact negatively on animals at emotional level as well as the physiological level (Bekoff, 2008). Conservation physiology is an integrative scientific discipline applying physiological concepts, tool and knowledge to characterize biological diversity and its ecological implications, understanding and predicting how organisms, populations and ecosystems respond to environmental change and stressors and solving conservation problems across the range of taxa (Cooke *et al*., 2013). The incorporation of physiology and ecology enable conservationists to understand the impacts of physiological effects related to anthropogenic disturbances and environmental perturbations at the individual level (Metcalfe *et al*., 2012). When the physiological knowledge is incorporated into ecological models, it can improve predictions of organism responses to environmental and human disturbances and provide tools to support management decisions (Cooke *et al*., 2013; Metcalfe *et al*., 2012). However, there are limited studies on the impact of tourism activities especially trophy hunting on both anxiety and physiological stress of wildlife subjected to elevated hunting levels (Maréchal *et al*., 2011).

Although trophy hunting related disturbances may represent a form of selective force in natural populations (Reeder and Kramer, 2005), most wildlife species have evolved a suite of behavioural and physiological strategies to cope with such disturbances (Baker *et al*., 2013). Wildlife species are known to cope with disturbances (e.g., presence of humans, noise from rifles) by mounting a stress response through by activating the hypothalamus-pituitary-adrenal axis and releasing glucocorticoid (GC) stress hormones such as cortisol and corticosterone (Romero, 2004; Setchell *et al*., 2010). Nevertheless, chronic stress and the corresponding elevated GC concentrations due to high hunting pressure may have deleterious effects on fitness and survival of targeted wildlife species (Sheriff *et al*., 2009). Repeated and frequent exposure to trophy hunting may cause prolonged stress and elevated GC concentrations in affected species. The cascading effects of elevated GC concentrations may lead to inhibition of growth, reproductive and immune system and alteration of animal behaviour (Romero, 2004). Setchell *et al*. (2010) noted that in some wildlife species, high GC concentrations may cause suppressed immunity system leading to elevated gastrointestinal parasitic infections. We argue that the amplitude and duration of stress responses as a result of trophy related disturbances may often correlate with the overall health of targeted species. Therefore, individual physiological responses to mild disturbances can be equally critical to the long-term survival of species (French *et al*., 2010).

Studies on stress physiology have concentrated on the influence of habitat disturbances (Ahlering *et al*., 2011; Deng *et al*., 2014; Tingvold *et al*., 2013), habitat quality (Creel *et al*., 2013; Dantzer *et al*., 2011), tourism (Maréchal *et al*., 2011), logging and hunting (Rimbach *et al*., 2013), translocation (Jachowski *et al*., 2013), climate change (Chown *et al*., 2010; Fuller *et al*., 2010) and other environmental stressors (Kight and Swaddle, 2011; Laske *et al*., 2011) among others. There are few studies done on stress physiology related to trophy hunting except for a few studies that report on poaching, social and ecological pressure on African elephant (Ahlering *et al*., 2011; Foley *et al*., 2001; Gobush *et al*., 2008). There is need for research on the possible physiological effects of trophy hunting on wildlife species and their persistence in natural ecosystems. To inform adaptive management initiatives in wildlife conservation programs, researches that seek to integrate the physiological mechanisms and behaviour responses into ecological models is critical (Metcalfe *et al*., 2012).

Genetic variability and desirable traits: Trophy hunters invariably exhibit some preference towards the choice of animal to harvest at any given time (Mysterud *et al*., 2006). Trophy hunting can be considered as an artificial selection approach where the natural selection, historically imposed by predation would have been modified or magnified in natural ecosystems (Allendorf and Hard, 2009). Nonetheless, predation does select individuals with weaker survival capabilities (except for a few ambush predators) whereas trophy hunters opt for those individuals in a population with superior and more desirable traits than others. Artificial selection through trophy hunting is therefore likely a pervasive force, whose potential genetic and evolutionary changes has far reaching conservation implications (Festa-Bianchet, 2003; Schneiders *et al*., 2012).

Genetic variation is considered an important factor in the long-term persistence of a population, especially in the ability of the population to respond to environmental change (Spielman *et al*., 2004). Allendorf *et al*. (2008) suggests that it is crucial to incorporate genetic considerations in wildlife management plans for harvested populations because hunting has the potential to cause three types of genetic changes, i.e., (1) alteration of population subdivisions, (2) loss of genetic variation and, (3) selective genetic changes. Usually traits associated with fitness are correlated with genetic variation, such as growth and development, fertility, survival, disease resistance and metabolic efficiency (Deyoung and Honeycutt, 2005). These factors have an impact on the sustainability of wildlife conservation programs in human mediated ecosystems. Regrettably, few studies have been conducted in most human-mediated tropical ecosystems which are endowed with much diversity and are preferred hunting destinations of trophy hunters.

Most studies on genetic and evolutionary impacts of selective harvesting have been done in fishes and a few wild ungulates as reviewed by Fenberg and Kaustuv (2008). However, it is important to take some cues from fisheries research and apply some of the molecular techniques in mammalian species exposed to hunting for management purposes (DeYoung and Brennan, 2005). This would be possible because the application of genetic analysis is becoming increasingly feasible and cost effective primarily due to recent advances in the number and types of genetic markers available, development of sophisticated data analysis methods, and increased automation of laboratory instrumentation (Deyoung and Honeycutt, 2005). With such advances in molecular ecology, it is possible to explore the evolutionary and or genetic changes associated with trophy hunting of wildlife species over time for management purposes.

Socio-economic imperatives in wildlife conservation policy measures: The sustainability of trophy hunting as a conservation tool has of recent years challenged the global community from moral, ethical and ecological perspective (Macdonald *et al*., 2016; Nelson *et al*., 2016; Ripple *et al*., 2016). Despite the polarity and lack of consensus among stakeholders, some researchers argues that if trophy hunting is given its rightful place in conservation; it may not compromise the population viability of a targeted wildlife population (Crosmary *et* *al*., 2015b; Damm, 2015; Di Minin *et al*., 2016b; Lindsey *et al*., 2016). Proposed trophy hunting bans by some countries may result in the loss of wildlife habitats due to the reduction of competitiveness of wildlife based land uses relative to ecologically unfavourable alternatives such as livestock and cropping (Di Minin *et al*., 2016a; Lindsey *et al*., 2012; McShane *et al*., 2011). We argue that the use of mutual gains concept in addressing contested and highly polarised conservation issues like trophy hunting becomes important (Dallimer and Strange, 2015; Fay, 2007). To achieve desired conservation outcomes, there is dire need to combining socio-ecological, and ecological approaches to understanding how people and wildlife are linked and the associated challenges in modern day conservation (Carter *et al*., 2014).

Trophy hunting is a common practice in several African countries because they are known for: (a) the prevalence of wildlife utilization, (b) a well established hunting industry and (c) an extraordinary alpha and gamma diversity of suitable and target wildlife species for trophy hunters. Countries like Namibia, Zambia and Zimbabwe have used trophy hunting to achieve the objectives of community based natural resources management through the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE), Communal Wildlife Conservancies and Administrative Management Design for Game Areas (ADMADE) (Bond, 2001; Gibson and Marks, 1995; Lewis and Alpert, 1997; Weaver and Skyer, 2003), respectively. For example, in Zimbabwe, CAMPFIRE is known to have generated over US$20 million of transfers to the participating communities during 1989-2001, of which 89% of which came from trophy hunting (Frost and Bond, 2008). Consequently, trophy hunting has contributed to poverty alleviation, local empowerment and community development though more administrative and legal structures that underlie the country's political ecology need to be strengthened (Logan and Moseley, 2002; Thakadu *et al*., 2005). On the contrast, in protected areas, i.e., where there is no trophy hunting, incidences of illegal hunting have been persistent at the detriment of the species under conservation such as elephants (Gandiwa *et al*., 2013; Muboko *et al*., 2016; Muboko *et al*., 2014).

A ban in trophy hunting would therefore result in the collapse of a well developed industry and revenue stream (Lindsey *et al*., 2007a) that would be difficult to replace. A loss of income and revenue from trophy hunting and the promotion of photographic tourism as an option would not be sustainable in most African countries. Most African protected areas are thought to be not functioning efficiently and are underperforming in ecological, economic and social terms because sometimes numbers of photographic tourists are low (Hamilton *et al*., 2007). Because of poor conservation funding issues, trade bans or enlisting species as endangered will not stop these species from declining because the greatest threat to species persistence has been poaching, habitat loss and human-wildlife conflicts (Di Minin *et al*., 2016a; Trethowan *et al*., 2011) and not sustainable utilization through trophy hunting.

Alternative sources of income through photographic tourism have been applied in other countries such as Botswana (Coria and Calfucura, 2012; Mbaiwa, 2015). However, such alternatives are suitable in countries with political stability whose perceived risk by tourists is low (Lepp *et al*., 2011; Lindsey *et al*., 2007b; Sönmez and Graefe, 1998). Accordingly wildlife managers and conservationists should consider among other interventions but not limited to: (1) prioritizing funds for habitat management and protection, water provision, anti-poaching operations, (2) implementing age based regulations in sustainable off-takes programs, wildlife conservation and trophy hunting policy reviews and strengthening implementation initiatives, and (3) improving governance of trophy hunting in order to curb corruption and illegal trade of wildlife species and or products (Lindsey *et al*., 2012).

However, the sustainability of trophy hunting industry may be hinged upon several other factors such as international legislation and local governance issues (Balme *et al*., 2010; Peterson, 2014; Shanee, 2012); communication and branding aspects of hunting related issues (Campbell and Mackay, 2009; Damm, 2015); stakeholder and hunter perceptions, hunter attitudes and motivations (Mangun *et al*., 2007; Miller, 2003); hunting ethics issues (Fox and Bekoff, 2011; Lunney, 2012; Paquet and Darimont, 2010); hunting leases and hunting fees (Mozumder *et al*., 2007; Rhyne *et al*., 2009), and marketing of permits and service (Little and Berrens, 2008) among others. Although these issues are being researched nowadays, we argue that they are being done in isolation without integrating and synthesizing them for the purposes of adaptive management.

Integration of factors affecting trophy hunting: We note that trophy hunting may have impacts on the ecology, physiology and genetic aspects of targeted wildlife species though the severity of these depends on the hunting pressure exposed to these species. In addition, in some cases, trophy hunting has been observed to cause a reduction in the trophy size of species over time. Some hunters prefer hunting destinations where there are species with exceptional trophy quality traits and high hunting success. We argue that low trophy quality may reduce the attractiveness of a trophy hunting destination resulting in loss of income and reduced funds for conservation and policy evolution and implementation. Here we present a conceptual framework that integrates the ecological, physiological, genetic and socio-economic dimensions of trophy hunting as a conservation tool (Figure 2).

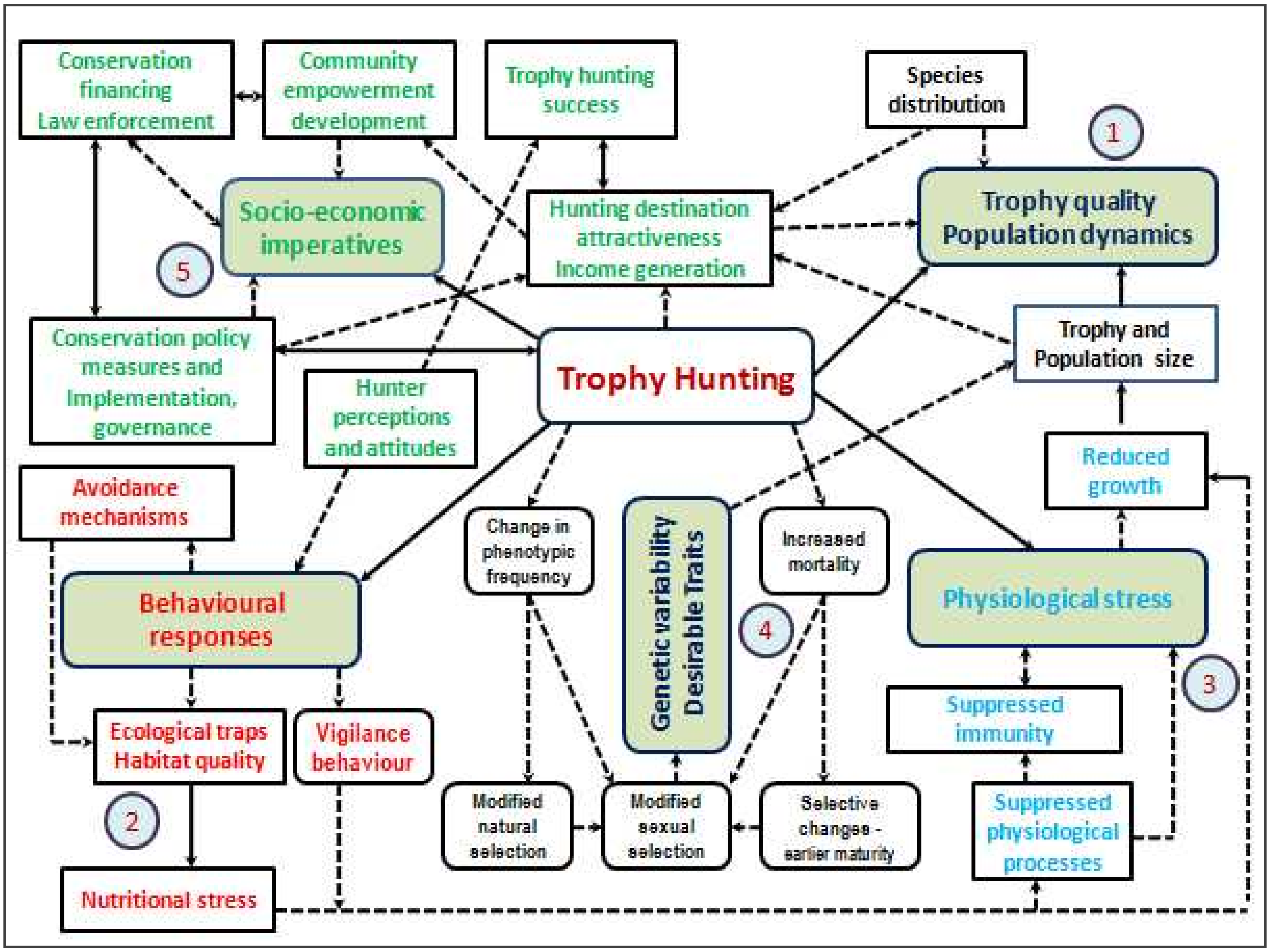

Figure 2: Conceptual framework for the integrated trophy hunting trade-offs: (1) trophy quality and population ecology of hunted species, (2) behavioural ecology of hunted populations and associated avoidance mechanisms, (3) physiological stress in hunted populations (4) genetic variability and desirable traits, and (5) socio-economic imperatives in wildlife conservation policy measures. Notes: Solid arrows indicate direct relationships; dotted arrows indicated indirect relationships between factors.

We believe that the nature and level of trophy hunting may directly or indirectly influence the behaviour of targeted species thereby shaping the landscape of fear for these species. Depending with the magnitude of behavioural plasticity and shifts in the habitat use as an avoidance mechanism, trophy hunting may cause ecological traps where individuals may utilize poor habitats which may result in nutritional stress. The direct effect of nutritional stress and the physiological stress emanating from the hunting pressure may reduce fitness of individuals hence may be more susceptible to parasitic infections. The cascading effects of all these may result in population decline of the affected species.

On the other hand, the selective nature of trophy hunting may result in the loss of genetic variability and low population growth of affected populations if there is minimum management intervention. Trophy hunting may result in a decline in the trophy size and possible increase in hunting effort which may reduce the attractiveness of a hunting destination (Muposhi *et al* 2016b). These factors combined with trophy hunting restrictions may result in loss of income which may translate to poor conservation financing and a resultant loss of species due to habitat loss and illegal hunting. Accordingly, a concerted effort towards the integration of these impacts in wildlife research and management interventions is essential in the conservation of wildlife species and their habitats.

Conclusion: There is mounting evidence of a downward trend in trophy quality of commonly hunted wildlife species associated with a decline in population sizes in most southern African countries. Aspects on behavioural change and the creation of ecological traps as a result of trophy hunting are however still less studied or documented. There is an increasing awareness on the need to incorporate stress physiology research aspects on trophy hunting activities albeit very little research on effect of trophy hunting on targeted species. Wildlife species develop behavioural mechanisms to evade trophy hunting disturbances and as such may reduce their reproductive success, suppress immunity and low population growth. Moreover, trophy hunting may induce nutritional stress and low fitness levels which may reduce resilience to parasitic infections and diseases over time if not managed properly. There is lack of integration of the five themes on trophy hunting as a conservation tool examined in this paper for broader analytical analysis and comparison purposes. It is recommended that conservationists should (1) consider the impacts of trophy hunting in entirety and endeavour to reduce their impact on wildlife species; (2) promote the enactment of progressive policies and action plans that promote innovation in the management of wildlife species e.g. establishing realistic and ecologically sound harvesting models and active monitoring of trophy hunts for sustainability.

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REFERENCES

Abrams, P.A., L. Ruokolainen, B.J. Shuter, and K.S. McCann. (2012). Harvesting creates ecological traps: Consequences of invisible mortality risks in predator-prey metacommunities. Ecology 93: 281-293.

Adams, W.M. (2013). Against extinction: the story of conservation. Earthscan, London.

Ahlering, M.A., J.J. Millspaugh, R.J. Woods, D. Western, and L.S. Egger. (2011). Elevated levels of stress hormones in crop-raiding male elephants. Anim Conserv. 14: 124-130.

Albrecht, G., C.R. McMahon, D.M. Bowman, and C.J. Bradshaw. (2009). Convergence of culture, ecology, and ethics: Management of feral swamp buffalo in northern Australia. J. Agric. Environ. Ethics. 22: 361-378.

Allendorf, F.W., P.R. England, G. Luikart, P.A. Ritchie, and N. Ryman. (2008). Genetic effects of harvest on wild animal populations. TTrends Ecol Evolut. 23: 327-337.

Allendorf, F.W., and J.J. Hard. (2009). Human-induced evolution caused by unnatural selection through harvest of wild animals. Proc. Natl. Acad. Sci. U.S.A. 106: 9987-9994.

Anthony, L.L., and D.T. Blumstein. (2000). Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce effective population size. Biol. Cons. 95: 303-315.

Baker, J.E. (1997). Trophy Hunting as a Sustainable Use of Wildlife Resources in Southern and Eastern Africa. J. Sustain. Tour. 5 306-321.

Baker, M.R., K.S. Gobush, and C.H. Vynne. (2013). Review of factors influencing stress hormones in fish and wildlife. J. Nat. Conserv. 25: 309-318.

Baldus, R.D. (2008). Wildlife: Can pay its way or must be subsidized? In: R. D. Baldus, G. R. Damm and K. Wollscheid (eds.) Best Practices in Sustainable Hunting- A guide to best practices from around the world. p 12-16. International Council for Game & Wildlife Conservation, Hungary.

Balme, G.A., L.T. Hunter, P. Goodman, H. Ferguson, J. Craigie, and R. Slotow. (2010). An adaptive management approach to trophy hunting of leopards Panthera pardus: a case study from KwaZulu-Natal, South Africa Biology and conservation of wild felids. p 341-352. Oxford University Press, Oxford, United Kingdom.

Battin, J. (2004). When good animals love bad habitats: ecological traps and the conservation of animal populations. Biol. Conserv. 18: 1482-1491.

Bekoff, M. (2008). Increasing our compassion footprint: the animals' manifesto. Zygon 43: 771-781.

Bond, I. (2001). CAMPFIRE & the incentives for institutional change. In: D. Hulme and M. Murphree (eds.) African Wildlife and Livelihoods: The promise and performance of community conservation. p 227-243. Cab Direct.

Campbell, M., and K.J. Mackay. (2009). Communicating the Role of Hunting for Wildlife Management. Hum. Dimens. Wildl. 14 21-36.

Carter, N.H., A. Viña, V. Hull, W.J. McConnell, W. Axinn, D. Ghimire, and J. Liu. (2014). Coupled human and natural systems approach to wildlife research and conservation. Ecol. Soc. 19: 43.

Chown, S.L., A.A. Hoffmann, T.N. Kristensen, M.J. Angilletta Jr, N.C. Stenseth, and C. Pertoldi. (2010). Adapting to climate change: a perspective from evolutionary physiology. Clim Res. 43: 3-15.

Ciuti, S., T.B. Muhly, D.G. Paton, A.D. McDevitt, M. Musiani, and M.S. Boyce. (2012). Human selection of elk behavioural traits in a landscape of fear. Proc. R. Soc. Biol. Sci. Ser. B: rspb20121483.

Coleman, B.T., and R.A. Hill. (2014). Living in a landscape of fear: the impact of predation, resource availability and habitat structure on primate range use. Anim. Behav. 88: 165-173.

Coltman, D.W., P. O'Donoghue, J.T. Jorgenson, J.T. Hogg, C. Strobeck, and M. Festa-Bianchet. (2003). Undesirable evolutionary consequences of trophy hunting. Nature 426: 655-657.

Cooke, S.J., L. Sack, C.E. Franklin, A.P. Farrell, J. Beardall, M. Wikelski, and S.L. Chown. (2013). What is conservation physiology? Perspectives on an increasingly integrated and essential science. Conservation Physiology. 1 cot001.

Cooley, H.S., R.B. Wielgus, G.M. Koehler, H.S. Robinson, and B.T. Maletzke. (2009). Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90: 2913-2921.

Coria, J., and E. Calfucura. (2012). Ecotourism and the development of indigenous communities: The good, the bad, and the ugly. Ecol. Econ. 73: 47-55.

Craigie, I.D., J.E. Baillie, A. Balmford, C. Carbone, B. Collen, R.E. Green, and J.M. Hutton. (2010). Large mammal population declines in Africa's protected areas. Biol. Conserv. 143: 2221-2228.

Creel, S., B. Dantzer, W. Goymann, and D.R. Rubenstein. (2013). The ecology of stress: effects of the social environment. Funct. Ecol. 27: 66-80.

Crosmary, W.-G., S. Chamaillé-Jammes, G. Mtare, H. Fritz, and S.D. Côté. (2015a). Decline of sable antelope in one of its key conservation areas: the greater Hwange ecosystem, Zimbabwe. Afr. J. Ecol. 53: 194-205.

Crosmary, W.G., S. Côté, and H. Fritz. (2015b). The assessment of the role of trophy hunting in wildlife conservation. Anim. Conserv. 18: 136-137.

Crosmary, W.G., S.D. Côté, and H. Fritz. (2015c). Does trophy hunting matter to long-term population trends in African herbivores of different dietary guilds? Anim. Conserv. 18: 117-130.

Crosmary, W.G., A.J. Loveridge, H. Ndaimani, S. Lebel, V. Booth, S.D. Côté, and H. Fritz. (2013). Trophy hunting in Africa: long-term trends in antelope horn size. Anim. Conserv. 16: 648-660.

Dallimer, M., and N. Strange. (2015). Why socio-political borders and boundaries matter in conservation. Trends Ecol. Evol. 30: 132-139.

Damm, G.R. (2008). Recreational trophy hunting: "What do we know and what should we do?". In: R. D. Baldus, G. R. Damm and K. Wollscheid (eds.) Best practices in sustainable hunting-A guide to bes practices from around the world. p 5-11. International Council for Game and Wildlife Conservation, Hungary.

Damm, G.R. (2015). Branding hunting. African Indaba eNewsletter 13: 1-3.

Dantzer, B., A.G. McAdam, R. Palme, S. Boutin, and R. Boonstra. (2011). How does diet affect fecal steroid hormone metabolite concentrations? An experimental examination in red squirrels. Gen. Comp. Endocrinol. 174: 124-131.

de Boer, H.Y., L. Van Breukelen, M.J. Hootsmans, and S.E. Van Wieren. (2004). Flight distance in roe deer Capreolus capreolus and fallow deer Dama dama as related to hunting and other factors. Wildl. Biol. 10: 35-41.

Deng, H., X. Jin, D. Hu, and D. Liu. (2014). Fecal cortisol content of wild giant pandas (*Ailuropoda melanoleuca*) to monitor human disturbance level in natural habitats. Anim. Biol. 64 75-86.

DeYoung, R.W., and L.A. Brennan. (2005). Molecular genetics in wildlife science, conservation, and management. J. Wildl. Manag. 69: 1360-1361.

Deyoung, R.W., and R.L. Honeycutt. (2005). The molecular tool box: Genetic techiques in wildlife ecology and management. J. Wildl. Manag. 69: 1362-1384.

Di Minin, E., N. Leader-Williams, and C.J. Bradshaw. (2016a). Banning Trophy Hunting Will Exacerbate Biodiversity Loss. Trends in Ecology & Evolution 31: 99-102.

Di Minin, E., N. Leader-Williams, and C.J. Bradshaw. (2016b). Trophy Hunting Does and Will Support Biodiversity: A Reply to Ripple *et al*. Trends Ecol. Evol. 31: 495-496.

Donadio, E., and S.W. Buskirk. (2006). Flight behavior in guanacos and vicunas in areas with and without poaching in western Argentina. Biol. Conserv. 127: 139-145.

Dunham, K.M. (2012). Trends in populations of elephant and other large herbivores in Gonarezhou National Park, Zimbabwe, as revealed by sample aerial surveys. Afr. J. Ecol. 50: 476-488.

Fay, D.A. (2007). Mutual gains and distributive ideologies in South Africa: theorizing negotiations between communities and protected areas. Hum. Ecol. 35: 81-95.

Fenberg, P.B., and R. Kaustuv. (2008). Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Mol. Ecol. 17: 209-220.

Festa-Bianchet, M. (2003). Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. In: M. Festa-Bianchet and M. Apollonio (eds.) Animal Behavior and Wildlife Conservation. p 191-210. Island Press, Washington, D.C.

Festa-Bianchet, M. (2007). Ecology, evolution, and ungulate management. In: T. E. Fulbright and D. G. Hewitt (eds.) Wildlife science: linking ecological theory and management applications. p 183-202. FL: CRC Pres, Boca Raton.

Fischer, A., C. Sandström, M. Delibes-Mateos, B. Arroyo, D. Tadie, D. Randall, F. Hailu, A. Lowassa, M. Msuha, V. Kereži, S. Reljić, J. Linnell, and A. Majić. (2013). On the multifunctionality of hunting – an institutional analysis of eight cases from Europe and Africa. J. Environ. Plann. Manag. 56: 531-552.

Foley, C.A.H., S. Papageorge, and S.K. Wasser. (2001). Noninvsive stress response and reproductive measures of social and ecological pressures in free-ranging african elephants. Conserv. Biol. 15: 1134-1142.

Fox, C.H., and M. Bekoff. (2011). Integrating values and ethics into wildlife policy and management—lessons from North America. Animals 1: 126-143.

French, S.S., D.F. DeNardo, T.J. Greives, C.R. Strand, and G.E. Demas. (2010). Human disturbance alters endocrine and immune responses in the Galapagos marine iguana (*Amblyrhynchus cristatus*). Horm. Behav. 58: 792-799.

Frost, P.G., and I. Bond. (2008). The CAMPFIRE programme in Zimbabwe: payments for wildlife services. Ecolog. Econ. 65: 776-787.

Fuller, A., T. Dawson, B. Helmuth, R.S. Hetem, D. Mitchell, and S.K. Maloney. (2010). Physiological Mechanisms in Coping with Climate Change. Physiol. Biochem. Zool. 83: 713-720.

Gandiwa, E. (2013). The Numbers Game in Wildlife Conservation: Changeability and framing of large mammal numbers in Zimbabwe. PhD Thesis, Graduate School of Production Ecology and Resource Conservation, Wageningen University, Wageningen, Netherlands.

Gandiwa, E., I.M.A. Heitkönig, A.M. Lokhorst, H.H.T. Prins, and C. Leeuwis. (2013). Illegal hunting and law enforcement during a period of economic decline in Zimbabwe: A case study of northern Gonarezhou National Park and adjacent areas. J. Nat. Conserv. 21: 133-142.

Gandiwa, E., S. Sprangers, S. van Bommel, I.M. Heitkönig, C. Leeuwis, and H.H. Prins. (2014). Spill-over effect in media framing: Representations of wildlife conservation in Zimbabwean and international media, 1989–2010. J. Nat. Conserv. 22: 413-423.

Gibson, C.C., and S.A. Marks. (1995). Transforming rural hunters into conservationists: an assessment of community-based wildlife management programs in Africa. World Dev. 23: 941-957.

Ginsberg, J.R., and E. Milner-Gulland. (1994). Sex-biased harvesting and population dynamics in ungulates: Implications for conservation and sustainable use. Conserv. Biol. 8: 157-166.

Gobush, K.S., B.M. Mutayoba, and S.K. Wasser. (2008). Long-Term Impacts of Poaching on Relatedness, Stress Physiology, and Reproductive Output of Adult Female African Elephants. Conserv. Biol. 22: 1590-1599.

Hamilton, K., G. Tembo, G. Sinyenga, S. Bandyopadhyay, A. Pope, B. Guilon, B. Muwele, S. Mann, and J. Pavy (Editors). 2007. The real economic impact of nature tourism in Zambia. Natural Resources Consultative Forum, Government of Zambia, and the World Bank. Overview, Lusaka, Zambia.

Harris, R.B., R. Cooney, and N. Leader-Williams. (2013). Application of the anthropogenic Allee effect model to trophy hunting as a conservation tool. Conserv. Biol. 27: 945-951.

Heffelfinger, J.R., V. Geist, and W. Wishart. (2013). The role of hunting in North American wildlife conservation. Int. J. Environ. Studies. 70: 399-413.

Holbrook, H.T., and L.E. McSwain. (1991). Influence of success on hunter satisfaction and deer management objectives. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 45: 133-139.

Hutton, J.M., and N. Leader-Williams. (2003). Sustainable use and incentive-driven conservation: realigning human and conservation interests. Oryx 37: 215-226.

Ingold, T., D. Riches, and J. Woodburn. (1991). Hunters and gatherers: volume 1: history, evolution and social change; volume 2: property, power and ideology. Berg Publishers Limited.

Jachowski, D., R. Slotow, and J. Millspaugh. (2013). Delayed physiological acclimatization by African elephants following reintroduction. Anim. Conserv. 16: 575-583.

Kight, C.R., and J.P. Swaddle. (2011). How and why environmental noise impacts animals: an integrative, mechanistic review. Ecol. Lett. 14: 1052-1061.

Kilgo, J.C., R.F. Labisky, and D.E. Fritzen. (1998). Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida panther. Conserv. Biol. 12: 1359-1364.

Laske, T.G., D.L. Garshelis, and P.A. Iaizzo. (2011). Monitoring the wild black bear's reaction to human and environmental stressors. BMC Physiol. 11: 13-26.

Laundré, J.W., L. Hernández, and W.J. Ripple. (2010). The landscape of fear: ecological implications of being afraid. OEJ. 3: 1-7.

Leader-Williams, N., and J.M. Hutton (Editors). 2005. Does extractive use provide opportunities to offset conflicts between people and wildlife? Conservation Biology Series, 9. Cambridge University Press, Cambridge, 140-161 pp.

Lepp, A., H. Gibson, and C. Lane. (2011). Image and perceived risk: A study of Uganda and its official tourism website. Tourism Manage. 32: 675-684.

Lewis, D.M., and P. Alpert. (1997). Trophy hunting and wildlife conservation in Zambia. Conserv. Biol. 11: 59-68.

Lindsey, P., G. Balme, P. Funston, P. Henschel, and L.T. Hunter. (2016). Life after Cecil: Channelling global outrage into funding for conservation in Africa. Conserv Lett. 9(4): 296–301

Lindsey, P., S. Romanach, and H. Davies-Mostert. (2009). The importance of conservancies for enhancing the value of game ranch land for large mammal conservation in southern Africa. J. Zool. 277: 99-105.

Lindsey, P., P. Roulet, and S. Romanach. (2007a). Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. Biol. Conserv. 134: 455-469.

Lindsey, P.A. (2008). Trophy hunting in sub-Saharan Africa: economic scale and conservation significance. In: R. D. Baldus, G. R. Damm and K. Wollscheid (eds.) Best Practices in Sustainable Hunting–A Guide to Best Practices from Around the World. p 41-47. International Council for Game and Wildlife Conservation, Hungary

Lindsey, P.A., R. Alexander, L.G. Frank, A. Mathieson, and S.S. Romanach. (2006). Potential of trophy hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable. Anim. Conserv. 9: 283-291.

Lindsey, P.A., R. Alexander, M. Mills, S. Romanach, and R. Woodroffe. (2007b). Wildlife viewing preferences of visitors to protected areas in South Africa: implications for the role of ecotourism in conservation. J. Ecotourism 6: 19-33.

Lindsey, P.A., G.A. Balme, V.R. Booth, and N. Midlane. (2012). The significance of African lions for the financial viability of trophy hunting and the maintenance of wild land. PloS One 7: e29332.

Lindsey, P.A., L.G. Frank, R. Alexander, A. Mathieson, and S.S. Romanach. (2007c). Trophy hunting and conservation in Africa: problems and one potential solution. Conserv. Biol. 21: 880-883.

Little, J.M., and R.P. Berrens. (2008). The Southwestern Market for Big- Game Hunting Permits and Services: A Hedonic Pricing Analysis. Hum. Dimens. Wildl. 13: 143-157.

Logan, B.I., and W.G. Moseley. (2002). The political ecology of poverty alleviation in Zimbabwe's Communal Areas Management Programme for Indigenous Resources (CAMPFIRE). Geoforum 33: 1-14.

Loveridge, A., C. Packer, and A. Dutton. (2009). Science and the recreational hunting of lions. In: B. Dickson, J. Hutton and B. Adams (eds.) Recreational hunting, conservation and rural livelihoods. p 108-124. Wiley-Blackwell, Oxford.

Loveridge, A.J., J.C. Reynolds, and E.J. Milner-Gulland. (2006). Is sport hunting part of conservation? In: D. W. Macdonald and K. Service (eds.) Key Topics in Conservation. p 224-240. Blackwell, Oxford.

Lunney, D. (2012). Wildlife management and the debate on the ethics of animal use. II. A challenge for the animal protection movement. PCB. 18: 81-99.

Macdonald, D.W., K.S. Jacobsen, D. Burnham, P.J. Johnson, and A.J. Loveridge. (2016). Cecil: A Moment or a Movement? Analysis of Media Coverage of the Death of a Lion, Panthera leo. Animals. 6: 26.

Mahoney, S.P. (2009). Recreational hunting and sustainable wildlife use in North America. Recreational hunting, conservation and rural livelihoods: Science and Practice: 266-281.

Mahoney, S.P., and J.J. Jackson III. (2013). Enshrining hunting as a foundation for conservation – the North American Model. Int. J. Environ. Studies. 70: 448-459.

Mangun, J.C., K.W. Throgmorton, A.D. Carver, and M.A. Davenport. (2007). Assessing Stakeholder Perceptions: Listening to Avid Hunters of Western Kentucky. Hum. Dimens. Wildl.12: 157-168.

Maréchal, L., S. Semple, B. Majolo, M. Qarro, M. Heistermann, and A. MacLarnon. (2011). Impacts of tourism on anxiety and physiological stress levels in wild male Barbary macaques. Biol. Conserv. 144: 2188-2193.

Mayaka, T.B., T. Hendriks, J. Wesseler, and H.T. Prins. (2004). Improving the benefits of wildlife harvesting in northern Cameroon: a co-management perspective. Ecol. Econ. 54: 67-80.

Mbaiwa, J.E. (2015). Ecotourism in Botswana: 30 years later. J. Ecotourism 14: 204-222.

McShane, T.O., P.D. Hirsch, T.C. Trung, A.N. Songorwa, A. Kinzig, B. Monteferri, D. Mutekanga, H. Van Thang, J.L. Dammert, and M. Pulgar-Vidal. (2011). Hard choices: making trade-offs between biodiversity conservation and human well-being. Biol. Conserv. 144: 966-972.

Metcalfe, J., W. Le Quesne, W. Cheung, and D. Righton. (2012). Conservation physiology for applied management of marine fish: an overview with perspectives on the role and value of telemetry. Philos. Trans. R. Soc. Lond. B Biol. Sci. 367: 1746-1756.

Miller, C. (2003). Hunter Perceptions and Behaviors Related to Chronic Wasting Disease in Northern Illinois. Hum. Dimens. Wildl. 8: 229-230.

Milner-Gulland, E.J., N. Bunnefeld, and G. Proaktor. (2009). The science of sustainable hunting. In: B. Dickson, J. Hutton and B. Adams (eds.) Recreational hunting, conservation and rural livelihoods. p 75-93. John Wiley & Sons, Oxford.

Milner-Gulland, E.J., and J.M. Rowcliffe. (2007). Conservation and sustainable use: a handbook of techniques. Oxford University Press, Oxford.

Milner, J.M., C. Bonenfant, A. Mysterud, J.M. Gaillard, S. Csanyi, and N.C. Stenseth. (2006). Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. J. Appl. Ecol. 43: 721-734.

Morrill, W.I. (1993). The tourist safari hunter's role in conservation. Paper prepared for Safari Club International, Herndon, VA.

Mozumder, P., C. Meghan Starbuck , R.P. Berrens, and S. Alexander. (2007). Lease and Fee Hunting on Private Lands in the U.S.: A Review of the Economic and Legal Issues. Human Dimensions of Wildlife: An Int. J. 12: 1-14.

Muboko, N., E. Gandiwa, V.K. Muposhi, and T. Tarakini. (2016). Illegal hunting and protected areas: Tourist perceptions on wild animal poisoning in Hwange National Park, Zimbabwe. Tourism Manage. 52: 170-172.

Muboko, N., V. Muposhi, T. Tarakini, E. Gandiwa, S. Vengesayi, and E. Makuwe. (2014). Cyanide poisoning and African elephant mortality in Hwange National Park, Zimbabwe: a preliminary assessment. Pachyderm. 55: 92-94.

Muboko, N., and F. Murindagomo. (2014). Wildlife control, access and utilisation: Lessons from legislation, policy evolution and implementation in Zimbabwe. J. Nat. Conserv. 22: 206-211.

Muposhi, V.K., A. Chanyandura, E. Gandiwa, J. Muvengwi, N. Muboko, P.Taru, and O.L. Kupika. (2014a). Post-release monitoring of diet profile and diet quality of reintroduced African buffalo (Syncerus caffer) in Umfurudzi Park, Zimbabwe. Trop. Conserv. Sci. 7: 440-456.

Muposhi, V.K., M. Ndlovu, E. Gandiwa, J. Muvengwi, and N. Muboko. (2014b). Vegetation structure and composition prior to wildlife reintroductions in southern Umfurudzi Park, Zimbabwe. J. Anim. Plant. Sci. 24: 1680-1690.

Muposhi, V.K., E. Gandiwa, S.M. Makuza, and P. Bartels. (2016a). Trophy hunting and perceived risk in closed ecosystems: Flight behaviour of three gregarious African ungulates in a semi-arid tropical savanna. Austral. Ecol. 41: 809-818.

Muposhi, V.K., E. Gandiwa, P. Bartels, S.M. Makuza, and T.H. Madiri. (2016b). Trophy Hunting and Sustainability: Temporal Dynamics in Trophy Quality and Harvesting Patterns of Wild Herbivores in a Tropical Semi-Arid Savanna Ecosystem. PloS one 11: e0164429.

Mysterud, A., P. Tryjanowski, and M. Panek. (2006). Selectivity of harvesting differs between local and foreign roe deer hunters: trophy stalkers have the first shot at the right place. Biol. Lett. 2: 632-635.

Nasi, R., D. Brown, D. Wilkie, E. Bennett, C. Tutin, G. Van Tol, and T. Christophersen. (2008). Conservation and use of wildlife-based resources: the bushmeat crisis. Secretariat of the Convention on Biological Diversity, Montreal and Center for International Forestry Research (CIFOR), Bogor. Technical Series 33. pp. 51.

Ndaimani, H., A. Murwira, and S. Kativu. (2013). Comparing terrain and vegetation- based visibility for explaining sable flight behaviour in a Southern African savanna. Geocarto. Int. 28: 130-143.

Nelson, M.P., J.T. Bruskotter, J.A. Vucetich, and G. Chapron. (2016). Emotions and the ethics of consequence in conservation decisions: Lessons from Cecil the Lion. Conserv. Lett. 9(4), 302-306

Nuzzo, M.C., and L.W. Traill. (2013). What 50 years of trophy records illustrate for hunted African elephant and bovid populations. Afr. J. Ecol. 52: 250-253.

Ochieng, A., W.M. Ahebwa, and I.J. Visseren-Hamakers. (2015). Hunting for Conservation? The Re-introduction of Sport Hunting in Uganda Examined Institutional Arrangements for Conservation, Development and Tourism in Eastern and Southern Africa. p 139-155. Springer.

Ogutu, J., N. Owen-Smith, H.P. Piepho, and M. Said. (2011). Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977–2009. J. Zool. 285: 99-109.

Ogutu, J., H.P. Piepho, H. Dublin, N. Bhola, and R. Reid. (2008). El Niño-Southern Oscillation, rainfall, temperature and Normalized Difference Vegetation Index fluctuations in the Mara-Serengeti ecosystem. Afr. J. Ecol. 46: 132-143.

Ogutu, J.O., and N. Owen-Smith. (2003). ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. Ecol. Lett. 6: 412-419.

Ottichilo, W.K., J. De Leeuw, A.K. Skidmore, H.H. Prins, and M.Y. Said. (2000). Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. Afr. J. Ecol. 38: 202-216.

Palazy, L., C. Bonenfant, J.-M. Gaillard, and F. Courchamp. (2011). Cat dilemma: too protected to escape trophy hunting? PLoS One 6: e22424.

Palazy, L., C. Bonenfant, J. Gaillard, and F. Courchamp. (2012). Response: rarity, trophy hunting and ungulates. Anim. Conserv. 15: 16-17.

Paquet, P., and C. Darimont. (2010). Wildlife conservation and animal welfare: two sides of the same coin. Anim. Welf. 19: 177-190.

Peterson, M.N. (2014). How Wildlife Management Agencies and Hunting Organizations Frame Ethical Hunting in the United States. Hum. Dimens. Wildl. 19: 523-531.

Reeder, D.M., and K.M. Kramer. (2005). Stress in free-ranging mammals: integrating physiology, ecology, and natural history. J. Mammal. 86: 225-235.

Rhyne, J.D., I.A. Munn, and A. Hussain. (2009). Hedonic Analysis of Auctioned Hunting Leases: A Case Study of Mississippi Sixteenth Section Lands. Hum. Dimens. Wildl. 14: 227-239.

Rimbach, R., A. Link, M. Heistermann, C. Gómez-Posada, N. Galvis, and E.W. Heymann. (2013). Effects of logging, hunting, and forest fragment size on physiological stress levels of two sympatric ateline primates in Colombia. Conservation Physiology. 1: cot031.

Ripple, W.J., T.M. Newsome, and G.I. Kerley. (2016). Does Trophy Hunting Support Biodiversity? A Response to Di Minin *et al*. Trends Ecol. Evol. 31: 495-496.

Ripple, W.J., T.M. Newsome, C. Wolf, R. Dirzo, K.T. Everatt, M. Galetti, M.W. Hayward, G.I. Kerley, T. Levi, and P.A. Lindsey. (2015). Collapse of the world's largest herbivores. Science Advances 1: e1400103.

Robertson, B.A., and R.L. Hutto. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87: 1075-1085.

Robinson, J.G., and E.L. Bennett. (2004). Having your wildlife and eating it too: an analysis of hunting sustainability across tropical ecosystems. Anim. Conserv. 7: 397-408.

Romero, L.M. (2004). Physiological stress in ecology: lessons from biomedical research. Trends Ecol. Evol. 19 249-255.

Romero, L.M., and L.K. Butler. (2007). Endocrinology of stress. International J. Comp. Psychol. 20: 89-95.

Rösner, S., E. Mussard-Forster, T. Lorenc, and J. Müller. (2014). Recreation shapes a "landscape of fear" for a threatened forest bird species in Central Europe. Landsc. Ecol. 29: 55-66.

Schneiders, A., T.V. Daele, W.V. Landuyt, and W.V. Reeth. (2012). Biodiversity and ecosystem services: Complementary approaches for ecosystem management. Ecol. Indic. 21: 123-133.

Setchell, J.M., T. Smith, E.J. Wickings, and L.A. Knapp. (2010). Stress, social behaviour, and secondary sexual traits in a male primate. Horm. Behav. 58: 720-728.

Setsaas, T.H., T. Holmern, G. Mwakalebe, S. Stokke, and E. Røskaft. (2007). How does human exploitation affect impala populations in protected and partially protected areas?–A case study from the Serengeti Ecosystem, Tanzania. Biol. Conserv. 136: 563-570.

Shanee, N. (2012). Trends in local wildlife hunting, trade and control in the Tropical Andes Biodiversity Hotspot, northeastern Peru. Endang. Species Res 19: 177-186.

Sharp, R., and K.U. Wollscheid. (2009). An overview of recreational hunting in North America, Europe and Australia. In: B. Dickson, J. Hutton and W. A. Adams (eds.) Recreational hunting, conservation and rural livelihoods. Science and practice , London. pp. p 25-38. Wiley-Blackwell, U.K.

Sheriff, M.J., C.J.Krebs, and R. Boonstra. (2009). The physiology of predator stress in free-ranging prey. J. Animal Ecology 78: 1103-1105.

Sönmez, S.F., and A.R. Graefe. (1998). Influence of terrorism risk on foreign tourism decisions. Ann. Touris. Res. 25: 112-144.

Sorensen, C.A.E. (2015). Trophy Hunting in the US Media: A macro-and micro-level frame analysis, Central European University, Budapest.

Spielman, D., B.W. Brook, and R. Frankham. (2004). Most species are not driven to extinction before genetic factors impact them. Proceedings of the National Academy of Sciences of the United States of America 101: 15261-15264.

Stankowich, T. (2008). Ungulate flight responses to human disturbance: a review and meta-analysis. Biol. Conserv. 141: 2159-2173.

Stankowich, T., and D.T. Blumstein. (2005). Fear in animals: a meta-analysis and review of risk assessment. Proc. R. Soc. Lond. B Biol. Sci. 272: 2627-2634.

Tambling, C.J., and J.T. Du Toit. (2005). Modelling wildebeest population dynamics: implications of predation and harvesting in a closed system. J. Appl. Ecol. 42: 431-441.

Tarakini, T., W.-G. Crosmary, H. Fritz, and P. Mundy. (2014). Flight behavioural responses to sport hunting by two African herbivores. S. Afr. J. Wildl. Res. 44: 76-83.

Thakadu, O., K. Mangadi, F. Bernard, and J. Mbaiwa. (2005). The economic contribution of safari hunting to rural livelihoods in the Okavango: The case of Sankuyo village. Botsw Notes Rec 37: 22-39.

Thiriet, D. (2009). Recreational hunting–regulation and animal welfare concerns. In: P. Sankoff and S. White (eds.) Animal Law in Australasia. p 259-288. Federation Press, Sydney, NSW, Australia.

Tingvold, H.G., R. Fyumagwa, C. Bech, L.F. Baardsen, H. Rosenlund, and E. Røskaft. (2013). Determining adrenocortical activity as a measure of stress in African elephants (Loxodonta africana) in relation to human activities in Serengeti ecosystem. Afr. J. Ecol. 51: 580-589.

Trethowan, P., P. Funston, and R. Groom. (2011). Response to the March 2011 petition to the list African lion (*Panthera leo*) as endangered. p 38.

Treves, A. (2009). Hunting for large carnivore conservation. J. Appl. Ecol. 46: 1350-1356.

Verdade, L.M. (1996). The influence of hunting pressure on the social behavior of vertebrates. Rev Bras Biol 56: 1-13.

Voeller, C. (2005). " He Only Looked Sad the Same Way I Felt": The Textual Confessions of Hemingway's Hunters. The Hemingway Review 25: 63-76.

von Brandis, R.G., and B.K. Reilly. (2007). A temporal analysis of trophy quality in South Africa: has trophy quality changed over time. S. Afr. J. Wildl. Res. 37: 153-158.

von Brandis, R.G., and B.K. Reilly. (2008). Spatial variation in trophy quality of popular hunted ungulate species in South Africa. S. Afr. J. Wildl. Res. 38: 17-21.

Weaver, L.C., and P. Skyer. 2003. Conservancies: Integrating wildlife land-use options into the livelihood, development and conservation strategies of Namibian communities, US AID/WWF, South Africa.

Wilfred, P. (2012). Trophy hunting and trophy size in Ugulla Game Reserve, Western Tanzania. Tanz. J. Sci. 38: 111-122.

THE LION’S SHARE?

ON THE ECONOMIC BENEFITS OF TROPHY HUNTING

A REPORT PREPARED BY ECONOMISTS AT LARGE
FOR HUMANE SOCIETY INTERNATIONAL

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SUMMARY

Pro-hunting group Safari Club International (SCI) recently published material entitled 'The Conservation Equation'. The claimed 'equation' is a simple one – that trophy hunting equals conservation of African wildlife and habitat.

SCI's claims are based on a commissioned study by consultants Southwick Associates. This study estimated the economic benefits of trophy hunting in eight African countries – Botswana, Ethiopia, Mozambique, Namibia, South Africa, Tanzania, Zambia and Zimbabwe (Southwick, 2015). They claim that the overall economic benefit from their estimated 18,815 trophy hunter visits is $USD 426 million to the studied eight countries, and that trophy hunting directly and indirectly supports 53,000 jobs.

In fact, trophy hunting contributes significantly less to the eight study economies, job markets, and African conservation. Reviewing the study behind The Conservation Equation, this analysis finds that:

- Economic benefits have been heavily overstated, with Southwick (2015) claiming that trophy hunting contributes $426 million; a more realistic estimate is less than $132 million per year.
- Marginal contribution from trophy hunting to employment is not 53,000 jobs, as claimed by Southwick (2015), but more likely in the range of 7,500 - 15,500 jobs.
- While overall tourism is between 2.8% and 5.1% of GDP in the eight study countries, the total economic contribution of trophy hunters is at most about 0.03% of GDP.
- Foreign trophy hunters make up less than 0.1% of tourists on average.
- The adjusted value of Southwick's economic contribution of trophy hunting ($132 million or less) amounts to only 0.78% or less of the $17 billion in overall tourism spending in the studied countries.
- Trophy hunting tourism employment is only 0.76% or less of average direct tourism employment in study countries.

ARE SCI'S COMMISSIONED ESTIMATES OF TROPHY HUNTING'S ECONOMIC IMPACT RELIABLE?

Southwick (2015) employ methods that substantially overstate the size of the hunting economy. The main methodological problems are:

1. Ignoring the opportunity cost of resources used for hunting activities by assuming that land and wildlife resources have no substitute uses at all. Clearly there are alternative uses, such as non-hunting tourism. Analysis that ignores the existence of alternative uses and industries cannot contribute to the key question of whether hunting is the most economically valuable use of resources in the regions where it occurs.

2. Non-hunting tourism by trophy hunters is attributed purely to trophy hunting. While this and other pro-trophy hunting economic studies proclaim that trophy hunters are motivated by more than just the hunt, and that trophy hunters value outdoor wildlife experiences in exotic locations, these same studies assume that no trophy hunters would visit these countries if not for trophy hunting, and that no non-trophy hunting activities would occur if hunting ceased.

3. Using multipliers to determine total economic contribution. This method of analysis assumes that not only would all businesses that earn revenue from trophy hunters find no alternative income sources, but neither would their suppliers, and their suppliers' suppliers, and so forth up the value chain. This method is unrealistic, and no longer an accepted method of economic analysis.

Adjusting the Southwick (2015) estimates to account for these problems helps provide an indication of the *marginal* economic benefit of trophy hunting. In other words, what is the benefit that hunting provides over and above what an alternative use of the land, wildlife, labour and other inputs would generate. This is the economically correct approach to assessing the value of an industry.

Making these adjustments, this marginal benefit would be less than $USD 132 million, depending on alternative wildlife uses. In terms of employment, the likely marginal effect of trophy hunting is in the range of 7,500 - 15,500 jobs, rather than the 53,000 claimed by Southwick (2015). A summary of the effect of adjusting for these methodological issues is in Figure 1. The graphic illustrates how Southwick (2015) was able to reach the inflated and inaccurate figure of a $426 million economic benefit and 53,000 employment benefit to the eight countries studied.

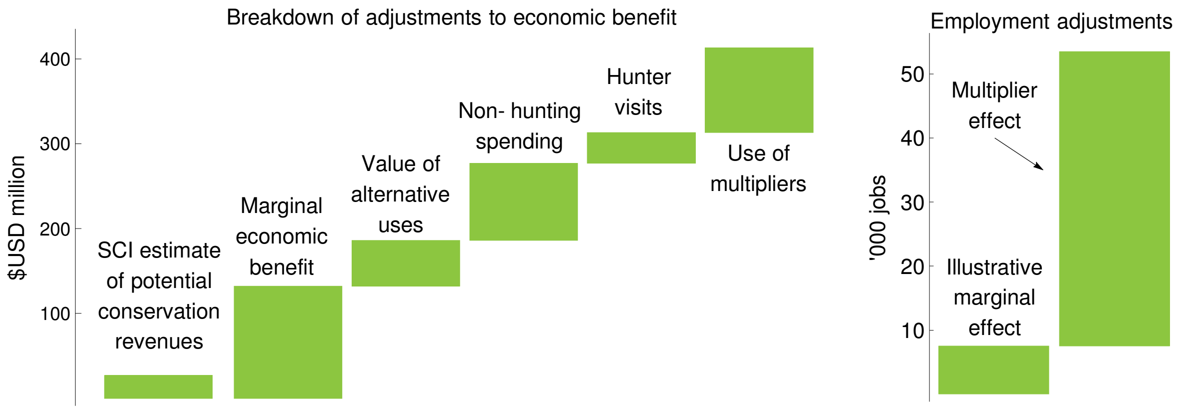

FIGURE 1: SUMMARY OF ADJUSTMENTS TO SOUTHWICK TROPHY HUNTING BENEFIT

WHAT DOES THE SIZE OF HUNTING INDUSTRY LOOK LIKE IN PERSPECTIVE?

Although often reported to be economically significant, or even critical, the gross tourism expenditure from trophy hunters claimed by Southwick (2015) is around 1.9% of overall (non-hunting and hunting) tourism expenditure in the study countries (while the marginal contribution from trophy hunting is far less). The tourism sector overall is between 2.8% and 5.1% of GDP in the study countries, meaning that the current total economic contribution of trophy hunters from their hunting-related, and non-hunting related, tourism is at most about 0.03% of GDP. Foreign trophy hunters make up less than 0.1% of tourists on average.

The comparison of tourist arrivals, spending, and direct employment of tourism overall, and the claimed contribution of trophy hunters in Southwick (2015) is in Figure 2, which shows clearly that the economic significance of trophy hunting is exaggerated.

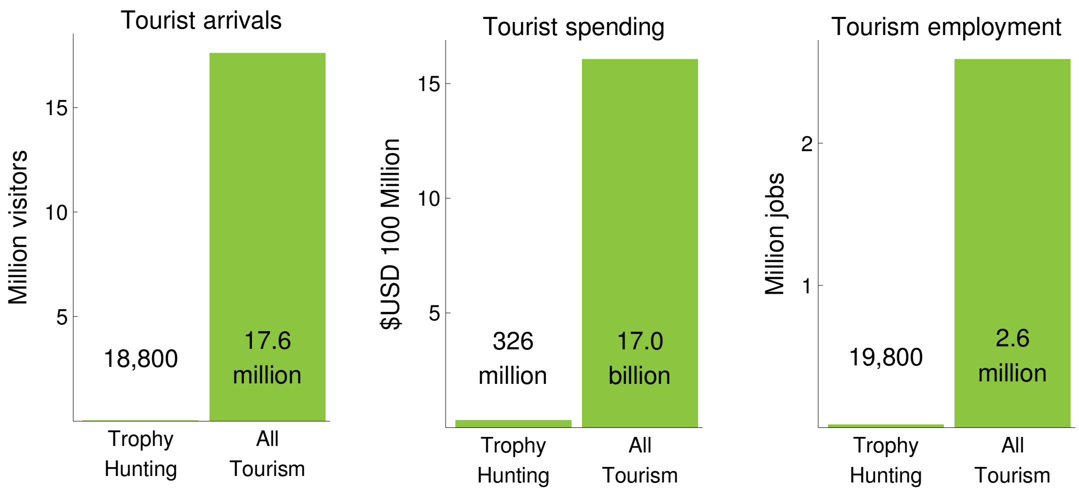

FIGURE 2: TROPHY HUNTING ESTIMATES IN PERSPECTIVE (WTTC, 2016)

In terms of the wider tourism economy, which relies heavily on wildlife resources, trophy hunting is relatively insignificant. Overall tourism spending grew by as much as the claimed direct value of the trophy hunting industry ($326 million) every four months on average in the eight study countries between 2000 and 2014. The average increase in tourist arrivals over 9 days in Botswana exceeded the total annual foreign trophy hunter arrivals as estimated by Southwick (2015). For the more established hunting markets of Namibia and South Africa, this was 54 and 60 days, meaning that just the growth over a year in tourist numbers is about six times larger than a year's worth of hunting tourists.

Thus, at the country level the overall financial contribution of trophy hunting is minor, though perhaps significant in a few small select regions. Some African countries have already instituted trophy hunting restrictions. Kenya, for example, banned almost all hunting in 1977 and has seen high growth in tourism industries, and a pushback by large eco-tourism operators against the reintroduction of hunting. In 2014, Botswana followed Kenya's example. Trophy hunting may actually deter growth in other forms of tourism, and these costs may overwhelm any economic benefits (already recognized to be minor) of the trophy hunting industry.

THE IMPLICIT CONSERVATION STORY

SCI claims that the economic benefits estimated by Southwick (2015) implicitly support their "conservation equation" view that hunting equals conservation because it generates economic activity which can help pay the cost of conservation. Yet the report only offers claims of total economic contribution, with no details provided on how much of the inflated total of $426 million actually goes to conservation. Instead, published studies have consistently shown that trophy hunting can have a detrimental effect on wildlife populations.

It is not impossible for conservation areas in some cases to have some amount of sustainable trophy hunting. But trophy hunting does not itself automatically lead to effective conservation. With minor exceptions, the causal link SCI claims simply does not exist. A well-regulated system is required for trophy hunting to be sustainable. For example, it must be void of corruption, offer accurate and regular monitoring of populations, ensure that hunting quotas are based on science, be properly regulated and enforced, etc. Given the complex political climates of many of the eight study countries – some of which are in fact extremely corrupt, lack accurate population monitoring, base quotas on factors other than science, ignore age restrictions for hunted animals, and allow hunting to disrupt social stability in animal groups - this perfect operating system is unattainable and therefore sustainability cannot be ensured. This presents clear evidence against SCI's conservation equation view. Southwick's (2015) findings that just an estimated 6 to 9% of economic benefits are potentially available to be directed towards conservation similarly undermines that view.

> *There are indeed examples where community-based hunting programs, in remote areas that are not suitable for tourism, do provide meaningful funding for communities and, ironically, do lead to the recovery of the targeted species (Namibia has a few such examples), but this is by no means the norm. And many trophy hunters get upset when it is suggested that these examples are few and far between and that the overall picture is not pretty. (Epsley, 2015)*

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INTRODUCTION

A recent study (Southwick, 2015) commissioned by international trophy hunting organization Safari Club International estimates that the economic benefit from trophy hunting in eight African countries - Botswana, Ethiopia, Mozambique, Namibia, South Africa, Tanzania, Zambia, and Zimbabwe - was $USD 426 million in 2012, and that 53,000 jobs are supported by this industry.

The study, written by consultants Southwick Associates, is interpreted by hunting advocates as demonstrating the large and positive economic impact of trophy hunting which, they allege, is a significant funding source for conservation. The following statements have been made about the report:

> *Our results show that a substantial number of jobs and income are created by each hunter who visits Africa, and when you add them all together, hunting becomes a critical sector of the region's economy. (Phillips, 2016)*
>
> *The results from this report show that hunting tourism is a driving force in conservation and positively contributes to a sustainable future for Africa's wildlife and local economies. (Ammoland, 2016)*

However, without context, these job and income numbers have little meaning. For example, what share of total tourism expenditure do trophy hunters comprise? What activities does trophy hunting displace? And what proportion of this economic contribution from trophy hunting actually provides incentives for greater conservation?

The aim of this report is to determine the merits of the Southwick (2015) results, and bring some rigour to the question of trophy hunting's marginal economic benefit by answering the following questions:

1. Are Southwick (2015) estimates of trophy hunting's economic impact reliable?
2. What does the economic size of trophy hunting industry look like in comparison to all tourism?

To accomplish this, this analysis reviews Southwick (2015) and its estimated economic value of trophy hunting, focussing on methodological shortcomings which overstate the relative economic significance of trophy hunting. Southwick's estimates of direct economic activity associated with trophy hunting are compared to national tourism statistics, showing that many of their estimates are implausibly large, and that even if they are believed, just the growth in the non-hunting tourism industry is often larger than the whole trophy hunting industry. Some overall perspective is then provided by looking at patterns of tourism as a whole in the study countries, and in Kenya, which has long had a trophy hunting ban.

LIMITATIONS OF PREVIOUS TROPHY HUNTING STUDIES

Very little data is available to determine the contribution of trophy hunting to tourism and economic activity in Eastern and Southern Africa. Despite this lack of data, some studies do attempt to estimate such impacts using surveys of trophy hunters and outfitters, particularly in a case study setting (Lindsey et al., 2007a; Samuelsson and Stage, 2007; Jorge et al., 2013; Southwick, 2015).

The latest is *The Economic Contributions of Hunting-Related Tourism in Eastern and Southern Africa*, by Southwick Associates, commissioned by Safari Club International (Southwick, 2015). Using a survey of 432 international trophy hunters, the study made the following claims:

1. Total spending by surveyed trophy hunters on all items in destination countries was $USD 20,602 on average.
2. Multiplying by the number of licenced international trophy hunters in each study country, the total spending by trophy hunters was estimated to be $USD 326 million.
3. Applying a "GDP per spending" multiplier to this figure provides a GDP (value added) estimate of $USD 426 million.[1]
4. Applying a total direct and indirect "jobs per GDP" multiplier to this GDP estimate provides an estimate of total jobs related to hunting tourism of 53,000.

This approach is similar to an earlier study by Samuelsson and Stage (2007), who surveyed 164 international hunting tourists in 2003 who visited Namibia between 1998 and 2002. Trophy hunting tourists in their survey spent $USD 3,900 on hunting-related activities in public conservancies (80% of trophy hunters) and $USD 2,700 in private farms (20% of trophy hunters). Conservancy hunters also spent $USD 2,100 on non-hunting related activities. In common $USD 2002 terms, their estimate of the average total hunter direct spending was $USD 5,500, or only 68% to Southwick's (2015) estimate of Namibian total trophy hunter spending, which deflated to 2002, is $USD 8,100 on average per person. A 2004 estimate by Damm (2005), put total expenditure by international trophy hunters in Namibia at $USD 5,700 (adjusted to 2014 dollar terms), again far below comparable estimates by Southwick (2015).

Southwick (2015) employed a survey sampling method that is likely to have inflated their estimates of trophy hunter spending. They sought participants over three rounds by having professional hunting organisations contact their clients. In their third round, which made up 60% of total survey participants, the average reported total expenditure on a hunting trip was $USD 25,600, compared to $USD 16,000 for survey participants from the first two rounds (a 60% difference). This possible sampling bias matches closely the difference in spending between Southwick (2015) and earlier estimates, especially for Namibia. Overall, the variation and scope for error in understanding the basic expenditure profile of international trophy hunters in this type of survey method appears large, and the Southwick (2015) estimates seem to be some of the highest estimates available.

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[1] The application of this multiplier is designed to capture potential indirect, or induced, economic activity that may occur in upstream supply industries and complementary industries. This assumes that not only would all businesses that earn revenue from trophy hunters find no alternative income sources, but neither would their suppliers, and their suppliers' suppliers, and so forth up the value chain. This method is no longer accepted by many governments and institutions as a valid form of economic analysis.

For example, Lindsay et al. (2007a) summarised the trophy hunter expenditure estimates from earlier studies, which lead to a widely reported figure that trophy hunting in Africa was a $200 million industry. This number was criticised for relying on similar survey estimates by pro-trophy hunting lobby groups of overall expenditure, rather than the economic benefit to local communities or wildlife management agencies who are actually engaged in conservation and wildlife management (Campbell, 2012). Furthermore, both the $200 million and $426 million figures fail to demonstrate how much the economic activity generated actually contributes to conservation efforts, as opposed to paying for overhead costs, salaries, or going into projects that have no direct benefit to wildlife, or indeed, if the economic gains simply further incentivize wildlife depletion. In other words, there is no debate that some money is generated by trophy hunting. But that is not the key question; the key question is whether or not that money is making a meaningful positive contribution to wildlife conservation.

More than this, however, is that both the Lindsay et al. (2007a) and Southwick (2015) studies do not estimate the *marginal* economic impact of trophy hunting. They estimate the *gross* economic activity associated with trophy hunting. When trying to establish the net economic difference between a scenario with no trophy hunting, compared to the scenario with current trophy hunting arrangements, it is only the marginal economic contribution of trophy hunting which is meaningful. This fundamental economic concept is illustrated in Figure 3 below, where the gross economic benefit from the next best alternative use of wildlife and conserved land resources must be known to understand what the marginal economic benefit from trophy hunting is.

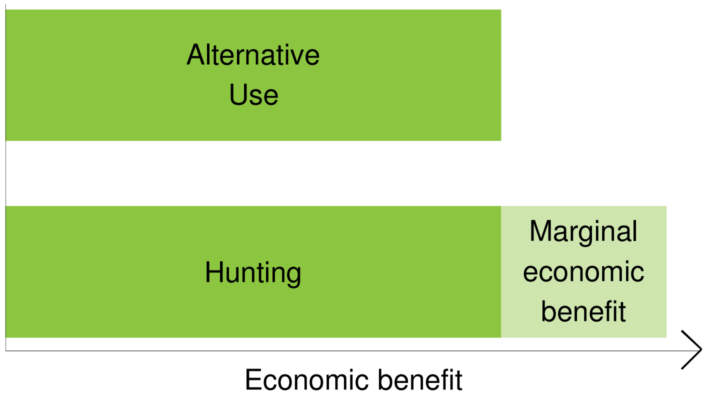

FIGURE 3: CONCEPT OF MARGINAL ECONOMIC BENEFIT

This fundamental confusion about what the relevant economic benefit measure should be when establishing the economic contribution of trophy hunting is responsible for three specific problems with the methods used by Southwick (2015), which also apply more generally to studies of this type: 1) ignoring the opportunity cost of land and wildlife resources by assuming no ability to substitute land and wildlife resources towards other uses (such as non-consumptive tourism), 2) attributing all non-trophy hunting tourism expenditure by trophy hunters to hunting, and 3) using economic multipliers to determine total economic contribution. These problems are discussed in turn.

IGNORING THE OPPORTUNITY COST OF RESOURCES

Quantifying the scope of gross economic activity currently related to the trophy hunting industry does not answer the important question of how much greater that economic contribution is than the next best alternative use of the wildlife and land resources (the opportunity cost). Even if trophy hunting is associated with a great deal of economic activity, the total value of that activity could still be lower than alternative non-trophy hunting uses of the natural and human resources. For example, a non-consumptive ecotourism private farm may bring in more money and greater conservation benefits than if the same land were used for trophy hunting. From the methods used by Southwick (2015), this can't be known, as they make the incorrect assumption that the next-best use of land and wildlife generates a total economic benefit of exactly zero. The economic benefits of alternative land and wildlife uses can be significant.

For example, Lindsey et al. (2013) show that ecotourism uses of private ranches is a growing alternative in Namibia, and is also associated with higher ranch employment than trophy hunting or agriculture, suggesting the rise of ecotourism as a viable alternative land use in many situations. Taylor et al. (2016) explain how the Zululand Rhino Reserve in South Africa over time moved from mixed uses of trophy hunting and ecotourism, to exclusively ecotourism, because trophy hunting uses where limiting expansion of higher-value ecotourism. Such conflicts between trophy hunting and alternative uses are captured in the below quote from a Tanzanian villager in a study on conservancy management.

> *We're more closely allied with the photographic operators than the hunters. They are finishing off the wildlife before we've had a chance to realize a profit from it. (Sachedina, 2008)*

While local conditions will determine the highest value alternative use of wildlife and conservation areas, the economic benefit from these uses is likely to be far from zero. For example, in the main trophy hunting areas that often adjoin national parks, there is clear opportunity for this land to be utilized for similar ecotourism purposes as the parks themselves.

Moreover, it is not always clear that the locations where trophy hunting takes place are even financially viable themselves. For example, Lindsay et al. (2012) studied the effect of restrictions on lion hunting on the amount of land where trophy hunting would remain commercially viable across Mozambique, Namibia, Tanzania, Zambia and Zimbabwe. While the study showed that a total ban on lion hunting across all the studied countries would reduce the viability of trophy hunting industries in 14% of the current hunting areas, and a reduction in offtake to previously estimated sustainable levels would reduce viable areas of hunting by 2%, the more interesting finding was that even under existing regulations, trophy hunting was financially viable in only 56% of the total area in which lion hunting was undertaken (Campbell, 2012). This suggests that across 44% of the land used for lion hunting, alternative wildlife uses (like non-consumptive tourism) would be more economically sustainable than trophy hunting. Why trophy hunting persists at all in these areas is more likely to be a product of political and social pressures, rather than economic ones.

ATTRIBUTING ALL IN-COUNTRY EXPENDITURE TO TROPHY HUNTING

Attributing all 'in-country' expenses of trophy hunters on their travels to the act of trophy hunting assumes that in the absence of trophy hunting, no trophy hunters would travel to these countries to enjoy other tourism experiences. Yet the Southwick (2015) study itself notes that 11% of the hunters answered that they would still travel to that destination country (8% were undecided), and that of the hunters surveyed, over half also participated in photo safari activities in addition to the trophy hunt. Some proportion of the money saved by not hunting on the trip could also be spent in the destination country. An adjustment for this is warranted if a credible estimate of the marginal economic contribution of trophy hunting is sought.

Southwick (2015) also attribute the $1,000 non-trophy hunting proportion of in-country spending by trophy hunters to hunting itself, reasoning that this spending - on photo-tourism, relaxing, hiking and visiting friends and family - would not occur in the absence of trophy hunting. This equates to 5% of spending attributable to non-trophy hunting activities, which is very low compared to previous hunter surveys.

Samuelsson and Stage (2007), for example, found that non-trophy hunting expenditure by trophy hunters in Namibia ranged from 25-49% of their trophy hunting expenditure, depending on their trophy hunting destination. Jorge et al. (2013) used a wide variety of primary data sources and surveys of hunters and outfitters to examine where hunter's spending during trips to Niassa National Reserve end up, finding that 58% of in-country expenditure is directly hunting related.[2] Based on these other studies, the share of non-hunting expenditure for international trophy hunters is more likely to be around 40% of total spending, in contrast to the 5% found in the survey by Southwick (2015). The stark contrast between these is suggestive of an over-attribution of spending to the activity of trophy hunting itself in Southwick (2015), and a 35% downward adjustment of their results would provide a trophy hunting-attribution of spending in keeping with previous research.

USE OF ECONOMIC MULTIPLIERS

The use of economic multipliers to total in-country spending to determine total economic benefits (in upstream supply industries for example) is misleading. Southwick (2015) apply economic multipliers for tourism from the World Trade and Tourism Council (WTTC) to their total $USD 326 million in-country spending estimate to suggest that $USD 426 million of GDP is attributable to trophy hunting. They also then apply a "GDP to jobs" ratio from WTTC analysis of the tourism sector to generate a figure of 53,000 "direct and indirect" jobs supported by trophy hunting.

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[2] Based on calculations from using Figures 1 and 2, which excluded travel, trophy shipping, and taxidermy. These costs are excluded for the purposes of this calculation because they are largely, ancillary, not fully incurred in the destination country, and in part account for missing information on alternative economic activities available.

For each of the eight study countries, Southwick (2015) first multiply their estimates of average per hunter spending from their survey by the number of licenced international hunters. With this estimate of total spending, they apply the economic multiplier used by the WTTC to inflate direct estimated tourism spending to total direct and indirect economic effects. These multipliers are between 1.1 and 1.8 across the countries studied. They then apply the per dollar ratio in the WTTC reports between total "direct and indirect" economic effects, and the WTTC estimates of total employment effects from tourism spending, to their own estimate to determine the employment effects of trophy hunter's spending.

This method hides an assumption that in the absence of trophy hunting, all upstream suppliers of economic inputs would leave their resources idle should trophy hunting cease, and conversely, that there are idle resources, such as land, labour, buildings and machines, available at all upstream suppliers that would be brought into production if trophy hunting increased. This method is no longer widely considered to be a valid way to assess economic benefits, particularly in tourism industries (Dwyer et al. 2004; Crompton, 2006).

However, it is possible to give an idea of how employment effects can be inflated by multiplier-type analysis when compared to alternative methods that account for resource constraints and behavioural adjustments. An economic analysis comparing evaluation methods in the case of a South African arts festival found that multiplier methods can overstate employment effect, with a resource-constrained model[3] providing an estimate of 29% of the jobs from the multiplier method (van Wyk et al. 2015).

Also, in Queensland, Australia, employment estimates for a new coal mine in the Galilee Basin were estimated to be 10,000 jobs using multiplier methods (GHD, 2013). However, independent estimates using alternative methods with more realistic considerations of economic constraints found that total national job creation was around 1,400, or just 14% of the estimate using multiplier methods (Fahrer, 2015). The enormous difference between these methods arises because the multiplier method assumes that every job created employed someone who was previously unemployed and waiting for work, as did all their upstream suppliers who expanded to accommodate the new mine. In reality however, many of those employed by the growth of any industry will be drawn from the pool of already employed people. If a similar difference in employment effects due to modelling choice applied to the WTTC multiplier estimates, and hence Southwick's (2015) estimates, the total trophy hunting jobs would be around 7,500 - 15,500 instead of 53,000 (i.e., between 14% and 29% of their estimate using multiplier methods).

A comparison of these two fundamentally different economic approaches should not be confused with simply removing the multiplier used in the Southwick (2015) analysis. There is no prior reason to estimate employment effects using a resource-constrained model to be at least as large as the direct employment

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[3] There are many classes of such models, often referred to as general equilibrium models. The main difference is that they account for the fact that if resources (like labour, land, buildings and machinery) are not used for one purpose, that there will be a second-best use of them that they will instead be utilized for when that first-best purposed is no longer available. Thinking about this in reverse, it means that if a new more profitable industry emerges, that it will have to compete to attract workers, machines, buildings and so forth away from their existing uses in other industries, meaning net effect of this new industry on overall economic activity must account for these forgone uses of resources.

in that industry, as both those employed directly as well as indirectly will have other options available to them.

ADJUSTING THE SOUTHWICK (2015) ESTIMATE

Taking into consideration these methodological shortcomings, it is possible to use Southwick's (2015) own data, along with the main findings in the literature, to generate a reasonable estimate of the *marginal* economic benefits of trophy hunting. Table 1 presents these adjustments.

The first row of Table 1 is the total direct trophy hunter expenditure in each country from Southwick (2015, p. iv). The next row adjusts for the fact that 89% of surveyed trophy hunters that said they would not travel to the destination country if they were unable to trophy hunt, meaning that according to Southwick (2015) 11% are likely to travel to the study countries for tourism and non-consumptive safaris. Row two assumes a trip is made with the same total spending. The third row adjusts for the share of non-trophy hunting related expenditure in each trip that appears underestimated. Because there is little information to go on about the average economic value of alternative uses of land and wildlife, the next four shaded rows show a range of scenarios about what the marginal economic benefit from trophy hunting would be when the next best alternative use of resources has economic benefits of 30%, 50%, 70%, or 100% as large as trophy hunting benefits. Obviously when the next best use of wildlife and conservation land resources is the same as trophy hunting there is zero marginal benefit.

TABLE 1: ADJUSTMENTS FOR METHODOLOGICAL PROBLEMS IN SOUTHWICK (2015).

		BOTSWANA	**ETHIOPIA**	**MOZAMBIQUE**	**NAMIBIA**	**SOUTH AFRICA**	**TANZANIA**	**ZAMBIA**	**ZIMBABWE**	**TOTAL**
HUNTER RECEIPTS	($USDm)	7.2	0.4	8.8	105.0	141.2	16.4	8.2	39.4	326
NON-HUNTING VISITS	(x0.89)	6.4	0.4	7.8	93.5	125.7	14.6	7.3	35.1	291
NON-HUNTING SPEND	(x0.65)	4.2	0.2	5.1	60.7	81.7	9.5	4.7	22.8	189
ECONOMIC BENEFIT OF ALTERNATIVE USE	30%	2.9	0.2	3.6	43	57	6.6	3.3	16.0	132
	50%	2.1	0.1	2.5	30	41	4.7	2.4	11.4	95
	70%	1.2	0.1	1.5	18	25	2.8	1.4	6.8	57
	100%	0	0	0	0	0	0	0	0	0
TOTAL EMPLOYMENT	No.	316	503	10,690	8,367	12,742	14,161	783	5,861	53,423
ADJUSTED NET EMPLOYMENT	(x0.14)	44.2	70.4	1,496	1,171	1,783	1,982	109	820	7,479
	(x0.29)	91.6	145.9	3,100	2,426	3,695	4,106	227	1,699	15,492

All values in $USD million.

In Table 1 the use of multipliers on economic benefit measures is ignored because of their inherent flaws. To give an indication of the potential overestimate of the employment effects from the multiplier methods used by Southwick (2015), the last two rows take their employment estimates, and adjust by the difference observed in the earlier-discussed studies which showed that alternative economic assessment methods generate only 14 to 29% of the number of jobs compared to the multiplier method. While the exact ratio will not be the same in the case of trophy hunting, this adjustment gives an approximation for the potential scale of the overestimation of employment effects.

These adjusted figures bring us closer to a useful figure for understanding the marginal economic value of trophy hunting, and therefore closer to understanding the potential size of the economic gains from trophy hunting that may be captured for conservation. Indeed, the Southwick (2015) report estimates that only $USD 27 to 40 million of their approximated economic benefits of trophy hunting, or only between 6 and 9%, can be regarded as potentially contributing to conservation.[4]

In sum, the above exercise illustrates the effect of the three main methodological flaws in Southwick (2015). Adjusting their own data to account for the marginal economic benefit of trophy hunting across the eight study counties provides a value between zero and $USD 132 million. The number of jobs supported by trophy hunting is likely to be between 7,500 and 15,500. This is a different story of economic significance from the Southwick estimates of $USD 426 million in benefits and 53,000 jobs.

TROPHY HUNTING IN CONTEXT

The core problem of Southwick's (2015) analysis is that it does not estimate the marginal economic impact of trophy hunting, and thus overstates the economic importance and any changes to trophy hunting regulations. Aside from this, the claim is that the estimate of economic activity associated with trophy hunting is economically significant. To allow the reader to judge for themselves the significance or not of trophy hunting based on Southwick's (2015) estimates, this section compares those estimates with estimates of overall tourism spending and other economic aspects of the eight study countries.

Even ignoring the fundamental methodological problems with the Southwick study previously discussed, we see that current size of economic activities related to trophy hunting are a small part of the overall tourism economy of the study countries, which is itself a relatively small part of the overall economy of those countries.

TROPHY HUNTING AND VISITOR NUMBERS

The Southwick estimate of trophy hunters traveling to the eight study countries was 18,815. These countries attract high numbers of tourists, with almost 18 million tourist arrivals per year on average between 2003 and 2013, as shown in Table 2 below. There are 1,000 tourists for every trophy hunter on average.

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[4] The Southwick report cites that this estimate does not include portions of trophy fees that are already included in the trophy hunting package cost and admits that "this area of research deserves dedicated in-depth analysis. . ." (Southwick, 2015, pg. 18).

TABLE 2: TROPHY HUNTING TOURIST ARRIVALS IN CONTEXT

		BOTSWANA	ETHIOPIA	MOZAMBIQUE	NAMIBIA	SOUTH AFRICA	TANZANIA	ZAMBIA	ZIMBABWE	TOTAL
HUNTER ARRIVALS		350	21	428	7,076	8,387	794	398	1,361	18,815
TOTAL TOURIST ARRIVALS	(million)	1.58	0.58	1.2	1.13	9.36	1.05	0.89	1.81	17.6
HUNTER TOURIST SHARE	(%)	**0.02**	**0.00**	**0.02**	**0.63**	**0.09**	**0.08**	**0.04**	**0.07**	**0.11**
MEAN TOURIST GROWTH	('000/yr)	**13.8**	**50.1**	**144.5**	**48.1**	**51.1**	**303.2**	**50.2**	**-42.3**	**669.4**
EQUIV. DAYS TOURIST GROWTH	(days)	**9.3**	**0.2**	**1.1**	**54**	**60**	**0.9**	**2.9**	**-11**	**10.3**

Source: Southwick (2015) and WTTC (2016). Mean tourist growth is from 2003-2013 where data for all countries is complete. Foreign trophy hunter arrivals are estimates for average annual from 2012-2014 from Southwick (2015), Table 16. Total tourist arrivals from World Tourism Organization, Yearbook of Tourism Statistics, 2003-2013 average for arrivals.

Table 2 shows that South Africa and Namibia have the highest number of foreign trophy hunters at over 15,000 between them. Outside of these countries, Southwick estimates that only Zimbabwe had over 1,000 trophy hunter arrivals. By contrast, WTTC figures show that South Africa had over nine million total tourist visitors, while all other countries had around 1 million visitors each. Only in Namibia do trophy hunters represent a larger share of arrivals, or 0.63 percent. In other words, in Namibia there are 160 tourists for every trophy hunter, while in the other study countries there are 1,430 tourists for every trophy hunter.

The final two rows in Table 2 provide some perspective on the relative size of the foreign trophy hunting cohort compared to overall tourist arrivals. Mean tourist growth shows the average annual increase in tourist arrivals from 2003 to 2013. The final row, equivalent days in tourist growth, is an estimate of how long it takes for total tourist arrivals to grow by as much as the total annual number of foreign trophy hunter arrivals. That is, the average increase in tourists each day in Mozambique exceeds the total annual foreign trophy hunter arrivals. For the more established trophy hunting markets of Namibia and South Africa, this was 54 and 60 days, meaning that just the growth over a year in tourist numbers is about six times larger than a year's worth of trophy hunting tourists.

The growing popularity of these African countries among non-trophy hunting tourists is more clearly shown in Figure 4, which shows the trend in tourist numbers in the study countries in since 1996, but also includes Kenya, which has had a trophy hunting ban in place since 1977.[5] Including Kenya in the

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[5] In 2014 Botswana banned all commercial hunting, though it had already removed lions from its hunting quota between 2001-2004 and from 2008 (Lindsey et al. 2013). Zambia imposed a moratorium on elephants and big cat

remaining analysis provides a point of comparison about the bigger overall tourism trends that are occurring in Africa, which also rely on non-consumptive wildlife use to some degree.

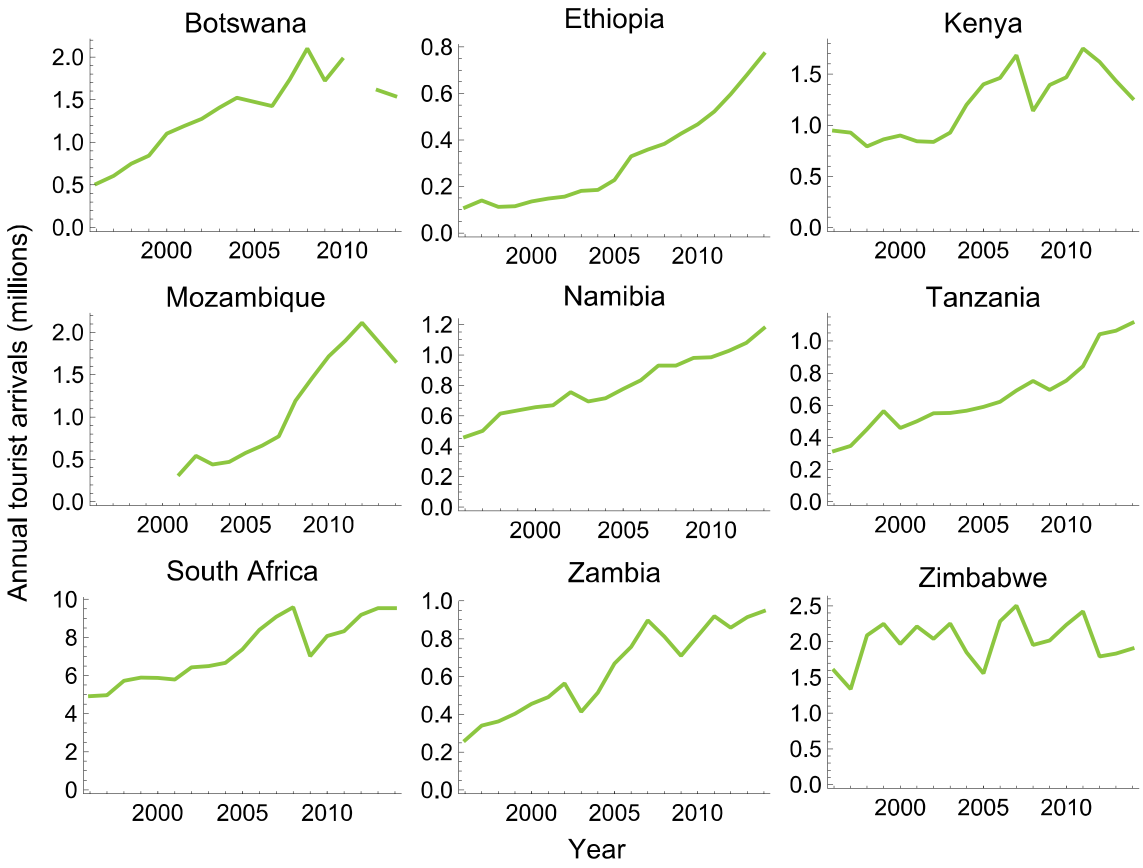

FIGURE 4: TOTAL TOURIST ARRIVALS IN STUDY COUNTRIES AND KENYA, 1996-2015 (WTO, 2016)

Overall the study countries have seen large increases in their tourist arrivals, though the tourism industry is a relatively small part of each economy because the tourism sector is between 2.8% and 5.1% of GDP in the study countries.

TROPHY HUNTING AND VISITOR SPENDING

In addition to putting into context the number of trophy hunters, we can provide some context on their estimated total spending compared to the overall tourism industries in the study countries. While Southwick (2015) suggest that their $USD 326 million of direct spending by trophy hunters is a large and important part of the tourism sectors of the eight study countries, it is less than 2% of the overall $USD 17 billion in direct tourist spending in these countries. Table 3 below compares the Southwick (2015) estimates in the first row, with earlier estimates compiled by Lindsey et al. (2007a) in the second row, and the overall tourism spending in the third row.

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hunting in 2013, while Tanzania cut the lion quota by almost half between 2008 and 2012 (Lindsey et al. 2013, ZAWA, 2014).

Overall, the share of tourist spending from trophy hunters is low, ranging from nearly 0% in Ethiopia, to a high of 10.5% in Namibia, which is shown for each study country in the first shaded row of Table 3. Some of the Southwick (2015) estimates of spending by hunter tourists seem implausibly high in some of countries. When a per tourist adjustment is made based on arrivals data from Table 2, it appears Southwick is claiming that the average trophy hunter is spending often more than 100x as much as the average tourist. While trophy hunters probably do spend much more than the average tourist, the upper end estimates implied here seem abnormally high compared to lower ratios seen in more developed trophy hunting industries of Namibia and South Africa.

TABLE 3: TROPHY HUNTER SPENDING IN THE CONTEXT OF OVERALL TOURISM SPENDING

		BOTSWANA	**ETHIOPIA**	**MOZAMBIQUE**	**NAMIBIA**	**SOUTH AFRICA**	**TANZANIA**	**ZAMBIA**	**ZIMBABWE**	**TOTAL**
HUNTER SPEND (SOUTHWICK)	$USDm	7.2	0.4	8.8	105.0	141.2	16.4	8.2	39.3	326.5
HUNTER SPEND (LINDSEY)	$USDm	20.0	1.3		28.5	100.0	27.6	5.0	16.0	198.4
TOURIST RECEIPTS	$USDm	36	1,980	224	598	11,202	1,754	518	749	17,061
HUNTER TOURIST SHARE	(%)	20.0%	0.0%	3.9%	17.6%	1.3%	0.9%	1.6%	5.2%	1.9%
HUNTER / AVERAGE		904	6.0	110	28.0	14.1	12.3	35.4	69.7	17.9

Source: Southwick (2015) in 2012$USD, Lindsey et al. (2007) in 2004$USD, and WTO (2016). 'Tourist receipts' is the mean estimate by WTTC from 2005 to 2012. This adjustment is necessary because the data variability is extremely high.

Figure 5 shows the trend in total tourist spending in the study countries since 1996, along with Kenya, which has had a trophy hunting ban since 1977. The two lines for each country represent two data sources for international tourism spending, with the inconsistencies between the two lines indicating just how poorly understood the overall economies of these countries are.[6] Overall there is fairly strong growth, though volatile and dependent on local and international economic and political factors. Like the data on trophy hunting, establishing reliable estimates of overall tourist spending is also a challenge in the study countries, as they have limited capacity for large scale statistical surveys. Despite this, these trends allow us to show the relative size of the total spending by trophy hunting tourists in the main trophy hunting countries of Namibia and South Africa. Between 2007 and 2012 tourism spending grew by more than Southwick's (2015) estimate of annual trophy hunting spending ($326 million), and by four times as much as other estimates of trophy hunter spending (Lindsey et. al. 2007). In South Africa, just the growth in total tourism spending was $2 billion between 2007 and 2012, which is fourteen times larger than the

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[6] The solid line is World Travel and Tourism Council (WTTC) data of international tourism spending in $USD2015 prices, while the dashed line is World Trade Organization (WTO) data in $USD2015 prices. WTTC data is used in the Table 3.

general estimates of the size of the trophy hunting industry in that country by Southwick (2015). Indeed, In Figure 5 we can see that Kenya has had sustained growth in tourism spending despite a long-term ban on trophy hunting.

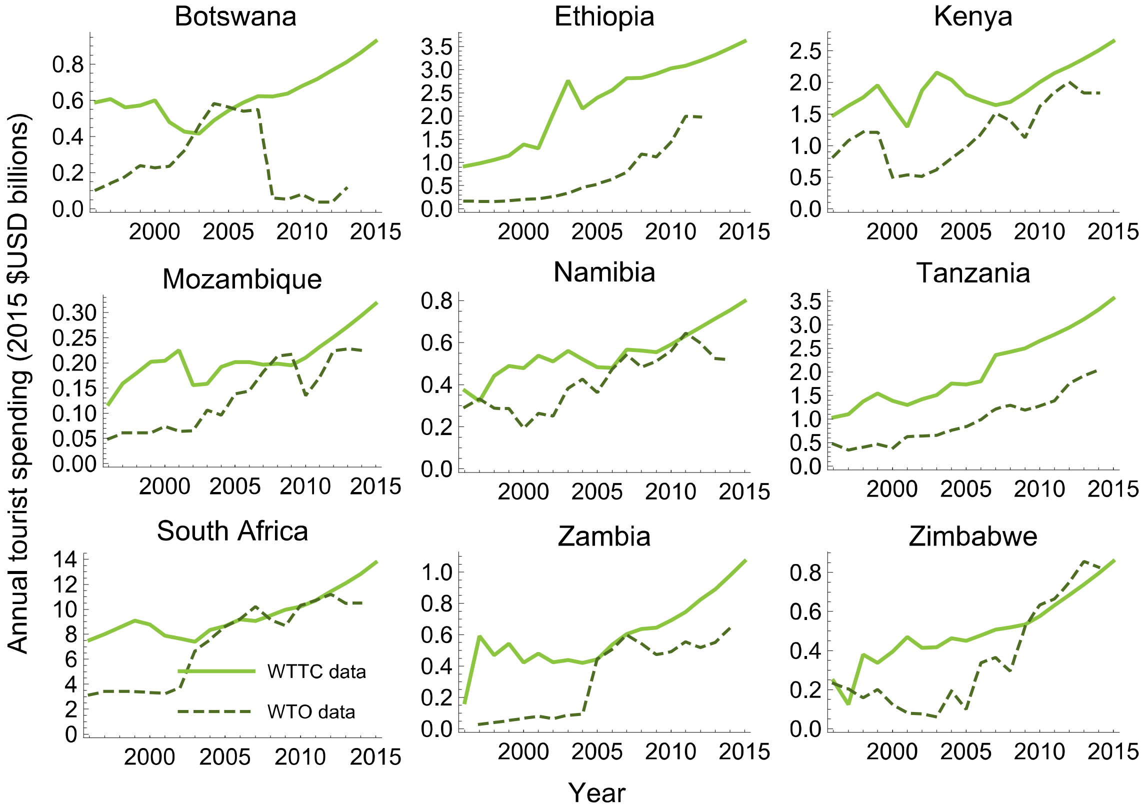

FIGURE 5: DIRECT TOURIST SPENDING, STUDY COUNTRIES AND KENYA, 1996-2015 (WTO, 2016; WTTC, 2016).

When the claimed size of trophy hunting tourist spending is put in the context of overall tourism, it is again shown to be relatively small, and certainly cannot be claimed to be a significant source of tourism growth, as the Kenyan experience shows.[7]

TROPHY HUNTING AND EMPLOYMENT

In addition to putting into context the number of trophy hunters, we can provide insights on their estimated share of overall tourism employment in the study countries. Recall that Southwick (2015)

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[7] Some trophy hunting advocacy groups cite current wildlife population declines in Kenya as an example of why trophy hunting should not be prohibited, but instead reinstated in Kenya. However, the very reason for the 1977 ban was the massive decline in wildlife populations when there was a poorly regulated trophy hunting industry and corruption, along with widespread poaching. In the three years prior to the ban, elephant numbers declined by half. Many studies show that reduced wildlife numbers since the trophy hunting ban have arisen due to human encroachment of land, the small size of conservation areas, and continued poaching (Ogutu et al. 2011, Ottichilo et al. 2000). These are challenges faced by all eight studied countries. Recent partial or complete bans on trophy hunting have been enacted in Botswana and Zambia. This was in response to species population declines, demonstrating that trophy hunting has not delivered the promised conservation successes to countries that continued to allow hunting after Kenya's ban.

included only the total direct and indirect employment using multiplier from WTTC; a method that is no longer considered credible among economists. Adjusting back these estimates by the multiplier used provides their own estimate of direct employment effects of 19,733 jobs (see row 3 of Table 4). This is still higher than the range estimated earlier in this analysis using adjustments from other studies (see section titled *Use of Economic Multipliers*) which have compared the multiplier method with resource-constrained methods.

TABLE 4: TROPHY HUNTING EMPLOYMENT CONTRIBUTION COMPARED TO OVERALL TOURISM

		BOTSWANA	ETHIOPIA	MOZAMBIQUE	NAMIBIA	SOUTH AFRICA	TANZANIA	ZAMBIA	ZIMBABWE	TOTAL
HUNTING EMP. (DIRECT & INDIRECT)		316	503	10,690	8,367	12,742	14,161	783	5,861	53,423
MULTIPLIER		2.2	2.5	2.6	4.3	2.2	3.0	2.9	2.3	2.7
HUNTING EMP. (DIRECT)		144	201	4,112	1,946	5,792	4,720	270	2,548	19,733
14% ADJUSTMENT		44	70	1,497	1,171	1,784	1,983	110	821	7,479
29% ADJUSTMENT		92	146	3,100	2,426	3,695	4,107	227	1,700	15,493
TOURISM EMP. (DIRECT)	(‘000)	28	1,001	247	25	661	340	85	202	2,589
HUNTING SHARE EMP.	(%)	0.51	0.02	1.66	7.78	0.88	1.39	0.32	1.26	0.76
HUNTING / AVERAGE		23.2	5.6	46.7	12.4	9.8	18.4	7.1	16.8	7.1
EQIV. MONTHS TOURIST GROWTH		2.0	0.05	4.6	15.9	3.8	3.9	0.7	3.0	1.7

Source: Southwick (2015) and WTTC (2016).

Despite their methodological limitations, the direct employment estimates derived from Southwick (2015) in row 3 of Table 4 can be compared with WTTC data on overall direct employment in tourism in the study countries to provide context on the relative size of the trophy hunting industry. Total direct tourism employment is estimated to be around 2.6 million. Put another way, 132x as many people are employed in non-trophy hunting tourism than in the trophy hunting industry. The first shaded row of Table 4 shows that trophy hunting tourism represented 0.76% of direct tourism employment on average (19,733 is 0.76% of 2,589,000), and is most significant in Mozambique (1.7%), Namibia (7.8%), and Tanzania (1.4%).

The second to last row of Table 4 provides a check on the plausibility of the Southwick estimates by showing the ratio of the number of direct jobs supported by a single trophy hunter tourist, compared to the average tourist. The ratio of 47x in Mozambique seems exceptionally high, and Botswana’s estimate of 23x is also on the high side, compared to the other estimates of 6 to 18 times in other countries.

Again, perspective on the significance of claimed employment supported by trophy hunting tourism can be assessed by comparing it with how long total tourism employment grows by that amount. The final row of Table 4 does this, and we can see that typically employment in the tourism sector grows by as much as total trophy hunting tourism in just a few months, the exception being Namibia, where it takes almost a year and a half.

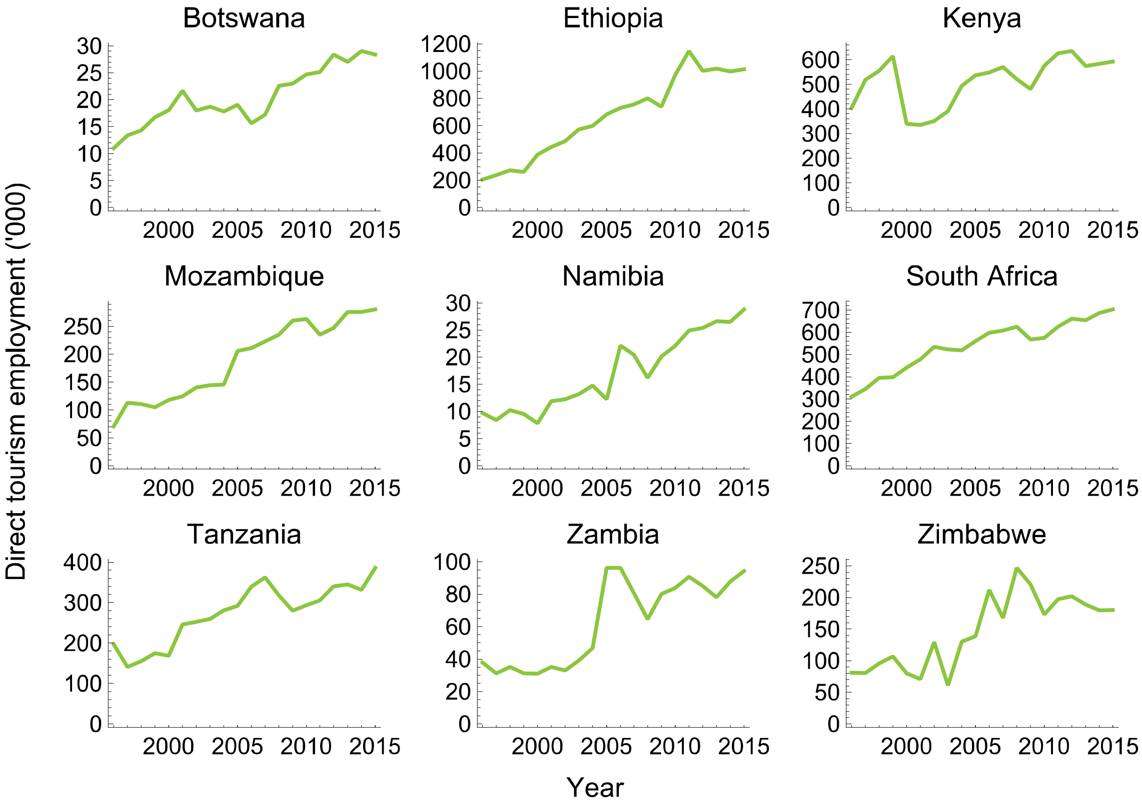

FIGURE 6: DIRECT TOURISM EMPLOYMENT IN STUDY COUNTRIES AND KENYA (WTTC 2016)

TOURISM IN CONTEXT

It is important to put into context the potential economic size of trophy hunting within the wider context of tourism growth in the study countries. In many cases the tourism drawcard for African nations is the abundance of wildlife in conservation areas. Ecotourism operators in Kenya, for example, are strongly opposed to the reintroduction of trophy hunting, which they believe will depress demand for their own tourism ventures (Elliot and Mwangi, 1998; Ngonyo, 2013). Because trophy hunting is such a tiny part of the overall tourism sector, with little scope for sustained future growth, even a small effect of trophy hunting deterring growth in other tourism uses may overwhelm its own economic benefits.

As a proportion of the national economies of the eight study countries, tourism-generated employment is most significant in South Africa and Ethiopia, with Kenya, having the third largest tourism sector. Yet while many factors are involved in determining tourism demand, including the political climate and international economic conditions, it is worth comparing the recent trends, and in particular, comparing the tourism industries of the eight study countries with Kenya, where trophy hunting has been banned for four decades. Table 5 makes this comparison.

TABLE 5: SUMMARY OF TOURISM IN RELATION TO TOTAL OUTPUT

	BOTSWANA	**ETHIOPIA**	**MOZAMBIQUE**	**NAMIBIA**	**SOUTH AFRICA**	**TANZANIA**	**ZAMBIA**	**ZIMBABWE**	**KENYA**
GDP (2014 $USD BN)	15.9	55.6	16.9	12.8	349.9	48.0	27.0	14.2	**61.4**
TOTAL TOURISM SPEND (2014 $USD BN)	0.7	1.2	0.7	1.0	12.4	0.8	0.7	0.7	**2.4**
TOURISM SHARE GDP (%)	4.1	4.1	3.1	2.8	3.0	3.6	3.0	5.1	**3.9**
TOURISM DIRECT SHARE EMPLOY. (%)	3.2	3.7	2.4	3.5	4.5	3.0	1.6	3.2	**3.6**
TOURISM GROWTH 2000-2014 (%)	9.1	11.5	14.6	22.4	4.6	7.2	7.7	16.4	**9.5**
GDP GROWTH RATE 2000-2014 (%)	4.4	9.2	7.8	5.0	3.0	6.7	6.8	-0.8	**4.7**

Sources: WTTC (2016) and World Bank (2016). Growth rates are mean annual.

Ethiopia has the smallest trophy hunting industry of the study countries, while Kenya has no trophy hunting industry, and South Africa has the largest trophy hunting industry. Overall there is no significant correlation between size of each county's trophy hunting industry and either tourism growth rates, GDP growth rates, or tourism share of GDP (statistical tests were run on all of these possible relationships). If trophy hunting truly was even a small but significant economic part of the tourism picture of these countries, some correlation would be expected.

Earlier it was shown that even the most generous estimates of trophy hunting tourism, which made no attempt to control for the marginal contribution of trophy hunting only, were around 1.9% of overall tourism spending, and 0.1% of overall tourist arrivals. Given that tourism accounts for between 2.8% and 5.1% of GDP, the broader economic significance of trophy hunting is low, accounting for about 0.03% of GDP.

CONCLUSIONS

The marginal economic benefit of trophy hunting is not well known, and rarely studied. Pro- trophy hunting organisations often present estimates of gross economic activity associated with hunting to promote their view that trophy hunting equals conservation because of its economic value. However, given past experiences of unsustainable trophy hunting leading to serious population declines and ultimately bans on trophy hunting, one cannot automatically conclude that simply because there are economic activities associated with trophy hunting, that this is inherently benefiting conservation.

The most recent attempt to understand the economic significance of trophy hunting by Southwick (2015) claimed that overall economic benefits of trophy hunting in eight countries was $USD 426 million. This estimate suffered from several methodological flaws that meant it grossly overstated the economic contribution of trophy hunting. The overarching reason the study was unable to show the economic contribution of trophy hunting was that the analysis provided an estimate of the gross economic activity associated with trophy hunting, rather than the marginal economic benefit of trophy hunting.

Estimates of marginal economic benefits must necessarily consider the next best alternative use of resources, and thus are useful for evaluating management options for wildlife and conservation areas. Estimates of gross economic activity associated with an activity are not themselves informative in this regard. Furthermore, Southwick (2015) does not account for the fact that 11% of the trophy hunters were likely to visit the African study countries and engage in other tourism activities even without the option to trophy hunt. Southwick (2015) also used multipliers to assume that businesses offering trophy hunting would find no alternative income source should trophy hunting be more tightly regulated; an economic analysis tool no longer widely accepted by economists.

Adjusting for the methodological shortcomings in Southwick (2015) shows that trophy hunting does not contribute $426 million to the study economies as claimed, and that the marginal economic contribution of trophy hunting is likely in the range between zero and $USD 132 million, depending on the alternative uses of land and wildlife resources. Meanwhile, trophy hunting activities do not generate 53,000 jobs as claimed but rather between 7,500 and 15,500 jobs. Lastly, regardless of what the marginal economic benefit of trophy hunting truly are, even if they are highly positive, this does not automatically provide incentives for wildlife conservation. Indeed, the Southwick (2015) study is cautious not to claim a direct link between trophy hunting and wildlife conservation, offering a rough estimate that only between $USD 27 and 40 million potentially contribute to funding conservation in the eight study countries.

REFERENCES

Ammoland. 2016. Hunting Tourism Contributes $426 Million to African Economy. Ammoland. June 13 2016. Accessed at http://www.ammoland.com/2016/06/hunting-tourism-contributes-426-million-african-economy/#ixzz4Rzp6uYTr

Campbell, R. 2012. Mane Assumptions: A review of Lindsey et al (2012) -- The Significance of African Lions for the Financial Viability of Trophy Hunting and the Maintenance of Wild Land, a report for the African Lion Coalition, prepared by Economists at Large, Melbourne, Australia

Crowley, K. 2016. Hunters' Answer to Cecil The Lion Outrage Is That We Create 53,000 Jobs. Bloomberg. June 10, 2016. Accessed at http://www.bloomberg.com/news/articles/2016-06-09/hunters-answer-to-cecil-the-lion-outrage-we-create-53-000-jobs

Crompton, J.L. 2006. Economic Impact Studies: Instruments for Political Shenanigans? Journal of Travel Research August 2006 45: 67-82, doi:10.1177/0047287506288870

Damm, G. R. 2005. Hunting in Namibia 2004: A Summary. African Indaba Vol 3, Nos 4 and 5, pages 1 – 14. http://www.africanindaba.com/wp-content/uploads/2014/03/AfricanIndabaVol3-4.pdf

Dwyer, L., Forsyth, P., and R. Spurr. 2004. Evaluating tourism's economic effects: new and old approaches, Tourism Management, Volume 25, Issue 3, Pages 307-317, ISSN 0261-5177, http://dx.doi.org/10.1016/S0261-5177(03)00131-6.

Elliot, J. and M. Mwangi. 1998. The opportunity cost of the hunting ban to landowners in Laikipia, Kenya. Laikipia Wildlife Economics Study Discussion Paper CEC-DP-4. African Wildlife Foundation. Accessed at http://www.awf.org/sites/default/files/media/Resources/Books%20and%20Papers/CEC-DP-4_hunting_ban.pdf

Epsley, S. 2015. Why the hunting conversation hurts conservation. Africa Geographic Magazine. 30 January 2015. Accessed at http://magazine.africageographic.com/weekly/hunting-canned-hunting-trophy-hunting-debate/

Fahrer, J. 2015. Carmichael coal and rail project: Economic assessment – Expert report by Jerome Fahrer, ACIL Allen consulting, report to Land Court of Queensland.

GHD. 2013. Carmichael Coal Mine and Rail Project SEIS: Report for Economic Assessment, available from Queensland Department of State Development website, http://www.statedevelopment.qld.gov.au/assessments-and-approvals/carmichael-coal-mine-and-rail-project.html

Jorge A.A., Vanak A.T., Thaker M., Begg C., Slotow R. 2013. Costs and benefits of the presence of leopards to the sport-hunting industry and local communities in Niassa National Reserve, Mozambique. Conservation Biology 27(4):832-43. doi: 10.1111/cobi.12082

Lindsey, P. A., Roulet, P. A., and S. S. Romanach. 2007a. Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. Biological Conservation. 134: 455-469

Lindsey P.A., Balme G.A., Booth V.R., Midlane N. 2012. The Significance of African Lions for the Financial Viability of Trophy Hunting and the Maintenance of Wild Land. PLoS ONE 7(1): e29332. doi:10.1371/journal.pone.0029332

Lindsey, P.A., Havemann, C.P., Lines, R.M., Price, A.E., Retief, T.A., Rhebergen, T., Van der Waal, C. and Romañach, S.S., 2013. Benefits of wildlife-based land uses on private lands in Namibia and limitations affecting their development. Oryx, 47(01), pp.41-53.

Ngonyo, J. 2013. The Usual Suspects Try Again to Reintroduce Trophy Hunting to Kenya. Greanville Post. Accessed at http://www.greanvillepost.com/2013/10/25/the-usual-suspects-try-again-to-reintroduce-trophy-hunting-to-kenya/

Phillips, K. 2016. Hunters Contribute $426 Million to African Economy. NRA Hunters Leadership Forum. Wednesday, June 15, 2016. Accessed at https://www.nrahlf.org/articles/2016/6/15/hunters-contribute-426-million-to-african-economy/

Ogutu, J.O., Owen-Smith, N., Piepho, H.P. and Said, M.Y. 2011. Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977–2009. Journal of Zoology, *285*(2), pp.99-109.

Ottichilo, W.K., De Leeuw, J., Skidmore, A.K., Prins, H.H. and Said, M.Y. 2000. Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. African Journal of Ecology, 38(3), pp.202-216.

Sachedina, H.T. 2008. Wildlife is Our Oil: Conservation, Livelihoods and NGOs in the Tarangire Ecosystem, Tanzania. PhD Thesis. School of Geography and the Environment, University of Oxford

Samuelsson, E. and Stage, J. 2007. The size and distribution of the economic impacts of Namibian hunting tourism. South African Journal of Wildlife Research 37 (1), 41-52

Southwick. 2015. The Economic Contributions of Hunting-Related Tourism in Eastern and Southern Africa. Southwick Associates. For Safari Club International Foundation. November, 2015. Accessed at http://safariclubfoundation.org/wp-content/uploads/2016/06/Southwick-Associates-2015_FINAL.pdf

Taylor, W.A., Lindsey, P.A. & Davies-Mostert, H. 2016. An assessment of the economic, social and conservation value of the wildlife ranching industry and its potential to support the green economy in South Africa. The Endangered Wildlife Trust, Johannesburg.

van Wyk, L., Saayman, M., Rossouw, R., & A. Saayman. 2015. Regional economic impacts of events: A comparison of methods. South African Journal of Economic and Management Sciences, 18(2), 155-176. https://dx.doi.org/10.17159/2222-3436/2015/v18n2a2

World Bank. 2016. World development indicators. Databank. http://databank.worldbank.org/data/home.aspx

WTTC. 2016. World Travel & Tourism Council Data Gateway. http://www.wttc.org/datagateway/

WTO. 2016. World Tourism Organization, Yearbook of Tourism Statistics, Compendium of Tourism Statistics and data files. Accessed at http://data.worldbank.org

ZAWA. 2014. ZAWA explains hunting ban lift. Zambia Wildlife Authority (ZAWA) Press release. September 14, 2014. Accessed at http://www.zambiatourism.com/zawa-explains-hunting-ban-lift

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Estimating economic losses to tourism in Africa from the illegal killing of elephants

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Recent surveys suggest tens of thousands of elephants are being poached annually across Africa, putting the two species at risk across much of their range. Although the financial motivations for ivory poaching are clear, the economic benefits of elephant conservation are poorly understood. We use Bayesian statistical modelling of tourist visits to protected areas, to quantify the lost economic benefits that poached elephants would have delivered to African countries via tourism. Our results show these figures are substantial (~USD $25 million annually), and that the lost benefits exceed the anti-poaching costs necessary to stop elephant declines across the continent's savannah areas, although not currently in the forests of central Africa. Furthermore, elephant conservation in savannah protected areas has net positive economic returns comparable to investments in sectors such as education and infrastructure. Even from a tourism perspective alone, increased elephant conservation is therefore a wise investment by governments in these regions.

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The conservation of savannah (*Loxodonta africana*) and forest (*Loxodonta cyclotis*) elephants in Africa is an issue of urgent global significance, as the recent upswing in poaching has resulted in reductions of up to 60% in elephant populations across the continent[1–3]. Demand for ivory, largely to supply Asian markets despite an international commercial trade ban[1], is reducing or eliminating elephants in large swathes of their former range, with recent surveys suggesting tens of thousands of elephants have been poached over the last 5 years from Tanzania and Mozambique alone[4]. Suggested conservation responses to this crisis have included reducing ivory demand in Asia[5,6], increasing incentives for local communities to act as elephant stewards[7] and strengthening the ability of frontline conservationists to prevent elephant poaching[8,9]. The latter two points require range-country governments to amplify their investments in elephant conservation efforts. However, given other pressing development priorities that compete for limited funding and attention, it is typically difficult to justify conservation via a return-on-investment basis, as the tangible economic benefits of biodiversity conservation are rarely understood[10,11].

Here we conduct an economic analysis of the contribution of elephants (grouping both species together) to tourism in Africa's protected areas (PAs). In taking this approach we aim to elucidate how the tourism benefits that are lost due to elephant poaching relate to the enforcement or anti-poaching costs required to prevent elephant population declines that arise from illegal killing. This benefit-cost framework, while addressing an important aspect of elephant conservation and management, is only one small component of what a total economic value study would estimate[12]. In a more comprehensive economic study with greater data availability, additional potential costs such as damages to local communities' crops and the opportunity costs of setting aside PAs[13,14], as well as additional potential benefits such as the ecosystem engineering role of elephants and the existence values that people hold for their conservation[15,16], would all be considered.

Our modelling builds on recent global and continental-scale models of tourist visits to PAs[17] and quantifies the marginal contribution of elephant densities to the expected number of visits to a PA. Conceptually, if fewer elephants are present at PAs due to poaching, and if elephant abundance is indeed an important driver of tourist visits (that is, all else equal, more elephants mean more tourists), the lost economic benefits due to poaching can be estimated as the spending of visitors at and near PAs that will no longer occur due to reduced visitation rates. To make such a valuation, we use information on the average number of annual visits to 164 PAs within 25 elephant range-state countries (these 25 countries collectively contain > 90% of Africa's elephants), including 110 PAs that contain elephants

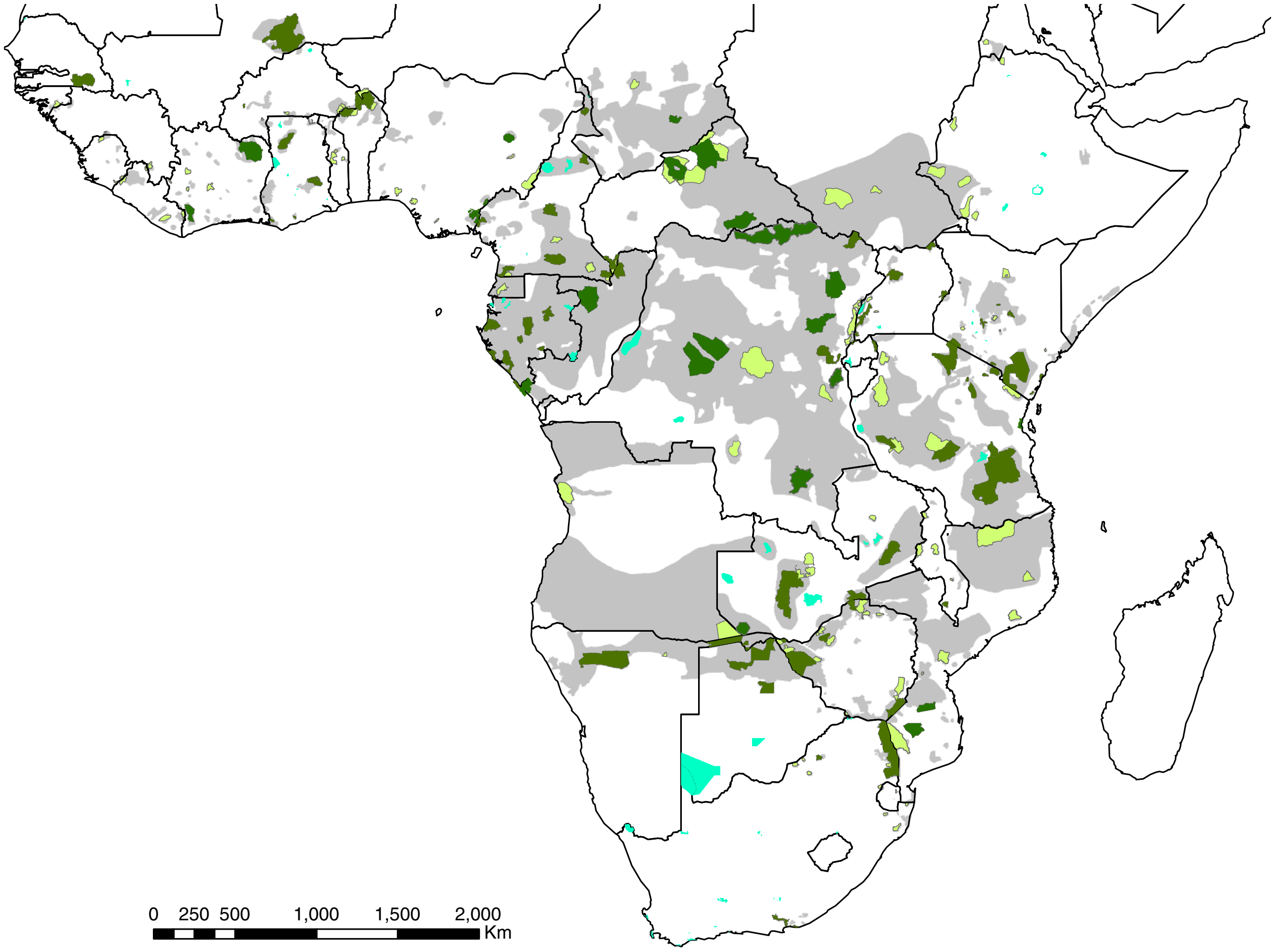

Figure 1 | Protected areas and elephant distribution in Africa. Combined range of the two African elephant species (grey), with International Union for Conservation of Nature Category II–VI protected areas[46] that harbour elephants (dark green indicating $n = 110$ that have tourist visitor data and light green indicating those without visitor data) and protected areas with no elephants for which we have tourist data (blue, $n = 54$).

(Fig. 1). In addition, we harnessed information on the most recent (typically *ca.* 2009–2013) comprehensive population estimates (http://elephantdatabase.org)[18] and rates of illegal killing at 216 PAs, and on the average direct and indirect spending levels of nature-based tourists visiting PAs in Africa (see Methods). Our figures for the per-unit-area spending necessary to effectively curtail elephant poaching are derived from empirical modelling work conducted at the height of the first wave of African elephant poaching during the 1980s (refs 19,20); to our knowledge, there have been no similarly thorough estimates derived during the current poaching crisis.

We find that the lost economic benefits that elephants could deliver to African countries via tourism are substantial (~ USD $25 million annually), and that these benefits exceed the costs necessary to halt elephant declines in east, southern and west Africa. Even if we entirely ignore other benefits that people derive from elephants[21], their conservation is a wise investment decision for countries in the savannah regions of Africa, although not currently so in the forested regions of central Africa.

Results

Aggregate impact and valuation of elephant losses to tourism. The tourism model we developed explains 44% of the variance in visitation rates to Africa's PAs (Fig. 2). After controlling for a number of other potentially confounding variables, there was very strong support (95% Bayesian credible intervals that do not overlap with zero) for elephant density as a positive predictor of the annual number of visits a PA receives (Table 1). There was also very strong evidence of an interaction between elephant density and whether PAs were forested or savannah (the positive effect of elephants on visits was much reduced in forests), a negative effect of PA size and a positive one of country-level wealth. In addition, there was substantial support (90% Bayesian credible intervals that do not overlap with zero) for the impacts of surrounding population (negative; PAs with smaller surrounding populations had more visits), the presence of another charismatic megafauna species, the lion *Panthera leo* (positive; PAs with lions had more visits) and a main effect of forested PAs (negative; fewer visits to forest PAs than savannah PAs). After controlling for all these independent variables, our model showed that a 1-unit increase in elephant density resulted in a $100 \times (e^{1.55} - 1) = 371\%$ increase in PA tourist visits. At the median number of PA visits in our data set (1,883), this result implies that an increase in elephant density of 0.1 km^{-2} resulted in an additional ~700 annual visits to a PA, all else equal.

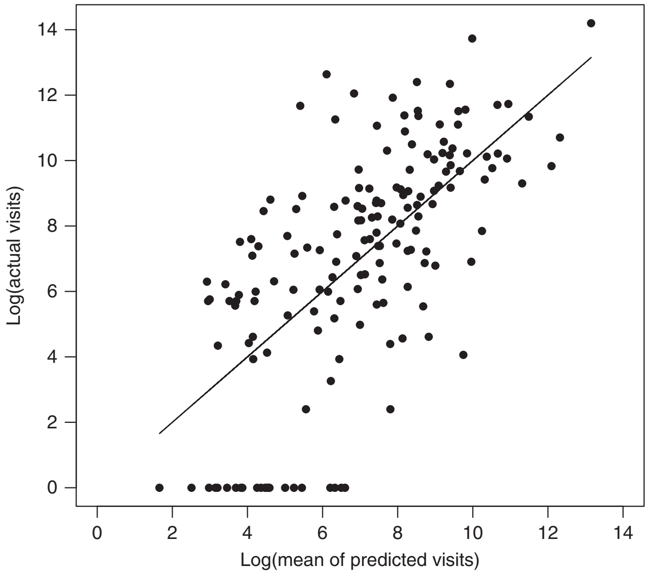

Figure 2 | Evaluating the predictive value of the tourist visitation model. Actual (*y* axis) versus median predicted (*x* axis) average annual tourist visits (log-transformed) from a Bayesian regression model of tourist visits to 164 protected areas in Africa. Regression equation: $Y = 1.02^{*}X - 0.14$, $R^2 = 0.44$, $P < 0.0001$.

We used our model to predict tourist visitation rates at all 216 PAs in Africa that currently harbour elephants. We then used population-specific estimates of changes in elephant densities[1], to estimate the annual number of elephants being lost to poaching at each PA, and simulated how this loss would reduce annual tourist visits by re-running our model using these new predicted elephant densities. To monetize the reduction in the flow of tourists to PAs due to elephant poaching, we simulated economic losses resulting from direct spending (using a best-fitting exponential distribution parameterized from 36 estimates of in-country, per-visit expenditure on nature-based tourism in Africa; Supplementary Fig. 1) and also from indirect and induced spending (using a best-fitting Gaussian distribution parameterized from 24 studies that estimated local economy 'multiplier' impacts of African nature-based tourism; Supplementary Fig. 2). We drew independently from each of these distributions for each PA, multiplied these values by the estimate of annual losses in tourist visits and repeated 100,000 times.

Using this valuation procedure we estimate that across Africa the annual, direct economic losses from reduced PA visitation due to elephant poaching run to a mean of $9.1 million (USD 2016; 95% Bayesian credible interval (CI) $4.86–$15.7 million), with an additional mean loss of $16.4 million (95% CI $8.56–$28.9 million) in indirect and induced spending. These estimates represent the first continent-wide assessment of the economic losses that the current elephant poaching surge is inflicting on nature-based tourism economies in Africa. Using a central figure of ~$25 million in lost economic benefits per year highlights the relative impact of these losses: this represents close to 20% of the receipts from all PA visits in 14 countries that contain half of Africa's elephants[22] and, tabulating ecoregion-level costs of effective biodiversity conservation[23], ~7% of the funding required to conserve biodiversity in ecoregions in which elephants occur. On the other hand, the economic difficulties of elephant conservation are also illustrated by the fact that annual losses to tourism are only a small fraction of the estimated $597 million that ivory from Africa's poached elephants was worth annually on Chinese black markets from 2010–2012 (see Supplementary Note 1).

Geographic variation in tourism loss from elephant poaching. Disaggregating the overall figures for the economic losses associated with poaching of elephants at PAs across the continent reveals substantial variability in their geographic distribution. Regionally, the greatest losses occur in east and southern Africa (Table 2). This is driven not by poaching rates, which are actually substantially lower in those regions than in central Africa[1–3], but rather by high visitation rates to PAs and the fact that the positive impact of elephant density on tourism visits is strongly reduced in the forested PAs of central Africa (Table 1). As such, the aggregate current tourism expenditures that are lost due to elephant poaching in central African forested PAs are negligible ($0.009 million with 95% CI $0.02–$0.05 million), but are several orders of magnitude higher in east Africa (mean $12.2 million; 95% CI $4.17–$27.8 million) and in southern Africa (mean $13.0 million; 95% CI $5.69–$24.8 million). These lost tourism benefits due to elephant poaching can be a substantial fraction of all nature-based tourism in countries where savannah, rather than forested, ecosystems predominate. For example, in Tanzania, we estimate that the average total tourism benefits lost due to elephant poaching are ~ \$540,000 per year, or between 4% and 11% of the total receipts from all visitors to PAs (estimated at \$5–\$15 million per year[22]).

Return-on-investment from elephant conservation. How do the lost benefits from reductions in elephant-based tourism compare with the costs that would be required to reduce or eliminate the poaching of elephants (and therefore sustain these benefits) at PAs across the continent? Few studies have analysed anti-poaching costs, in particular with varying effectiveness targets and across large scales encompassing different habitat types. The only such study we are aware of was conducted during the height of elephant poaching in the 1980s and developed a regression model of the relationship between changes in large ($>$1,000) elephant populations and per-unit-area investment in conservation across 14 African countries[19,20]. To achieve no decline in elephant populations required spending levels of \$215 km^{-2} in USD 1981, equivalent to \$565 km^{-2} in USD 2016 (converted using the United States' Department of Labor Consumer Price Index inflation calculator; http://data.bls.gov/cgi-bin/cpicalc.pl). We used this regression model to estimate the shortfall (based on changes in PA-specific elephant populations from illegal killing) required to stabilize elephant populations for each of 58 PAs containing over 1,000 elephants.

The overall costs for reducing poaching to a level that rendered elephant populations stable (that is, no growth but no decline) in PAs with large elephant populations were estimated at \$26.5 million annually across the 58 PAs, with almost two-thirds of this cost (\$16.9 million) occurring in the large, mostly forested PAs of central Africa where poaching has been heaviest (Table 2). Comparing these costs with the total lost tourism benefits due to elephant poaching at the same sites reveals average rates of return (the difference between average benefits and costs, divided by the costs) on elephant conservation that are highly negative in central Africa (−100%, because of a large shortfall in spending and few visitors), positive in west Africa (16%; modest visitation but also—because of low elephant numbers—a limited spending gap), and strongly positive in southern Africa (54%) and east Africa (78%; where gains in visitor spend would substantially outweigh the necessary increases in anti-poaching expenditure). From a regional, return-on-investment point of view, elephant conservation in the savannah PAs of east, southern and west Africa is justifiable based on the economic returns from tourism alone. The average rate of return on elephant conservation in these regions also compares favourably with estimated rates of return to investments in education[24], agriculture[25], electricity[26] and infrastructure[26] that governments in African elephant range countries routinely make (Fig. 3).

Changes in elephant density and tourist visits over time. Our results are based on across-site variation in tourism visits and changes in elephant densities for a large set of African PAs. How do these results compare with changes in visits and elephant numbers within a single site? Acquiring a large panel data set on changes over time in tourists, elephant densities and additional covariates across many PAs would have been ideal, but in practice we were only able to locate one PA with sufficient data to do a within-site comparison. Addo Elephant National Park in South Africa has a published time series from 1954 to 2010 on elephant numbers and visitors[27], and a bivariate plot of the two indicates a general positive relationship split into two distinct phases (1956–1995 and 1996–2010; Supplementary Fig. 3). Although our model of tourist visits across African PAs mostly contains

Table 1 | Bayesian regression model results.

	Mean	s.d.	2.5%	97.5%	Number effective samples	R-hat
Intercept	6.38	4.18	−1.83	14.49	4479	1
Area	−0.83	0.36	−1.54	−0.11	21508	1
Elephant density	1.55	0.39	0.80	2.32	3633	1
Forest	−1.26	0.68	−2.59	0.05	3181	1
Elephant density × forest	−2.02	0.69	−3.39	−0.73	2098	1
Lion	1.00	0.58	−0.14	2.14	27139	1
Natural attractiveness	−0.18	0.34	−0.84	0.49	18595	1
Nearby human population	−0.34	0.21	−0.75	0.07	18652	1
Accessibility	−0.70	0.49	−1.65	0.25	3595	1
Country PPP	2.05	0.53	1.02	3.08	4588	1

Bayesian regression model results for a model of the average number of annual tourist visits (log-transformed) across 164 protected areas in sub-Saharan Africa. The mean, s.d., 2.5% quantile and 97.5% quantile of posterior coefficient estimates are presented, as well as the number of effective samples and the R-hat measure of parameter convergence. PPP, Purchasing Power Parity.

Table 2 | Estimating the lost tourism benefits from the illegal killing of elephants.

Region	All PAs with elephants				PAs > 1,000 elephants				
	Predicted annual visits	Direct tourism benefits lost*	Indirect/induced tourism benefits lost*	Total benefits lost*	Cost to maintain population*	Direct tourism benefits lost*	Induced tourism benefits lost*	Total benefits lost*	Rate of return (%)
Central	8,412	0.003	0.006	0.009	16.9	0.003	0.005	0.008	−100
East	384,439	4.37	7.83	12.2	3.29	2.13	3.83	5.31	78
South	1,605,487	4.64	8.32	13.0	6.14	3.45	6.19	5.52	54
West	55,405	0.12	0.22	0.34	0.14	0.06	0.10	0.16	16

PA, protected area.

Regional distribution of predicted annual visits and lost tourism benefits across all PAs containing elephants, as well as investment costs required to halt poaching, lost tourism benefits and rates of return across 58 African protected areas that contain large ($>$1,000) elephant populations.

*\$2016 USD millions.

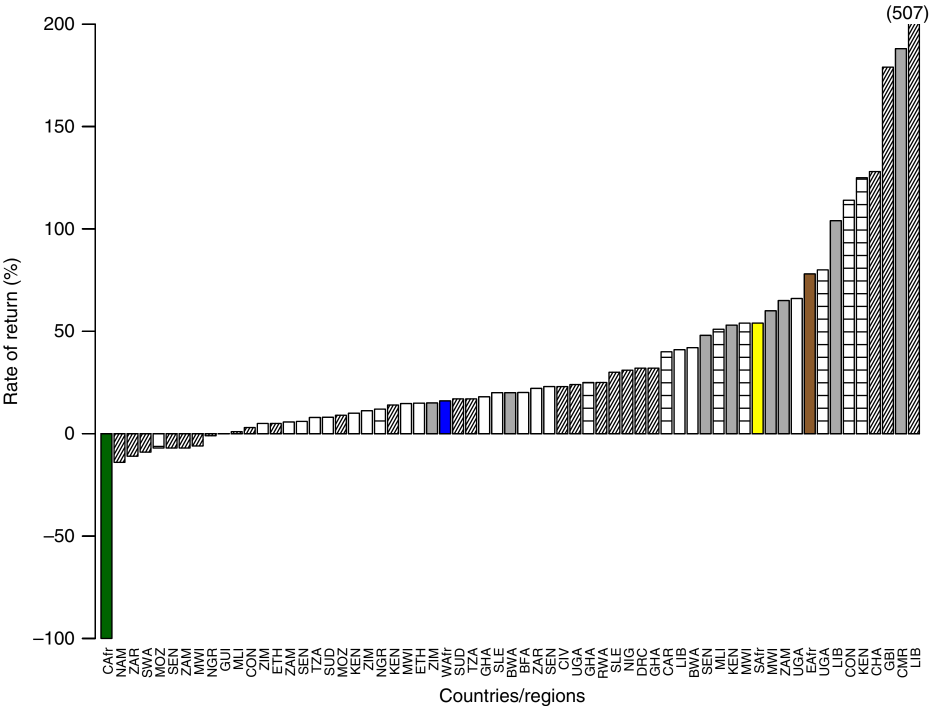

Figure 3 | Comparing rates of return in African elephant conservation to other investments. Mean rates of return to tourism from investing in efforts to reduce elephant poaching in central (green), west (blue), southern (yellow) and east (brown) Africa, along with a sample of rates of return estimated for investments in education (white bars[24]), agriculture (grey bars[25]), electricity (horizontal cross-hatched bars[26]) and infrastructure (angled cross-hatched bars[26]) in 33 African elephant range state countries (country abbreviations on bottom axis of figure).

Table 3 | Models of tourist visitation and elephant densities at Addo Elephant National Park.

	Mean	s.d.	2.5%	97.5%	Number effective samples	R-hat
1965–2010						
Intercept	10.91	7.09	– 2.94	24.91	1,490	1
Area	0.47	0.1	0.27	0.66	2,104	1
Country GDP	– 0.46	0.9	– 2.22	1.3	1,494	1
Elephant density	0.67	0.21	0.26	1.08	1,355	1
σ (tourists)	0.38	0.04	0.31	0.47	2,456	1
1965–1995						
Intercept	13.12	6.38	0.72	25.2	1,661	1
Area	0.22	0.09	0.05	0.4	1,978	1
Country GDP	– 0.59	0.81	– 2.13	0.99	1,652	1
Elephant density	0.55	0.18	0.19	0.9	1,549	1
σ (tourists)	0.3	0.04	0.23	0.39	1,864	1
1996–2010						
Intercept	9.72	0.58	8.56	10.87	2,011	1
Elephant density	0.66	0.19	0.27	1.05	1,978	1
σ (tourists)	0.15	0.04	0.09	0.26	1,560	1

Bayesian regression model results for a model that predicts annual tourist visits (log-transformed) at Addo Elephant National Park in South Africa. The mean, s.d., 2.5% quantile and 97.5% quantile of posterior coefficient estimates are presented, as well as the number of effective samples and the R-hat measure of parameter convergence.

variables that are time invariant (that is, forest/non-forest, year of establishment, access, surrounding population and natural attractiveness), country gross domestic product (GDP) and park area did change over time at Addo. We therefore built a subset of our main model by regressing tourist visits against park area, country GDP and elephant density. Despite this different set of independent variables, the coefficient on elephant density remained positive, with Bayesian credible intervals above zero and overlapping the range of our across-site analysis (0.67, with 95% CI of 0.26–1.08; Table 3). The coefficient on elephant density remained positive when we restricted the analysis to the 1956–1995 period (0.55; 95% CI 0.15–0.9) and also for the 1996–2010 period (0.66; 95% CI 0.27–1.05; it is noteworthy that here we regressed tourist visits on elephant density alone, as the sample size was too small to include the other independent variables). These results suggest a degree of concordance between the among- and within-site analyses (Supplementary Note 2), although Addo may only be representative of those PAs that, similar to itself, are fenced and where elephant populations have been strictly managed. Additional data at non-fenced, less heavily

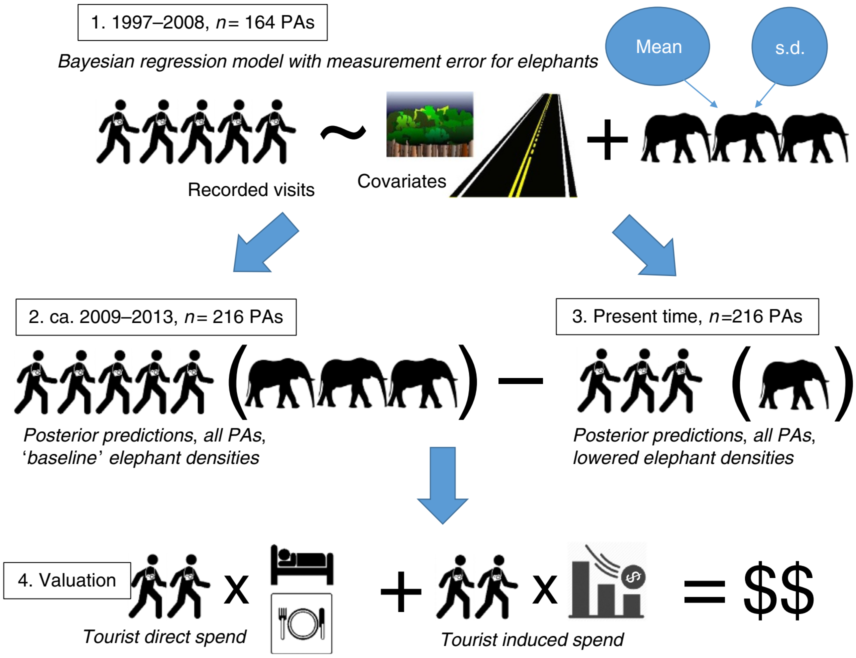

Figure 4 | Workflow representation of methods. Our modelling methodology involved the following steps: (1) Bayesian model estimation of tourist visits at 164 PAs; (2) predicted visits at 216 PAs, no elephant poaching; (3) predicted visits at 216 PAs, with reduced elephant densities from poaching; (4) stochastic valuation of lost visits via distributions of the direct and indirect spending of tourists at PAs.

managed PAs would have been useful to further assess the generality of our results for individual sites.

Discussion

Although our results make use of comprehensive, spatially explicit data on elephant densities at PAs across Africa, emerging results from the most recent census efforts suggest that declines in elephant populations in some countries have been even steeper than those previously documented[1,28]. As such, our estimates of the economic losses to tourism from elephant poaching may well be conservative, although we also understand that tourism takes time to evolve in places, and that responses to elephant decreases will not happen immediately at any given site. Despite the recognized importance of Africa's natural assets, especially wildlife, to tourism and other development pathways[29], our analyses were limited by the amount, quality and spatial resolution of data on the nature-based tourism sector. This was particularly true for expenditures that tourists make during PA visits and the associated impacts this injection of money can have in local economies[30]. Finally, the increasing magnitude and sophistication of elephant poaching may necessitate higher per-unit-area anti-poaching costs in heavily hit areas, although the deployment of novel, high-tech solutions such as unmanned aerial vehicles and infrared remote cameras may simultaneously drive costs down[31]. Anti-poaching costs also no doubt vary across sites due to other ecological and socioeconomic factors, but data to address this variation are sorely lacking and we were therefore obliged to rely on rigorous but dated information on anti-poaching costs collected during the 1980s wave of elephant poaching in Africa. Moreover, although anti-poaching efforts have strong positive impacts on elephant populations in both forest[32] and savannah[8] systems despite being generally underfunded across African PAs[33,34], they are not the only site-level actions that are important for elephant conservation[35].

Despite these caveats, our results suggest two broad conclusions. The first is that elephant conservation in PAs of the savannahs of Africa represents a wise investment with immediate and ongoing payback for tourism. Rates of return are positive, sometimes strongly, in these areas, indicating that tourists' willingness to pay, to see elephants as part of a visit to a PA, are sufficient to offset the increased costs necessary to safeguard elephant populations. These results align with surveys that have shown that elephants are among the most desired of African wildlife species for tourist viewing[36,37], suggesting that declines in elephants from poaching drive tourism losses, rather than the converse. Anecdotal information on the impacts of the even more catastrophic recent losses of elephants across Africa also suggests that tourism is under threat or has already declined (see Supplementary Note 3).

The second conclusion is that elephant-based tourism cannot currently be expected to contribute substantially to the conservation of forest elephants in central Africa. In these remote, difficult-to-access areas where tourism levels are currently lower than in savannahs and where elephants, with few exceptions[38], are difficult to see, different funding mechanisms that capture public concern and the 'existence value' of elephants will be necessary to halt recent declines[2]; examples include the Partnership to Save Africa's Elephants (a Clinton Global Initiative) and the Elephant Crisis Fund. Global forest-based conservation schemes, such as Reducing Emissions from Deforestation and Degradation (REDD +), may also have a role to play if associated biodiversity considerations, such as the conservation of elephants, can be incorporated[39]. Our results additionally highlight that the conservation of biodiversity cannot always be justified from a purely financial point of view, and that the 'use values' or 'ecosystem services' that biodiversity provides are complementary to, rather than substitutes for, moral or aesthetic reasons for conservation[40].

Although the value of ivory from poached elephants on Chinese black markets swamps that of the resulting losses in tourism, ivory benefits are not realized by governments or the people of African range states, apart from the few that are involved in the illegal killing. In contrast, tourism benefits from elephant conservation have the potential to reach a much broader cross-section of Africans, although financial considerations, such as the profit margins of tourism operators and the ability of policy makers to channel revenues from tourism to key stakeholder groups, are obviously critical to ensuring these net benefits are translated into effective conservation action. In particular, it will be fundamental to ensure that local communities and landholders are sufficiently incentivized to embrace living alongside elephants, or at minimum, are sufficiently compensated so as to not collaborate with poaching syndicates (for example, see www.ecoexistproject.org)[41]. Although there is a long history of nature-based tourism benefits not reaching local communities[42], recent experiences in African elephant range countries have demonstrated some successes in the devolution and capture of benefits from local natural resource management[43,44]. Ensuring that those who live with elephants are sufficiently compensated and motivated to do so, whether via tourism or other avenues, will play a central role in the success or failure of Africa's elephant conservation efforts.

Methods

Tourism data. For tourist visits to African PAs, we extended the visitor database of a recent global study[17], compiling data at additional PAs from published research, the grey literature and personal contacts familiar with tourism in various regions across sub-Saharan Africa. This resulted in a database with information on annual visitation rates for 164 PAs that occur in countries that contain African elephants. We simultaneously searched the literature for estimates of the economic importance of tourism visits to PAs in Africa via (1) the direct, in-country expenditure (not including the costs of international airfare) that a tourist spends at a PA[17,22] and (2) the economic impact, or 'multiplier' effect, that a tourist dollar has as it trickles through the local economy after its initial expenditure[30,45]. We were able to compile $N=36$ and $N=24$ such estimates, respectively, which we used in valuation simulations as described in the main text and below (Supplementary Figs 1 and 2).

Elephant and PA data. We extracted data on the size and location of elephant populations across Africa from the African Elephant Database (http://elephantdatabase.org)[18]. G. Wittemyer kindly provided annual growth rates (*ca.* 2012), including the proportion of elephants killed illegally (PIKE), for these same populations[1]. We cross-referenced these spatial estimates of elephant populations and their growth rates with International Union for Conservation of Nature (IUCN) PAs in categories II–VI (excluding category I PAs where tourism is largely prohibited) using the World Database on Protected Areas[46], extracting all PAs that overlap with known elephant populations (Fig. 1). For each of these 216 PAs, we extracted information on additional potential predictors of tourist visitation rates as per the model in ref. 17 and as described below.

Modelling PA visitation rates. We built a model of the average annual number of visits to PAs across the African elephant's range using 164 PAs for which we had information on tourist visits, elephant populations and a set of additional predictor variables previously used in modelling tourist visits to PAs[17]. Briefly, these additional variables were as follows: (1) PA size—we expected larger PAs to have more visitors; (2) surrounding population—we expected PAs with more people living around them to have higher numbers of visitors; (3) accessibility—we expected more accessible PAs (measured by the minutes to get to the PA over land and/or water routes from the nearest large city) to be more heavily visited; (4) national income (2006 PPP)—we expected richer countries to have greater levels of PA visits; and (5) natural attractiveness—we expected PAs with a higher such score (measured subjectively as a 1–5 index of the attractiveness of the birds and mammals a visitor might expect to observe for 65 biome-realm combinations) to have more visitors. In addition to the predictors in ref. 17 and elephant density (the result of the stochastic draw of elephant population mean divided by the area that was censused at each PA), we also included the interaction between elephant density and forest/non-forest land cover type (based on an assessment of the dominant land cover contained within each PA[47]), as we expected elephants to be less important draws for tourists in forested areas where they are difficult to observe. In addition, and recognizing that other charismatic megafauna have the potential to drive tourism, we used recent and comprehensive rangewide distributions[48,49] of the lion *P. leo* to include lion presence/absence at a PA as a further predictor in our visitation models. Our previous work[17] investigated other possible variables of importance that were ultimately not included in the final visitation model (for example, distance to major airport and incidence of armed conflict) and data availability constraints precluded other potential drivers, such as the activities on offer at a park (for example, mountain biking, hiking and fishing), from being included.

As our tourism data were almost entirely from 1998–2007 (ref. 17), we used elephant population estimates that overlapped with this time period where possible (75% of cases). We used a Bayesian regression modelling approach that offered several advantages to traditional/frequentist multiple linear regression methods. First, elephant populations are estimated with uncertainty and our Bayesian framework explicitly incorporated this uncertainty by using as the predictor a normal distribution for the population at each PA (defined by the mean and s.d.), rather than a point estimate as required by ordinary multiple linear regression[50]. A majority (55%) of the elephant populations had estimates of the uncertainty around the population size, expressed either as a s.d. from an assumed normal distribution (43%) or as a range (12%). In the latter case, we assumed a normal distribution centred around a mean at the midpoint of the range and assumed the range endpoints represented 95% CIs, following best practice in such instances[50]. A second advantage of Bayesian regression methods is that for the 45% of population estimates where no uncertainty estimate was provided, these missing values can be stochastically and simultaneously imputed within the same model, using the strong positive linear relationship we observed between the s.d. and mean of elephant population sizes ($\text{s.d.}=192+0.122\times\text{mean}$, $n=49$, $R^2=0.85$).

We (natural) log-transformed tourism visits so that the resulting distribution better approximated the normal and also log-transformed most of the predictor variables (Supplementary Table 1) to reduce differences in scale that could affect the Bayesian estimation procedures[51]. We used the modelling language Stan and the R statistical computing software to develop our models, using 4 Monte Carlo chains of 25,000 iterations after a 25,000-iteration warmup period each, for a total of 100,000 samples (a figure necessary to stabilize resulting value estimations that we derived from preliminary trials). Priors on all estimated parameters were uninformative[51]. We assessed convergence of the chains by ensuring that effective sample sizes were large and by ensuring that the potential scale reduction statistic, R-hat, was ≤ 1.01 for all estimated parameters[52]. See Supplementary Note 4 for a more detailed exposition of the model. We did not define a threshold cutoff for statistical 'significance', but rather interpret variable coefficients where 95% Bayesian credible intervals do not overlap with zero as providing very strong evidence for a variable's impact, with more moderate support for variables whose 90% Bayesian credible intervals do not overlap with zero.

Economic valuation of elephant losses from poaching. We used our Bayesian regression model to generate posterior predictions on the impact of the most recent reductions in elephants due to illegal killing. We first updated our estimates of tourist visits at all 216 PAs that contain elephants by holding all variables at their mean values and generating a set of predictions for tourist visits reflecting elephant population numbers from the most recent round of elephant censusing at sites across Africa (typically *ca.* 2009–2013, as opposed to the *ca.* 1998–2007 population estimates that coincided with our tourism data, and that we used to parameterize the PA visits model). We then used the site-specific PIKE estimates to calculate current annual reductions in elephant densities due to poaching for each site and, keeping all other predictor variables at their mean values, used these new, lowered elephant densities to generate predictions of annual visitation rates to all 216 PAs under expected current changes in elephant densities due to poaching. Taking the difference between the median visits with and without PIKE at each PA and summing these estimates resulted in a range-wide, aggregate annual reduction in PA visitation rates due to current illegal killing rates of elephants of $\sim$12,500 tourist visits.

As described in the Results, we then monetized this reduced flow of tourists by drawing direct expenditure values and indirect/induced multiplier effects from their respective distributions for each PA, multiplying these values by the predicted reduction in the PA's tourist visits due to elephant poaching and repeating this 100,000 times. Figure 4 provides a pictorial summary of the methods we used to assess the impact of elephant poaching on PA visits and the subsequent valuation of these visit losses.

To estimate the investment necessary to prevent the illegal killings of elephants calculated to be occurring at each PA, we drew on the only published studies that have quantitatively assessed the relationship between per-unit-area anti-poaching costs and changes in elephant populations across multiple study sites and habitat types[19,20]. These studies were conducted across 14 African countries (covering both forest and savannah habitats) during the height of the first wave of elephant poaching in the 1980s and resulted in a regression model of change in elephant population size as a function of per km^2 conservation expenditure. The model is applicable to large elephant populations ($>$1,000 individuals) and resulted in an estimate of \$215 km^{-2} in 1981 USD (\$565 km^{-2} in 2016 USD) in conservation spending necessary to prevent elephant declines. We view this \$565 km^{-2} estimate as conservatively high, given that it is several times higher than site-level cost estimates to halt elephant poaching in Zambia[53] and in Ghana[54].

Using this benchmark cost estimate of \$565 km^{-2}, we estimated the shortfall in spending that would be necessary to reduce the illegal killing of elephants at PAs containing $>$1,000 elephants such that populations were in equilibrium, by: (1) using PA-specific estimates of changes in elephant populations under current PIKE levels to generate, via the regression equations in refs 19,20, the expected amount of km^{-2} conservation spending occurring at each site[1] and (2) subtracting these spending estimates from the \$565 km^{-2} benchmark level. This resulted in conservation spending estimates that would be required to stabilize elephant populations for the 58 PAs that contained $>$1,000 elephants, which we then compared against the direct and total tourism benefits lost due to elephant poaching at these same sites.

Data availability. The data used to build the Bayesian regression models of tourist visitation to African PAs are given in Supplementary Data 1. Additional data are available from the authors upon request.

References

1. Wittemyer, G. *et al.* Illegal killing for ivory drives global decline in African elephants. *Proc. Natl Acad. Sci. USA* **111,** 13117–13121 (2014).
2. Maisels, F. *et al.* Devastating decline of forest elephants in Central Africa. *PLoS ONE* **8,** e59469 (2013).
3. Wasser, S. K. *et al.* Genetic assignment of large seizures of elephant ivory reveals Africa's major poaching hotspots. *Science* **349,** 84–87 (2015).
4. Schiffman, R. Four countries are acting as safe havens for elephants. *New Scientist* https://www.newscientist.com/article/dn27665-four-countries-are-acting-as-safe-havens-for-african-elephants/ (2015).
5. Patel, N. G. *et al.* Quantitative methods of identifying the key nodes in the illegal wildlife trade network. *Proc. Natl Acad. Sci. USA* **112,** 7948–7953 (2015).
6. Wasser, S. *et al.* Elephants, Ivory, and Trade. *Science* **327,** 1331–1332 (2010).
7. Challender, D. W. S. & MacMillan, D. C. Poaching is more than an enforcement problem. *Conserv. Lett.* **7,** 484–494 (2014).
8. Hilborn, R. *et al.* Effective enforcement in a conservation area. *Science* **314,** 1266 (2006).
9. Keane, A., Jones, J. P. G., Edwards-Jones, G. & Milner-Gulland, E. J. The sleeping policeman: understanding issues of enforcement and compliance in conservation. *Anim. Conserv.* **11,** 75–82 (2008).
10. Naidoo, R., Weaver, L. C., Stuart-Hill, G. & Tagg, J. Effect of biodiversity on economic benefits from communal lands in Namibia. *J. Appl. Ecol.* **48,** 310–316 (2011).
11. Gascon, C. *et al.* The importance and benefits of species. *Curr. Biol.* **25,** R431–R438 (2015).
12. Hanley, N. & Barbier, E. B. *Pricing Nature: Cost-Benefit Analysis and Environmental Policy* (Edward Elgar Publishing, 2009).
13. Mackenzie, C. A. & Ahabyona, P. Elephants in the garden: financial and social costs of crop raiding. *Ecol. Econ.* **75,** 72–82 (2012).
14. Naidoo, R. *et al.* Integrating economic costs into conservation planning. *Trends Ecol. Evol.* **21,** 681–687 (2006).
15. Alexander, R. R. Modeling species extinction: the case for non-consumptive values. *Ecol. Econ.* **35,** 259–269 (2000).
16. Valeix, M. *et al.* Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biol. Conserv.* **144,** 902–912 (2011).
17. Balmford, A. *et al.* Walk on the wild side: estimating the global magnitude of visits to protected areas. *PLoS Biol.* **13,** e1002074 (2015).
18. Blanc, J. *et al. Status of African Elephant Populations and Levels of Illegal Killing and the Illegal Trade in Ivory: A Report to the African Elephant Summit* (IUCN/SSC African Elephant Specialist Group, 2013).
19. Leader-Williams, N. The cost of conserving elephants. *Pachyderm* **17,** 30–34 (1993).
20. Leader-Williams, N. & Albon, S. D. Allocation of resources for conservation. *Nature* **336,** 533–535 (1988).
21. Ngouhouo Poufoun, J., Abildtrup, J., Sonwa, D. J. & Delacote, P. The value of endangered forest elephants to local communities in a transboundary conservation landscape. *Ecol. Econ.* **126,** 70–86 (2016).
22. World Tourism Organization. *Towards Measuring the Economic Value of Wildlife Watching Tourism in Africa - Briefing Paper* (UNWTO, 2014).
23. Moore, J., Balmford, A., Allnutt, T. & Burgess, N. Integrating costs into conservation planning across Africa. *Biol. Conserv.* **117,** 343–350 (2004).
24. Psacharopoulos, G. & Patrinos, H. A. Returns to investment in education: a further update. *Educ. Econ.* **12,** 111–134 (2004).
25. Benin, S. *Returns to Agricultural Public Spending in Africa South of the Sahara* (International Food Policy Research Institute, 2015).
26. Canning, D. & Bennathan, E. *The Social Rate of Return on Infrastructure Investments* (The World Bank, 1999).
27. Maciejewski, K. & Kerley, G. I. H. Elevated elephant density does not improve ecotourism opportunities: convergence in social and ecological objectives. *Ecol. Appl.* **24,** 920–926 (2014).
28. Chase, M. J. *et al.* Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ* **4,** e2354 (2016).
29. OECD. *Natural Resources and Pro-Poor Growth: The Economics and Politics* (OECD Publishing, 2009).
30. Saayman, M. & Saayman, A. Estimating the economic contribution of visitor spending in the Kruger National Park to the regional economy. *J. Sustain. Tour.* **14,** 67–81 (2006).
31. Mulero-Pázmány, M., Stolper, R., van Essen, L. D., Negro, J. J. & Sassen, T. Remotely piloted aircraft systems as a rhinoceros anti-poaching tool in Africa. *PLoS ONE* **9,** e83873 (2014).
32. Beyers, R. L. *et al.* Resource wars and conflict ivory: the impact of civil conflict on elephants in the democratic Republic of Congo - the case of the Okapi Reserve. *PLoS ONE* **6,** e27129 (2011).
33. Barnes, M., Craigie, I. D. & Hockings, M. in *Protected areas: are they safeguarding biodiversity?* (eds Joppa, L. N., Bailie, J. E. M. & Robinson, J. G.) (Wiley-Blackwell, 2016).
34. Jachmann, H. Monitoring law-enforcement performance in nine protected areas in Ghana. *Biol. Conserv.* **141,** 89–99 (2008).
35. de Merode, E. *et al.* The impact of armed conflict on protected-area efficacy in Central Africa. *Biol. Lett* **3,** 299–301 (2007).
36. Di Minin, E., Fraser, I., Slotow, R. & MacMillan, D. C. Understanding heterogeneous preference of tourists for big game species: implications for conservation and management. *Anim. Conserv.* **16,** 249–258 (2013).
37. Lindsey, P. A., Alexander, R., Mills, M. G. L., Romanach, S. & Woodroffe, R. Wildlife viewing preferences of visitors to protected areas in South Africa: implications for the role of ecotourism in conservation. *J. Ecotour* **6,** 19–33 (2007).
38. Remis, M. J. & Hardin, R. Transvalued species in an African forest. *Conserv. Biol.* **23,** 1588–1596 (2009).
39. Gardner, T. A. *et al.* A framework for integrating biodiversity concerns into national REDD + programmes. *Biol. Conserv.* **154,** 61–71 (2012).
40. Kleijn, D. *et al.* Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* **6,** 7414 (2015).
41. Pinter-Wollman, N. Human-elephant conflict in Africa: the legal and political viability of translocations, wildlife corridors, and transfrontier parks for large mammal conservation. *J. Int. Wildl. Law Policy* **15,** 152–166 (2012).
42. Bookbinder, M. P., Dinerstein, E., Rijal, A., Cauley, H. & Rajouria, A. Ecotourism's support of biodiversity conservation. *Conserv. Biol.* **12,** 1399–1404 (1998).
43. Naidoo, R., Weaver, L. C., De Longcamp, M. & Du Plessis, P. Namibia' s community-based natural resource management program: an unrecognized payments for environmental services scheme. *Environ. Conserv.* **38,** 445–453 (2011).
44. Frost, P. G. H. & Bond, I. The CAMPFIRE programme in Zimbabwe: payments for wildlife services. *Ecol. Econ.* **65,** 776–787 (2008).
45. Hamilton, K. *et al. The Real Economic Impact of Nature Tourism in Zambia* (Natural Resources Consultative Forum, 2007).
46. IUCN and UNEP-WCMC. *The World Database on Protected Areas (WDPA)* Available at www.protectedplanet.net (UNEP-WCMC: Cambridge, UK, 2013).
47. Bontemps, S. *et al. GLOBCOVER 2009-Products Description and Validation Report* (European Space Agency, 2011).
48. Riggio, J. *et al.* The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiversity Conserv.* **22,** 17–35 (2013).
49. Bauer, H. *et al.* Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proc. Natl Acad. Sci. USA* **112,** 14894–14899 (2015).
50. McElreath, R. *Statistical Rethinking: A Bayesian Course with Examples in R and Stan* (Chapman and Hall/CRC, 2015).
51. Gelman, A. *et al. Bayesian Data Analysis* 3rd Edition (CRC Press, 2013).
52. Stan Development Team. Stan Modeling Language: User's Guide and Reference Manual. Version 2.9.0 (2015).
53. Jachmann, H. & Billiouw, M. Elephant poaching and law enforcement in the Central Luangwa Valley, Zambia. *J. Appl. Ecol.* **34,** 233–244 (1997).
54. Jachmann, H. Illegal wildlife use and protected area management in Ghana. *Biol. Conserv.* **141,** 1906–1918 (2008).

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Author contributions

R.N. conceived of extending the original protected area visitation model of A.M. and A.B. R.N., A.M. and A.B. compiled the data. R.N. analysed the data with input from B.F., A.M. and A.B. R.N., B.F., A.M. and A.B. wrote the paper.

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Home range sizes and space use of African elephants (*Loxodonta africana*) in the Southern Kenya and Northern Tanzania borderland landscape

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The African elephant (*Loxodonta africana*) require vast areas to meet their survival needs such as food, mates, water, resting sites, and look up positions; the area referred to as home range. We collared 9 bull and 3 female elephants using satellite-linked Geographic Positioning System (GPS) collars in February 2013. Their movements were monitored up to April 2016 in the wider Amboseli landscape. We estimated their home ranges using 100% minimum convex polygon (MCP) and 95% Fixed Kernel Density Estimator (KDE) methods. A total of 48,852 GPS points were used representing 77% of the expected GPS points. This study revealed that bulls had a larger total home range size (MCP = 32,110 km²; KDE = 3,170 km² compared to females (MCP = 10,515 km²; KDE = 3,070 km²). The 95% confidence interval of the monthly range (95% KDE) for all elephants was 6,130 to 7,025 km² with the minimum and maximum range being 5,200 and 7,790 km² respectively. Females had smaller home ranges during the dry and wet season (MCP: dry = 2,974 km²; wet = 1,828 km²; KDE: dry = 2,810 km²; wet = 3,070 km²) than bulls (MCP: dry = 3,312 km²; wet = 13,288 km²; KDE: dry = 2,960 km²; wet = 3,720 km²). The variations of the elephant home range could have been influenced by an interaction of factors including rainfall, human disturbances and land use (e.g., farms, settlements, road network, and fences), water availability, bush cover, food availability, and tracking period. The most important areas that had key habitats for elephants were scattered throughout the Kenya/Tanzania borderland. The Amboseli-Tsavo-Magadi-Natron-West Kilimanjaro elephant population roams within specific areas of the landscape. Trans-boundary efforts should be enhanced to ensure sound management of the elephant-habitat-people interface for continued well-being of the elephant population.

Key words: Amboseli ecosystem, elephant, home range, minimum convex polygon, Kenya/Tanzania borderland, kernel density estimator.

INTRODUCTION

The African elephant (*Loxodonta africana*) are mega-herbivores that require large areas for acquisition of the necessary resources for self-sustenance. Ecologists refer to this area as the home range. The initial definition of home range was provided by Burt (1943) as, “the area traversed by individual in the normal activities of food gathering, mating and caring of the young”. Mohr (1947) estimates home range using the minimum convex polygon method that completely encloses all data points by connecting the outer locations in such a way as to create a convex polygon. The area under the polygon is used by the animal to satisfy its resource requirements over a specified time (e.g., mates, food, water, escape routes from enemies, resting sites, and look up positions; Delany, 1982; Jewell, 1966).

The concept of animal home range has been discussed in detail by different authors including Osborn (2004), Walter et al. (2011), Odrenj (2011), Douglas-Hamilton et al. (2005), Lyons et al. (2013) and Kie et al. (2016). The authors agree that the size of an animal home range is an exact area whose size depends on the method and parameters used to define and estimate it. Some methods used to estimate home range include: 100% minimum convex polygon (MCP) (Mohr, 1947; Leuthold and Sale 1973; Lindeque and Lindeque, 1991; Thouless, 1996; Whyte, 1996; Getzand Wilmers, 2004; Getz et al., 2007; Foguekem et al., 2007; Ipavec et al., 2007), squared grids (SG) (Douglas-Hamilton et al., 2005), 95% kernel density estimation (KDE; Leggett, 2006; Lyons et al., 2013), and Brownian Bridge Movement Models (BBMM) (Horne et al., 2007; Fischer et al., 2013; Walter et al., 2011). More recent home range estimation methods that combine the simplicity of polygon methods with the robustness of kernel methods have been developed (Lyons et al., 2013). These methods superimpose and then aggregate non-parametric shapes constructed around each point and include Voronoi polygons (Casaer et al., 1999), Delaunay triangles (Downs and Horner, 2009) and Local Convex Hull (LoCoH) approach (Getz and Wilmers, 2004; Getz et al., 2007). These current methods (e.g., LoCoH and BBMM) better estimate animal home range than the old methods e.g., MCP (Kie et al., 2016). However, the current methods have not been used long enough and researchers are still using the old methods to facilitate comparison of home range sizes over time (Kie et al., 2016).

Individual elephants are known to range over vast areas, varying from 10^1 to 10^3 km^2 (Leuthold and Sale, 1973; Lindeque and Lindeque, 1991; Thouless, 1995, 1996; Whyte, 1996; Douglas-Hamilton et al., 2005; Leggett, 2006; Foguekem et al., 2007; Ipavec et al., 2007; Ngene et al., 2009). Table 1 provides a summary of the sizes of African elephants in different ecosystems. Elephant home ranges were small in fenced areas (10 km^2 to about 80 km^2) and large in open areas (90 to about 800 km^2; Douglas-Hamilton et al., 2005; Leggett, 2006; Dolmia et al., 2007; Ngene et al., 2009; Kikoti, 2009). Long distance migrations of over 90 and 400 km in length have been reported from Kenya (Ngene et al., 2009), Mali (Blake et al., 2003) and Namibia (Leggett, 2006; Lindeque and Lindeque, 1991).

Despite the importance of the home range concept, there is no consensus among scientists studying animal movements on how to estimate the home range size of animals (Reinecke et al., 2014). However, in this paper, we estimate the home range of elephant in Amboseli ecosystem using the MCP and KDE methods. Despite its limitations (Powell, 2000; Osborn, 2004), the 100% MCP method was selected to facilitate comparisons of Amboseli elephant home ranges with those of West Kilimanjaro-Loliondo-Natron-Manyara areas in northern Tanzania (Kikoti, 2009). The 95% KDE method will provide a baseline for future comparisons of elephant home ranges in the study area. Although the MCP method estimates a larger home range size than KDE, it has been used for a long time and therefore, it offers an opportunity for comparing elephant home range in different areas (Osborn, 2004; Worton, 1989; Powell, 2000; Lyons et al., 2013; Kie et al., 2016). However, there is need to use another method to accurately estimate the elephant home range and offer an opportunity for future comparisons, especially with the current challenges of land use changes and their implications on elephant ranging patterns in the area. The 95% KDE method is popular (Worton, 1989; Lyons et al., 2013) because it is based on the superposition of Gaussian or compact (e.g., uniform or Epinechnikov) kernels and is more suitable for concave geometries (Lyons et al., 2013). Also, the method can estimate probability contours, and is easy to use due to its implementation in a variety of software packages (Lyons et al., 2013; Laver and Kelly, 2008). Regardless of the methodology used to estimate home range, changes of land use and land tenure systems affect utilization of range by elephants and constrict their home ranges (Doughlas-Hamilton et al., 2005; Gara et al., 2016a, b). The increase in human population and changes in lifestyles have resulted to changes in land use emanating from mushrooming of human infrastructure (e.g., roads, human settlements, fences and crop fields) within elephant ranges (Gara, 2014; Gara et al., 2016a, b). These changes impede wildlife movement and fragment prime elephants habitats (Burn Silver et al., 2008). Understanding elephant home range and space use in fragmentation landscape is critical for conservation and mitigating human-elephant conflicts (Gara et al., 2016a, b). In most savanna ecosystem across Africa landscape fragmentation due to land use and land tenure changes is understood to be a major threat to elephant and other

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Table 1. Size of elephant home range in different ecosystems.

Location	Home range size (km^2)	Country	Reference
Amboseli NP	100-200	Kenya	Douglas-Hamilton et al. (2005)
Shimba Hills	10-80	Kenya	Douglas-Hamilton et al. (2005)
Meru NP	200-300	Kenya	Douglas-Hamilton et al. (2005)
Marsabit	260-910	Kenya	Ngene et al. (2009)
Samburu-Laikipia	100-700	Kenya	Douglas-Hamilton et al. (2005)
West Kilimanjaro-Natron	191-3698	Tanzania	Kikoti (2009)
Krugar NP	129-1255	South Africa	Whyte (1993)
Hwange NP	1038-2981	Zimbabwe	Conybeare (1991)
Waza NP	248-3066	Cameroon	Tchamba et al. (1995)
Queen Elizabeth NP	363-500	Uganda	Abe (1994)
Sengwa	322	Zimbabwe	Osborn (1998)
Lake Manyara NP	10-57	Tanzania	Douglas-Hamilton (1972)
Tsavo East NP	1035-2380	Kenya	Leuthold (1977) and Leuthold and Sale (1973)
Tsavo West NP	294-408	Kenya	Leuthold (1977) and Leuthold and Sale (1973)
Etosha NP and Kaokoveld	5800-8700	Namibia	Lindeque and Lindeque (1991)
Northern Namib desert	1763-2944	Namibia	Viljoen (1989)

NP = National Park.

large mammals' distribution (Groom and Western, 2013). In Kenya, most protected area (parks, reserves and sanctuaries) aimed at *in-situ* conservation of different types of wildlife are bordered by human settlements (Graham et al., 2009). The Amboseli National Park is surrounded by six community ranches that are used by the Maasai agro-pastoralists for livestock grazing and subsistence and commercial crop farming (Hobbs et al., 2008; Gara, 2014).

These ranches act as dispersal areas and migratory corridors for elephants as they endeavor to connect cut off habitats (Burn Silver et al., 2008; Gara, 2014). However, these community ranches have experienced increased landscape fragmentation as a result of sedentarization of the Maasai, intensification of different landuse types and changing land tenure system (Ogutu et al., 2009; Gara et al., 2016a, b).

Landscape fragmentation as a result of sedentarization in the ranches has resulted in the increase of human-elephant conflict. The human-elephant conflicts in the area around Amboseli National Park are intensified by the fact that the elephants spend over 63% of their time outside the Amboseli National Park (Okello and D'Amour, 2008).

This paper maps the home ranges of 12 GPS-collared elephants in the Amboseli ecosystem using the 100% MCP and 95% KDE methods. We estimate the total and seasonal home range of the elephants (all combined, by sex [bull and females], and individual elephant). We also identify core areas utilized by the elephants using the 95% KDE method to discern key habitats important to the elephants as well as identify ranches important for elephant conservation.

MATERIALS AND METHODS

Study area

The Amboselie cosystem is located in Loitoktok Sub-County of Kajiado County. The ecosystem stretches between Mount Kilimanjaro, Chyulu Hills, Tsavo West National Park and the Kenya/Tanzania border. The current study area covers about 3,400 km^2 (Figure 1). Administratively, the Amboseli ecosystem consists of Amboseli National Park and the surrounding six group ranches (KWS, 2014). The six group ranches include: Kimana/Tikondo, Olgulului/Olararashi, Selengei, Mbirikani, Kuku, and Rombo and cover an area of about 506,329 ha (KWS, 2014). In addition, it includes the former 48 individual ranches located on the slope of Kilimanjaro Mountain that are now under rain fed crop farming (KWS, 2014). These ranches were all once connected together and with Amboseli National Park but today, human settlements, farms, fences and road networks are slowly making them more isolated from each other and the park (Kioko and Okello, 2010).

The area falls in the agro-ecological zones V and VI, and is hence classified as arid to semi-arid savanna (Gara, 2014). It is more suitable for pastoralism rather than crop farming and has a high potential for conservation of wildlife and tourism based enterprises. The rainfall shows spatiotemporal variations during the year. Annual rainfall ranges from 500 to 600 mm in the north to 250 to 300 mm in Amboseli National Park (Gara, 2014). The rain falls in two seasons with short rains being experienced from November to January and long rains from March to April. The two rainy seasons are interspersed by two dry periods (February, May, June, July, August, September, October; Altmann et al., 2002; Gara, 2014). Surface water is scarce other than permanent water in swamps and artificial waterholes in the southeast part of the ecosystem (BurnSilver et al., 2008). Temperature varies from 20 to 30°C (Gara, 2014). Elevation ranges from 850 m above sea level to 1350 m above sea level (Gara, 2014). The ecosystem is dominated by the following vegetation types: The broad leaf, dry tropical forests and woodlands on the Kilimanjaro and Chyulu slopes; open grassland, riverine forest, halophytic grass and scrubland in the Amboseli Basin; and, scattered *Commiphora* and *Acacia*

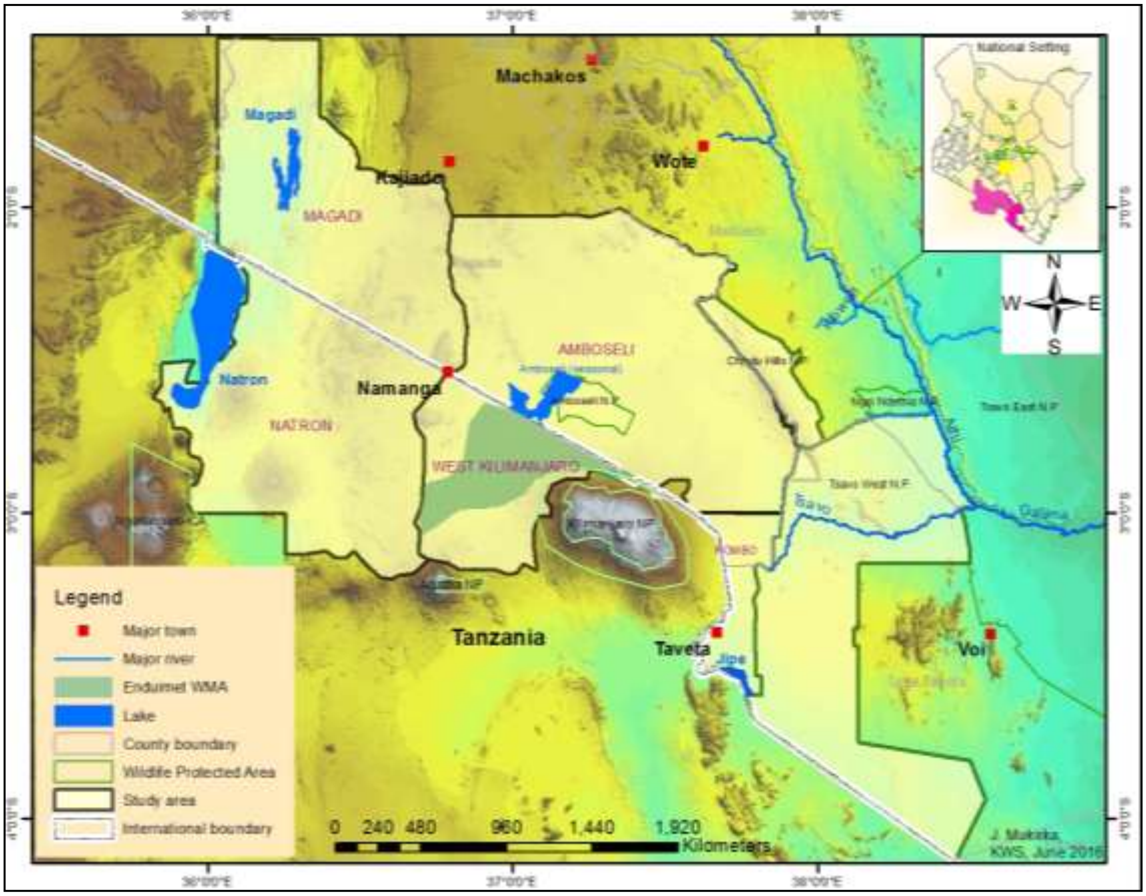

Figure 1. Map of the Amboseli ecosystem that includes the Amboseli National Park, Tsavo West National Park, Chyulu National Park and surrounding areas.

woodlands within the surrounding ranches (Howe et al., 2013; Western, 2007).

Data on elephant locations

Data on the space-use of elephants were collected from 12 elephants (9 bulls and 3 females) collared with satellite-linked GPS collars in 2013 (between: 18thFebruary 2013 and 15th March 2013; and, 2nd December 2013 and 5th December 2013) and 2014 (between 23rd April 2014 and 24th April 2014) by Kenya Wildlife Service (KWS) and the International Fund for Animal Welfare (IFAW). The collars were supplied by African Wildlife Tracking, South Africa and were satellite GPS/VHF model. The collaring operation followed procedures described by Ngene et al. (2013). The collared elephants belonged to different family groups. All the elephants were collared outside Amboseli National Park, with the objective of observing and monitoring their movement patterns outside the park and understanding when the elephants utilize the park. Table 1 provides details of the collared elephants. Figure 2 shows the point data of all the 12 collared elephants.

The collared elephants were immobilized with *Etorphine hydrochloride* (18 mg) administered using a dart gun. The immobilized elephants were then revived using *diprenorphine* (54 mg). The GPS collars were configured to acquire one GPS fix after every four hours. The GPS fixes were acquired in form of geographic coordinates (latitude/longitude) format but were re-projected to Universal Transverse Mercator (UTM) WGS-84 reference system (Zone 37M) using ArcGIS 10.1 (ESRI, 2011).

Before analysis the GPS fixes were checked for any positional irregularities that included checking whether GPS fixes were within acceptable locations within and around study area. All the elephant location data were screened for accuracy following procedures described by Bjørneraas et al. (2010). Dataset that had GPS errors like missing coordinates were removed from the dataset before analysis. The causes of GPS errors are: Temporal malfunction of the GPS collars (Gala, 2014), canopy cover (Jiang et al., 2008; Sager-Fradkin et al., 2007; Heard et al., 2008), topography (terrain and slope; Hebblewhite et al., 2007; Frair et al., 2004) and collar orientation (Sager-Fradkin et al., 2007; Heard et al., 2008; Moen et al., 1996; Frair et al., 2010). The data available for analysis after screening ranged between 58 and 92% (Table 2), which is within acceptable range to characterize wildlife movement patterns and make sound inference (Frair et al., 2010). After GPS tracking data screening a total of 48,852GPS points were used for analysis (Figure 2).

The datasets for each collared elephant were then classified into two seasons including wet(January, March, April, November and December) and dry (February, May, June, July, August, September and October) seasons respectively. The two seasons were selected as the study area falls within the tropical areas, which has only the wet and dry seasons. The seasons were selected based on monthly rainfall data from January 1976 to October 2015 (Figure 3; Altmann and Alberts, 2016). Months with average rainfall of below

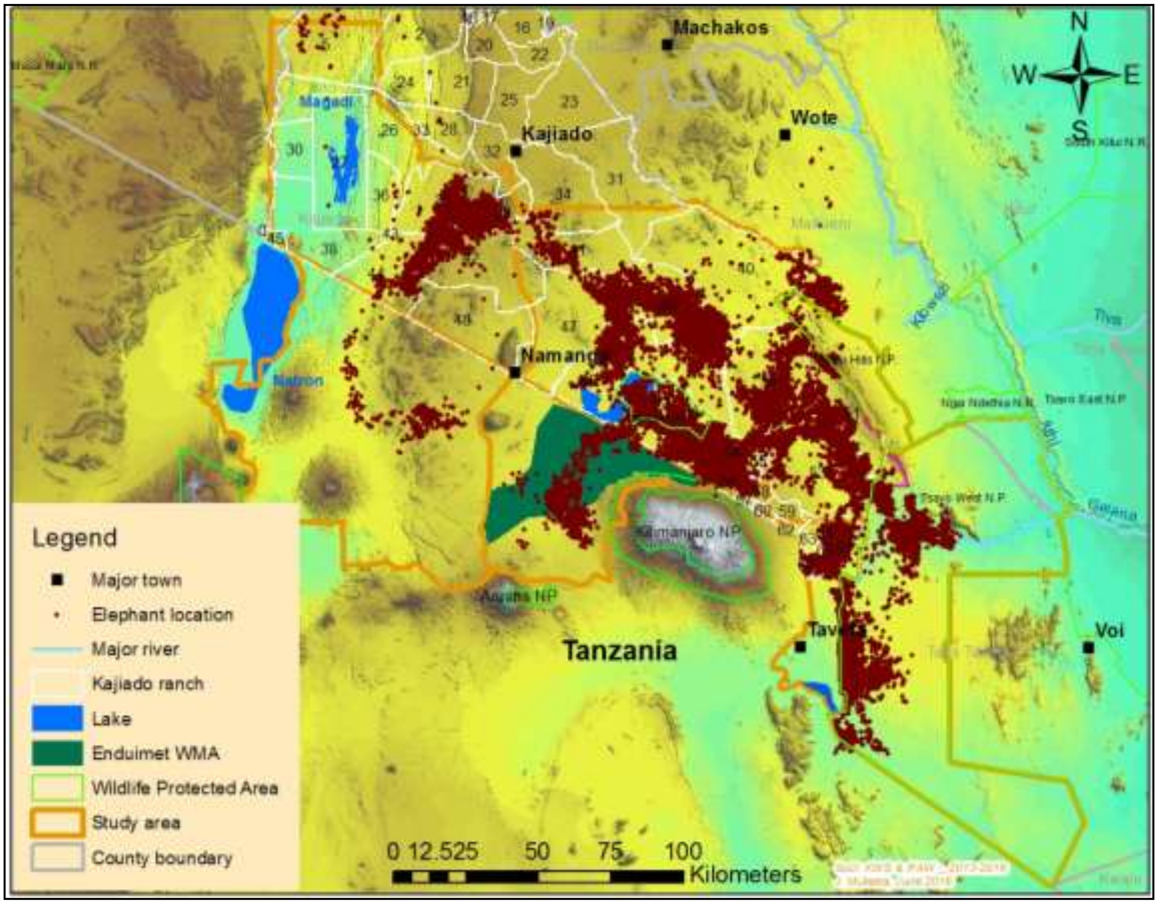

Figure 2. Location of 12 elephants collared in Amboseli ecosystem (2 February 2013 to 16 April 2016).

and above 30 mm were categorized as dry and wet respectively (Altmann and Alberts, 2016; Figure 3). The elephant locations datasets were grouped into these two seasons because previous studies demonstrate that elephant behavior is season dependent (Douglas-Hamilton *et al.*, 2005; Ngene et al., 2010). For example, the speed of elephant movement has been shown to vary from one season to another (Buij et al., 2007; de Beer and van Aarde, 2008; Ngene et al., 2010). Also, Gara (2014) reported that seasonality has a significant effect on the speed of elephant movement and habitat utilization.

Estimation of elephant home range

Home range of the elephant was estimated using the 100% Minimum Convex Polygon (MCP) method (Mohr, 1947) following procedures described by Beyer (2005) and implemented using Hawth's tools as an ARCGIS extension. The Hawth's tools were uploaded to ARCGIS 10 and used to calculate the MCP for each elephant. Based on the number of fixes (Table 2), the range used by all the elephants was estimated. In addition, individual elephant total and seasonal (dry and wet) home ranges were estimated. The MCP was used in different studies ((Leuthold and Sale 1973; Lindeque and Lindeque, 1991; Thouless, 1996; Whyte, 1996; Foguekem et al., 2007; Ipavec et al., 2007; Ngene et al., 2010), including in Tanzania (Kikoti, 2009) allowing comparisons with our study.

Space use by elephants

We established space use by the elephants using the 50 and 95% fixed kernel density estimator (KDE) method (Worton, 1989) implemented with the ARCMET tool (Wall, 2016) under the ARCGIS 10.3 environment (Worton, 1989; Fieberg, 2007; ESRI, 2013). The 95% KDE method quantified the probability density of elephant occurrence in the study area (Worton, 1989; Fieberg, 2007). The KDE was estimated for: all elephants for all seasons; all elephants during the wet and dry seasons; all bull and female elephants; and individual elephants in all seasons. The 50% KDE was used to isolate the core areas utilized by elephants. This is the areas that have the highest probability of being used by the elephants within their home ranges (Worton, 1989; Fieberg, 2007). The 95% and 50% KDE was estimated using a fixed bivariate normal kernel with a choice of ad hoc bandwidth (*h-ad hoc*) smoothing parameter as recommended by Worton (1989) and Schuler et al. (2014). We used the fixed kernel method rather than the adaptive kernel method as fixed kernel estimators are sensitive to multiple areas of concentrated use, and produce less area bias and better surface fit than adaptive kernel estimates (Seaman and Powel, 1996; Seaman at al., 1999).

Data analysis

Datasets for use in parametric tests were tested for normality and homogeneity of variances using the *Shapiro-Wilk Test* (Shapiro et

Table 2. Characteristics of the 12 collared elephants in Amboseli ecosystem including duration of tracking, number of fixes and GPS-fix success rate

No.	EID	Name	Sex	Age (year)	Collar Number or Frequency (freq)	Date of collaring	Date first GPS fix	Date last GPS fix	Days	Expected fixes	Fixes used	% Fixes used
1	KM	Kimana	Bull	26	00580824VTI9E75	19/2/2013	19/2/2013	6/4/2016	1127	6,762	6254	92
2	OSW	Osewan	Bull	30	00580819VTI0A5C	20/2/ 2013	20/2/ 2013	8/7/2016	1218	7308	4646	64
3	ESM	Eselengei	Bull	33	00580810VTI662F	20/2/ 2013	20/2/ 2013	22/2/2015	1082	6,492	3778	58
4	RF	Rombo	Female	15	00580811VTIEA34	14/3/2013	14/3/2013	6/4/2016	11102	6,612	5392	82
5	KUF	Kuku	Female	26	00580813VTIF23E	14/3/2013	14/3/2013	6/4/2016	11102	6,612	6031	91
6	MBM	Mbirikani	Bull	22	00580812VTI6E39	15/3/2013	15/3/2013	8/7/2015	1193	7,158	4278	60
7	ELM	Elerai	Bull	20	126150.620415freq	23/4/2014	23/4/2014	17/12/2015	594	3,564	3285	92
8	EWM	Elengata	Bull	40	124150.310B550freq	3/12/2013	3/12/2013	26/5/2015	533	3,198	2587	81
9	EWM2	Elengata2	Bull	30	125150.600BD5Afreq	3/12/2013	3/12/2013	6/4/2016	843	5,058	4250	84
10	KIM	Kitirua	Bull	22	Not recorded	23/4/2014	23/4/2014	6/4/2016	703	4,218	2933	70
11	MAF	Mailua	Female	25	129150.7906187freq	4/12/2013	4/12/2013	29/7/2014	235	1,410	1247	88
12	MAM	Mailua	Bull	25	128150.770DD82freq	4/12/2013	4/12/2013	6/4/2016	842	5,052	4171	83
Total										**63,444**	**48,852**	**77**

al., 1968; Fowler et al., 1998) with normality and homogeneity of variances being assumed when P> 0.05 (Shapiro et al., 1968). The *Shapiro-Wilk* test is the preferred test of normality because of its good power properties as compared to a wide range of alternative tests (Shapiro et al., 1968). For datasets that were not normally distributed and the variances were heterogeneous, they were Log$_{10}$ transformed to normalize them and ensure homogeneity of variances (Fowler et al., 1998). For datasets that could not attain normality non-parametric test were used. For parametric and non-parametric tests, we then used *T*-test, one-way ANOVA *F*-tests and chi-square goodness of fit test to analyze the data (Fowler et al., 1998) following procedures described by Statsoft (2002). Significant differences were at P ≤0.05 (Fowler et al., 1998).

RESULTS

Annual home range size

The annual range of the 12 elephants as estimated using the 100% MCP and 95% KDE methods was about 37,167 km^2 (Figure 4A) and 5,360 km^2 (Figure 4B) respectively. Bull elephants (n = 9) ranged in an area of about 32,110 km^2 (100% MCP; Figure 5A) and 3,170 km^2 (95% KDE; Figure 5B). The total home range of female elephant (n = 3) was about 10,515 km^2 (100% MCP; Figure 5A), 3,070 km^2 (95% KDE; Figure 5A) respectively. The home range of individual elephants is summarized in Table 3, Figure 6A (MCP method) and Figure 6B (95% KDE method). Female elephants did not range into Tanzania but three bulls (Kitirua, Osewani and Elengata) extended their range from Southern Kenya into the northern parts of Tanzania. The bull named Kimana ranged within the border area of Kenya and Tanzania, with some time being spent in Tanzania (Figure 6B). All the elephants utilized Amboseli National Park but the frequency of use varied among them (Supplementary Table). Rombo, a female elephant, was frequently located in Tsavo West National Park whereas the bull Erelai spent sometime in the same park (Supplementary Table).

The core areas used by all elephants were located in Lengesim and Kimana/Tikodo ranches (Figure 4B). However, individual elephant core areas were located in the following ranches and parks: Mbuko, Lorngosua, Mailua, Lengesim, Amboseli National Park, Kimana/Tokondo, Endonet, Rombo Block II, Kuku, Tsavo West National Park, Chyulu West Game Conservation Area (Figure 6B; Supplementary Table). The 95% confidence interval of the monthly range (95% KDE) for all elephants was 6,130 to 7,025 km^2 with the minimum and maximum range being 5,200 and 7,790 km^2. The monthly range for all elephants varied significantly (t = 279; df = 11; p < 0.05; Figure 7). There was a significant variation of monthly home range with amount of rainfall with smaller home ranges being recorded in dry months than in wet months (t = 12; df = 1; p <

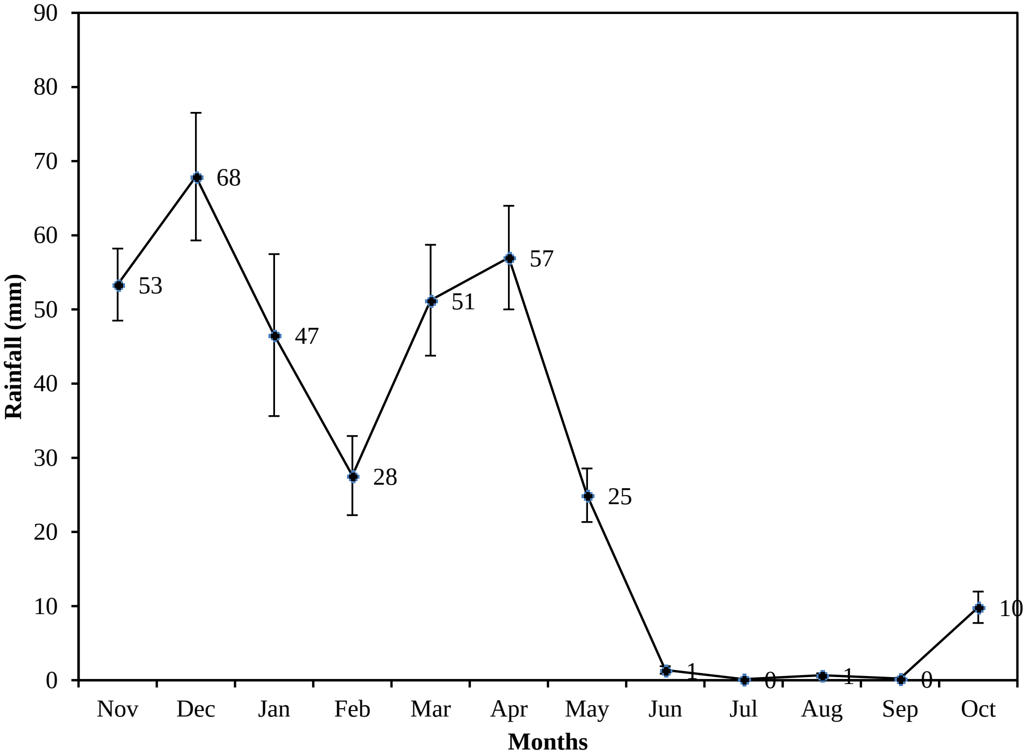

Figure 3. Mean monthly rainfall from January 1976 to October 2015 (Source: Altmann and Alberts, 2016). Months with less than 30mm of rainfall were categorized as dry season whereas those with more than 30 mm of rainfall were categorized as wet season.

0.05; Figure 7). The smallest (5,200 km^2) and largest (7,710 km^2) range were observed in August and April, respectively (Figure 7).

Seasonal home range

The elephants covered a range (100% MCP) of 31,404 and 33,471 km^2 during the dry and wet seasons respectively (Figure 8A). The dry and wet season home range (100% MCP) varied from 932 to 9,034 km^2 and 671 km^2 and 4,954 km^2 respectively (Table 4). There was a significant seasonal variation of elephant home range sizes with smaller home ranges being recorded during the wet season than dry season (dry: X^2 = 16,751; df = 11; $p < 0.05$; wet: X^2 = 14730.94 df = 11 $p < 0.05$; Table 3).Some of the elephants showed larger and small home range (100% MCP) during the dry season than the wet season respectively (Table 4). Females had a significantly smaller mean home range (100% MCP: dry = 2,974 km^2; wet = 1,828 km^2) than bulls (100% MCP: dry = 3,312 km^2; wet = 3,288 km^2) during the dry and wet seasons respectively (dry season: t = 645; df = 22; p <0.05; wet season: t = 610; df = 22; $p < 0.05$).

The elephants ranged (95% KDE) in an area of about 5,448 and 6,129 km^2 during the dry and wet seasons respectively (Figure 8B). Results for 95% KDE showed the home range of females during the dry and wet season as 2,810 and 3,070 km^2 respectively, while that of bulls was 2,960 km^2 (dry season) and 3,720 km^2 (wet season; Figure 9). Table 4 also summarizes home range of individual elephants using the 95% KDE method. The 95% KDE home range sizes vary as those reported for the MCP method. However, the 95% KDE method recorded smaller home ranges than those calculated using the MCP method (Table 4).

DISCUSSION

Our results reveal that individual elephants ranged from 1,839 to 10,016 km^2 (100% MCP) and 290 to 1,226 km^2 (95% KDE; Figure 10). Similar results of large variation of home range area (100% MCP) have been reported in other studies in East Africa (Ngene et al., 2009; Kikoti, 2009). For example, Kikoti (2009) reported that annual range of 21 elephants collared with satellite-linked GPS collars in northern Tanzania varied from 191 to 3,698 km^2 (100% MCP).

In northern Kenya, Thouless (1996) reported that range area (100% MCP) for 20 female elephants varied from 102 to 5,527 km^2. Also, Douglas-Hamilton et al. (2005) reported the home ranges size (100% MCP) for 11 elephants varied from 11 to 5,520 km^2 in

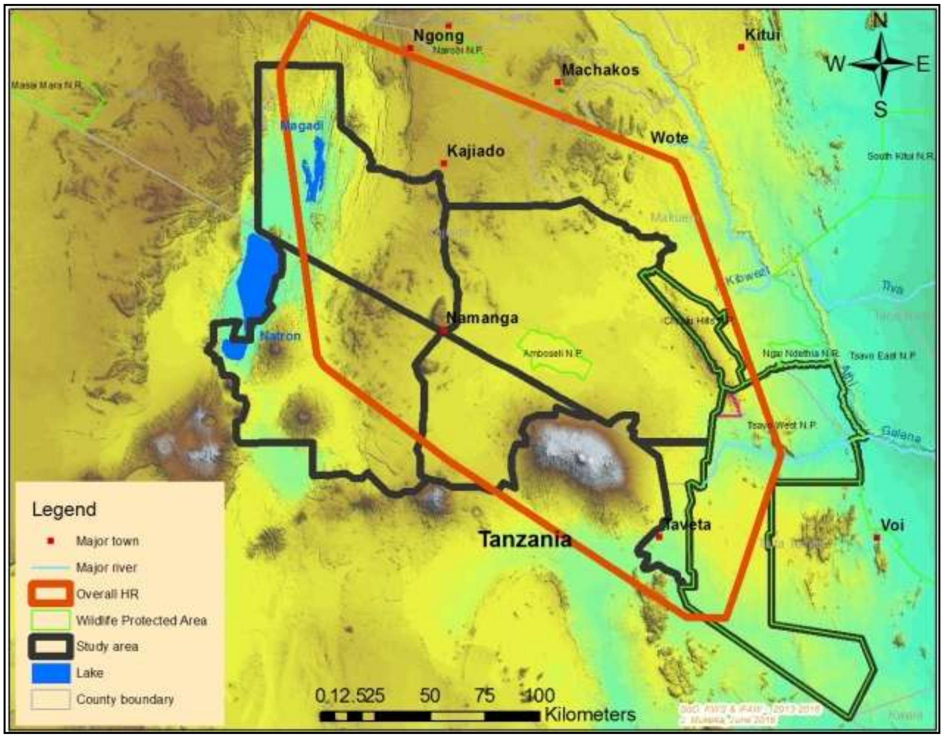

Figure 4A. Total home range (MCP method) of 12 elephants collared in Amboseli ecosystem (2 February 2013 to 16 April 2016). The numbers represent the group ranches in the study area (Supplementary Table

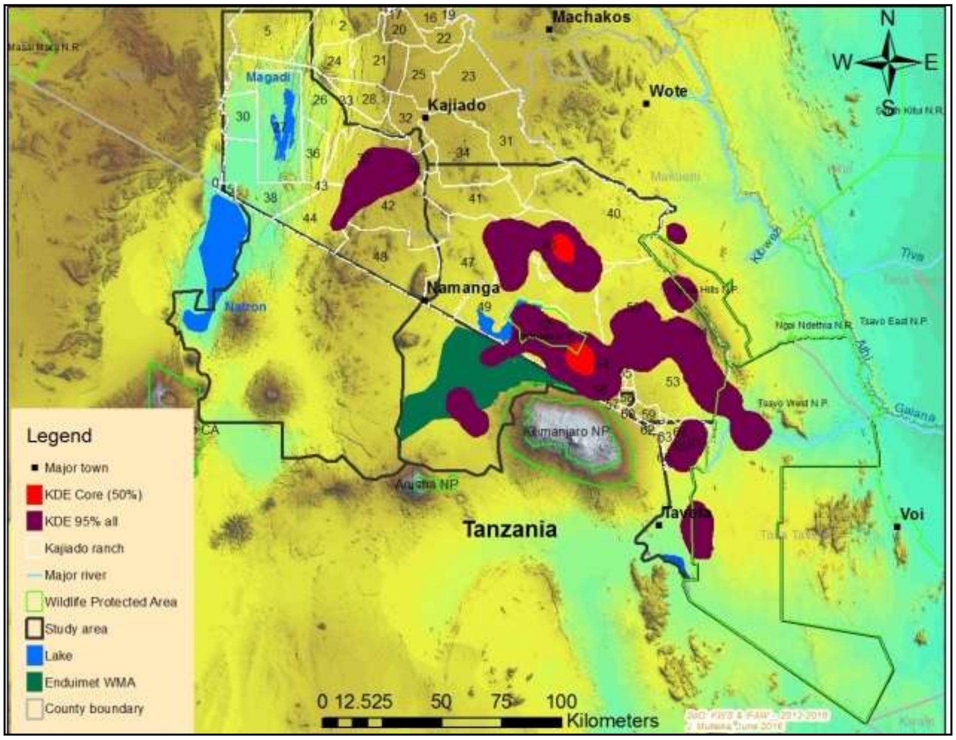

Figure 4B. Total home range (KDE method) of 12 elephants collared in Amboseli ecosystem (2 February 2013 to 16 April 2016). The numbers represent the group ranches in the study area (Supplementary Table).

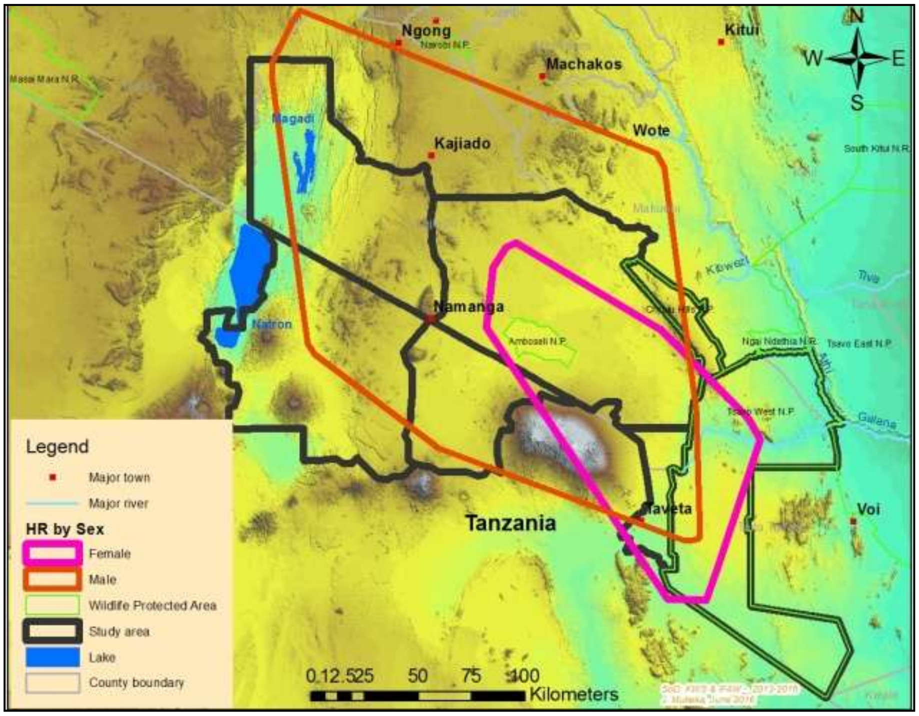

Figure 5A. Total home range (MCP method) of bull (n = 9) and female (n = 3) elephants collared in Amboseli ecosystem (2 February 2013 to 16 April 2016).

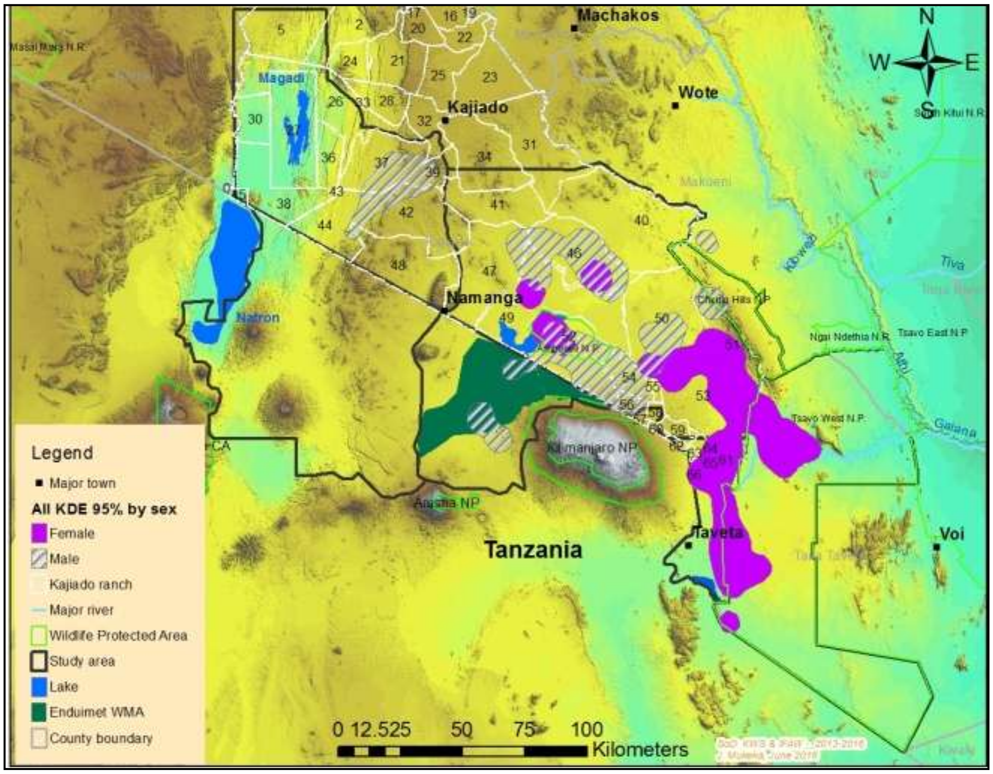

Figure 5B. Total home range (KDE method) of bull (n = 9) and female (n = 3) elephants collared in Amboseli ecosystem (2 February 2013 to 16 April 2016). The numbers represent the group ranches in the study area (Supplementary Table).

Table 3. Total home range (MCP and KD) of 12 elephants collared in Amboseli ecosystem (values for MCP and KDE are in km^2).

EID	Name	Sex	Age (years)	Fixes used	MCP	KDE
KM	Kimana	Bull	26	6254	2,005	290
OSW	Osewan	Bull	30	4646	4,040	769
ESM	Porini	Bull	33	3778	5,449	669
RF	Rombo	Female	15	5392	3,444	1226
KUF	Kuku	Female	26	6031	4,995	749
MBM	Mbirikani	Bull	22	4278	3,314	704
ELM	Elerai	Bull	20	3285	2,602	223
EWM	Elengata	Bull	40	2587	5,143	1073
EWM2	Elengata2	Bull	30	4250	10,016	1162
KIM	Kitirua	Bull	22	2933	2,745	903
MAF	Mailua	Female	25	1247	1,839	606
MAM	Mailua	Bull	25	4171	3,695	208

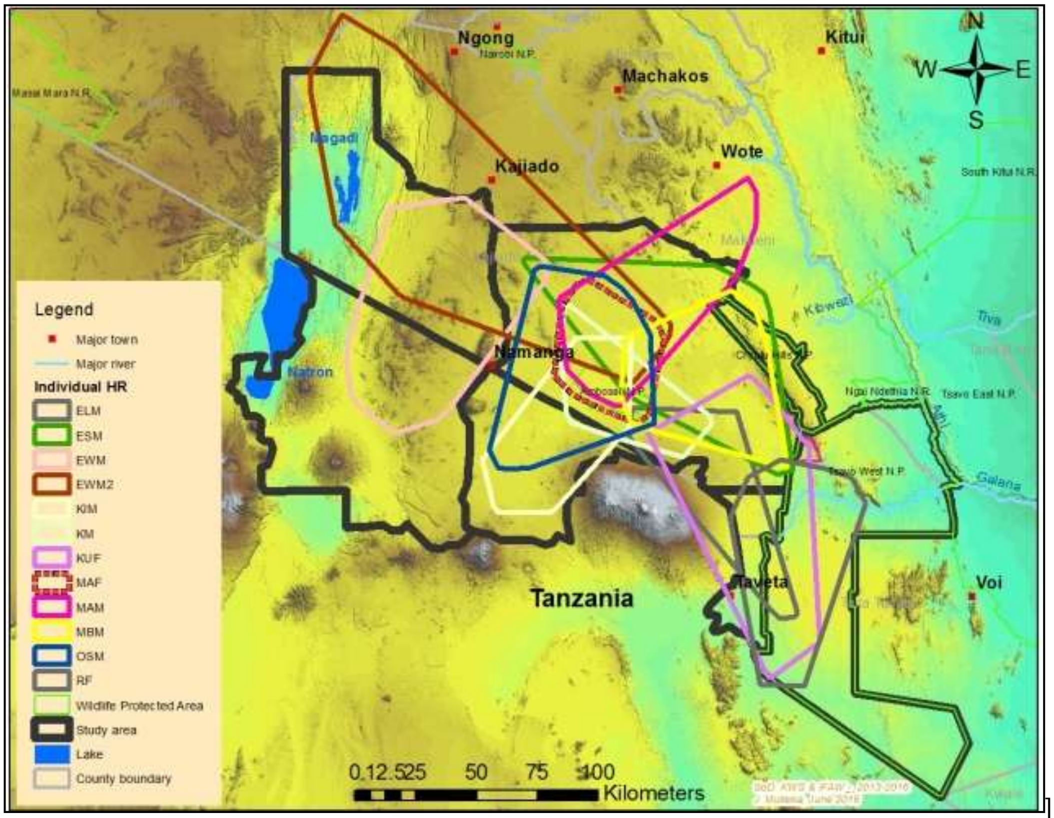

Figure 6A. Home range (MCP method) of individual elephants collared in Amboseli ecosystem (2 February 2013 to 16 April 2016).

southern and central Kenya. The average home range of bulls (100% MCP), was much larger than the range of two bulls (M86: 210 km^2; M169: 140 km^2) collared in Amboseli National Park (Douglas-Hamilton et al., 2005). However, the two bulls were monitored for very short periods (134 and 168 days respectively) compared to this study that monitored the elephants from February 2013 to April 2016. The general implication of these space use patterns is that the elephants require space outside the protected areas within the larger Amboseli ecosystem. It is important to secure the space for elephants outside the protected areas for their continued use and future

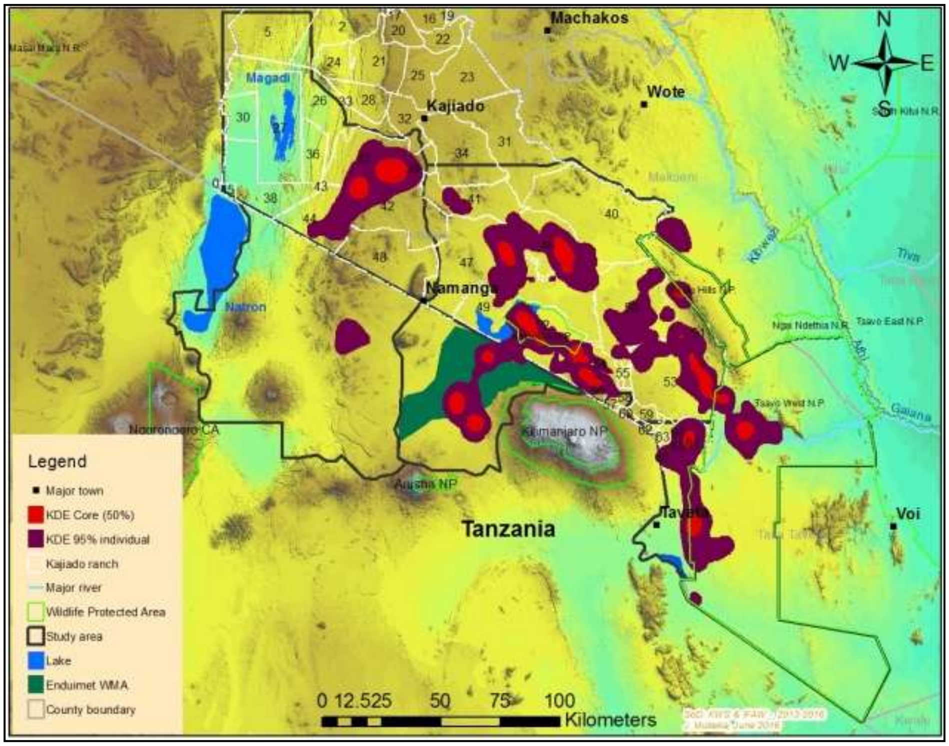

Figure 6B. Home range (KDE method) of individual elephants collared in Amboseli ecosystem (2 February 2013 to 16 April 2016). The numbers represent the group ranches in the study area (Supplementary Table)

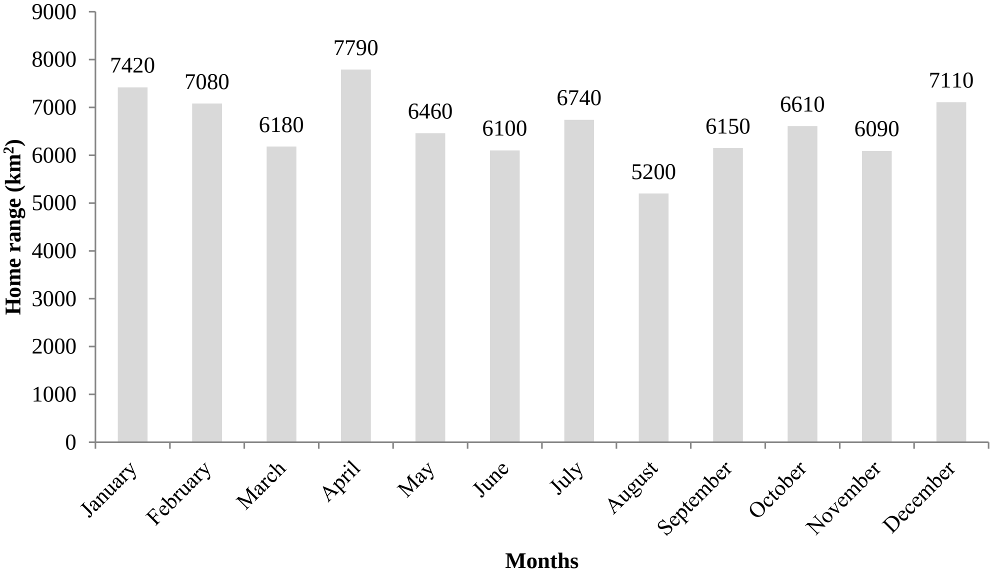

Figure 7. The monthly range (95% KDE) covered by all elephants in Amboseli ecosystem (February 2013 to April 2016).

existence in the ecosystem. This can be achieved by direct purchase of land used by elephants outside the protected areas as well as establishment of successful community and private conservancies on space utilized by elephants outside the protected areas.

Only three females compared to nine bulls were

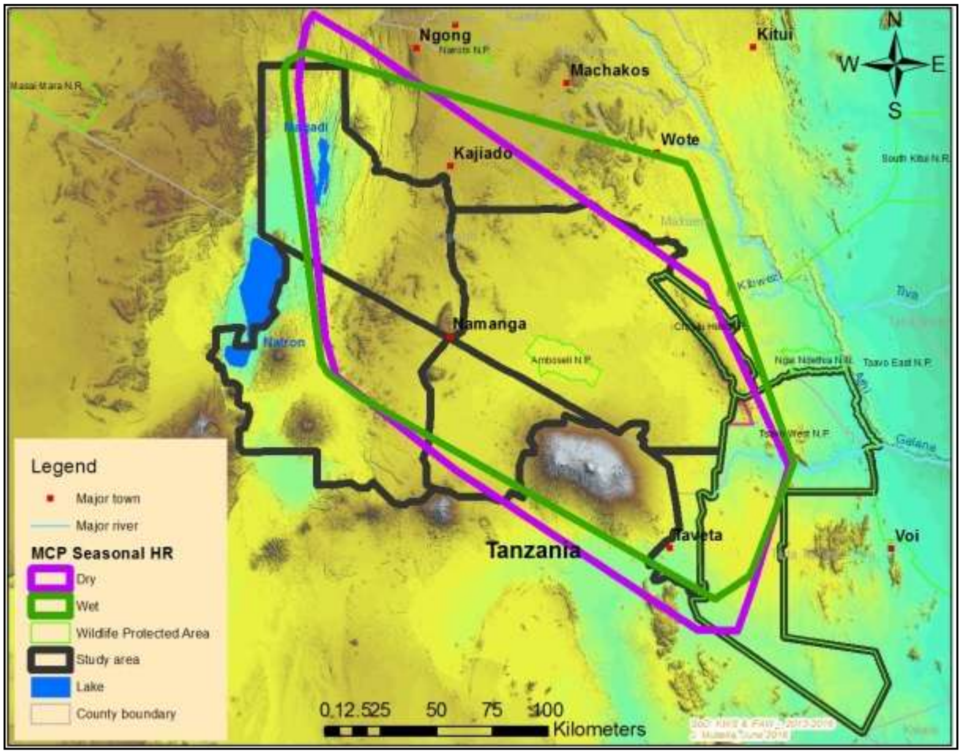

Figure 8A. Seasonal home range (MCP method) of all 12 elephants collared in Amboseli ecosystem (2 February 2013 to 16 April 2016).

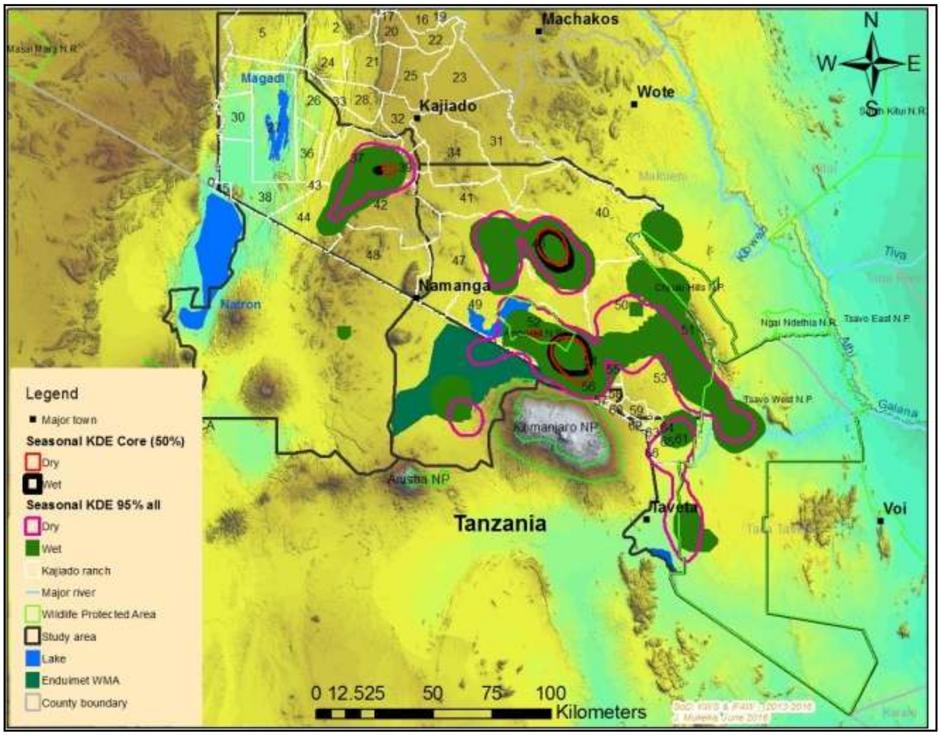

Figure 8B. Seasonal home range (KDE method) of all 12 elephants collared in Amboseli ecosystem (2 February 2013 to 16 April 2016). The numbers represent the group ranches in the study area (Supplementary Table).

Table 4. Seasonal home range (dry and wet) for 12 elephants collared in Amboseli ecosystem

EID	Name	Sex	Age (years)	Dry season (km^2) MCP	Dry season (km^2) KDE	Wet season (km^2) MCP	Wet season (km^2) KDE
KM	Kimana	Bull	26	1,896	256	671	280
OSW	Osewan	Bull	30	1,764	697	3,957	954
ESM	Porini	Bull	33	4,762	925	3,716	1,244
RF	Rombo	Female	15	3,107	791	2,693	495
KUF	Kuku	Female	26	4,882	617	1,013	475
MBM	Mbirikani	Bull	22	2,612	205	2,915	266
ELM	Elerai	Bull	20	2,341	808	770	1,102
EWM	Elengata	Bull	40	3,894	1,247	4,954	1,021
EWM2	Elengata2	Bull	30	9,034	711	7,610	875
KIM	Kitirua	Bull	22	1,994	278	2,201	546
MAF	Mailua	Female	25	932	164	1,777	321
MAM	Mailua	Bull	25	1,515	256	2,796	280

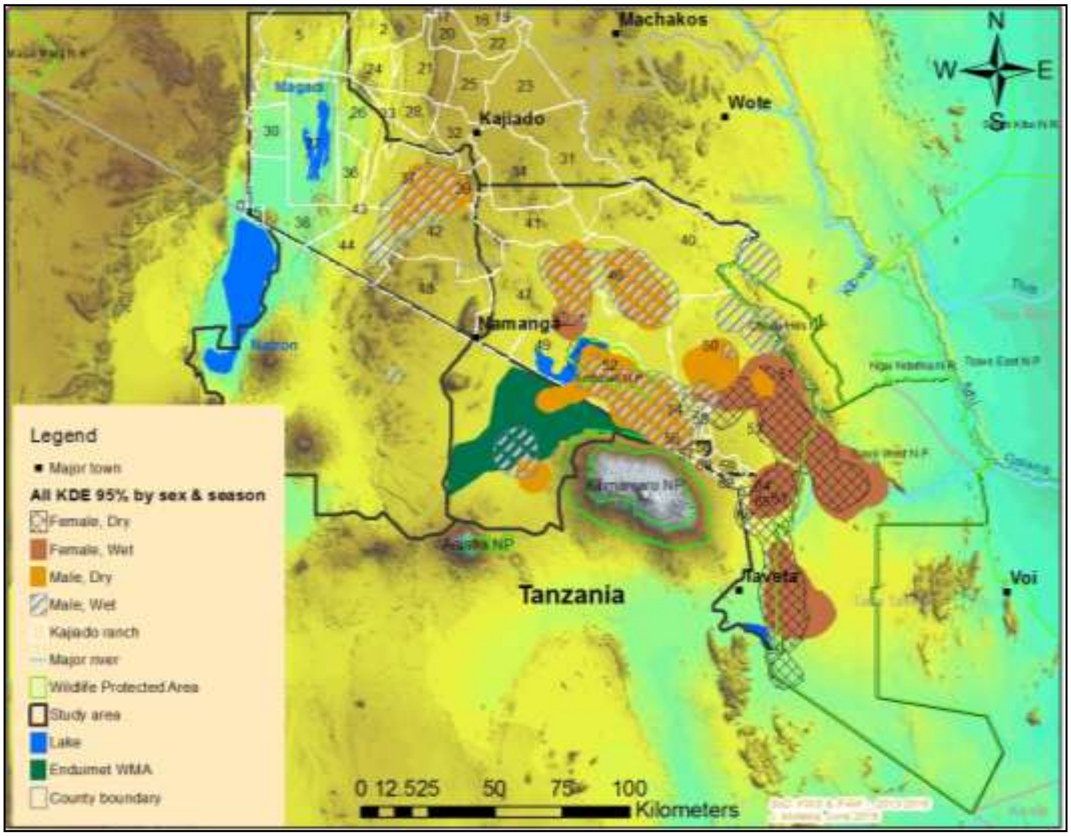

Figure 9. Seasonal home range (95% KDE) of bulls and female elephants collared in Amboseli ecosystem (2 February 2013 to 16 April 2016). The numbers represent the group ranches in the study area (Supplementary Table).

collared during the study. However, our results showed that bulls had a larger total range (100% MCP) than females (bulls range: 2,005 to 10,016 km^2; female range: 1,839 to 4,995 km^2). However, when the 95% KDE was used, females had a larger total range than bulls (bulls: 208 to 1,162 km^2; female: 606 to 1,226 km^2). Similar

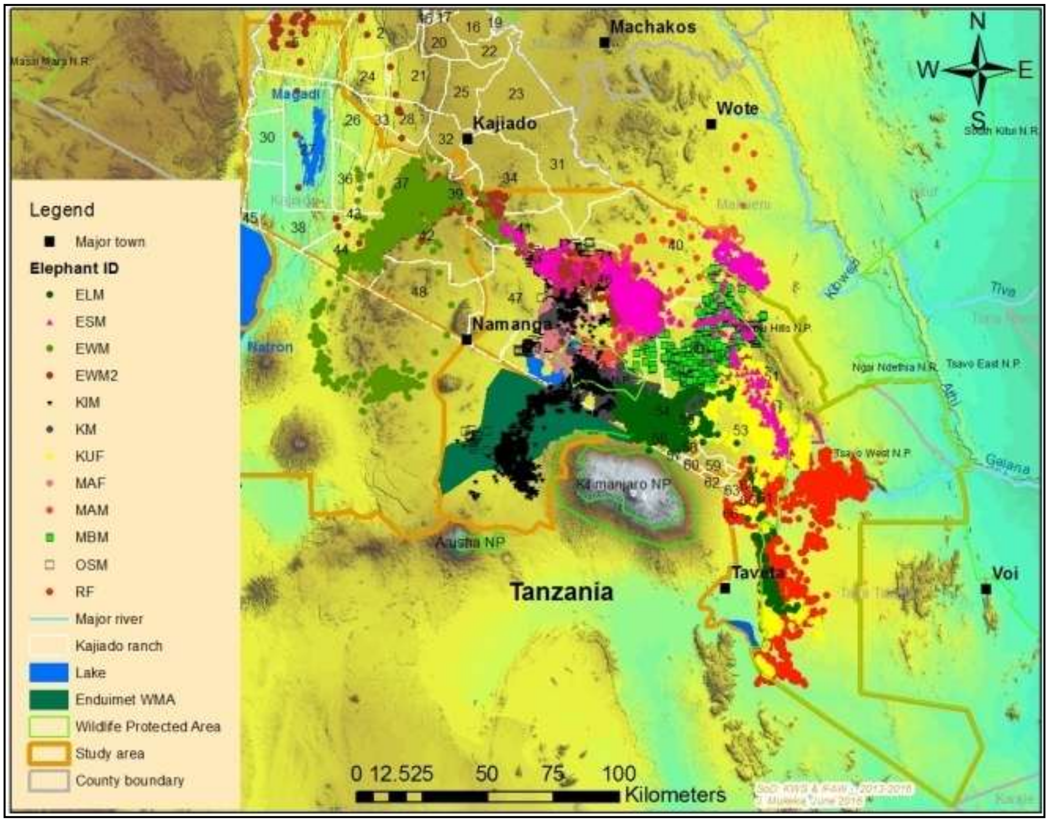

Figure 10A. The areas utilized by the 12 elephants in the borderland (February 2013 to April 2016). Point data of all areas utilized by the elephants. The numbers represent the group ranches in the study area (Supplementary Table).

results (100% MCP) were observed by Kikoti (2009) in Northern Tanzania where bulls had a larger home range than females (bulls: 700 to 3,698 km^2; females (100% MCP): 191 to 2,590 km^2). During the dry and wet seasons, bulls had larger mean home range than females (bulls dry: 3,312 km^2; female dry = 2,974 km^2; bull wet = 3,288 km^2; female wet = 1,828 km^2). Similar observations were made when the 95% KDE was used (bulls dry: 598 km^2; Female dry = 143 km^2; bull wet = 730 km^2; Female wet = 430 km^2). Our results match with similar previous studies on elephant home range (Stokke and du Toit, 2002; Jackson and Erasmus, 2005; Chase, 2007; Kikoti, 2009), which reported the home range sizes (95% fixed kernel) of bulls were larger than that of females. The female herds mostly consist of young elephants that cannot cope with extensive movements, therefore making female elephants to range in smaller areas than bulls (Ngene et al., 2009; Leggett, 2006). However, males consist of bulls of almost the same age and they are able to roam around in larger areas as their movements are not interfered with by young individuals who cannot cope with rigorous movements like females (Douglas-Hamilton et al., 2005; Ngene et al., 2009). It is evident that bulls will therefore require more space than females, a factor critical for them to continue accessing females on estrous at different localities within the larger Amboseli landscape. Efforts to secure space outside the protected areas should be enhanced to ensure it is available to the bull elephants.

Overall, the variations of elephant home range are influenced by an interaction of factors including rainfall, human disturbances (e.g., farms, settlements, fencing, urban development and road network), pressure from poaching, water availability, bush cover, food availability, habitat fragmentation, tracking period, and fencing of parcels of land (Esikuri, 1998; Douglas-Hamilton et al., 2005; Leggett, 2006; Foguekem et al., 2007; Mutima et al., 2009; Kikoti, 2009; Ngene et al., 2009; Gara, 2014). For Amboseli ecosystem, the elephant range has increasingly come under threat due to four factors including: Conversion of rangeland to farmland, increase of settlements, increase of human population, and shift of the Maasai community from nomadic pastoralism and transhumance to sedentary intensive agro-pastoralism (Esikuri, 2009; Okello and Kioko, 2010; Kioko and Okello, 2010). These factors have resulted to fragmentation of elephant range in Amboseli ecosystem as described and discussed in details by Gara (2014) and Gara et al. (2016a,

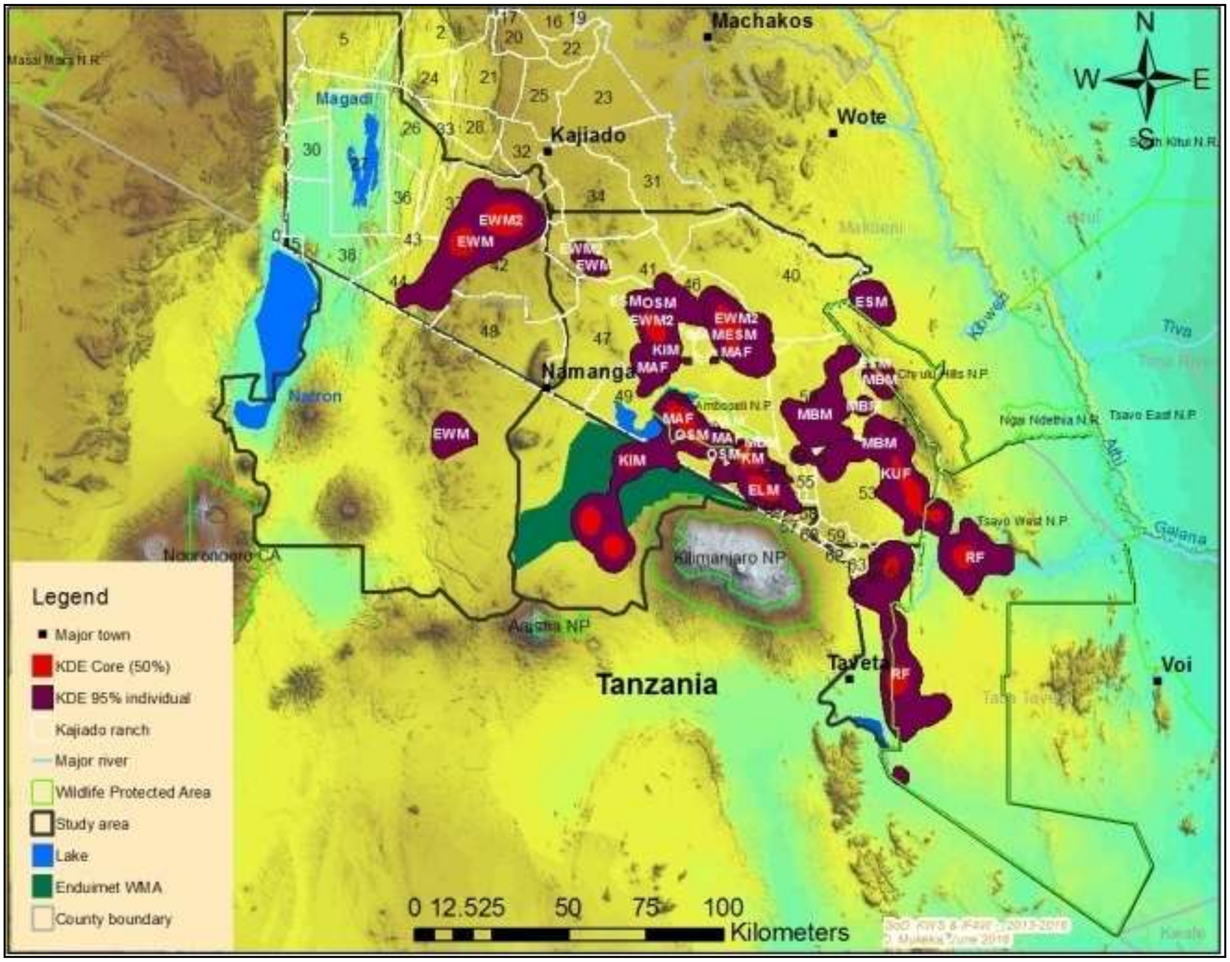

Figure 10B. The areas utilized (95 and 50% KDE) by the 12 elephants in the borderland (February 2013 to April 2016). The white labels are the names of elephants. The numbers represent the group ranches in the study area (Supplementary Table).

b). The fragmentation has resulted to reduction of elephant home range as the elephants only utilize secure habitats (Gara, 2014; Gara et al., 2016a, b). Gara et al. (2016a, b) reported that habitat utilization by elephants in human-dominated landscapes of Amboseli landscape was mostly explained by a combination of landscape fragmentation and vegetation productivity during the dry and transition seasons, than each of the factors alone.

The proof of continued habitat fragmentation in the Amboseli ecosystem has been by many authors including Eskuru (1993), Kioko and Okello (2010) and Nyamasio and Kihima (2014). For example Esikuri (1993) reported over 70% of conversion of rangeland to crop land in Amboseli ecosystem with the trend being on the increase over the years. For example, Eskuru (1993) reported an increase of area under crop farming in Amboseli basin by 273, 461 and 733% for the time periods 1975-1988, 1988-1993, and 1975-1993 respectively. Kioko and Okello (2010) reported an increase of land under irrigated and rain-fed crop farming by 2,217 and 96% between 1976 and 2007. A more recent study by Nyamasio and Kihima (2014) at Kimana Wetland Ecosystem (KWE; 3,349 km^2) reported increase of area under crop farming from about 70 km^2 in 1980 to about 438 km^2 in 2013, which represents a 526% increase in 33 years. During the same period land area under woodlands, wetlands and grassland decreased by 5.35, 69 and 8% respectively. These conversions are a pointer to constriction of elephant home range due to habitat fragmentation (Gara et al., 2016a, b). It is evidenced by avoidance of farmed or heavily settled areas of Kimana, Nguruman, Njukini, and Rombo in larger Amboseli ecosystem (Figure 10A and B; Gara et al., 2016a, b). Settlements and mushrooming of urban centers have ncreased over the past years (Gara et al., 2016a, b). For example, in KWE, which comprises of Entonet division, Central division, Imbirikani Location, and Amboseli National Park, land under settlements and urban areas increased by 682% between 1980 and 2013 (Nyamasio and Kihima, 2014). Human population has also increased in the ecosystem as more people and other communities (especially Changa, Kamba and Kikuyus) move to the area to undertake irrigation and rain fed crop farming (Okello, 2005; Kioko et al., 2006; Okello and Kioko, 2010; Kioko and Okello, 2010). For instance, over the past three decades, KWE has experienced an estimated annual human population growth rate of 4.67 as per the 2009 census, which translates to 84,297 persons and a population density of about 25 persons/km^2 in 2009 (Nyamasio and Kihima, 2014). The human population in KWE is projected to be about 210,789 individuals and a population density of 63 persons/km^{2}by 2030 (Nyamasio and Kihima, 2014). This will further constrict the elephant range within the ecosystem. From the results, the KWE was avoided by the collared elephants during the study period (Figure 10A and B). This is because of settlements and farms therein. The shift of the Maasai community from nomadic pastoralism and transhumance to sedentary intensive agro-pastoralism has increased land fragmentation in Amboseli ecosystem (Kioko and Okello, 2010; Western, 1990). The land fragmentation has been aggravated by the development of infrastructure, demand for more land as the population increases, migration of people from crop farming communities, and sub-division of group ranches as individual members realize the need to own land and use it for other activities like farming and for selling (Kioko et al., 2006; Kioko and Okello, 2010; Gara, 2014; Gara et al., 2016a; Gara et al., 2016b).The above observations reveal massive conversion of Amboseli elephant range to farmlands and settlement areas (Esikuri, 1998; Kioko et al., 2006; Nyamasio and Kihima, 2014; Gara, 2014). The resultant effect is reduced elephant range, increased human-elephant conflicts, increased mortality of elephants and reduced income from farming (Okello, 2005; Okello and Kioko; 2010; Kioko et al., 2006; Kioko and Okello, 2010; Nyamasio and Kihima, 2014; Gara, 2014; Gara et al., 2016a, b). The above explains why elephants avoided the Kimana, Nyukini, Ngurumani, and Rombo area of Amboseli ecosystem as shown in Figure 10a and B.

Conclusion

In this study, we describe the home range of elephants in Amboseli ecosystem using the 100% MCP and 95% KDE. Bulls had larger home ranges than females. The elephant home range was larger during the dry season than wet season. The most important ranches that offer key habitats for elephants include: Lolarashi/Olgulului, Rombo, Mbirikani, Kimana/Tikondo, Endonet, Lengesim, Kaputei south, Kuku, Lorngosua, Mbuko, and ElangataWuas, Torosei, Kimana/Tikondo Small Holdings and Dalalakutuk. The Isilalei ranch was used as a corridor to and from Elengata Wuas, Lorngosua and Torosei ranches. These are priority ranches where efforts to establish community conservancies should be enhanced. Other important areas used by the elephants include Chyulu West Game Management Area (CWGMA) in Kenya and Endimet Wildlife Management Area (EWMA) in Tanzania. Amboseli, Tsavo West and Chyulu National Parks in Kenya as well as parts of the Natron area in Tanzania were also utilized by elephants. The elephant population utilizes the range in both Southern Kenya and Northern Tanzania. Therefore, trans-boundary efforts should be enhanced to ensure sound management of the elephant-habitat-people interface for continued wellbeing of the elephant population and communities living with the elephants in Southern Kenya and Northern Tanzania.

Conflicts of Interests

The authors have not declared any conflict of interests.

REFERENCES

Altmann J, Alberts S, Altmann S, Roy S (2002). Dramatic change in local climate patterns in the Amboseli basin, Kenya. Afr. J. Ecol. 40(3):248-251.

BurnSilver S, Worden J, Boone R (2008). Processes of Fragmentation in the Amboseli Ecosystem, Southern Kajiado District, Kenya. In Galvin K, Reid R, Hobbs RBNT (Eds.), Fragmentation in Semi-Arid and Arid Landscapes: Springer Netherlands. pp. 225-253.

Burt WH (1943). Territoriality and home range concepts as applied to mammals. J. Mammol. 24:346-352.

Casaer JIM, Hermy M, Coppin POL, Verhagen RON (1999). Analyzing space use patterns by Thiessen polygon and triangulated irregular network interpolation: A non-parametric method for processing telemetric animal fixes. Int. J. Geogr. Inform. Sci. 13:499-511.

Douglas-Hamilton I, Krink T, Vollrath F (2005). Movement and corridors of African elephants in relation to protected areas. Naturwissenschaften 92:158-163.

Downs J, Horner M (2009). A Characteristic-Hull Based Method for Home Range Estimation. Transactions in GIS 13:527-537.

Esikuri EE (1998). Spatio-Temporal Effects of Land Use Changes in A Savanna Wildlife Area of Kenya. PhD Thesis, Virginia Polytechnic Institute and State University, Virginia, USA.

ESRI [Environmental Systems Research Institute] (2010). ArcGIS: Arc Map Version 10.3. ESRI, California, USA.

Fieberg J (2007). Kernel density estimators of home range: smoothing and the autocorrelation red herring. Ecology 88(4):1059-1066.

Frair JL, Nielsen SE, Merrill EH, Lele SR, Boyce MS, Munro RHM, Stenhouse GB, Beyer HL (2004). Removing GPS collar bias in habitat selection studies. J. Appl. Ecol. 41:201-212.

Frair JL, Fieberg J, Hebblewhite M, Cagnacci F, DeCesare NJ, Pedrotti L (2010). Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philos. Trans. R. Soc. B: Biol. Sci. 365(1550):2187-2200.

Fowler J, Cohen L, Larvis P (1998). Practical statistics for field biology. John Wiley and Sons. West Sussex, England.

Gara TW, Wang TJ, Skidmore AK, Zengeya FM, Ngene SM, Murwira A, Ndaimani H (2016a). Understanding the effect of landscape fragmentation and vegetation productivity on elephant habitat utilization in Amboseli ecosystem, Kenya: Open access. Afr. J. Ecol.

Gara TW, Wang TJ, Skidmore AK, Ngene SM, Dube T, Sibanda M (2016b). Elephants move faster in small fragments of low productivity in Amboseli ecosystems Kenya. Geocarto International,

Gara TW (2014). Effect of Water Availability, Landscape Fragmentation and Forage Abundance on the Movement and Habitat Utilization of Elephants. MSc Thesis, University of Twente, Faculty of Geo-Information Science and earth Observation (ITC), Enschede, The Netherlands.

Getz W, Fortmann-Roe S, Cross P, LyonsA, Ryan S, Wilmers C (2009). LoCoH:Non-parameteric Kernel Methods for Constructing Home Ranges and Utilization Distributions. PLoS ONE 2:e207.

Getz WM, Wilmers CC (2004). A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. Ecography 27:489-505.

Graham MD, Douglas-Hamilton I, Adams WM, Lee PC (2009). The movement of African elephants in a human-dominated land-use mosaic. Anim. Conserv. *12*(5):445-455.

Groom, RJD, Western D (2013). Impact of Land Subdivision and Sedentarization on Wildlife in Kenya's Southern Rangelands. Rangeland Ecol. Manage. 66(1):1-9.

Heard DC, Ciarniello LM, Seip DR (2008). Grizzlybear behavior and global positioning system collar fix rates. J. Wildlife Manage.72:596-602.

Hebblewhite M, Percy M, Merrill EH (2007). Are all global positioning system collars created equal? Correcting habitat-induced bias using three brands in the Central Canadian Rockies. J. Wildlife Manage. 71:2026-2033.

Hobbs NT, Reid R, Galvin K, Ellis J (2008). Fragmentation of Arid and Semi-Arid Ecosystems: Implications for People and Animals. In Galvin K, R Reid RB Hobbs N T (Eds.) Fragmentation in Semi-Arid and Arid Landscapes: Springer Netherlands. pp. 25-44.

Horne JS, Garton EO, Krone SM, Lewis JS (2007). Analyzing Animal Movements Using Brownian Bridges. Ecol. 88:2354-2363.

Howe M, Okello MM, Davis JM (2013). Inter-specific Variation in the Distribution of Ungulates Relative to Human Infrastructure Surrounding Amboseli National Park. Afr. Zool. 48(1):159-166.

Jiang Z, Sugita M, Kitahara M, Takatsuki S, Goto T, Yoshida Y (2008). Effects of habitat feature, antenna position, movement, and fix interval on GPS radio collar performance in Mount Fuji, central Japan. Ecol. Res. 23:581-588.

Kie JG, Matthiopoulos J, Fieberg J, Powel RA, Cagnaccia F, Mitchell MS, Gaillard J, Moorcroft PR (2016).The home range concept: A traditional estimator still relevant with modern telemetry? Phil. Trans. R. Soc. 365:2221-2231.

Kikoti AP (2009). Seasonal home range sizes, trans-boundary movements and conservation of elephants in Northern Tanzania. PhD Thesis, University of Massachusetts, Massachusetts, USA.

Kioko J, Kiringe J, Omondi P (2006).Human–elephant conflict outlook in the Tsavo–Amboseli ecosystem, Kenya. Pachyderm 41:53-60.

Kioko J, Okello MM (2010).Land use cover and environmental changes in a semi-arid rangeland, Southern Kenya. J. Geogr. Regional Plann. 3(11):322-326.

Laver PN, Kellyn MJ (2008). A Critical Review of Home Range Studies. J. Wildl. Manage. 72:290-298.

Legget KEA (2006). Home range and seasonal movement of elephants in the Kunene Region, northwestern Namibia. Afr. Zool. 41:17-36.

Lyons JA, Turner WC, Getz WM (2013). Home range plus: a space-time characterization of movement over real landscapes. Mov. Ecol. 1(2):1-14.

Moen R, Pastor J, Cohen Y, Schwartz CC (1996). Effects of moose movement and habitat use on GPScollar performance. J. Wildl. Manage. 60:659-668.

Mohr CO 1(947). Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37:223-449.

Ngene SM, Njumbi S, Ngoru B, Nzisa M, Bitok E, Poghon J, Gombe A, Koech E, Sangawe O, Wambua D, Omondi C, Korir W (2013). Satellite-Linked GPS Collars Deployed on Elephants in Tsavo Ecosystem, Kenya. In: Recent Advances in Satellite Research and Development (Eds. S. Gardiner and K.P. Olsen). Nova Publishers, New York, USA.

Ogutu JO, Piepho HP, Dublin HT, Bhola N, Reid RS (2009). Dynamics of Mara-Serengeti ungulates in relation to land use changes. J. Zool. 278(1):1-14.

Okello MM, D'Amour DE (2008). Agricultural expansion within Kimana electric fences and implications for natural resource conservation around Amboseli National Park, Kenya. J. Arid Environ. 72(12):2179-2192.

Okello MM (2005). Land use changes and human-wildlife conflicts in theAmboseli area, Kenya. Hum. Dimens. Wildl. 10(1):19-28.

Okello MM, Kioko J (2010). Contraction of wildlife dispersal area in Olgulului-Ololorashi Group Ranch around Amboseli National Park,Kenya. Open Conserv. Biol. J. 4:28-39.

Osborn FV (2004). The concept of home range in relation to elephants in Africa. Pachyderm 37:37-44.

Powell RA (2000). Animal home ranges and territories and home rangeestimators. Research Techniques in Animal Ecology: Controversies and Consequences (Eds L. Boitani& T.K. Fuller). Columbia University, NewYork. pp. 65-110.

Reinecke H, Leinen L, Thißen I, Meißner M, Herzog S, Schütz S, Kiffner C (2014). Home range size estimates of red deer in Germany: environmental, individual and methodological correlates. Eur. J. Wildl. Res. 60:237-247.

Sager-Fradkin KA, Jenkins KJ, Hoffman RA, Happe PJ, Beecham JJ, Wright RG (2007). Fix success and accuracy of global positioning system collars in oldgrowthtemperate coniferous forests. J. Wildl. Manage. 71:1298-1308.

Seaman DE, Powell RA (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. Ecol. 77:2075-2085.

Schuler KL, Schroeder GM, Jenks JA, Kie JG (2014). Ad hoc smoothing parameter performance in kernel estimates of GPS-derived home ranges. Wildl. Biol. 20:259-266.

Stokke S, Du Toit JT (2002). Sexual segregation in habitat use by elephants in ChobeNational Park, Botswana. African J. Ecol. 40:360-371.

Wall J (2016). Movement Ecology for ArcGIS (ArcMet) [Online]. Available: www.movementecology.net [Accessed 10th June 2013].

Walter WD, Fischer JW, Baruch-MorDo S, Vercauteren KC (2011). What is the proper method to delineate home range of an animal using today’s advanced GPS telemetry systems: the initial step, pp.249-268. In O. Krejcar (ed.), Modern telemetry. InTech, Rijeka, Croatia.

Worton BJ (1989). Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. Ecol. 70:164-168.

SUPPLEMENTARY MATERIAL

Table 1. List of number and names of Kajiado ranches.

S/N	Ranch name
1	EwuasoKidong
2	EwuasoKidong
3	Embakasi Forest
4	Ngong Scheme 2
5	Suswa
6	Not Named
7	Ngong Scheme 1a
8	Ngong Scheme 3
9	Ngong Scheme 1b
10	Ololua Forest
11	Ngong Town
12	Ngong Scheme 5
13	Ngong Scheme 4
14	Ngong Scheme 4b
15	Olteyani
16	Kitengela Game Conserv. Area
17	Ngong Scheme 6
19	Nairobi National Park
20	OlochoroOnyore
21	Kipeto
22	Olooloitikoishi
23	Kaputei North
24	LoodoAriak
25	Kisaju
26	Oldoinyoke
27	Magadi Concession
28	Kilonito
30	Olkiramatian
31	Kaputei Central
32	Ildamat
33	Lake Kwenia
34	Dalalakutuk
36	Olkeri
37	Erangata-Wuas
38	Shombole
39	Mbuko
40	Kaputei South
41	Osilalei
42	Lorngosua
43	Lake Kabongo
44	Torosei
45	Magadi Concession
46	Lengesim
47	Mailua
48	Meto
49	Lolarashi/Olgulului
50	Mbirikania
51	Chyulu West Game Conservation Area
52	AmboseliNp
53	Kuku
54	Kimana/Tikondo
55	Kimana/Tikondo Small Holdings
56	Endonet
57	EnkariakRongena
58	Emperon
59	Olkarkar
60	Nkama
61	Rombo B
62	Entarara
63	Rombo A
64	Rombo Block II
65	Rombo Block II
66	Rombo Block III

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Tuberculosis in captive Asian elephants (*Elephas maximus*) in Peninsular Malaysia

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SUMMARY

A cross-sectional study was conducted from 10 January to 9 April 2012, to determine the seroprevalence of tuberculosis (TB) of all captive Asian elephants and their handlers in six locations in Peninsular Malaysia. In addition, trunk-wash samples were examined for tubercle bacillus by culture and polymerase chain reaction (PCR). For 63 elephants and 149 elephant handlers, TB seroprevalence was estimated at 20·4% and 24·8%, respectively. From 151 trunk-wash samples, 24 acid-fast isolates were obtained, 23 of which were identified by *hsp*65-based sequencing as non-tuberculous mycobacteria. The *Mycobacterium tuberculosis*-specific PCR was positive in the trunk-wash samples from three elephants which were also seropositive. Conversely, the trunk wash from seven seropositive elephants were PCR negative. Hence, there was evidence of active and latent TB in the elephants and the high seroprevalence in the elephants and their handlers suggests frequent, close contact, two-way transmission between animals and humans within confined workplaces.

Key words: Captive Asian elephants, elephant handlers, *Mycobacterium tuberculosis*, non-tuberculous mycobacteria (NTM), Peninsular Malaysia.

INTRODUCTION

Tuberculosis (TB) is a serious chronic infection in humans and animals throughout the world. It affects a large variety of animal hosts including non-human primates, marine mammals like seals and sea lions, psittacine and other birds, domestic, captive and wild animals like cats, rats, cattle, sheep, goats, swine, deer, fox, badgers, moles and elephants [1–5]. Transmission between human and captive animals has occurred following close and frequent contact [6].

TB has been recognized as a disease of elephants for over 2000 years [7, 8]. However, naturally occurring TB has not been reported in wild elephants, suggesting that captive elephants could most likely have contracted the disease via contact with infected humans [1]. In captive elephants, the disease is primarily caused by *Mycobacterium tuberculosis*, although infection with *Mycobacterium bovis* has been recorded [9]. Asian elephants (*Elephas maximus*) are more frequently infected with TB compared to African elephants (*Loxodonta africana*) [10]. The difference in prevalence may reflect a closer association of Asian

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elephants with humans [1]. Rothschild & Laub [11] identified tuberculous lesions in 52% (59/113) of mastodon (*Mammut americanum*) skeletons, and implied that pandemic TB may be one of the probable causes of the mastodons' extinction. This discovery has alerted us to the need to protect living elephants from TB.

Transmission of TB from captive Asian elephants to other animals and humans has been described in several outbreaks [12–14]. Clinical signs in infected elephants are usually absent or only shown in the terminal stages of the chronic disease. Transmission of *M. tuberculosis* occurs by aerosolization of infectious respiratory droplets when the animals cough, trumpet or trunk spray, and is affected by the bacterial load, droplet size, duration of exposure, proximity to infected animals and the immune status of the exposed individual. TB can only be transmitted from elephants with active pulmonary disease following primary infection or after reactivation of latent infection [6].

The interest in elephant TB has been increasing over the past years due to its public health threat as well as increased concern for the healthcare and conservation of elephants. According to the World Conservation Union (IUCN red list 2006), the Asian elephant is an endangered species. There are probably about 1100–1200 Asian elephants in the wild and slightly more than 60 captive Asian elephants in Peninsular Malaysia. Although there are a number of recent reports of TB in captive Asian elephants from the USA [9], Sweden [14], Thailand [15], Nepal [16] and Sri Lanka [17], very little is known about its prevalence in Peninsular Malaysia. The aim of this study is to determine the prevalence of TB in captive Asian elephants in zoos and conservation centres in Peninsula Malaysia and to assess its potential risk of transmission between elephants and to elephant handlers. TB surveillance data would provide important information to determine the need for a strategy to prevent and control TB in elephants as well as a specific occupational health programme for elephant handlers and caregivers.

METHODS

Animal and human samples

We conducted a cross-sectional study between 10 January and 9 April 2012 to estimate the seroprevalence of *M. tuberculosis* infection in all 63 captive elephants in six locations (zoos and elephant conservation centres) across Peninsular Malaysia. Only 58 elephants that were approachable and allowed handling, without imposing significant risk to both elephants and handlers were sampled. At the same time, blood samples from elephant handlers (zoo keepers and workers, veterinary staff and *mahouts*) who gave informed consent for participation in the study were collected to estimate the extent of human exposure to TB. Only those with direct contact with elephants were screened. The Animal Care and Use Committee at the University Putra Malaysia and Department of Wildlife and National Parks Malaysia (DWNP) granted approval for the study on captive Asian elephants while the Medical Ethical Committee from the University Malaya Medical Centre granted approval for the study on elephant handlers.

Blood sampling and testing in elephants

We collected blood from the auricular vein behind the elephant's ear, using a 21-gauge needle butterfly catheter and a 10-ml syringe to draw blood into a plain tube. Blood was allowed to clot at room temperature and samples were shipped in an ice chest to the laboratory within 3–12 hours. Sera were collected by centrifuging the blood tubes at 600 ***g*** for 10 min at ambient temperature (25–30 °C) and then used in the ElephantTB Stat-Pak assay (ChemBio, USA) which contains a cocktail of recombinant antigens for rapid detection of antibodies to the *M. tuberculosis* complex in elephants [18].

Trunk-wash collection in elephants

Trunk-wash samples were collected by the elephant handlers under the supervision of the veterinarians in zoos and conservation centtes, using the 'triple sample method' [19]. A series of three trunk-wash samples was collected on separate days within a 1-week period. Each elephant was carefully restrained by its *mahouts* and 60 ml of sterile normal saline was instilled into a nostril using a 60-ml syringe. The trunk was lifted up and then lowered to collect the fluid in a sterile plastic bag. The wash was later split into two 25-ml aliquots and transferred into a 50-ml sterile Falcon tube™ (BD Biosciences, USA). One set of samples was taken for liquid culture (BACTEC MGIT960 system, BD Biosciences) and polymerase chain reaction (PCR) at the University of Malaya (UM), and the other set for culture on

Lowenstein–Jensen (LJ) agar (Oxoid, UK) at the University Putra Malaysia (UPM). A total of 154 trunk-wash samples were collected of which only 151 could be used.

Decontamination of trunk-wash samples

Prior to culture, trunk-wash samples were decontaminated using the modified Petroff method [20]. Briefly, the samples were centrifuged at 13 000 ***g*** for 15–25 min at 4 °C. The supernatant was discarded and 5 ml was retained in the tube to which 5 ml 2% NaOH was added. The mixture was incubated at 37 °C for 15 min. After incubation, 40 ml phosphate buffered saline (1 × PBS) was added and the mixture was centrifuged at 13 000 ***g*** for a further 15–25 min. The supernatant was then discarded, 1 ml 1 × PBS was added to resuspend the pellet and the sample was transferred into a labelled sterile bijou bottle.

Culture and microscopic identification

A loopful of each decontaminated sample was inoculated onto a LJ slant and incubated at 37 °C for up to 8 weeks. The cultures were examined daily for 7 days, then weekly for 7 weeks, during which time the growth rate and pigmentation of visible colonies were recorded. Ziehl–Neelsen staining was performed to look for acid-fast bacilli under a light microscope.

TB antigen rapid test (TiBilia™ TB, Genesis, China)

The TiBilia test, an immunochromatographic assay that detects the presence of MPB64 antigens exclusively found in the *M. tuberculosis* complex, was conducted for all acid-fast positive isolates. One loopful of each colony was suspended in 200 μl extraction buffer in a 1·5-ml tube. The mixture was vortexed and 100 μl was dropped into the sample well of the test device at room temperature. Results were read after 15 min and the presence of two red lines at the test and control areas indicated positive detection for *M. tuberculosis*, while a red line only at the control area was considered negative. Test results showing no red line or a red line at the test area only were considered invalid.

PCR detection of *M. tuberculosis* in trunk wash

DNA in the trunk wash was extracted and purified using DNA-sorb-B Nucleic Acid Extraction kit (AmpliSens Biotechnologies, Russia), according to the manufacturer's instructions. The purified DNA then served as a template for PCR amplification of the *M. tuberculosis* complex using the AmpliSens MBT-EPh PCR kit (AmpliSens Biotechnologies).

Identification of non-tuberculous mycobacterium (NTM) species

One loopful of an isolate on LJ medium was suspended in 0·2 ml sterile distilled water. The resulting suspension was boiled at 100 °C for 30 min and then centrifuged at 16 100 ***g*** for 2 min. The resulting supernatant was used for the subsequent *hsp*65-based PCR analysis, as described by McNabb *et al.* [21]. PCR amplicons were purified by the QIAquick PCR Purification kit (Qiagen, Germany) and sequenced by 1st BASE Laboratories (Malaysia). The resulting DNA sequences were aligned, using BLAST, against *hsp*65 locus sequences in a web-accessible database (http://msis.mycobacteria.info/). The most probable species of each isolate was identified based on the sequence similarity with reference strains and the expectation value (E value).

Blood sampling and testing of elephant handlers

Venous blood samples from the elephant handlers, caregivers and veterinary staff were collected by medical staff from the Ministry of Health, Malaysia, for testing with the QuantiFERON®-TB Gold In-Tube test (Cellestis Inc., Australia), which detects the release of interferon (IFN)-γ from TB-specific T lymphocytes [22]. Three millilitres of blood was drawn directly into three blood collection tubes, i.e. 1 ml each into a nil control tube with saline, TB antigen tube with a mixture of synthetic peptides representing ESAT-6, CFP-10 and TB7·7 test antigens, and a mitogen control tube containing phytohaemagglutinin. To ensure complete mixing of the blood with the tube contents, the tubes were shaken immediately after blood collection and again just before they were incubated at 37 °C, within 16 h of collection. After 16–24 h incubation, the tubes were centrifuged and the supernatant containing IFN-γ released from the antigen-stimulated T lymphocytes was harvested for testing by QuantiFERON-TB Gold ELISA. As recommended by the manufacturer, optical density readings >0·35 IU/ml were interpreted as indicative of latent or active TB infection, depending on clinical presentation.

Table 1. *TB Stat-Pak test results for captive Asian elephants by location*

Location	No. of elephants	No. of sera collected	No. of sera tested	No. of Elephant TB Stat-Pak positives	Seroprevalence (%)
A	27	27	27	7	25·9
B	8	8	8	2	25·0
C	8	6	5	0	0·0
D	9	9	6	1	16·7
E	3	3	2	0	0·0
F	8	3	1	0	0·0
Total	63	58	49	10	20·4

Data analysis

TB seroprevalence was estimated by the number of seropositives divided by the total number tested, and reported as a percentage (%). Statistical analysis was performed using Fisher's exact test from GraphPad InStat version 3 (GraphPad Inc., USA). A P value <0·05 was considered statistically significant.

RESULTS

Fifty-eight serum samples were obtained from 63 elephants in captivity, of which only 49 could be tested as the rest were haemolysed. Using the rapid Stat-Pak assay, 10/49 (20·4%) elephants tested were seropositive (Table 1). Herd prevalence ranged from 0% to 25·9% in the six study locations. Of 149 staff who had contact with elephants, the overall seroprevalence by QuantiFERON test was 24·8% (range 18·6–50%) (Table 2). Besides Malaysians, there were 19 foreign nationals among the elephant handlers. There was no significant difference in seropositivity ($P=0·2537$) between Malaysian (23·18%, 30/130) and foreign (36·8%, 7/19) workers. Neither was there any significant association with duration of employment ($P>0·9999$ for duration ~1 year and $P>0·9999$ for duration ~5 years).

The TB detection results for trunk-wash samples are given in Table 3. Samples were only collected from five locations as the elephants in location F were not approachable. TB PCR was performed on all 10 seropositive elephants and 12 of the seronegatives animals. Of these 22 elephants, three (13·6%) were positive in both tests and therefore considered to have laboratory evidence of active TB. Eight elephants (with negative serology and PCR) were probably not infected. Seven (seropositive but PCR-negative) were considered to have latent infection and the remaining four (seronegative but PCR-positive) could be false-positive PCR or false-negative serology results.

Table 2. *QuantiFERON test results of elephant handlers by location*

Location	No. of human samples tested	No. of QuantiFERON test positives	Prevalence (%)
A	70	13	18·6
B	21	5	23·8
C	20	5	25·0
D	12	6	50·0
E	18	6	33·3
F	8	2	25·0
Total	149	37	24·8

All trunk-wash samples were cultured; none grew *M. tuberculosis.* Most of the liquid cultures were heavily contaminated by non acid-fast bacteria and fungi, despite prior decontamination and the incorporation of antibiotics (BBL, MGIT PANTA; BD Biosciences) into the MGIT culture medium. However, on LJ slants it was possible to obtain pure subcultures of acid-fast bacteria, but 23/24 positive cultures turned out to be NTM species, identified by a negative TiBilia test followed by *hsp*65gene amplification and sequence alignment with reference NTM species. *M. arupense* and *M. colombiense* made up 50% of the NTM species recovered (Table 4).

DISCUSSION

Many techniques have been used for the detection of TB in elephants but few have been reported to be entirely satisfactory when used alone. A combination of diagnostic assays is often required [15]. The Chembio TB Stat-Pak assay used in this study is

Table 3. *Culture and TB PCR results of elephant trunk washes by location*

Location	No. of elephants	No. of trunk washes collected	No. of acid-fast positive cultures	No. of elephants TB PCR positive
A	27	78	13	0
B	8	24	4	2
C	8	18	2	0
D	9	27	4	3
E	3	4	1	2
F	8	0	0	0
Total	63	151	24*	7†

PCR, Polymerase chain reaction.
* From 55 elephants.
† From 22 elephants tested.

Table 4. *Non-tuberculous mycobacteria (NTM) identification by hsp65 sequencing*

Most probable species	No. of isolates
M. arupense	7
M. colombiense	5
M. intracellulare	2
M. asiaticum	2
M. mantenii	2
M. fortuitum	2
M. gilvum	1
M. hiberniae	1
M. kumamotonense	1
Total	23*

* Of 24 acid-fast bacilli-positive cultures, 23 were NTM species. The remaining isolate was identified as *Nocardia nova*.

licensed by the U.S. Department of Agriculture as a screening test for TB in elephants. The sensitivity and specificity of this test for the detection of anti-*M. tuberculosis* complex antibodies have been reported to be 100% and 95%, respectively [23]. However, other workers have noted an inadequacy of the Stat-Pak assay for the unequivocal identification of TB-infected animals [9, 15]. Our results also showed poor correlation between serology and trunk-wash culture and PCR. In humans, serological results are affected by the phase of TB infection and the immune competence of the host. A positive serological result in the absence of clinical features and *M. tuberculosis* detection is usually interpreted as indicative of latent infection, while negative serology in the presence of positive TB culture or PCR can be explained by immunological anergy. It is not known whether the same interpretations are applicable in elephants. With trunk-wash tests, sensitivity has been reported to be poor [18, 23] and affected by collection and processing methods as well as the degree of contamination in the samples collected. The PCR assay we used is designed for a wide range of human specimen types but has not been adequately evaluated for elephant respiratory samples. Hence, although the combined use of both the Stat-Pak assay and TB PCR did provide some evidence for active and latent TB infection in our captive elephants, continued monitoring of the health of elephants, particularly those seropositive, and repeated examination of trunk washes are required to confirm TB infection in elephants. Nevertheless, there is sufficient indication that there exists a sizable reservoir of silent infection in the elephants that would maintain continued transmission if not controlled.

The QuantiFERON test has been well established for the diagnosis of latent TB in humans and is often used as a supplementary test to aid the diagnosis of active TB. None of the 37 staff who tested positive in this study had TB-like symptoms. All 13 seropositive individuals from location A were examined by a chest physician and found to have no physical or radiological signs. Only one gave a history of recent contact with a known case of TB. The 24·8% seroprevalence is probably entirely due to latent infection but it is substantially higher than the seroprevalence previously obtained (authors' unpublished data) for asymptomatic university lecturers and students (4%), general laboratory staff (6%) and staff working in a TB diagnostic laboratory (12·5%). The overall 20·4% seroprevalence in our elephants is comparable to reports of 20% from Nepal [16] and 12–25% from India (25% of elephants in temples *vs.* 12–15% in other elephant groups) [16]. This finding is rather unexpected as the human TB incidence in Malaysia (3-year average of 83/100 000 population from 2008 to 2010) is substantially lower than incidences in Nepal (163/100 000 population) and India (190/100 000 population) [24]. Hence, the high seroprevalence in elephants and their handlers in this study could be the result of frequent, close contact, two-way transmission between animals and humans within confined workplaces.

The isolation of NTM from trunk wash illustrates the ubiquitous presence of these environmental bacteria. Many of the species recovered are potential animal and human pathogens. *M. avium* has been reported to be the most frequently isolated mycobacterial species from trunk washes in the USA [9]. Similarly, in this study, among the most frequently isolated NTM were two members of the *M. avium* complex, *M. colombiense* (a new sequevar of *M. avium* [25]) and *M. intracellulare. M. arupense,* the other common isolate, is associated with human respiratory infections and has been isolated from various domestic and wild animals [26]. The role of these NTM species as elephant pathogens requires further investigation.

There is a paucity of information of TB in elephants particularly in Asia. To the best of our knowledge, this study is the first to look at the extent of TB infection in captive Asian elephants in Peninsular Malaysia. Our findings could contribute to the development of a long-term surveillance and healthcare programme for this endangered species. From the conservation point of view, the implication of potential transmission and spread to wild elephant populations cannot be underestimated, e.g. if TB-infected elephants are used during rescue and release operations [27]. Just as important is the prevention of elephant–human transmission in zoos and conservation centres. Elephant handlers need to be aware of the risk of TB acquisition from infected animals and be educated with regard to infection control measures. On the other hand, as elephants become infected by humans with open TB, there must be workplace policies (e.g. pre-employment screening and annual chest X-rays) to ensure that elephant handlers are free from active TB. Hence, a One Health approach [16] involving both animal and human health sectors should be undertaken to develop a comprehensive prevention, treatment and prophylaxis control strategy to protect the elephants and their caregivers from TB.

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DECLARATION OF INTEREST

None.

REFERENCES

1. **Montali RJ, Mikota SK, Cheng LI.** *Mycobacterium tuberculosis* in zoo and wildlife species. *Revue Scientific et Technique de l'Office International des Epizooties* 2001; **20**: 291–303.
2. **Cousins DV, *et al.*** Tuberculosis in seals caused by a novel member of the *Mycobacterium tuberculosis* complex: *Mycobacterium pinnipedii* sp. nov. *International Journal of Systematic and Evolutionary Microbiology* 2003; **53**: 1305–1314.
3. **Washko RM, *et al.*** *Mycobacterium tuberculosis* infection in a green-winged macaw (*Ara chloroptera*): Report with public health implications. *Journal of Clinical Microbiology* 1998; **36**: 1101–1102.
4. **Kremer K, *et al.*** *Mycobacterium microti*: more widespread than previously thought. *Journal of Clinical Microbiology* 1998; **36**: 2793.
5. **Millan J, *et al.*** Disseminated bovine tuberculosis in a wild red fox (*Vulpes vulpes*) in Southern Spain. *Journal of Wildlife Diseases* 2008; **44**: 701–706.
6. **Michalak K, *et al.*** *Mycobacterium tuberculosis* infection as a zoonotic disease: transmission between humans and elephants. *Emerging Infectious Disease* 1998; **4**: 283–287.
7. **Iyer AK.** Veterinary science in India, ancient and modern with special reference to tuberculosis. *Agriculture Livestock India* 1937; **7**: 718–724.
8. **McGaughley CA.** Diseases of elephants: part III. *Ceylon Veterinary Journal* 1961; **9**: 94–98.
9. **Payeur JB, *et al.*** Mycobacterial isolation in captive elephants in the United States. *Annals of the New York Academy of Sciences* 2002; **969**: 256–258.

10. **Isaza R.** Tuberculosis in all taxa. In: Fowler ME, Miller RE eds. *Zoo and Wild Animal Medicine*. Pennsylvania: Saunders, 2003, pp. 689–696.
11. **Rothschild BM, Laub R.** Hyperdisease in the late Pleistocene: validation of an early 20th century hypothesis. *Naturewurwissenschaften* 2006; **93**: 557–564.
12. **Oh P, *et al.*** Human exposure following *Mycobacterium tuberculosis* infection of multiple animal species in a Metropolitan Zoo. *Emerging Infectious Disease* 2002; **8**: 1290–1293.
13. **Murphree R, *et al.*** Elephant-to-human transmission of tuberculosis. *Emerging Infectious Disease* 2011; **17**: 366–370.
14. **Lewerin SS, *et al.*** Outbreak of *Mycobacterium tuberculosis* infection among captive Asian elephants in a Swedish zoo. *Veterinary Record* 2005; **156**: 171–175.
15. **Angkawanish T, *et al.*** *Mycobacterium tuberculosis* infection of domesticated Asian elephants, Thailand. *Emerging Infectious Disease* 2010; **16**: 1290–1293.
16. **Mikota S, Maslow JN.** Tuberculosis at the human-animal interface: an emerging disease of elephants. *Tuberculosis* 2011; **91**: 208–211.
17. **Dangolla A, Silva I.** The status and veterinary problems in captive elephants in Sri Lanka. In *Proceedings of the 54th Annual Convention of the Sri Lanka Veterinary Association*. Gannoruwa, Sri Lanka: Plant Genetic Resource Centre, 3–4 May 2002, pp. 19 (http://www.aserc.org/index.php?option=com_content&task=view&id=37). Accessed 7 January 2013.
18. **Lyashchenko KP, *et al.*** Tuberculosis in elephants: antibody responses to defined antigens of *Mycobacterium tuberculosis*, potential for early diagnosis, and monitoring of treatment. *Clinical and Vaccine Immunology* 2006; **13**: 722–732.
19. **Isaza R, Ketz CJ.** A trunk wash technique for the diagnosis of tuberculosis in elephants. *Verhandlungsbericht des Internationalen Symposiums uber die Erkrankungen der Zootiere Vienna* 1999; **39**: 121–124.
20. **Cruickshank R, *et al.*** *Medical Microbiology*, 12th edn. Edinburgh: Churchill Livingstone, 1975, pp. 390.
21. **McNabb A, *et al.*** Assessment of partial sequencing of the 65-kilodalton heat shock protein gene (*hsp65*) for routine identification of *Mycobacterium* species isolated from clinical sources. *Journal of Clinical Microbiology* 2004; **42**: 3000–3011.
22. **Mori T, *et al.*** Specific detection of tuberculosis infection with an interferon-gamma based assay using new antigens. *American Journal of Respiratory and Critical Care Medicine* 2004; **170**: 59–64.
23. **Greewald R, *et al.*** Highly accurate antibody assays for early and rapid detection of tuberculosis in African and Asian elephants. *Clinical and Vaccine Immunology* 2009; **16**: 605–612.
24. **World Health Organization.** Global tuberculosis control report 2011 (http://whqlibdoc.who.int/publications/2011/9789241564380_eng.pdf), pp. 216–231 Accessed 7 January 2013.
25. **Murcia MI, *et al.*** *Mycobacterium colombiense* sp.nov., a novel member of the *Mycobacterium avium* complex and description of MAC-X as a new ITS genetic variant. *International Journal of Systematic and Evolutionary Microbiology* 2006; **56**: 2049–2054.
26. **Neonakis IK, *et al.*** *Mycobacterium arupense* pulmonary infection: antibiotic resistance and restriction fragment length polymorphism analysis. *Indian Journal of Medical Microbiology* 2010; **28**: 173–176.
27. **Mikota SK.** Review of tuberculosis in captive elephants and implications for wild population. *Gajah* 2008; **28**: 8–18.

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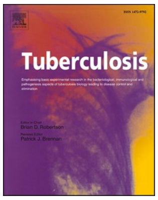

Review

Tuberculosis in elephants: Origins and evidence of interspecies transmission

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Mycobacterium tuberculosis

ABSTRACT

Tuberculosis (TB) is a devastating disease in elephants caused by either *Mycobacterium tuberculosis* or *M. bovis*. It is an ancient disease, and TB in elephants was first reported over two millennia ago in Sri Lanka. Outbreaks of TB worldwide, in captive and free-ranging elephant populations, have been recorded. Interspecies transmission of TB among elephants and humans has been confirmed in several geographic localities using spoligotyping, MIRU-VNTR analysis, and/or comparative genomics. Active surveillance of TB in wild and captive elephants and their handlers is necessary to prevent TB transmission at the elephant-human interface and to aid in the conservation of Asian and African elephants. In this review, we present an overview of diagnosis, reports of TB outbreaks in the past 25 years, TB in wild elephants, its transmission, and possible prevention and control strategies that can be applied at the elephant-human interface.

1. Introduction

Tuberculosis (TB) in elephants is primarily caused by *Mycobacterium tuberculosis* (*M.tb*); however, infection with *M. bovis* has also been reported in some cases [1,2]. *M. szulgai*, an opportunistic pathogenic non-tuberculous *Mycobacterium*, has been reported as the cause of death of two African elephants in a zoo in Illinois in the US [3]. *M. avium* has been frequently isolated from trunk washes of elephants but it has not been associated with clinical disease [1]. *M. caprae* has been isolated from an elephant that was imported from Borneo to a zoo in Japan [4]. A majority of TB-infected elephants do not manifest clinical signs. Some may demonstrate exercise intolerance, anorexia, and weight loss. TB-infected elephants may present clinical signs only in advanced stages and sometimes TB is diagnosed only at necropsy [2].

TB is an ancient disease of humans and animals, including elephants. TB in Asian elephants was first described by ancient Ayurvedic physicians more than 2000 years ago in Sri Lanka [5,6]. Pathognomonic granulomatous lesions resembling TB were discovered in 59 out of 113 (52%) mastodon skeletons [7], evidence of the long history of this disease, and susceptibility of elephant ancestors to TB. This finding has led to the speculation that TB may have played a role in the extinction of the mastodon (*Mammut americanum*).

In more recent history, TB infection was reported in an Asian elephant at the London Zoo, and elephant died in the society's garden in mid-1875 [8]. Most of the published reports on elephant TB from the early and mid-nineteenth century were exclusively in captive Asian elephants [9,10]. TB has also been suspected in an African elephant from Israel [11] based on typical necropsy findings. A retrospective study conducted in North American Zoos between 1908 and 1994 identified 8 TB-related deaths among 379 elephants. However, privately-owned elephants were not included in this study likely leading to an underestimation of the true prevalence of TB cases in North America [12].

2. Diagnosis of TB in elephants

Elephant trunk wash culturing for mycobacteria is considered as a "gold standard" for TB diagnosis [13]. However, this technique has several limitations [14]. Elephants are intermittent shedders of mycobacteria. As the elephants use their trunks for multiple tasks, the possibility of contamination of trunk wash samples with soil bacteria is always high. This is further complicated by the fact that mycobacteria are slow growers and it takes about eight weeks for final culture results. Furthermore, microbial culturing requires a well-equipped biosafety level 3 (BSL3) laboratory and only a few such laboratories are located in the elephant range countries. The isolation of mycobacteria provides a definitive diagnosis and the opportunity for strain identification, source

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tracking, and drug susceptibility testing [14].

Surveillance of TB in elephants across the globe has been performed by serological assays, viz.: ElephantTB STAT-PAK ® (STAT-PAK), DPP VetTB ® assays (Dual-path platform; DPP) (Chembio Diagnostic Systems, Inc., NY, USA), or ELISA using six TB antigens. These assays detect antibodies against putative immune-dominant TB antigens in serum/plasma samples of elephants [15]. The production of STAT-PAK was discontinued in 2012 and replaced with a more refined DPP assay for antibody screening in elephants.

The ELISA technique using six TB antigens demonstrated 100% sensitivity and specificity in elephants. The six antigens used in this study were the same as those used for the detection of *M. bovis* infection in cattle and cervids [16]. This study was conducted using a relatively small sample size (n = 47) of Asian and African elephants and included seven culture-positive animals. Since the assay was performed in an endemic area where all elephants are expected to be exposed with some progressing to disease while others would be subclinical, these results of sensitivity and specificity would need to be reconfirmed with multiple tests on a larger number of TB confirmed, exposed, and healthy (confirmed unexposed) elephants.

In humans, tuberculin skin tests (TST) and chest radiography are used for TB diagnosis, which are not applicable nor practical in elephants. Chest radiography is impractical for elephant TB diagnosis due to their larger size, and the intradermal tuberculin test has demonstrated low sensitivity [17].

The interferon- γ release assay (IGRA) has been successfully developed and is used in cattle and humans. Cytokine gene expression studies among STAT-PAK reactive and non-reactive Asian elephants revealed that mRNA of interferon-γ was upregulated among reactive elephants [18]. IGRA has been attempted in elephants with promising results [19,20]. However, IGRA needs to be validated in a larger population of TB confirmed, exposed, and healthy elephants.

3. TB outbreaks in elephants in the past 25 years (1996–2020)

Scientific studies on elephant TB cases began when TB was identified as a cause of death of two circus elephants in the US in 1996 [17]. An Elephant Tuberculosis Advisory Panel formed thereafter by the United States Department of Agriculture (USDA) developed the first set of elephant TB guidelines in 1997, providing recommendations for TB surveillance, testing, and treatment in elephants. These guidelines underwent multiple revisions as new information on diagnosis, treatment, and management of TB in elephants became available [13]. Between 1996 and 2018, 60 elephants were confirmed with TB infection in the US [21] with one case caused by *M. bovis* [2]. In addition to the US, TB has also been identified in captive elephants in Sweden [22], Thailand [23], Australia [24], Nepal [25], and Switzerland [26] (Table 1).

In Sweden, between 2001 and 2003, an outbreak of TB was reported in multiple species of zoo animals including Asian elephants [22]. At necropsy, *M.tb* was isolated from five elephants and one giraffe. Although the source of infection in such a large number of zoo animals could not be determined, it is likely elephants were exposed to and infected with *M.tb* from people during recreational elephant rides or circus-related activities. Four domesticated Asian elephants were confirmed as infected with *M.tb* in Thailand between 2005 and 2008 [23]. Based on 16S–23S-rDNA internal transcribed spacers (ITS) and *gyrB* sequence analyses on the isolates, it was established that *M.tb* was transmitted to these four elephants from humans. Unique genotypes among these isolates suggest that these transmission events may have occurred multiple times from people carrying organisms from different ancestry. In Thailand, tourists participate in activities that bring people and elephants close providing an opportunity for interspecies transmission.

Table 1
TB outbreaks in captive and wild elephants in different countries with the number of cases diagnosed in various settings, 1996–2018.

Country	Number of TB-confirmed elephants	Year of TB diagnosis	Setting	Reference
Sweden	5	2001–2003	Captive	[22]
Thailand	4	2005–2008	Captive	[23]
Australia	1	2010	Captive	[24]
Nepal	5	2009–2013	Captive	[25, 29]
Sri Lanka	1	2014	Free-ranging	[36]
Switzerland	3	2015	Captive	[26]
South Africa	1	2016	Free-ranging	[41]
India	4	2007–2016	Free-ranging	[37, 38]
Japan	1	2016	Captive	[4]
USA	60	1996–2018	Captive	[21]

In 2010, 1 out of 5 Asian elephants imported from Thailand to Australia were diagnosed with *M.tb* infection. Interestingly, interspecies transmission of TB was implicated, as the infecting strain of *M.tb* was identical to one isolated from a chimpanzee housed in the same zoo [24]. The exact route of transmission of *M.tb* between an elephant and chimpanzee was not established as they were kept 110 m apart. Researchers suspected that transmission likely occurred through fomites in which feed was provided regularly to the chimpanzee.

A TB outbreak in three captive Asian elephants was reported in Switzerland. Infection with *M.tb* complex (MTBC) was suspected in 2015 based on the clinical signs such as weight loss, weakness and exercise intolerance, as well as reactivity on DPP. As these elephants were seropositive for TB and their general body condition deteriorated over time, they were euthanized by the attending veterinarian. *M.tb* was cultured from tissues collected at necropsy from all three animals [26]. These elephants were likely subclinically infected with TB via human contact in Indonesia (a high TB burden country [27]) before arriving in Switzerland where they progressed to clinical disease. *M. caprae*, a MTBC member, was isolated from a captive elephant in Japan after being brought from Borneo island several years earlier [4]. This was likely the first report of *M. caprae* infection in elephants. The regions of difference (RD) analysis revealed that this isolate belonged to the Allgäu genotype which is present in red deer (*Cervus elephas*). *M. caprae* has been detected primarily in central Europe among cattle, pigs, red deer, and wild boars [28] and has not been reported in humans or other animal species from Asian countries, so the source of infection of *M. caprae* in this elephant remains indeterminate.

M.tb was isolated from five government-owned captive elephants in Nepal that died between 2009 and 2013 with granulomatous lesions in the lungs [25,29]. Captive elephants in Nepal are used for tourist safaris, patrolling of protected areas, elephant bathing, rhino census, and other activities, all of which bring them into intimate contact with humans and providing multiple opportunities for TB transmission among elephants and humans. Furthermore, captive elephants in Nepal are housed in close proximity to each other in sheds, and they play and graze together which may aid in elephant-to-elephant transmission of TB.

TB screening in elephants in Asian elephant range countries and elephant facilities across the globe has been regularly carried out using serology (STAT-PAK and DPP). A study conducted in India revealed that 45 of 300 captive elephants tested were reactive on STAT-PAK and 25.4% of these were from temples, where they had frequent and intimate contact with humans [30]. Serological surveillance of captive elephants in Malaysia in 2012 showed that 20.4% of the tested elephants (n = 63) were reactive. Three of these seropositive animals also tested positive in a *M.tb*-specific PCR [31] in trunk wash samples. STAT-PAK-based serology conducted on captive elephants in Laos PDR in 2012 revealed that 36% of the tested elephants (N = 80) were reactive [32]. Among seropositive animals, 31% had frequent contact with wild elephants, posing a high risk of TB transmission to the wild elephants. TB screening was also carried out in 35 captive African elephants in Zimbabwe in 2014 using STAT-PAK and DPP. The study indicated that six elephants (17.1%) were seropositive [33]. Seroprevalence was higher among the animals having frequent contact with wild elephants suggesting that they may have been transmitting TB to their wild counterparts. Elephants can be seroreactive to TB antigens and shed bacteria intermittently, long before they are culture-positive on trunk washes, and are likely to serve as a source of *M.tb* infection to other healthy wild elephants [21].

Asian elephant range countries in Southeast Asia have about 41% of the global burden of TB among the human population [27]. In these countries, there are close interactions between humans and elephants during various activities like tourist safaris, religious ceremonies, elephant races, etc. The prolonged close contact between TB-infected humans and healthy elephants or vice versa provides ideal conditions for the transmission of TB between elephants and humans. However, the real risk and directionality of transmission of TB at the human-elephant interface during these activities are largely unknown.

Captive elephants have been treated with anti-tubercular drugs in the US and other parts of the world. Treatment algorithms used in the US follow the protocols in The Guidelines to Control Tuberculosis in Elephants [13]. As in humans, first-line anti-TB drugs isoniazid, rifampin, ethambutol, and pyrazinamide are used in elephants. Drug-resistant cases of elephant TB have been reported in the zoological settings in the US and the elephants have had to be euthanized due to public health concerns [21,34]. Treatment of TB in elephants with anti-TB drugs is further complicated by adverse effects such as anorexia, constipation, ataxia, tremors, limb paresis, and depression [35].

4. TB in wild elephants

TB has been recently diagnosed in wild elephants in Asia and Africa. The first report of TB in wild Asian elephants was from Sri Lanka in 2014. A 35-year old female elephant was found in a moribund condition in the corridor between Udawalawe and Lunugamwehera National Parks. She died two days after supportive therapy and TB-like gross lesions were discovered in the lungs at necropsy. TB was confirmed in this elephant by histopathology and culture [36]. Three wild male Asian elephants that died between 2007 and 2013 in a wildlife sanctuary in southern India were confirmed to be TB positive by histopathology, tetraplex PCR and sequencing of 16S–23S internal transcribed spacer region, *hsp65*, and *rpoB* [37]. One wild Asian elephant that died of suspected TB lesions in the forest of Rajiv Gandhi National Park, Karnataka, India in 2016, was confirmed as TB positive by PCR and nucleotide sequencing [38].

The first case of TB infection in wild African elephants was reported in Kenya in 2011 based on post-mortem lesions and histological examinations; however, no samples were submitted for culture. This elephant was an orphaned calf rescued from a national park in Kenya and raised with other rescued orphans and then was eventually released back into the wild [39]. Serology (using STAT-PAK) was performed on banked serum samples collected from free-ranging African elephants between 2004 and 2018 in Kruger National Park (KNP) in South Africa. The results show that 9.3% of 161 elephants tested were positive [40]. *M.tb* was isolated for the first time from a wild African elephant from KNP in South Africa in 2016 [41]. *M. bovis* has been reported from multiple species in KNP where it is endemic [42]. Despite this fact, it is speculated that this elephant might have become infected with *M.tb* (rather than *M. bovis*) through human-derived contaminated food or infectious biological discharges that might have been disposed of within the national park [41].

The precise source of infections in these wild elephants is unknown. Increasing activities of humans in protected areas, as well as roaming of wild elephants into the human settlements due to habitat fragmentation, might have led to multiple opportunities for TB transmission through fomites into the wild elephant population. If this insidious infection gets established in wild African and Asian elephants, it will eventually threaten the conservation efforts of the flagship species globally. Due to the intimate contact of captive elephants with humans, a reverse zoonosis also cannot be ruled out. More detailed genomic studies are necessary to evaluate the status of TB among wild elephants and other wildlife to evaluate them as potential reservoirs of TB.

5. Genotyping of TB isolates from elephants

A few studies have investigated the genotype profiles and the population genetic frameworks of TB isolates derive from diseased elephants. Spoligotyping, multilocus variable-number of tandem repeat analysis (VNTR), large sequence polymorphisms (LSP), and whole-genome sequencing have all been applied for genotyping elephant TB isolates.

Forty-eight isolates obtained from 33 elephants between 1997 and 2010 located in 11 states across the US were genotyped at National Veterinary Services Laboratories (NVSL), USDA in Ames, Iowa using spoligotyping and VNTR. Fourteen spoligotypes were detected representing common lineages present globally including Beijing, Euro-American, and Latino-American and Mediterranean (LAM). Of these 14, 11 spoligotypes matched CDC in-house reference database, and three spoligotypes were unique and had no matches in the International Type Strains database [43]. The fact that multiple spoligotypes identified matched with fingerprints reported in human cases of TB, suggests that there likely were multiple transmission events (or introductions) and that *M.tb* was transmitted to the captive elephants via human contact.

Genotyping of five *M.tb* isolates from Asian elephants of Nepal using spoligotyping, VNTR, and LSP revealed that all the isolates belonged to Indo-oceanic lineage. Interestingly, mixed *M.tb* lineage infection was reported in two elephants. One elephant was infected with East African-Indian and Indo-Oceanic lineages while other was infected with East Asian and Indo-Oceanic lineages [25,29]. A study on *M.tb* isolated from human TB patients (n = 261) in Nepal revealed that East African-Indian was the most common lineage (≈41%) followed by East-Asian lineage (≈33%). The Indo-Oceanic lineage was present in 11.5% of TB-infected human patients [44], which is likely common among the TB patients dwelling near the elephant facilities in Nepal. Indo-Oceanic lineage was reported in all five elephant isolates studied from Nepal [25,29]. Although this number is too low to draw any conclusions on common strain types, Indo-Oceanic lineage may be well-established among the elephants in Nepal.

Genotyping of TB isolates from three Asian elephants held in a Swiss zoo using spoligotyping identified an identical profile (SIT276) in all three isolates, evidence of a common source of infection in all three elephants. Whole-genome sequence analysis revealed that all isolates belonged to MTBC Lineage 4 [26], which is commonly present globally [45]. As these three elephants moved across different zoos in Europe before arriving at a Swiss Zoo, their exposure to the TB-infected humans likely occurred during these movements. Among the three, one elephant is likely to have become infected with MTBC Lineage 4 and then transmitted it to the other two elephants.

M.tb isolated from an African wild elephant belonged to SIT33/LAM3 spoligotype. Whole-genome sequencing of this isolate clustered it in the LAM3/F11 family [41], which is established as the most common MTBC lineage among human TB patients (21.4% of isolates studied) in South Africa, followed by the Beijing strain (16.5%) [46]. It is speculated that there may have been aerosol transmission of TB to this wild elephant from contaminated food or domestic waste discarded by the TB patient(s) in the vicinity of KNP.

Thus, these studies on strain typing of *M.tb* isolates from the elephants establish that interspecies transmission occurs regularly between elephants and humans. The application of whole-genome sequencing has been useful in the identification of the source of *M.tb* infection in elephants. Since a single transmission event would lead to the establishment of infection in an elephant population, spill back into humans cannot be ruled out. When this interspecies or within-species transmission ricochets, the directionality of spread and its extent across humans, elephants, and other wildlife species is difficult to establish without active surveillance, epidemiological tracking, and genotyping information.

6. TB transmission at the elephant-human interface

Transmission of TB among elephants and humans has been reported in different elephant facilities in the US and other countries. In an exotic farm in Illinois, the USA, three elephants died of *M.tb* infection and the bacterium was isolated from one living elephant. Tuberculin test conducted in the handlers showed that 11 out of 22 handlers were reactive on the tuberculin test performed in 1996 and 1997, and the sputum from one elephant handler was positive for *M.tb*. A comparison of DNA fingerprint by IS*6110* and TBN12 typing revealed that the isolates from four elephants and a culture-positive handler carried identical genetic fingerprints. This was the first report that confirmed the transmission of TB among elephants and humans [47]. These handlers worked near these TB infected elephants during training as well as in other activities including cleaning the barn, participation in necropsies, and residing close to the elephant barns. Thus, the transmission of TB among elephants and humans may have occurred via the aerosol route in this exotic animal farm in Illinois.

In a Los Angeles zoo, *M.tb* was isolated from two elephants and two other species between 1997 and 2000. Among 307 staff screened by tuberculin testing in 2000, 15 personnel who were largely involved in necropsy and elephant training were reactive revealing that interspecies transmission of TB among elephants and humans had likely occurred [48]. In an elephant refugee in Tennessee, one animal was diagnosed with active TB. Nine employees working with the elephant had tuberculin skin test conversion during 2006–2009; however, no one was diagnosed with active TB [49]. Based on the epidemiological and observational data, it was speculated that TB was indirectly transmitted from this TB-confirmed elephant to humans working at the barn through aerosolized *M.tb* that had been expelled or excreted by this elephant. Similarly, four staff working with a TB-confirmed captive elephant that was imported from Thailand were positive on the tuberculin skin test in 2011 in Australia [24]. These four cases spent at least 10 h within the elephant barn after TB was confirmed and this proximity with TB-infected elephant was likely the cause of a positive TST.

In Malaysia, TB testing of captive Asian elephants ($N = 63$) and their handlers ($N = 149$) from six different facilities revealed that 20.4% of elephants were reactive on STAT-PAK and 24.8% elephant handlers reacted positively on QuantiFERON-TB Gold In-Tube test (Cellestis Inc., Australia) [31]. All the QuantiFERON positive handlers were from the same facility. Since *M.tb* was not isolated from trunk washes and no sputum samples were collected from the handlers for culture, the source of infection and direction of transmission among elephants and handlers could not be established. The handlers also could have acquired TB via community spread before subsequently transmitting it to the elephants.

An outbreak of active TB in three bull elephants in a zoo in Oregon was reported in 2013. Ninety-six people who came in contact with the elephant were screened for TB using TST or IGRA and among the contacts, seven close contacts were diagnosed with latent TB infection based on these tests [50]. Genotyping using whole-genome sequencing revealed that one elephant's *M.tb* isolate was identical to the isolate from a person with pleural TB who worked at the zoo intermittently during 2012 and had limited contact with the elephants [50]. The protracted contact among elephants and humans provides an ideal condition for interspecies transmission of TB. These findings provide evidence of the likelihood of interspecies transmission of TB among elephants and humans in different zoological settings. There exists a greater risk of TB exposure to staff working in elephant facilities as well as the risk of transmission of TB to elephants.

7. Surveillance and control strategies of TB in elephants

Active surveillance of TB in both captive, as well as free ranging elephants, should be carried out routinely in elephant range countries as well as elephant facilities across the globe using the tests approved for elephants. Serological tests including STAT-PAK and DPP can be used for screening for TB; however, TB in elephants should always be confirmed by culture, a diagnostic gold standard. The validation of elephant specific interferon-γ release assay (IGRA), as well as identification of novel biomarkers during TB infection in elephants, will help in the early diagnosis of exposure of TB in elephants.

Elephant TB is primarily caused by *M.tb*, indicating that elephants are likely acquiring infections mostly from humans. Thus, TB screening of all handlers working with captive elephants should be performed regularly. Another major impact to the wildlife conservation would be when *M.tb* gets established in wild elephants and is transmitted to other susceptible endangered species. Thus, TB surveillance should also be performed in wild elephants and opportunistic samples collected for TB diagnosis. For the control and prevention of TB, regular TB screening of all captive elephants as well as the people working with them should be performed. Increased surveillance of TB at the elephant-human interface and future studies on *M. tuberculosis* genotypes isolated from the elephants and humans using whole-genome sequencing will clarify the transmission pattern and source of infection of TB in elephants.

8. Conclusions

This review presents the diagnosis of TB, documented TB outbreaks over the past 25 years, TB in wild elephants, its transmission at the elephant-human interface, and surveillance and control strategies as well as knowledge-gaps in the field of elephant TB. We present that *M.tb* is prevalent in captive elephants in the zoological settings as well as elephant range countries globally. TB in free-ranging elephants is limited to only a few countries in Asia (India and Sri Lanka) and Africa (South Africa), at present. The presence of TB in wild elephants suggests a great threat to the survival of these flagship species in the elephant range countries across the globe. A holistic approach is recommended to control this disease at the human-elephant interface to prevent interspecies transmission. Strict hygienic measures should be followed in elephant facilities to prevent disease transmission among elephants and other susceptible hosts. Surveillance for TB in captive and wild elephants, as well as in their handlers, and implementation of effective control strategies will aid in the conservation of this species across the globe.

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Declaration of competing interest

There is no conflict of interest associated with this publication.

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References

[1] Payeur JB, Jarnagin JL, Marquardt JG, Whipple DL. Mycobacterial isolations in captive elephants in the United States. Ann N Y Acad Sci 2002;969:256–8.

[2] Mikota SK. Tuberculosis in elephants. In: Fowler ME, Miller RE, editors. Zoo and wild animal medicine, current therapy. sixth ed. St. Louis: Saunders/Elsevier; 2008. p. 355–64. St. Louis.

[3] Lacasse C, Terio K, Kinsel MJ, Farina LL, Travis DA, Greenwald R, et al. Two cases of atypical mycobacteriosis caused by *Mycobacterium szulgai* associated with mortality in captive African elephants (*Loxodonta africana*). J Zoo Wildl Med 2007; 38:101–7. https://doi.org/10.1638/06-051.1.

[4] Yoshida S, Suga S, Ishikawa S, Mukai Y, Tsuyuguchi K, Inoue Y, et al. *Mycobacterium caprae* infection in captive Borneo elephant. Japan. Emerg Infect Dis 2018;24:1937–40. https://doi.org/10.3201/eid2410.180018.

[5] Iyer AK. Veterinary science in India, ancient and modern with special reference to tuberculosis. Agric Livest India 1937;7:718–24.

[6] McGaughey CA. Diseases of elephants: part III. Ceylon Vet J 1961;9:94–8.

[7] Rothschild B, Laub R. Hyperdisease in the late Pleistocene: validation of an early 20th century hypothesis. Naturwissenschaften 2006;93:557–64. https://doi.org/10.1007/s00114-006-0144-8.

[8] Garrod AH. Report on the Indian elephant which died in the Society's gardens on July 7th, 1875. Proc Zool Soc Lond 1875:542–3.

[9] Seneviratna P, Wettimuny SG, Seneviratna D. Fatal tuberculosis pneumonia in an elephant. Vet Med Small Anim Clin 1966;60:129–32.

[10] Saunders G. Pulmonary Mycobacterium tuberculosis infection in a circus elephant. J Am Vet Med Assoc 1983;183. 1311–2.

[11] Gorovitz C. Tuberculosis in an african elephant. Norden Vet Med 1962;14:351–2.

[12] Mikota SK, Sargent EL, Ranglack GS. Medical management of the elephant. Bloomfield, Michigan. Bloomfield: Indira Publishing House; 1994. p. 123–8.

[13] Proceedings USAHA. Guidelines for the control of tuberculosis in elephants. In: Proceedings of 114th Annual Meeting of the United States Animal Health Association. 114; 2010. p. 578–639.

[14] Mikota SK, Lyashchenko KP, Lowenstine L, Agnew D, Maslow JN. Mycobacterial infections in elephants. In: Mukundan H, Chambers MA, Waters WR, Larsen MH, editors. Tuberculosis, leprosy and other mycobacterial diseases of man and animals: the many hosts of mycobacteria, Wallingford, UK. Wallingford: CABI Publishing House; 2015. p. 259–76.

[15] Lyashchenko KP, Greenwald R, Esfandiari J, Mikota S, Miller M, Moller T, et al. Field application of serodiagnostics to identify elephants with tuberculosis prior to case confirmation by culture. Clin Vaccine Immunol 2012;19:1269–75. https://doi.org/10.1128/CVI.00163-12.

[16] Larsen RS, Salman MD, Mikota SK, Isaza R, Montali RJ, Triantis J. Evaluation of a multiple-antigen enzyme-linked immunosorbent assay for detection of *Mycobacterium tuberculosis* infection in captive elephants. J Zoo Wildl Med 2000; 31:291–302.

[17] Mikota SK, Peddie L, Peddie J, Isaza R, Dunker F, West G, et al. Epidemiology and diagnosis of *Mycobacterium tuberculosis* in captive Asian elephants (*Elephas maximus*). J Zoo Wildl Med 2001;32:1–16. https://doi.org/10.1638/1042-7260(2001)032[0001:EADOMT]2.0.CO;2.

[18] Landolfi JA, Mikota SK, Chosy J, Lyashchenko KP, Giri K, Gairhe K, et al. Comparison of systemic cytokine levels in *Mycobacterium* spp. seropositive and seronegative Asian elephants (*Elephas maximus*). J Zoo Wildl Med 2010;41:445–55.

[19] Angkawanish T, Morar D, van Kooten P, Bontekoning I, Schreuder J, Maas M, et al. The elephant interferon gamma assay: a contribution to diagnosis of tuberculosis in elephants. Transbound Emerg Dis 2013;60(Suppl 1):53–9. https://doi.org/10.1111/tbed.12098.

[20] Paudel S, Villanueva MA, Mikota SK, Nakajima C, Gairhe KP, Subedi S, et al. Development and evaluation of an interferon-γ release assay in Asian elephants (*Elephas maximus*). J Vet Med Sci 2016;78. https://doi.org/10.1292/jvms.15-0701. 1117–21.

[21] Miller MA, Finnegan M, Storms T, Garner M, Lyashchenko KP. Outbreak of *Mycobacterium tuberculosis* in a herd of captive Asian elephants (*Elephas maximus*): antemortem diagnosis, treatment, and lessons learned. J Zoo Wildl Med 2018;49: 748–54. https://doi.org/10.1638/2017-0200.1.

[22] Lewerin SS, Olsson SL, Eld K, Röken B, Ghebremichael S, Koivula T, et al. Outbreak of *Mycobacterium tuberculosis* infection among captive Asian elephants in a Swedish zoo. Vet Rec 2005;156:171–5. https://doi.org/10.1136/vr.156.6.171.

[23] Angkawanish T, Wajjwalku W, Sirimalaisuwan A, Mahasawangkul S, Kaewsakhorn T, Boonsri K, et al. *Mycobacterium tuberculosis* infection of domesticated Asian elephants, Thailand. Emerg Infect Dis 2010;16:1949–51. https://doi.org/10.3201/eid1612.100862.

[24] Stephens N, Vogelnest L, Lowbridge C, Christensen A, Marks GB, Sintchenko V, et al. Transmission of *Mycobacterium tuberculosis* from an Asian elephant (*Elephas maximus*) to a chimpanzee (*Pan troglodytes*) and humans in an Australian zoo. Epidemiol Infect 2013;141:1488–97. https://doi.org/10.1017/S095026881300068X.

[25] Paudel S, Mikota SK, Nakajima C, Gairhe KP, Maharjan B, Thapa J, et al. Molecular characterization of *Mycobacterium tuberculosis* isolates from elephants of Nepal. Tuberculosis (Edinb) 2014;94:287–92. https://doi.org/10.1016/j.tube.2013.12.008.

[26] Ghielmetti G, Coscolla M, Ruetten M, Friedel U, Loiseau C, Feldmann J, et al. Tuberculosis in Swiss captive Asian elephants: microevolution of *Mycobacterium tuberculosis* characterized by multilocus variable-number tandem-repeat analysis and whole-genome sequencing. Sci Rep 2017;7:14647. https://doi.org/10.1038/s41598-017-15278-9.

[27] WHO, Regional Office for South-East Asia. Ending TB in the South-east Asia region: regional strategic plan 2016-2020. 2016. WHO regional office for South-east Asia, http://www.who.int/iris/handle/10665/250292.

[28] Domogalla J, Prodinger WM, Blum H, Krebs S, Gellert S, Müller M, et al. Region of difference 4 in alpine *Mycobacterium caprae* isolates indicates three variants. J Clin Microbiol 2013;51:1381–8. https://doi.org/10.1128/JCM.02966-12.

[29] Paudel S, Nakajima C, Mikota SK, Gairhe KP, Maharjan B, Subedi S, et al. Mixed *Mycobacterium tuberculosis* lineage infection in 2 elephants, Nepal. Emerg Infect Dis 2019;25:1031–2. https://doi.org/10.3201/eid2505.181898.

[30] Abraham D, Cheeran JV, Sukumar R, Mikota SK, Rao S, Ganguly S, et al. Health assessment of captive Asian elephants in India with special reference to tuberculosis. Report to Project Elephant. New Delhi: Ministry of Environment and Forests, Government of India; 2008.

[31] Ong BL, Ngeow YF, Razak MF, Yakubu Y, Zakaria Z, Mutalib AR, et al. Tuberculosis in captive asian elephants (*Elephas maximus*) in peninsular Malaysia. Epidemiol Infect 2013;141:1481–7. https://doi.org/10.1017/S0950268813000265.

[32] Lassausaie J, Bret A, Bouapao X, Chanthavong V, Castonguay-Vanier J, Quet F, et al. Tuberculosis in Laos, who is at risk: the mahouts or their elephants? Epidemiol Infect 2015;143:922–31. https://doi.org/10.1017/S0950268814002180.

[33] Rosen LE, Hanyire TG, Dawson J, Foggin CM, Michel AL, Huyvaert KP, et al. Tuberculosis serosurveillance and management practices of captive african elephants (*Loxodonta africana*) in the kavango-zambezi transfrontier conservation area. Transbound Emerg Dis 2018;65:e344–54. https://doi.org/10.1111/tbed.12764.

[34] Dumonceaux GA, Leger St, Olsen JH, Burton MS, Ashkin D, Maslow JN. Genitourinary and pulmonary multidrug resistant *Mycobacterium tuberculosis* infection in an Asian elephant (*Elephas maximus*). J Zoo Wildl Med 2011;42: 709–12. https://doi.org/10.1638/2011-0040.1.

[35] Rosen LE, Olea-Popelka F, Deem SL, Isaza R, Schmitt D, Miller M. Survey of antituberculosis drug administration and adverse effects in elephants in North America. J Zoo Wildl Med 2019;50:23–32. https://doi.org/10.1638/2018-0028.

[36] Perera BVP, Salgadu MA, Gunawardena Gsps, Smith NH, Jinadasa HRN. First confirmed case of fatal tuberculosis in a Wild Sri Lankan elephant. Gajah 2014;41: 28–31.

[37] Zachariah A, Pandiyan J, Madhavilatha GK, Mundayoor S, Chandramohan B, Sajesh PK, et al. *Mycobacterium tuberculosis* in wild asian elephants, southern India. Emerg Infect Dis 2017;23:504–6. https://doi.org/10.3201/eid2303.161741.

[38] Chandranaik BM, Shivashankar BP, Umashankar KS, Nandini P, Giridhar P, Byregowda SM, Shrinivasa BM. *Mycobacterium tuberculosis* infection in free-roaming wild asian elephant. Emerg Infect Dis 2017;23:555–7. https://doi.org/10.3201/eid2303.161439.

[39] Obanda V, Poghon J, Yongo M, Mulei I, Ngotho M, Waititu K, et al. First reported case of fatal tuberculosis in a wild African elephant with past human-wildlife contact. Epidemiol Infect 2013;141:1476–80. https://doi.org/10.1017/S0950268813000022.

[40] Kerr TJ, de Waal CR, Buss PE, Hofmeyr J, Lyashchenko KP, Miller MA. Seroprevalence of *Mycobacterium tuberculosis* complex in free-ranging african elephants (*Loxodonta africana*) in kruger national park, South Africa. J Wildl Dis 2019;55:923–7. https://doi.org/10.7589/2018-12-292.

[41] Miller MA, Buss P, Roos EO, Hausler G, Dippenaar A, Mitchell E, et al. Fatal tuberculosis in a free-ranging african elephant and one health implications of human pathogens in wildlife. Front Vet Sci 2019;6:18. https://doi.org/10.3389/fvets.2019.00018.

[42] Michel AL, Bengis RG, Keet DF, Hofmeyr M, de Klerk L-M, Cross PC, et al. Wildlife tuberculosis in South African conservation areas: implications and challenges. Vet Microbiol 2006;112:91–100.

[43] Higgins J. Genotyping of *Mycobacterium tuberculosis* cultured from elephants. Tuberculosis in elephants: science, myths, and beyond. Kansas City, Missouri: USDA, APHIS, Center for Animal Welfare; April 5–6, 2011. https://www.aphis.usda.gov/animal_welfare/downloads/elephant/Genotyping%20of%20Mycobacterium%20Tuberculosis%20cultured%20from%20Elephants.pdf.

[44] Malla B, Stucki D, Borrell S, Feldmann J, Maharjan B, Shrestha B, et al. First insights into the phylogenetic diversity of *Mycobacterium tuberculosis* in Nepal. PloS One 2012;7:e52297. https://doi.org/10.1371/journal.pone.0052297.

[45] Stucki D, Ballif M, Egger M, Furrer H, Altpeter E, Battegay M, et al. Standard genotyping overestimates transmission of *Mycobacterium tuberculosis* among immigrants in a low- incidence country. J Clin Microbiol 2016;54:1862–70. https://doi.org/10.1128/JCM.00126-16.

[46] Victor TC, de Haas PE, Jordaan AM, van der Spuy GD, Richardson M, van Soolingen D, et al. Molecular characteristics and global spread of *Mycobacterium tuberculosis* with a Western Cape F11 genotype. J Clin Microbiol 2004;42:769–72. https://doi.org/10.1128/JCM.42.2.769-772.2004.

[47] Michalak K, Austin C, Diesel S, Bacon MJ, Zimmerman P, Maslow JN. *Mycobacterium tuberculosis* infection as a zoonotic disease: transmission between humans and elephants. Emerg Infect Dis 1998;4:283–7. 1998.

[48] Oh P, Granich R, Scott J, Sun B, Joseph M, Stringfield C, et al. Human exposure following *Mycobacterium tuberculosis* infection of multiple animal species in a Metropolitan Zoo. Emerg Infect Dis 2002;8:1290–3. https://doi.org/10.3201/eid0811.020302.

[49] Murphree R, Warkentin JV, Dunn JR, Schaffner W, Jones TF. Elephant-to-human transmission of tuberculosis. Emerg Infect Dis 2009;17:366–71. https://doi.org/10.3201/eid1703.101668. 2011.

[50] Zlot A, Vines J, Nystrom L, Lane L, Behm H, Denny J, et al. Diagnosis of tuberculosis in three zoo elephants and a human contact - Oregon. MMWR Morb

Mortal Wkly Rep 2013;64(52):1398–402. https://doi.org/10.15585/mmwr.mm6452a2. 2016 Jan 8.