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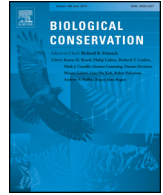**168** PUBLICATIONS **3,574** CITATIONS

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Big cats kill more livestock when wild prey reaches a minimum threshold

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A B S T R A C T

Livestock predation by big cats, i.e., lion (*Panthera leo*), tiger (*Panthera tigris*), leopard (*Panthera pardus*), jaguar (*Panthera onca*), snow leopard (*Panthera uncia*), puma (*Puma concolor*), and cheetah (*Acinonyx jubatus*), creates conflicts with humans which challenge biodiversity conservation and rural development. Deficiency of wild prey biomass is often described as a driver of such conflicts, but the question "at which level of prey density and biomass do big cats begin to kill livestock?" still remains unanswered. We applied logistic regression to meta-data compiled from recent peer-reviewed scientific publications and show that cattle predation is high when prey biomass is $<812.41 \pm 1.26$ kg/km^2, whereas sheep and goat predation is high at $<544.57 \pm 1.19$ kg/km^2, regardless of sizes of study areas and species, body masses, and population densities of big cats. Through mapping cases with known prey biomass and case-specific comparison of actual vs. threshold-predicted livestock predation we confirm the reliability of these thresholds in predicting livestock predation by big cats. The map also demonstrates that some protected areas of India, Nepal lowlands, and South Africa contain sufficient prey that makes big cats less likely to kill livestock, but in other sampled areas prey biomass is not high enough and the probabilities of livestock predation are moderate to high. We suggest that these thresholds represent important landmarks for predicting human–felid conflicts, identifying conflict hotspots, and setting priorities for targeted conservation actions. It is essential to maintain and restore wild prey to forestall local extinctions of big cats.

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1. Introduction

Mammalian carnivores inflict socio-economic losses to rural livelihoods, mainly due to predation on domestic livestock, and are intensively wiped out because of retaliatory or preventive persecution (Treves and Karanth, 2003; Baker et al., 2008; Gusset et al., 2009; Loveridge et al., 2010). These losses and arising human–carnivore conflicts are particularly strong for small-scale households and near protected areas, thus challenging a synergy between rural development and biodiversity conservation (Treves and Karanth, 2003; Bauer and de Iongh, 2005; Namgail et al., 2007; Baker et al., 2008; Lagendijk and Gusset, 2008; Dar et al., 2009; Loveridge et al., 2010). Encroachment of carnivore habitats by expanding human populations is a potential spark for new conflicts, which deteriorate the complex functioning of the environment at all levels, from individuals to ecosystems (Ripple et al., 2014). Big cats, namely the lion (*Panthera leo*), tiger (*Panthera tigris*), leopard (*Panthera pardus*), jaguar (*Panthera onca*), snow leopard (*Panthera uncia*), puma (*Puma concolor*), and cheetah (*Acinonyx jubatus*), are among the best-known carnivores responsible for conflicts with humans (Inskip and Zimmermann, 2009). Retaliatory killing, poaching and prey loss are the main threats for these species, of which six are classified by the IUCN Red List of Threatened Species as "Endangered" to "Near Threatened" and only puma is still common having the "Least Concern" status (Macdonald et al., 2010).

Albeit the density and biomass of livestock exceed those of wild prey manifold, big cats would prefer to kill wild prey to avoid human retribution (Loveridge et al., 2010). When prey, especially medium-sized and large ungulates, becomes scarce due to population declines or seasonal migrations felids increase predation on livestock to survive (Polisar et al., 2003; Bauer and de Iongh, 2005; Azevedo and Murray, 2007; Kumaraguru et al., 2011; Mondal et al., 2011; Amador-Alcalá et al., 2013; Zhang et al., 2013; Kabir et al., 2014). In some areas, cats kill livestock mostly during the wet season when prey disperses into lush vegetation, regains fitness and thus becomes less available, whereas livestock enters these areas for uncontrolled grazing (Polisar et al., 2003; Patterson et al., 2004; Kissui, 2008). In other areas, livestock predation is minimal during winter when prey attains high densities in certain areas with little snow (Dar et al., 2009) or it is maximal during the dry season when limited cover decreases hunting success, prey moves away and livestock concentrates around a few waterholes (Schiess-Meier et al., 2007). Overall, the relationships between prey availability and livestock predation by big cats appear to be straightforward, but some more intricate cause-and-effect patterns are also possible. For example, Harihar et al. (2011) found out that the natural recovery of prey after relocation of local people has led to a sharp rise, and not a decline as expected, of livestock predation by leopards because recovering tigers displaced them closer to villages. Moreover,

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Suryawanshi et al. (2013) concluded that snow leopard predation on livestock may intensify with more abundant prey, presumably because higher stock of prey supports a greater number of cats. Therefore, these authors recommend that prey recovery programs should be accompanied by strengthening livestock protection measures.

If the causality between wild prey scarcity and increased livestock predation is real, then a new question arises: at what threshold levels of prey density/biomass are attacks on livestock triggered? We did not find such information in the scientific literature. Such a threshold may vary with the species, body masses and population densities of big cats, as well as with size of the study areas. Although being similar in regard to obligatory meat eating, big cats may differ in livestock predation patterns due to species-specific ecological properties. For example, snow leopards are known for surplus killing and group-living lions might be expected to kill more livestock than other cats, which are solitary (Jackson et al., 2010; Loveridge et al., 2010). Livestock predation can also be allometric, because large-bodied big cats select cattle and buffaloes, and smaller species usually prefer sheep, goats, and juveniles of larger species (Dar et al., 2009; Zarco-González et al., 2013; Kabir et al., 2014). Population density of felids and other carnivores is positively related to prey biomass and this relationship is so strong that it allows estimating carnivore densities and carrying capacity from current prey resources (Carbone and Gittleman, 2002; Hayward et al., 2007; Carbone et al., 2011). However, this rule relies only on bottom–up processes (carnivores controlled by prey) and fails when ever-increasing top–down processes (carnivores controlled by humans, e.g., via poaching) limit carnivore numbers while prey remains sufficient (Khorozyan et al., 2008; Kiffner et al., 2009; Zhang et al., 2013; Bauer et al., 2014). Unlike other big cats, cheetah density is related more to competition with larger competitors than to prey availability (Carbone and Gittleman, 2002; Carbone et al., 2011). Sizes of study areas are inversely related to carnivore and prey densities, so they can mediate the strength of predator–prey relationships and livestock predation (Carbone and Gittleman, 2002). For instance, for practical reasons prey populations are often studied in relatively small high-density enclaves or protected areas, which may represent the areas of low predation on livestock (Biswas and Sankar, 2002).

In this paper, we (a) study the linkage between livestock predation by big cats, wild prey biomass and above-mentioned confounders, (b) identify and estimate the minimum thresholds of prey biomass that move predation rates up, and (c) discuss these thresholds as a potentially useful metric for assessing and predicting human–felid conflicts.

2. Materials and methods

2.1. Literature

We retrieved peer-reviewed English language scientific articles and book chapters dated 2000–2014 through the ISI Web of Knowledge (http://www.webofknowledge.com) and the IUCN/SSC Cat Specialist Group Digital Library (http://www.catsg.org). Only recent publications were considered to assure the most accurate and consistent data on predictors and confounders, especially on prey biomass, prey density, and cat density, which are particularly demanding for up-to-date research techniques. As information on wild prey density and its derivate prey biomass was a priori assumed to be most limited in livestock predation studies, we used the search words "panthera*livestock", "acinonyx*livestock", "puma*livestock", "panthera*prey density", "acinonyx*prey density" and "puma*prey density". These combinations gave us more output than if we used narrower options, e.g., "panthera*livestock*prey density", because the "*prey density" combination revealed control studies without livestock predation. In an array of publications that met these criteria, we selected those which contained at least some of the predictors and confounders (see below) or held sufficient information so that we

could calculate them (Appendix A). Original data are provided in Appendix B. Each publication contained one livestock predation/no predation case (one study area for one big cat species) or more cases (2–5 study areas for a species, e.g. different protected areas in a puma study by Donadio et al. (2010) in which each protected area was considered a separate case). We took the cases as independent if they described different big cat species, areas and/or study periods in the same area. Otherwise, we considered the cases as dependent and lumped them into a single case.

2.2. Input data

The numbers of livestock killed per year, which are reported in publications, usually do not represent actual livestock losses to carnivores. They come mostly from interviews and also from carnivore diets, livestock carcasses, farm reports and authority appraisals for compensation. Interviews may underestimate losses if remote or less and accessible villages are under-represented, if villagers forget cases or if they are reluctant to share information (Holmern et al., 2007; Kissui, 2008). On the other hand, villagers may overestimate losses if they assign other mortality causes to carnivore attacks, if they perceive carnivores as evil disproportionally to actual threat or if they want to attract attention or get compensation (Holmern et al., 2007; Gusset et al., 2009; Suryawanshi et al., 2013). Such biases are common, since in most cases villagers do not get compensations for losses and therefore they are not obliged to accurately document them. Although some authors try to minimize these biases by field verification of reported losses, it is applicable only to the most recent and identifiable cases and when verifying researchers are available on place (Azevedo, 2008; Kabir et al., 2014). Feces and livestock records suffer from low detection probabilities and underestimate livestock losses (Bagchi and Mishra, 2006; Sollmann et al., 2013; but see Wegge et al., 2012). Authority appraisals also tend to underestimate losses because they record only the most recent cases confirmed by carcasses or other irrefutable evidence (Sangay and Vernes, 2008). Farm reports are the most accurate, but their published data are only few (Patterson et al., 2004; Schiess-Meier et al., 2007; Wegge et al., 2012). As a result, inaccurate data on livestock losses may hide a relationship between livestock losses and predictors, which is present but goes undetected (type II error of false negatives, non-detections or underestimations; Zarco-González et al., 2013).

To overcome these issues, we considered livestock predation rates in terms of binary response variables: probability of cattle predation (CP) and probability of sheep and goat predation (SP). We lumped sheep and goats as "shoats" as they usually graze together and chose cattle and shoats because of their ubiquitous predation by big cats (Inskip and Zimmermann, 2009; Loveridge et al., 2010). We coded CP and SP as 1 if predation was high and 0 if it was none or minimal as described in references. If a livestock species was not taken, we coded it as 0 only if that species was bred, i.e. available for predation. Alternatively, we left CP or SP blank, as in the case of shoats not bred on cattle ranches (Rosas-Rosas et al., 2008).

Although the published numbers of livestock kills can be inaccurate, they allow getting an impression of whether livestock losses in a study are high or low, especially when they are discussed further by the authors. Our recent studies (Khorozyan et al., 2015a, in press) showed that the numbers of killed livestock are random and unpredictable while the binary data of high and low predation can be well described and predicted by variables. Dietary studies routinely use the correction factors that estimate the proportions of the numbers of livestock consumed to the numbers of all prey consumed, which are also useful for classifying livestock predation as high or low (Marker et al., 2003; Azevedo, 2008; Athreya et al., in press). The main criterion that we used to separate the cases of high and low predation was whether the studied big cat species depended on livestock as staple food (high

predation) or they did not kill livestock or did that sporadically (low predation).

The following predictors were considered and retrieved from the references in Appendix A: (1) cattle holdings, individuals/household, (2) shoats holdings, individuals/household, (3) cattle density, individuals/km^2, (4) shoats density, individuals/km^2, (5) cattle biomass, kg/km^2, (6) shoats biomass, kg/km^2, (7) wild prey density, individuals/km^2, and (8) wild prey biomass, kg/km^2. When predictors were not provided in publications directly, we estimated them from other data available in these publications, e.g. by estimating prey biomass from species densities and body masses. Livestock and prey body masses were reported as either average masses taken by a given big cat species or as 3/4 of female body mass, to account for juveniles (Zhang et al., 2013). We took wild prey density and biomass data mostly for ungulates, which are the staple prey for big cats (Inskip and Zimmermann, 2009; Loveridge et al., 2010). However, we also included the capybara (*Hydrochoerus hydrochaeris*), caiman (*Caiman yacare*), nine-banded armadillo (*Dasypus novemcinctus*) and giant anteater (*Myrmecophaga tridactyla*) for jaguar and the common langur (*Semnopithecus entellus*), rhesus monkey (*Macaca mulatta*) and black-naped hare (*Lepus nigricollis*) for leopard, which are intensively hunted by these cats (Polisar et al., 2003; Azevedo and Murray, 2007; Kumaraguru et al., 2011; Mondal et al., 2011; Bhattarai and Kindlmann, 2012).

We also considered four confounders which might affect the relationships between above-mentioned predictors and response variables: (1) big cat species, (2) big cat body mass, kg, (3) big cat density, individuals/100 km^2, and (4) size of study area, km^2 (Appendix C). We took the species-specific body masses from PanTHERIA database (Jones et al., 2009). We obtained the sizes of study areas and big cat densities from the references in Appendix A.

We took the coordinates of livestock predation/no predation cases from the references (Appendix A) or, if unavailable there, from the case locality names in Geoplaner v. 2.7 (http://www.geoplaner.com). When a study included several cases, like Donadio et al. (2010) mentioned above, we selected a midpoint as a plausible reference. We took the country midpoints for the nationwide cheetah studies in Namibia and for the jaguar and puma study in anonymous ranches of Venezuela (Marker et al., 2003; Hoogesteijn and Hoogesteijn, 2008; Marker et al., 2010). We mapped the cases in WGS84 georeference system in QGIS v. 2.8.1 Wien (http://www.qgis.com).

2.3. Data analysis

First, we used chi-square (χ^2) test to check the difference between the actual and expected numbers of publications as the indicators of their bias and representativeness for each big cat species. Predictors and confounders were ln-transformed to reduce intrinsic variation and minimize the effect of outliers. Estimation of lethal dose 50% (LD$_{50}$), which we borrowed for this study from toxicological practice (see below), also uses ln-transformation of concentrations as predictors (Faraggi et al., 2003). We identified significant predictors by comparing them between predation and no predation cases by Mann–Whitney test. We tested the relationships between significant predictors, response variables and confounders by means of logistic regression models. We studied the effect of confounders by comparing the values and 95% confidence intervals (95% *CI*) of the odds ratios exp(slope) of significant predictors with and without the confounders in the models (Yan and Su, 2009). We excluded outlier predictors with Cook's distance ~1 and higher and multicollinear predictors with significant Spearman's correlation coefficient r_s (Yan and Su, 2009). We applied two-way ANOVA and r_s to check the dependence of big cat density upon density and biomass of wild prey (Appendix D). The area under curve of receiver operating characteristic (ROC), denoted as AUC, indicated strong predictive capacity of logistic models if it exceeded 0.7 (Zarco-González et al., 2013).

We determined the threshold values of predictors from the best logistic regression models by estimating the values of predictors, which would cause *CP* and *SP* to equal 0.5, i.e. a 50:50 chance of livestock to be killed by big cats. These threshold values were calculated as -(intercept β_0/slope β_1) of the logistic model (Faraggi et al., 2003). The standard errors (*SE*) and 95% *CI* of these thresholds were estimated in Bioassay, Dose response and LD$_{50}$ option of Simfit 7.0 package (University of Manchester, UK). This approach is similar to determining a LD$_{50}$, the dose of an experimentally administered substance, which kills 50% of subjected individuals. Apart from toxicological applications, it is also efficient in wildlife ecology, for example in calculating the critical size of protected areas, which ensures 50% probability of survival of large carnivores inside these areas (Woodroffe and Ginsberg, 1998; Woodroffe, 2001). We used Wilcoxon signed-rank test to check how significant, in the same cases, is the difference between the actual predation/no predation status and the predation/no predation status predicted by thresholds. All analyses were performed in SPSS 17.0 (IBM Corp., USA) at two-tailed significance level *P* = 0.05.

3. Results

A total of 99 publications fulfilled the search criteria for leopard, 78 for lion, 74 for puma, 73 for tiger, 55 for cheetah, 38 for jaguar and 26 for snow leopard. They represented 315 publications, but only 107 (34.0%) of them contained at least part of required information and served as references (leopard — 38, 38.4%, lion — 27, 34.6%, tiger — 21, 28.8%, puma — 20, 27.0%, jaguar — 19, 50.0%, cheetah — 15, 27.3%, snow leopard — 11, 42.3%; Appendices A and B). The numbers of these references per species were significantly different (χ^2 = 21.497, *df* = 6, *P* = 0.001), implying an objective reality that, for example, leopard and lion are much better studied and published than snow leopard. However, the numbers of references did not differ from the expected ones within the species, given their unequal studiedness (χ^2 = 6.323, *df* = 6, *P* = 0.388); therefore, our meta-data were unbiased and representative. Our dataset contained 146 geographically diverse livestock predation/no predation cases, ranging from 11 cases from 5 countries for cheetah to 33 cases from 12 countries for leopard (Table 1).

There were 39 cases of prey biomass from 13 countries and 63 cases of prey density from 15 countries (Table 1). The cases with cattle predation had significantly lower wild prey density (Mann–Whitney *U* = 259.5, *P* = 0.024) and prey biomass (*U* = 87.0, *P* = 0.020) than those without cattle predation. Similarly, the cases with sheep and goat predation had lower prey density (*U* = 76.5, *P* = 0.006) and prey biomass (*U* = 29.5, *P* = 0.028) than those without it. No other predictors showed significant difference between predation and no predation cases (*P* > 0.05). The jaguar, lion and snow leopard took mostly cattle and all big cats, except for tiger, exhibited strong predation on sheep and goats (Fig. 1).

The significant logistic regression models show that the probability of cattle predation (*CP*) and the probability of sheep and goat predation (*SP*) strongly depended on prey biomass (Table 2; Fig. 2). *CP* and *SP* also depended on prey density (Wald = 4.855, *P* = 0.028 and Wald = 6.847, *P* = 0.009, respectively), but we excluded these models because of low predictive capacity of the *CP* model (AUC = 0.662) and the estimation of *SP* > 1 at low-density values.

The probability of livestock killing by big cats significantly increased when prey biomass fell below certain minimum thresholds. According to the models in Table 2, the threshold values of ln-transformed prey biomass were 6.70 ± 0.23 (95% *CI* = 6.21–7.19) for *CP* and 6.30 ± 0.17 (95% *CI* = 5.94–6.66) for *SP* (Fig. 2). Back-transformation of these estimates produced the threshold values of prey biomass to equal 812.41 ± 1.26 kg/km^2 (95% *CI* = 497.70–1326.10 kg/km^2) for *CP* and 544.57 ± 1.19 kg/km^2 (95% *CI* = 379.93–780.55 kg/km^2) for *SP* (Fig. 2). The map of 39 studied cases of prey biomass in relation to these thresholds confirmed the areas with and without known livestock predation, with a few exceptions (Fig. 3). In Gir Protected Area (India),

Table 1
The distribution of predictor sample sizes across the big cat species and livestock (cattle and shoats = sheep and goats) in this study. Abbreviations: B — biomass, D — density, H — holdings, hh — household, ind — individuals, N — number of studied cases.

Species	N	Livestock H (ind/hh)		Livestock D (ind/km²)		Livestock B (kg/km²)		Prey D (ind/km²)	Prey B (kg/km²)
		Cattle	Shoats	Cattle	Shoats	Cattle	Shoats		
Cheetah	11	7	5	6	4	1	0	3	1
Jaguar	19	16	1	12	0	4	0	2	3
Leopard	33	17	16	16	9	5	2	17	13
Lion	22	12	10	10	6	3	1	9	5
Puma	29	17	5	19	6	3	1	7	2
Snow leopard	13	1	5	2	6	0	1	11	4
Tiger	19	6	3	7	3	3	1	14	11
Total	146	76	45	72	34	19	6	63	39

the threshold model predicted low conflicts while the actual conflicts are high. In the national parks of Emas (Brazil) and Pench (India) and in the Wanda Mts. (China), the model predicted high predation but it is not recorded. Despite this, in the same 39 cases the difference between the actual predation/no predation status and the status predicted by the thresholds was insignificant (Wilcoxon $Z = -0.577$, $P = 0.564$).

The parameters and performance of the models in Table 2 were not confounded by big cat species, big cat body mass, big cat density and size of study area as the odds ratios and their 95% CI from different models significantly overlapped (Table 3). In all models, the odds ratios were <1 indicating that less prey biomass caused higher CP and SP (Table 3).

4. Discussion

Our research shows that big cats are much more likely to kill cattle, sheep, and goats when the biomass of wild prey is decreased (Table 2 and Fig. 2). This result is in agreement with local studies which hypothesized a direct causal link between prey biomass and livestock predation by big cats (Bagchi et al., 2003; Namgail et al., 2007; Gusset et al., 2009; Harihar et al., 2011; Kumaraguru et al., 2011;

Fig. 1. The distribution of publications about predation vs. no predation on cattle (a) and sheep and goats (b) by cheetah (CH), jaguar (JA), leopard (LE), lion (LI), puma (PU), snow leopard (SL) and tiger (TI).

Amador-Alcalá et al., 2013; Kabir et al., 2014). The probability of livestock killing by big cats significantly increases when prey biomass reaches some minimum thresholds. More specifically, these carnivores are more likely to kill cattle when prey biomass is less than 812.41 kg/km² and to kill sheep and goats when prey biomass is below 544.57 kg/km² (Fig. 2). We suggest that these thresholds may represent important landmarks for predicting human–felid conflicts and identifying conflict hotspots for priority actions in conflict mitigation and species conservation.

The map of cases with known prey biomass and predicted livestock predation shows that some protected areas of India, Nepal lowlands, and South Africa contain sufficient prey that makes big cats less likely to kill livestock. In all other sampled areas, which included mostly protected areas and also ranches and forestry areas, prey biomass is insufficient and the probabilities of livestock predation are moderate to high (Fig. 3). Our threshold model in Table 2 accurately predicted the areas of high and low predation, but four exceptions were found. From Banerjee et al. (2013), we have estimated prey biomass in Gir Protected Area (India) to equal 1984.0 kg/km², which is well above the threshold. However, lion attacks on livestock (cattle) are common in Gir because local people are officially permitted to graze livestock inside the park and to get compensations to tolerate conflicts with lions. Gir lions kill cattle proportionally to their availability and strongly prefer wild ungulates (Banerjee et al., 2013). In Pench National Park (India), Biswas and Sankar (2002) estimated prey biomass as 6013.25 kg/km² in 1998–1999 in a 61.1-km² area, whereas Majumder et al.'s (2013) data collected in 2007–2010 over 758 km² enabled us to estimate prey biomass as only 369.54 kg/km² for tiger and 314.03 kg/km² for leopard. The discrepancy in prey biomass could ensue from spatial inconsistency or prey declines over time, but none of these authors indicated livestock predation in Pench. Possibly, this pattern resulted from a preference for abundant, but smaller, prey like chital (*Axis axis*) instead of livestock, which was available only along the park boundaries (Majumder et al., 2013; also see below). With our threshold model, we assume a conservative low estimate of prey biomass and predict moderate to high livestock predation in Pench. The other two exceptions from Emas National Park (Brazil) and the Wanda Mts. (China) are described below.

Survival of the largest big cats – tiger, lion and jaguar – is significantly limited by the availability of large-bodied ungulates whose consumption would offset high energetic costs associated with hunting, maintenance of vast home ranges, and other activities (Carbone et al., 2011). The snow leopard also demands high energy intake because of living in cold, low productive and prey-poor highlands of Central Asia (Namgail et al., 2007; Jackson et al., 2010). These four big cats are the first candidates to switch to killing the most profitable, large-bodied domestic animals such as cattle when wild prey biomass becomes insufficient and drops below ca. 800 kg/km² (Fig. 1). Other big cats, especially leopard, are also able to take cattle (Loveridge et al., 2010; Fig. 1). When prey biomass falls below ca. 540 kg/km² even cattle cannot compensate for the lack of food and big cats turn to killing small livestock such as sheep and goats. This strategy strives to maximize the net energy budget of
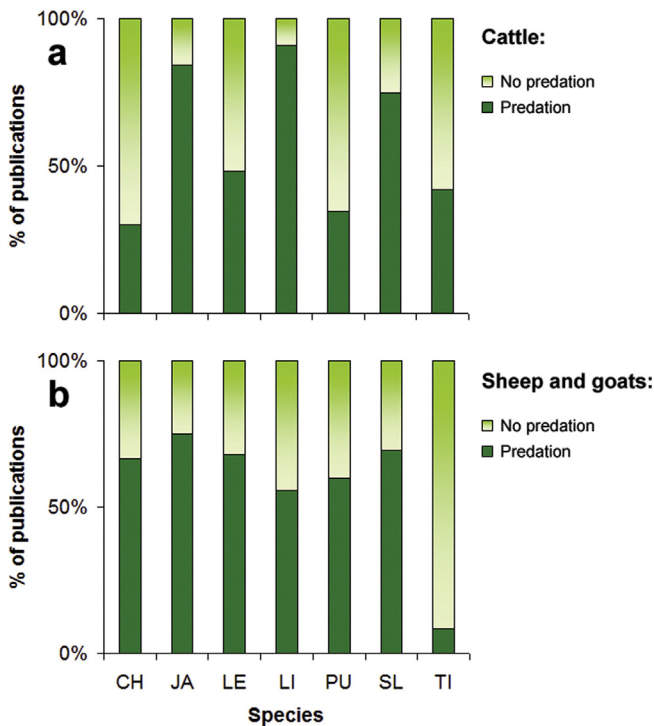
Table 2

The logistic regression models of the dependence of the probability of cattle predation (*CP*) and the probability of sheep and goat predation (*SP*) upon wild prey biomass (*preybio*, kg/km^2). Abbreviations: AUC — area under curve of Receiver Operating Characteristic (ROC), P_{model} — significance level of the model, P_{AUC} — significance level of the AUC, SE — standard error.

Model	Wald statistic	P_{model}	AUC $\pm$ SE	P_{AUC}
$CP = 1 / [1 + \exp(0.729 * \ln(preybio) - 4.885)]$	6.889	0.009	0.791 ± 0.081	0.005
$SP = 1 / [1 + \exp(1.119 * \ln(preybio) - 7.054)]$	4.422	0.035	0.885 ± 0.075	0.004

surviving felids by taking out the best available alternative prey (cattle) when prey biomass begins to dwindle, and by killing all available alternative prey (cattle, sheep and goats) when prey resources are too low.

It is imperative to study, monitor, maintain and restore the populations of wild prey, especially preferred ungulates, to forestall livestock predation, human–felid conflicts and further escalation of local extinctions of big cats. Fig. 3 shows that even many protected areas contain insufficient prey resources, implying an even worse status of prey in unprotected lands. Suryawanshi et al. (2013) suggest that high prey abundance may accelerate livestock-taking by supporting high numbers of carnivores which need more food. Although we did not find support for this opinion, a possibility of bimodal distribution of livestock predation at low and high levels of prey abundance is interesting and deserves further investigations.

Apparently, big cats cannot survive when ln-transformed prey biomass plummets to less than 2, i.e., prey biomass about 7 kg/km^2 (Fig. 2). The only known exception is the leopard, which can even attain high densities in some prey-free anthropogenic landscapes by killing domestic animals (Athreya et al., in press; Shehzad et al., 2015).

Our logistic model of the relationships between livestock predation and wild prey biomass consists of three zones: high predation risk zone (low prey and high predation on livestock), low predation risk zone (high prey and low predation) and uncertainty zone (low prey and low predation) (Fig. 2). The uncertainty zone is realistic in several cases. Very small populations of big cats are likely to subsist on limited prey resources without a need to depend on livestock (Zhang et al., 2013). In the worst case, these populations may vanish and nullify livestock predation in spite of existence of wild prey. Also, big cats can select abundant, but smaller, prey species instead of raiding livestock (e.g., jaguars specializing on killing giant anteaters — Sollmann et al., 2013; tigers and leopards selecting chitals — Majumder et al., 2013). These cases may explain why our threshold model predicted livestock predation by tigers in the Wanda Mts., China (Zhang et al., 2013), tigers and leopards in Pench National Park, India (Majumder et al., 2013) and jaguars in Emas National Park, Brazil (Sollmann et al., 2013), but actually this predation is none or minimal (Fig. 3). The other option can take place in situations when low prey biomass drives big cats to kill domestic animals, which were not considered in this study. In this case, Fig. 2 would show "false zeroes" (no or low predation) because our model was developed only for cattle, sheep, and goats. For example, in areas with insufficient prey snow leopards can take mostly horses, tigers can kill high numbers of buffaloes and leopards can rely mainly on domestic dogs (Bagchi et al., 2003; Bagchi and Mishra, 2006; Athreya et al., in press).

We did not observe a confounding effect of species on the relationship between prey biomass and livestock predation. Perhaps, this discrepancy was caused by an insufficient contrast between the species: only three
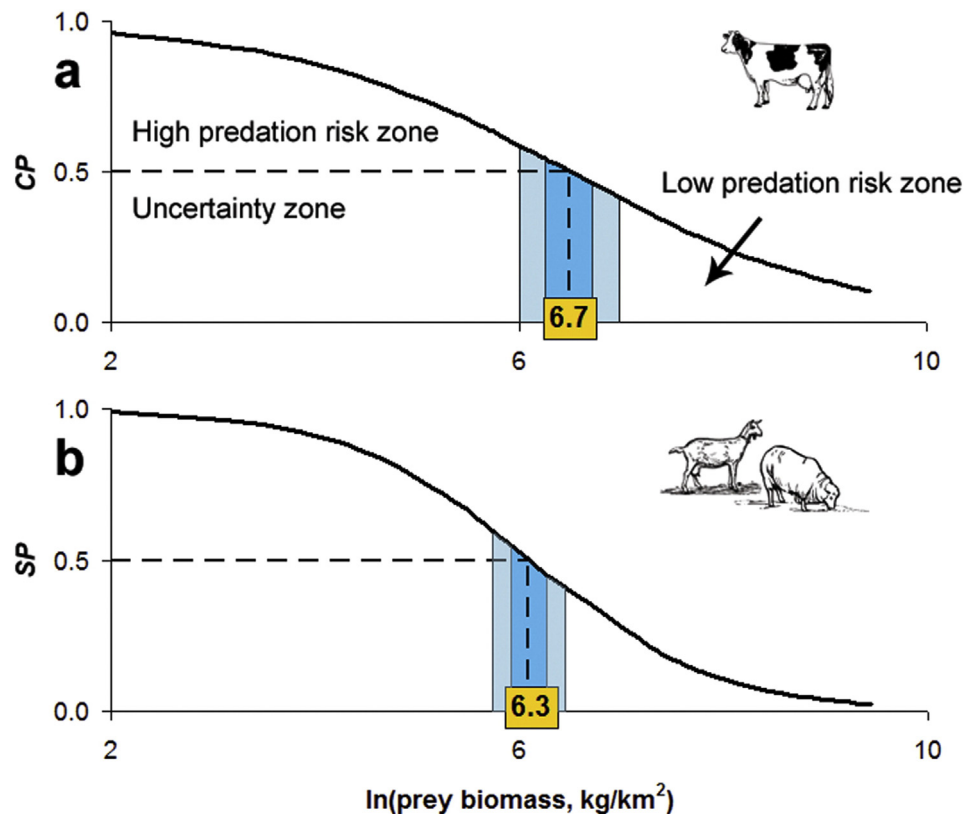
Fig. 2. The logistic regressions describing the effect of prey biomass on (a) the probability of cattle predation (*CP*) and (b) the probability of sheep and goat predation (*SP*) by big cats. See their equations in Table 2. The threshold values of ln-transformed prey biomass are provided in boxes. The standard error margins and the 95% confidence intervals of these thresholds are marked by dark and light colors, respectively.
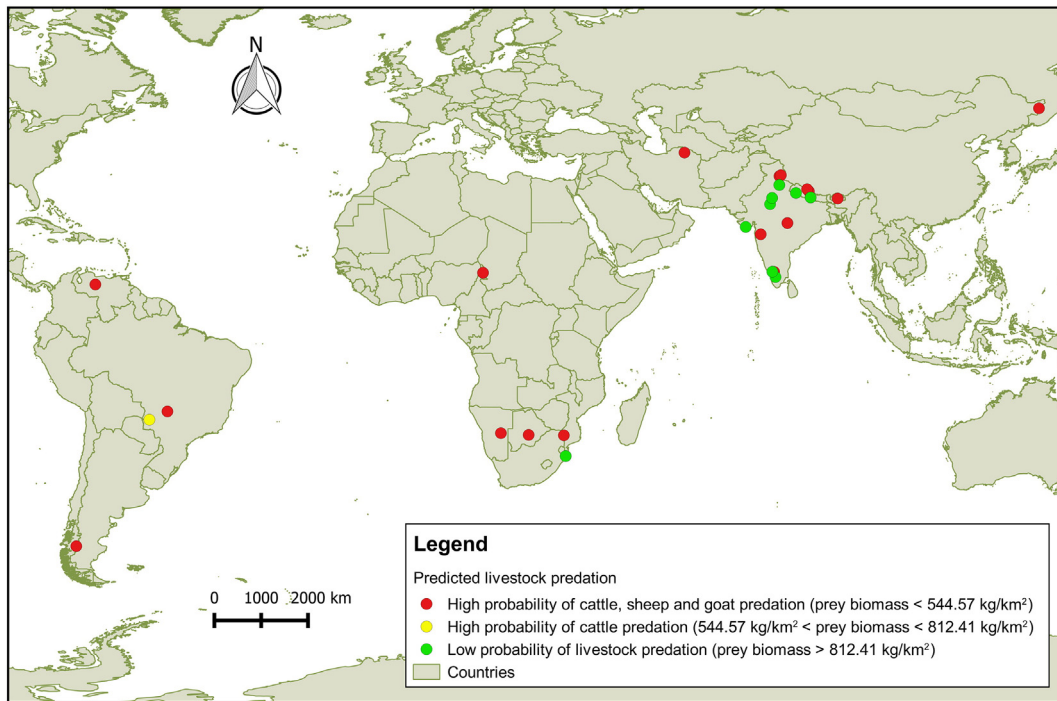
Fig. 3. The distribution of studied cases (n = 39) predicting the probabilities of livestock predation by big cats from currently known prey biomass. Some overlap of cases may take place when the same area is studied for different big cat species. High probability of predation >0.5 and low probability <0.5.

species avoided some livestock (cattle — cheetah and puma, sheep and goats — tiger), while the others took them readily (Fig. 1). Also, the habit to kill cattle or small livestock is variable within a species depending on a pressure from larger competitors. For examples, leopards can kill cattle when they are the top carnivores in the area, but tend to take more sheep and goats when co-existing with ecologically dominant lions or tigers (Holmern et al., 2007; Bhattarai and Kindlmann, 2012;

Thorn et al., 2013; Khorozyan et al., 2015b). The same pattern is documented in pumas living in areas with and without jaguars (Rominger et al., 2004; Azevedo, 2008; Rosas-Rosas et al., 2008; Amador-Alcalá et al., 2013).

Likewise, we did not find support for the hypothesis that body mass of big cats would affect the prey biomass–livestock predation relationship by skewing cattle killing to larger cats and sheep and goat killing

Table 3

The odds ratios and their 95% confidence intervals (95% CI) of ln-transformed wild prey biomass (*preybio*, kg/km^2) in livestock predation models with and without the confounders. Confounders: big cat species (*species*, dummy variables) and ln-transformed big cat body mass (*bodymass*, kg), size of study area (*studyarea*, km^2) and big cat density (*catdens*, individuals/100 km^2).

Models	Probability of big cat predation on cattle (CP)		Probability of big cat predation on shoats (SP)	
	Odds ratio	95% CI of odds ratio	Odds ratio	95% CI of odds ratio
preybio	0.48	0.28–0.83	0.33	0.12–0.93
preybio + species	0.49	0.28–0.87	0.33	0.10–1.02
preybio ∗ species	0.61	0.33–1.13	0.45	0.14–1.48
preybio + bodymass	0.47	0.26–0.83	0.42	0.13–1.30
preybio ∗ bodymass	0.34	0.10–1.18	0.90	0.13–6.40
preybio + studyarea	0.57	0.33–1.00	0.07	0.00–3.13
preybio ∗ studyarea	0.51	0.28–0.94	0.04	0.00–2.78
preybio + catdens	0.58	0.25–1.41	—	—
preybio ∗ catdens	0.69	0.27–1.75	—	—
preybio + bodymass + studyarea	0.55	0.31–1.00	0.15	0.01–2.63
preybio + bodymass + catdens	0.59	0.24–1.44	—	—
preybio + studyarea + catdens	0.96	0.33–2.81	—	—
preybio + species + bodymass	0.47	0.25–0.87	0.38	0.11–1.29
preybio + species + studyarea	0.56	0.30–1.04	0.07	0.00–1.77
preybio + species + catdens	0.96	0.33–2.81	—	—
preybio ∗ bodymass ∗ studyarea	0.50	0.27–0.93	0.05	0.00–2.88
preybio ∗ bodymass ∗ catdens	0.63	0.25–1.60	—	—
preybio ∗ studyarea*catdens	0.60	0.24–1.49	—	—
preybio ∗ species ∗ bodymass	0.57	0.31–1.04	0.50	0.15–1.64
preybio ∗ species ∗ studyarea	0.63	0.35–1.11	0.07	0.00–1.56
preybio ∗ species ∗ catdens	0.74	0.31–1.81	—	—
preybio + bodymass ∗ studyarea	0.57	0.33–1.00	0.07	0.00–3.22
preybio + bodymass ∗ catdens	0.56	0.23–1.34	—	—
preybio + studyarea ∗ catdens	0.57	0.25–1.29	—	—
preybio + species ∗ bodymass	0.50	0.29–0.88	0.36	0.11–1.17
preybio + species ∗ catdens	0.61	0.25–1.47	—	—
preybio + species ∗ studyarea	0.51	0.28–0.92	0.11	0.01–2.33

to smaller cats. There are two possible reasons for this. The snow leopard, which is the smallest and most light-weighted of big cats, is known to actively kill cattle and also other large-bodied animals like yaks and horses (Fig. 1; Bagchi and Mishra, 2006; Namgail et al., 2007; Sangay and Vernes, 2008; Jackson et al., 2010). Also, all the largest big cats, except for the tiger, are keen to kill sheep and goats (Fig. 1; Bauer and de Iongh, 2005; Amador-Alcalá et al., 2013). Reliance of livestock predation upon prey biomass appears to be stable regardless of big cat densities and sizes of study areas. Higher prey biomass leads to higher densities of big cats, which are inversely proportional to sizes of study areas (Appendix D; Carbone and Gittleman, 2002; Carbone et al., 2011; Zhang et al., 2013). On the other hand, more prey means less livestock predation (Fig. 2), but we did not find differences in big cat densities or sizes of study areas in predation vs. no predation areas. Our results did not confirm that high prey abundance may contribute to higher predation on livestock by supporting more carnivores (Suryawanshi et al., 2013).

A recent overview by Ripple et al. (2014) claims that expanding animal husbandry, which strives to meet increasing human demand for meat, poses a threat to carnivores by intensifying their clashes with livestock. Machovina and Feeley (2014) further suggest that reducing livestock numbers and their substituting by alternative proteins, such as soybeans, would negate human–carnivore conflicts. We do not agree with these views, as we did not find the effect of livestock holdings, density or biomass on its predation by big cats. Livestock predation depends more on favorable conditions for successful hunting (e.g., dense cover or lax husbandry) rather than on mere availability of livestock (Bagchi and Mishra, 2006; Sangay and Vernes, 2008; Kabir et al., 2014). Earlier studies have revealed that felid predation rates can increase with livestock abundance and density, decrease or remain unaffected by them (Azevedo, 2008; Amador-Alcalá et al., 2013; Zarco-González et al., 2013).

5. Conclusions

This study suggests that livestock predation by big cats can be reliably determined and predicted by biomass of wild prey species. Predation rates significantly increase when prey biomass decreases below certain minimum thresholds, which are higher for cattle (812.41 kg/km^2) than for sheep and goats (544.57 kg/km^2). Being optimal for net energy maximization by larger big cats and snow leopards, cattle are expected to be killed by these species first when prey biomass becomes insufficient. When prey biomass is below ca. 540 kg/km^2, sheep and goats are more intensively killed along with cattle to optimize energy intake. These threshold values of wild prey biomass can be used as important predictors of human–felid conflicts allowing the identification of conflict hotspots and targeted conservation actions. Therefore, more efforts are required to study, monitor, maintain, and restore the populations of wild prey, especially preferred ungulates, to forestall livestock predation, human–felid conflicts and further escalation of local extinctions of big cats.

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