

## REVIEW

## Global patterns in biomass models describing prey consumption by big cats

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### Keywords

depredation, Felidae, human-carnivore conflict, livestock, predator

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### ABSTRACT

1. Widespread prey depletion forces carnivores to rely more on livestock, which may lead to increased persecution by humans. Reliable quantification of livestock consumption is essential for understanding depredation scales, but a comparative analysis of extant biomass models used for this purpose has never been done before.
2. We conducted a global meta-analysis of two linear and three non-linear biomass models used to estimate consumption of prey biomass and individuals by seven big cat species. We applied the z-test to perform pairwise comparisons of estimates produced by five models for each prey record. Further, we used logistic regression to assess the effects of species of big cats and their prey, scat sample size, prey body mass, and study sites on significantly different and similar estimates.
3. The analysis of 769 prey records from 47 sites demonstrated that, in over 95% of cases, linear and non-linear biomass models produced similar estimates of prey biomass and individuals consumed. Significantly different estimates of prey biomass consumed (in 1.5% of cases) and prey individuals consumed (4%) were obtained only in certain study sites and for a few big cat species (tiger *Panthera tigris*, leopard *Panthera pardus*, and puma *Puma concolor*). Due to the paucity of different estimates, the effects of predictors could not be ascertained.
4. Our study demonstrated that linear models tend to estimate higher biomass of large prey, lower biomass of medium-sized prey and fewer individuals of large and medium-sized prey consumed than non-linear models. This disagreement in estimates suggests that the numbers of livestock lost to depredation can be underestimated by linear models, and that re-calculation by

non-linear models is required. However, the difference between estimates produced by linear and non-linear models is generally small and such re-calculation may be recommended only for tiger, puma and leopard in certain areas.

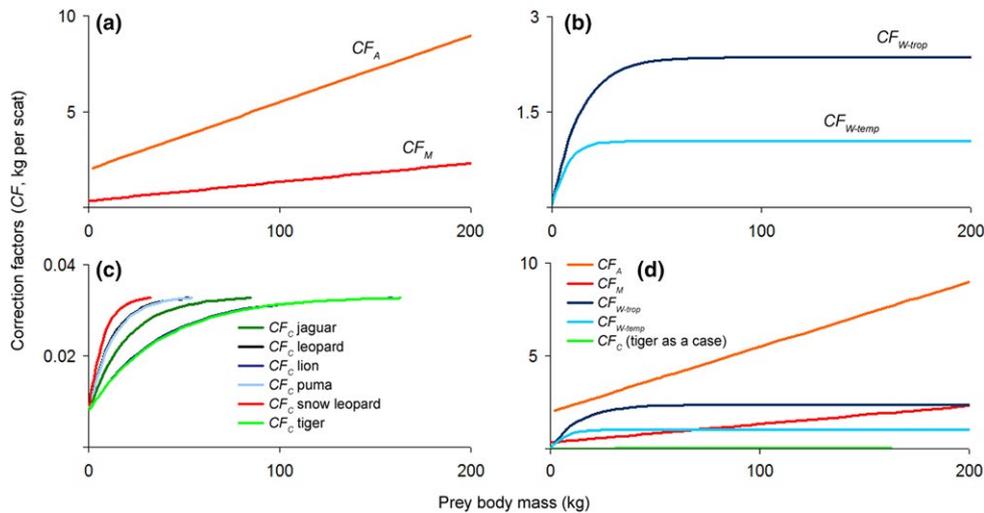
## INTRODUCTION

Feeding habits shape the population structure of large carnivores and determine their interactions with prey species, competitors and humans (Ripple et al. 2014). Body size and biomass of prey exert a direct and profound effect on carnivore densities (Carbone et al. 2011, Hatton et al. 2015). As ungulates and other prey species have been depleted through human persecution and habitat loss, carnivores increasingly rely on domestic animals to survive (Azevedo 2008, Inskip & Zimmermann 2009, Ripple et al. 2014, Khorozyan et al. 2015, Ghoddousi et al. 2016). Depredation often leads to retaliatory killing of large carnivores by humans, especially of big cats such as the lion *Panthera leo*, tiger *Panthera tigris*, jaguar *Panthera onca*, leopard *Panthera pardus*, snow leopard *Panthera uncia*, puma *Puma concolor*, and cheetah *Acinonyx jubatus*, which prey on economically valuable livestock and occasionally may attack humans (Inskip & Zimmermann 2009, Loveridge et al. 2010, Marchini & Macdonald 2012, Banerjee et al. 2013, Tumenta et al. 2013, Swanepoel et al. 2014). Due to prey depletion and human persecution, six of the seven big cat species (86%) are classified by the International Union for Conservation of Nature (IUCN; Anonymous 2016) as Near Threatened to Endangered, in spite of their flagship status which stimulates substantial research and conservation efforts worldwide. For comparison, this percentage is 66% in all felids (25 of 38 species) and only 39% (101 of 259 species) in all terrestrial carnivores (Anonymous 2016). Therefore, clear understanding of carnivore diets is not only an ecological topic, but also a fundamental part of socio-economic, psychological and even political aspects of conservation (Dickman et al. 2011, Eklund et al. 2011, Carter et al. 2012). This is in line with a stance that ecological science should be focused more on finding practical solutions for conservation of felids and other carnivores (Balme et al. 2014).

Few other aspects of carnivore ecology enjoy as comprehensive research effort as the diets of big cats (Brooke et al. 2014). Very often, contributions of different prey species to felid diets have been quantified through the analysis of undigested remains in faecal samples (scats). This is because scat surveys are relatively easy, non-invasive, affordable, and produce more representative results than alternative methods such as investigations of prey carcasses

or stomach contents (Thompson et al. 2009, Bacon et al. 2011, Martins et al. 2011). Determination of diet from scats can be done by calculating the frequency of prey occurrence, using conversion factors or applying biomass models. Frequency of prey occurrence significantly overestimates the share of small animals because of their complete consumption and high surface-to-volume ratio, which results in a high proportion of undigested fur and bones (Floyd et al. 1978). Conversion factors, which estimate prey biomass from dry scat mass, are laborious to apply and specific to each prey species, so are impractical for carnivores with diverse diets (Rühe et al. 2008). Therefore, biomass models are most widely used in carnivores, especially big cats (Andheria et al. 2007, Azevedo 2008, Meena et al. 2011, Mondal et al. 2011, Banerjee et al. 2013, Ghoddousi et al. 2016). Biomass models allow researchers to calculate the percentages of prey biomass and prey individuals, and thus to identify the key prey species.

Biomass models have been developed through feeding trials and use correction factors ( $CF$ ) and equations based on prey body mass and numbers of collectable scats to estimate the percentages of prey biomass and number of individuals consumed. The  $CF$ s can be linear in a simple form of  $CF$  (kg/scat) =  $a \times$  prey body mass (kg) +  $b$ , e.g. Ackerman's  $CF_A$  and Marker's  $CF_M$  (Ackerman et al. 1984, Marker et al. 2003).  $CF_A$  was developed in the puma, and is still most widely applied in felid studies, whereas  $CF_M$  was developed and verified only in the cheetah (see Fig. 1 and Appendix S1). Recently, several new non-linear biomass models were proposed for big cats, taking into account that  $CF$ s do not increase infinitely with increasing prey body mass as linear biomass models would suggest, but reach a plateau with heavy prey due to physiological constraints of defecation (Fig. 1; Appendix S1). These models suggest that  $CF_A$  and  $CF_M$  overestimate the biomass contribution of heavy prey and, thus, are intrinsically biased. The non-linear biomass models include Wachter's  $CF_{W-trop}$  for tropical felids, which was developed by using feeding trials in cheetahs (Wachter et al. 2012); Wachter's  $CF_{W-temp}$  for felids in temperate regions, which was developed in the Eurasian lynx *Lynx lynx* (Wachter et al. 2012); and Chakrabarti's  $CF_C$  for all felids, which was developed in the lion, leopard, jungle cat *Felis chaus* and domestic cat *Felis catus* (Chakrabarti et al. 2016). The authors of non-linear biomass models



**Fig. 1.** The patterns of correction factors ( $CF$ ) applied in big cats to calculate prey biomass consumed per scat produced. The graphs show (a) linear Ackerman's  $CF_A$  for prey weighing more than 2 kg and Marker's  $CF_M$  for prey weighing more than 0.35 kg; (b) non-linear Wachter's tropical  $CF_{W-trop}$  and Wachter's temperate  $CF_{W-temp}$ ; (c) non-linear Chakrabarti's  $CF_C$  scaled to body masses of big cat species; and (d) all correction factors overlaid to demonstrate the differences in their scales.  $CF_C$  reaches an asymptote as prey body mass approaches felid body mass (Jones et al. 2009) and becomes unrealistic thereafter. The cheetah line is excluded from graph (c) because of the different way in which cheetahs use prey carcasses. The  $CF_C$  lines are close together, so only tiger  $CF_C$  is shown in graph (d). Only prey with individuals of up to 200 kg is shown, as the trends in heavier prey remain unchanged.

advocated them as physiologically more justified and, thus, more realistic than linear  $CF$ s. Nonetheless, most big cat researchers still use Ackerman's  $CF$  and far fewer apply Marker's and Wachter's  $CF$ s (Farhadinia et al. 2012, Sollmann et al. 2013, Ghoddousi et al. 2016). Chakrabarti's  $CF_C$  is brand new and has not yet been applied elsewhere.

The development and application of so many  $CF$ s in big cats brings into question the comparability of biomass models. The authors of non-linear  $CF$ s made some attempts to conduct a comparative analysis. Wachter et al. (2012) compared  $CF_{W-trop}$  and  $CF_M$  for cheetah from Marker et al. (2003) and found that  $CF_M$  overestimated the biomass of small scrub hares *Lepus saxatilis*. Further, Wachter et al. (2012) compared  $CF_{W-trop}$  and  $CF_A$  in tiger and leopard diets from Andheria et al. (2007) and concluded that  $CF_A$  overestimated biomass of large gaur *Bos gaurus* and underestimated that of medium-sized chital *Axis axis* in the diet of the tiger, but not in the leopard. Chakrabarti et al. (2016) included 10 tiger studies, one leopard study (Mondal et al. 2011), and one lion study (Banerjee et al. 2013) in a comparison of prey biomass consumption estimated by  $CF_C$  and  $CF_A$ . This comparison has shown that  $CF_A$  overestimated the biomass consumption of all large prey consumed and underestimated medium-prey biomass in tigers, lions, and leopards (Chakrabarti et al. 2016). Particularly, it was concluded that economic losses from lion depredation were

overestimated by  $CF_A$  by 32% (Banerjee et al. 2013, Chakrabarti et al. 2016).

Comparisons also showed that biomass models produce much more distinct differences in estimates of numbers of prey individuals consumed than in those of prey biomass consumed. Estimation of prey individuals consumed by big cats can be done directly from  $CF_A$ ,  $CF_M$  or  $CF_C$  as shown above, or by using special equations developed by Wachter et al. (2012) for tropical and temperate felids (Appendix S1). The advantage of Wachter's equations is that they consider partial consumption of prey by big cats, which is much more realistic taking into account the fact that about 20–30% of prey biomass is composed of inedible matter (e.g. bones), and quite frequent cases of kleptoparasitism by co-existing carnivores (Bissett & Bernard 2007, Wachter et al. 2012). However, Wachter's equations could be biased towards cheetahs as they usually consume prey in a single bout, and therefore underestimate prey consumption by other cats, which return to carcasses and consume more (Hayward et al. 2006). All other models assume full consumption of prey, which may hold true only for small prey. The described trend is that  $CF_A$  and  $CF_M$  substantially underestimate numbers of large prey individuals, including livestock, and overestimate numbers of small prey, which actually play a negligible role in big cat diets (Marker et al. 2003, Andheria et al. 2007, Wachter et al. 2012).

The main conclusion of these comparisons is that linear biomass models overestimate biomass and underestimate

individuals in large prey, whereas in medium-sized and small prey they underestimate biomass and overestimate individuals consumed. However, the weakest points of these comparisons is that, except in the study of tigers by Chakrabarti et al. (2016), the researchers making the comparisons used only one study per big cat species and did not apply statistical tests to check the significance of difference in estimates of prey biomass and individuals consumed ensuing from different  $CF$ s. As a result, it remains unclear whether the authors' conclusions are generally applicable, specific to a given big cat species, prey species or study area, or depend on the sample size (number of scats). Knowing this is crucial to our understanding of how to assess the contribution of livestock and other prey to big cat diets accurately, where depredation hotspots are located, and how to make management decisions to minimise human-felid conflicts over livestock depredation. The differences in the estimation of the importance of large and medium-sized prey by biomass models are applicable to livestock, which also can be large (cattle *Bos taurus*, yak *Bos grunniens*, water buffalo *Bubalus bubalis*, horse *Equus caballus*, and donkey *Equus asinus*) and medium-sized (sheep *Ovis aries*, goat *Capra hircus*, and domestic pig *Sus domesticus*).

In this paper, we conduct a global meta-analysis of the diets of big cats, as determined from scats, and attempt to find answers to the following ecologically and practically important questions:

1. How different are the same dietary profiles if estimated by different biomass models?
2. Does this difference, if any, depend on the species of big cats and prey, study areas, prey body mass and sample size (numbers of scats analysed)?
3. As non-linear biomass models are more plausible and biologically justified, which of them is most appropriate and practical to use in big cats?
4. How do answers to these questions affect estimates of the contribution of domestic animals, especially livestock, to big cat diets, and how can they improve the evaluation of depredation rates in general?

## METHODS

We retrieved peer-reviewed English language scientific articles and book chapters dated 1984–2016 through the ISI Web of Knowledge (<http://www.webofknowledge.com>) and the IUCN Species Survival Commission Cat Specialist Group Digital Library (<http://www.catsg.org>). We began the literature search from 1984, a year when the first felid-specific correction factor  $CF_A$  was published (Ackerman et al. 1984). As search words, we used the combinations of the species common names 'lion', 'tiger',

'jaguar', 'leopard', 'snow leopard', 'puma', 'cougar', 'mountain lion', 'Florida panther', and 'cheetah' with the words 'diet', 'food habit', 'scat', and 'prey selection'. Several common names (puma, cougar, mountain lion and panther) are used for *Puma concolor* in different parts of the Americas, so we used all of them in the literature search (Macdonald et al. 2010). We also checked publications in which the original  $CF$  works (Ackerman et al. 1984, Marker et al. 2003, Wachter et al. 2012, Chakrabarti et al. 2016) were cited, and amended our reference list as necessary. Then, we selected papers in which  $CF$ s were used to estimate the percentage of prey biomass consumed ( $B\%$ ) and the percentage of prey individuals consumed ( $N\%$ ) from prey remains in scats (Table 1). We did not use dissertations, theses, reports and conference proceedings as literature sources. Also, we disregarded papers in which  $CF$ s were used, but in which the underlying quantitative information needed for our analysis was not provided, e.g. prey body masses or sample sizes were not given, prey were grouped, or  $B\%$  or  $N\%$  were represented only graphically.

We used the two linear correction factors ( $CF_A$  and  $CF_M$ ) and the three non-linear correction factors ( $CF_{W-trop}$ ,  $CF_{W-temp}$ , and  $CF_C$ ; Appendix S1; Fig. 1) that have been developed so far in big cats. We took prey body mass ( $BM$ , kg) from the literature. We retrieved body masses of big cats, which are required to calculate  $CF_C$ , from the PanTHERIA database: 32.5 kg for snow leopard, 50.5 kg for cheetah, 52.4 kg for leopard, 53.9 kg for puma, 84.9 kg for jaguar, 159 kg for lion, and 163 kg for tiger (Jones et al. 2009). We did not apply  $CF_A$  to prey weighing <2 kg and  $CF_M$  to prey weighing <0.35 kg, as these limits indicate the minimum body mass of small prey producing one scat from consuming a whole body, i.e.  $CF_A = BM$  and  $CF_M = BM$  (see Appendix S1; Ackerman et al. 1984). We considered sheep and goats as a single or separate livestock species, depending on how they were treated in literature sources.

We calculated  $B\%$  and  $N\%$  as indicated in Appendix S1. We clearly distinguished between Wachter's correction factors for tropical and temperate felids ( $CF_{W-trop}$  and  $CF_{W-temp}$ ) and Wachter's equations for tropical and temperate felids, because the  $CF$ s were used to calculate  $B\%$  and the equations were used to calculate  $N\%$  (Appendix S1). As the number of scat samples with remains of the  $i$ -th prey ( $n_i$ ) was not always reported in literature sources, we calculated it from available data on the frequency of prey occurrence in scats ( $f_i$ ) and the total number of collected scats ( $n_{total}$ ) using the relationship  $f_i = (n_i/n_{total}) \times 100$  (Ghoddousi et al. 2016). As Wachter et al.'s (2012) equations of  $N\%$  require knowledge of group size ( $G_j$  in Appendix S1), we took  $G = 4$  individuals for the lion, which is the only social big cat, and  $G = 1$  for all other big cats (Banerjee et al. 2013). The group size of lions in India and West Africa, which we sampled in

**Table 1.** The numbers of prey records and literature sources used in this study for each big cat species

Species	Number of prey records	Number of prey species consumed			Number of literature sources
		Wild	Domestic	Not specified*	
Cheetah <i>Acinonyx jubatus</i>	13	10	2	0	2
Jaguar <i>Panthera onca</i>	67	25	2	8	6
Leopard <i>Panthera pardus</i>	369	117	7	25	23
Lion <i>Panthera leo</i>	36	26	2	2	3
Puma <i>Puma concolor</i>	143	53	3	14	13
Snow leopard <i>Panthera uncia</i>	44	10	6	3	4
Tiger <i>Panthera tigris</i>	97	18	4	3	12
Total†	769	189	10	40	50

\*Remains of consumed organisms in scats are not determined to species level, considered as several species together, or cannot be identified.

†The total numbers of prey species and literature sources are not equal to the sums of species-specific numbers because some prey species are consumed by several big cats and some literature sources describe several big cats.

this study, is smaller than that in East and Southern Africa (Macdonald et al. 2010).

Ultimately, we produced a database of prey records in big cat scats, in which each record (row) contained five different estimates of  $B\%$  and  $N\%$  (columns) from the application of five  $CF$ s. Each record comprised a prey species consumed by a big cat species in a particular site, in a given study period. Therefore, prey records from the same big cat species and site, but from different periods, were treated separately (Bodendorfer et al. 2006, Meena et al. 2011, Banerjee et al. 2013).

For each prey record, we conducted six pairwise comparisons between  $B\%$  calculated from two linear and three non-linear  $CF$ s, e.g. between  $B\%$  from  $CF_A$  and  $B\%$  from  $CF_{W-temp}$ . We did the same for  $N\%$ , e.g. between  $N\%$  from  $CF_M$  and  $N\%$  from  $CF_C$ . For this, we used the one-sample z-test in MedCalc 16.2.1 (MedCalc Software bvba, Ostend, Belgium) with the significance level set to  $\alpha = 0.008$ . We defined  $\alpha$  by applying the Bonferroni correction for multiple testing, in which  $\alpha$  is the significance level 0.05 divided by the number of tests applied, i.e. six in our case (Armstrong 2014). The application of the Bonferroni correction was justified by using a single z-test when most of z-values are non-significant (see Results) and driven by an imperative to avoid a Type I error of false positives, i.e. significant z-values, which are actually not (Armstrong 2014). The difference between estimates in each pairwise comparison was statistically significant if one estimate fell beyond the 95% exact Clopper-Pearson confidence interval (95%  $CI$ ) of the other estimate.

Thus, in each prey record we obtained six z-values for  $B\%$  and six z-values for  $N\%$ , which were either statistically significant or non-significant. We assigned significantly different cases as 1 and similar cases as 0 and checked their dependence on prey body mass and scat sample size by using logistic regression in IBM SPSS Statistics 23.0 (IBM Corp., Armonk NY, USA). We included in the

logistic model factors such as study sites, big cat species and prey species, and their interactions, to explore the confounding effect of sites and species of big cats and their prey on  $B\%$  and  $N\%$  estimates. We excluded prey species indicated as 'not specified' in Table 1. We used Kruskal–Wallis tests to conduct multiple sample comparisons (Dytham 2011). We evaluated the power of logistic models by calculating the odds ratio  $\exp^\beta$ , where  $\beta$  is model slope. Odds ratios  $>1$  indicate a positive effect of factors and those  $<1$  show a negative effect (Dytham 2011).

## RESULTS

We obtained and analysed 769 prey records from 47 sites retrieved from 50 literature sources; the smallest sample size was for cheetah ( $n = 13$ ) and the largest was for leopard ( $n = 369$ ; Table 1, Appendix S2). The 769 records included 79 records (10%) of livestock depredation: 28 cattle, 26 sheep and goats, 8 water buffaloes, 6 horses, 5 yaks, 3 yak-cattle hybrids, 2 donkeys, and 1 domestic pig. In addition, big cats preyed on domestic dogs ( $n = 8$  records) and cats ( $n = 2$ ). The leopard had the most diverse diet and killed most domestic animals (Table 1). The snow leopard and cheetah consumed the lowest number of wild prey species (10 species each), and snow leopards killed all available domestic animals. Scat sample size was significantly larger in tigers ( $n = 26.6 \pm 4.1$  scats; Kruskal–Wallis  $\chi^2 = 32.82$ ,  $P < 0.0001$ ) and did not differ between the other six big cats ( $n = 11.5 \pm 0.9$  scats;  $\chi^2 = 8.47$ ,  $P = 0.132$ ). Prey body mass significantly differed between all big cats ( $\chi^2 = 91.03$ ,  $P < 0.0001$ ), except for puma and jaguar ( $\chi^2 = 0.64$ ,  $P = 0.426$ ).

### Percentage of prey biomass consumed ( $B\%$ )

Out of 4614 pairwise comparisons (769 prey records by six comparisons) in all species, only 69 (1.5%) yielded

significantly different estimates of  $B\%$  between linear and non-linear  $CFs$  and most estimates of  $B\%$  were similar within a record (Appendix S3). Linear  $CFs$  produced lower estimates of  $B\%$  for medium-sized prey (10–60 kg) and higher estimates of  $B\%$  for large prey weighing more than 60 kg and for small prey weighing <10 kg, but in 99% of cases this trend was not significant.

Significantly different estimates between linear and non-linear  $CFs$  were found over a wide range of scat sample sizes and prey body masses, but only for 12 prey species (6% of all) in 13 sites (28% of all). They comprised only one record of livestock depredation: calf consumption by pumas in Aravaipa-Klondyke, USA (Appendix S3). There were no significantly different estimates in cheetah, jaguar and snow leopard, but the maximum numbers of such estimates were in tiger ( $n = 36$ ) and puma ( $n = 23$ ). This contrast between big cat species was significant as Kruskal–Wallis  $\chi^2$  varied from 20.99 to 31.04 and  $P$  from <0.001 to 0.002 depending on the  $CFs$  that were compared.

Due to the paucity of significantly different estimates, logistic regression failed to find effects of scat sample size, prey body mass, species of big cats and their prey, and sites on difference or similarity of  $B\%$  based on the odds ratios  $\exp^{\beta} \approx 1$  in all logistic models (range 1.000–1.036; Appendix S4). This pattern was completely identical also in tigers and pumas, which contained most significantly different estimates, as their  $\exp^{\beta}$  varied from 0.999 to 1.035.

### Percentage of prey individuals consumed ( $N\%$ )

The number of significantly different estimates of  $N\%$  between linear and non-linear  $CFs$  was 169 out of 4614 (4%) pairwise comparisons, which included 35 prey species (18% of all) in 27 (57%) sites (Appendix S3). There was a complete 100% overlap of sites holding significantly different estimates of  $B\%$  and  $N\%$ . Linear  $CFs$  produced lower estimates of  $N\%$  for large and medium-sized prey and higher estimates for small prey, but this trend was not significant in 96% of cases.

Most of the significantly different estimates were in the puma ( $n = 86$ ), leopard ( $n = 38$ ) and tiger ( $n = 30$ ); the lowest numbers were in the snow leopard ( $n = 7$ ), jaguar ( $n = 5$ ), lion ( $n = 3$ ), and cheetah ( $n = 0$ ). This contrast between big cat species was significant, as Kruskal–Wallis  $\chi^2$  varied from 16.35 to 47.11 and  $P$  from <0.001 to 0.012. Significantly different estimates in the depredation of domestic animals included only three records: one of calf depredation in Aravaipa-Klondyke, USA, and two of dog depredation in western Maharashtra and Sanjay Gandhi National Park, India (Appendix S3).

Logistic regression did not reveal effects of scat sample size, prey body mass, species of big cats and their prey, and sites on difference or similarity of  $N\%$  based on the odds ratios  $\exp^{\beta} \approx 1$  in all logistic models (range 0.995–1.051). This pattern was true also in pumas, leopards and tigers, which showed most significantly different estimates, as their  $\exp^{\beta}$  varied from 0.975 to 1.102.

## DISCUSSION

Our extensive global meta-analysis of scat-based dietary studies of seven big cat species has demonstrated that, in over 95% of cases, linear and non-linear biomass models produced similar estimates of prey biomass and individuals consumed. We obtained significantly different estimates of prey biomass consumed (1.5% of cases) and prey individuals consumed (4%) only in certain study sites and big cat species, namely the tiger, puma and leopard. As most prey estimates were similar, we could not determine the effects of species of big cats and their prey, scat sample size, prey body mass, and study sites on the similarities or differences in prey estimates obtained by linear and non-linear biomass models.

Wachter et al. (2012) and Chakrabarti et al. (2016) concluded that linear models tend to estimate higher biomass and fewer prey individuals for large prey, but for medium-sized and small prey they estimate lower biomass and more individuals than non-linear models. Our results confirm this pattern, but linear models estimated higher biomass of small prey and fewer individuals of medium-sized prey than non-linear models. This disagreement in estimates may suggest that the numbers of livestock lost to depredation can be underestimated by linear models, and that the re-calculation of livestock losses and consumption is required by using more advanced non-linear models (Wachter et al. 2012, Chakrabarti et al. 2016). Our study provides some evidence for this disagreement, but in most cases it is not statistically significant, and the re-calculation of livestock losses can be justified only for the tiger, leopard and puma. For domestic animals, linear and non-linear models produced similar estimates, except for three records (one of cattle and two of dogs) out of the total of 89 records (3%). Particularly, in Aravaipa-Klondyke, USA, the biomass and number of calves consumed by pumas were higher by about 10% (biomass) and lower by over 10% (individuals) when estimated by linear models than by a non-linear one (Cunningham et al. 1999). Numbers of dogs consumed by leopards in Sanjay Gandhi National Park and western Maharashtra, India, were three times lower if estimated by linear models than if estimated by non-linear models (Edgaonkar & Chellam 2002, Athreya et al. 2016).

Estimates of prey biomass and individuals consumed are affected by the sample size (number of scats collected). Suppose that the percentage of consumed individuals of prey A is calculated as 15% from Ackerman's linear correction factor and 30% from Wachter's non-linear equation for tropical felids. This difference would be non-significant if the number of A-containing scats was only 10 ( $z = 1.035$ ,  $P = 0.301$ ), but would become significant at 70 samples ( $z = 2.739$ ,  $P = 0.006$ ). This is because the 95% confidence intervals of small samples are much wider, encompassing both estimates, than those of larger samples (Dytham 2011). However, in our study the scat sample size of big cats containing significantly different estimates (tiger, puma, and leopard) was large only for tiger, while puma and leopard samples were similar to those of other big cats.

We recognise that this study unintentionally underrepresents depredation by lions, leopards and cheetahs in Southern and East Africa, where human-felid conflicts over livestock killing are rather frequent (Inskip & Zimmermann 2009, Loveridge et al. 2010, Tumenta et al. 2013, Balme et al. 2014, Swanepoel et al. 2014). This is because the diet of big cats in these regions has been studied from prey kills and not from scats (Hayward et al. 2006, Bissett & Bernard 2007, Tambling et al. 2012, Tumenta et al. 2013). As a result, we used only limited scat-based data from Marker et al. (2003) for cheetahs in Namibia and from Brackzkowski et al. (2012) for leopards in South Africa. We could not incorporate data from Martins et al. (2011) on leopard diet in South Africa because the authors did not provide body masses of all prey found in scats and averaged livestock body masses between species. We are not aware of dietary studies from African lion scats other than that by Bodendorfer et al. (2006) in West Africa, which we used in this study. In this context, it would be useful to estimate prey (including livestock) biomass and individuals from prey kills and compare them with estimates from scats. The application of standardised prey body mass assessment as  $\frac{3}{4}$  of adult female body mass is of great advantage (Jooste et al. 2013), but it should be used carefully with livestock because their body sizes vary greatly depending on breeds and local conditions. Currently, comparative analyses of prey occurrence in scats and kills related to the same big cat species, study sites, and periods are limited in Africa and beyond (Ackerman et al. 1984, Bacon et al. 2011, Martins et al. 2011, Meena et al. 2011, Tambling et al. 2012, Banerjee et al. 2013). In addition, more studies on prey consumption and depredation should be conducted on the cheetah, as this species differs from other big cats by consuming its prey in a single bout (Hayward et al. 2006). There were no differences between linear and non-linear model outputs in the cheetah, but whether or not this is related to

feeding ecology of cheetah is unclear and requires more research.

In conclusion, we did not find sufficient evidence of differences between estimates of prey biomass and individuals consumed produced by linear and non-linear biomass models describing prey consumption by big cats. Very rare cases of significantly different estimates were found in certain study sites and in certain big cat species: tiger, puma, and leopard. As the difference between linear and non-linear model estimates is generally small, the recalculation of livestock losses due to depredation may be recommended only for tiger, puma, and leopard in certain areas.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

**Appendix S1.** Correction factors and related parameters.

**Appendix S2.** Reference studies and literature sources.

**Appendix S3.** Information on significantly different estimates of prey biomass and individuals consumed.

**Appendix S4.** Performance of logistic regression models.