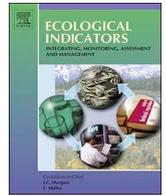




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The balancing act: Maintaining leopard-wild prey equilibrium could offer economic benefits to people in a shared forest landscape of central India

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ABSTRACT

Human-felid interactions impose financial burden on people through livestock loss, and on wildlife managers and conservationists through investments in conflict resolution measures. Leopards (*Panthera pardus*) are among the most adaptable carnivores, but their widespread occurrence in human-dominated landscapes makes them highly vulnerable to negative interactions with people. Beyond their role in maintaining ecological balance, they may also provide economic benefits through control of wild prey populations in human-use areas. We assessed leopard distribution based on indirect sign surveys, and spatial drivers of livestock/human attacks by leopards based on interview surveys of local residents, in a forest landscape shared by humans and leopards in central India. We also examined the role of wild prey in leopard diet and the extent to which they offset leopard depredation on domestic livestock. Leopards occupied 80% of the landscape, positively influenced by forest cover and relative abundance of wild prey; size of human settlements had a negative influence. Average probability of livestock/human attacks was 84%, driven mostly by size of cattle-holding by local residents and anthropogenic disturbance within forests. Nearly 90% of leopard diet was composed of primates or wild ungulate herbivores; non-wild prey (domestic livestock and free-ranging dogs) accounted for less than 3% of total biomass consumed. Under hypothetical scenarios wherein wild prey population reduced by 25%, 50% and 75%, we estimated that the contribution of domestic livestock towards leopard diet would increase to 21%, 40% and 60% respectively in order to support the current leopard population. We demonstrate that adequate forest cover and wild prey abundance allow leopards to persist in shared, human-modified landscapes. We use a novel approach for mapping spatial risk of livestock depredation and predict future scenarios under reduced wild prey populations. An ecological imbalance caused by decline in either leopard or wild prey populations could result in a concomitant increase in crop loss (to wild herbivores) or livestock depredation (by leopards), ensuing greater financial losses to local residents. An understanding of the ecological services and economic benefits conferred by carnivores could help in better valuing and conserving conflict-prone species in shared habitats.

1. Introduction

Interactions between people and large felids are among the most documented human-wildlife associations, globally (Inskip and Zimmermann, 2009; Macdonald et al., 2010). These interactions entail significant financial losses to people, primarily through livestock deaths and investment in mitigation measures (Dickman et al., 2011). Predator-related losses can have consequences for human lives, safety, well-being and livelihoods. Conversely, conflict-induced mortality

remains a critical deterrent for survival of large felids, negatively impacting their populations and consequently, their conservation (Miquelle et al., 2005; Holmern et al., 2007). Governments, wildlife managers and conservationists worldwide spend substantial monetary resources towards offsetting people's losses to large felids, through a suite of preemptive, assistive, or reactive measures (Thirgood et al., 2005; Dickman et al., 2011). Unfortunately, the multifaceted nature of these interactions together with local socio-cultural, economic and political complexities, preclude formulation of successful models that

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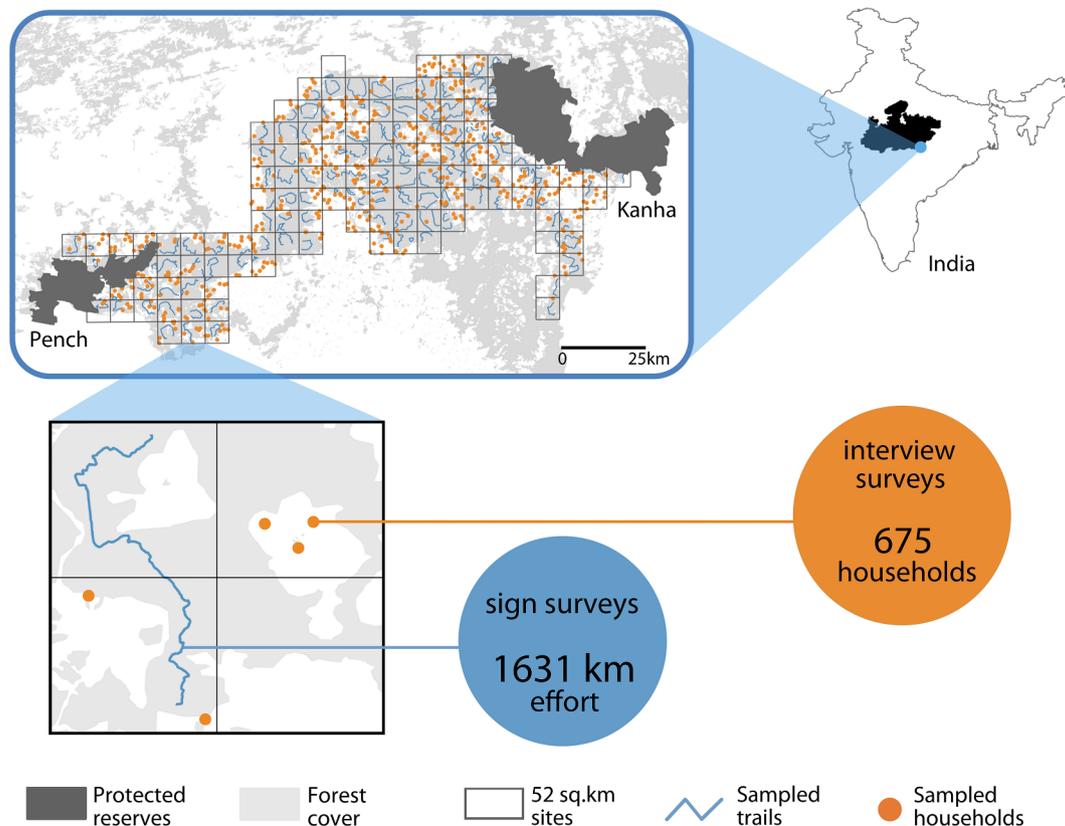


Fig. 1. Study area and design for sign surveys and questionnaire-based interview surveys in the Kanha–Pench forest landscape in 2015–2016. The map shows location of study area in the State of Madhya Pradesh, India, forest cover, protected reserves, grid network with 128 cells of 52 sq. km size each, and, surveyed forest trails and households. The focal grid-cell shows 13 sq. km sub-sites from which villages/households were chosen ensuring maximum spatial coverage for interview surveys.

are applicable across regions (Treves and Karanth, 2003; Lute et al., 2018).

The specific factors that engender adverse interactions between people and feline predators vary by species and locations. Although they attract disproportionate public and media attention, felid attacks on humans (leading to injury or death) are relatively rare (Inskip and Zimmermann, 2009). In shared habitats, domestic livestock can become primary prey for large felids, and depredation ensues monetary losses to people (Baker et al., 2008). Depletion of wild prey populations is presumed to predominantly shape the probability and extent of livestock depredation by large felids, even after controlling for variation in local or regional contexts, husbandry practices or proximity between people and predators (Khorozyan et al., 2015). Given the high economic costs involved in preventing, mitigating or compensating for livestock depredation, a vast majority of human-felid conflicts are in fact latent human–human conflicts that are rooted in different interests/priorities, power imbalances, and historical issues (Peterson et al., 2010; Redpath et al., 2015; Pooley et al., 2017). This interaction between predators–prey–people is commonplace in developing countries, where people’s direct dependence on land and livestock is higher than elsewhere in the world (e.g., Woodroffe et al., 2005; Suryawanshi et al., 2013; Khorozyan et al., 2015).

Leopards are perhaps the most versatile and adaptable large carnivores, found in a wide diversity of habitats around the world (Stein et al., 2016). Despite their large geographic range, leopards still face a host of anthropogenic threats and are extremely vulnerable to local extinctions (Jacobson et al., 2016). Their wide-ranging habits and high overlap with human-dominated areas make them highly prone to conflict; in the past decade alone, > 40 studies from multiple regions have investigated negative interactions between leopards and humans (Jacobson et al., 2016). In India, leopards occupy around 68% of the country’s land area, sharing space with a population of 1.3 billion

people (Karanth et al., 2009). Their presence is more common where anti-poaching laws are enforced and local cultural tolerance is high (Karanth et al., 2010; Athreya et al., 2013, 2015). A series of recent studies have contributed towards our understanding of leopard ecology in human-dominated areas of India, addressing issues like livestock depredation, attacks on humans, human perceptions, management interventions and conservation (Athreya et al., 2011, 2013, 2015; Ghosal et al., 2013; Odden et al., 2014; Ghosal and Kjosavik, 2015; Miller et al., 2016a; Kshetry et al., 2017; Naha et al., 2018).

Domestic livestock are primary prey species for leopards in human-use landscapes of India (Athreya et al., 2014; Kshetry et al., 2018). In some cases, free-ranging dogs serve as principal prey, and livestock depredations or human attacks are incidental when leopards foray into human-use areas in pursuit of dogs (Athreya et al., 2014, 2015). However, leopards—among other carnivores and scavengers—purportedly confer economic benefits to people through a suite of ecosystem services (O’Byrne et al., 2018). We empirically test this claim through parallel assessments of leopard diet, distribution, and livestock/human attacks in a landscape shared by leopards and people in central India. Specifically, we examine (1) how landscape features and spatial patterns of wild prey abundance influence distribution of leopards, (2) determinants of livestock/human attacks by leopards, (3) the role of wild prey in leopard diet, and (4) the extent to which wild prey species can offset leopard depredation on domestic livestock. Based on these observed relationships, we discuss the implications for managing wild prey species, potential economic benefits of sharing space with leopards, and large felid conservation in shared landscapes.

2. Material and methods

2.1. Study area

The Kanha–Pench corridor is among several multi-use forest landscapes of India where human activities and settlements overlap with wildlife habitats. We focused on the reserve forests connecting Kanha (940 sq. km) and Pench (411 sq. km) National Parks, spread across nearly 10,000 sq. km in the State of Madhya Pradesh (Fig. 1). The multi-use forests in the landscape support populations of leopard, tiger (*Panthera tigris*), striped hyena (*Hyaena hyaena*), sloth bear (*Melursus ursinus*), four species of wild canids, several medium- to large-bodied ungulate herbivores and two species of primates. The land cover consists of deciduous forests, degraded forests, and scrublands which are embedded in a mosaic of agricultural lands, and ~ 400 human settlements (DeFries et al., 2010). With large family sizes (average 6 members per household) and low literacy levels (~65% population studied up to class 8 or were illiterate; M. Puri, unpublished results), local residents mostly depend on agriculture and animal husbandry. In addition, people are also involved in collecting non-timber forest products for local markets, small-scale mining, and, wage labor in towns and cities. The forests linking Kanha and Pench reserves harbor resident and transient leopard populations (Dutta et al., 2013). Studies have also documented cases of livestock depredation by leopards in the landscape (Karanth et al., 2012; Miller et al., 2016b).

2.2. Field surveys

We overlaid an array of 128 grid-cells, each of 52 sq. km area across the study region (Fig. 1). The sampling units (grid-cells) were designed based on ecological, logistical, and sampling considerations. The grid-cells were chosen such that each cell was larger than the home range size of leopards, while also allowing us to optimize spatial coverage of the study area and obtain adequate sample sizes. Within each grid-cell (henceforth, site), we surveyed forest roads and trails for indirect signs of leopard presence (scats and tracks), following survey protocols as described in Karanth et al. (2011). While leopards are known to occur in human-use areas like agricultural areas and settlements, we sampled only in forests to maximise sign detections. Detection/non-detection data (1/0) were recorded in every 1-km spatial segment, along with data on signs of prey species (ungulates and primates), free-ranging dogs, and domestic livestock. Only those signs which could be identified unambiguously were recorded to avoid issues of false positive detections (Miller et al., 2011). Field surveys were carried out between October 2015 and January 2016; this corresponded to the dry season in the study landscape and allowed us to maintain uniformity in the detection process. Within the survey period, we assumed that there would be no changes in leopard distribution across the landscape. We expended a total of 1631 km of walk effort; the number of spatial replicates ranged from 2 to 23 across sites, proportional to the forest cover in each site.

We divided each 52 sq. km site into four sub-sites of 13 sq. km each and conducted structured questionnaire surveys with local residents between September 2015 and January 2016. To enable systematic sampling of the vast landscape, we sampled 50% of the sub-sites in a checkerboard pattern (Fig. 1), following the survey design as in Karanth et al. (2012). To ensure adequate spatial coverage, we selected up to four settlements within each sub-site, and in each settlement we interviewed one household. Adult household members were first asked to identify leopards from photographs. Upon correct identification, they were asked if they had seen a leopard in or near their village, and, if livestock depredation or human injury/death due to leopard was experienced by their household or others in the village. In order to obtain accurate information, recall period was restricted to the previous 12 months. We also collected additional information related to family demographics, household dependence on forests, land and livestock

ownership, conflict mitigation measures adopted, and compensation claimed for livestock losses. Data from 13 sq. km sub-sites were pooled to the corresponding 52 sq. km sites so that inferences for the two surveys (indirect sign surveys and questionnaire surveys) could be made at the same spatial scale. A total of 675 households were surveyed and the number of interviews ranged from 1 to 8 within each 52 sq. km site. Madhya Pradesh State Forest Department provided necessary research permits to carry out the study. Sign surveys were completely non-invasive and did not involve capture or handling of animals; animal care and use committee approval was not required. Interviews were completely voluntary and conducted following verbal consent of the local residents.

2.2.1. Leopard distribution and its correlates

We used an occupancy modeling framework for single species, accounting for imperfect detection, to estimate the proportion of the landscape occupied by leopards. Since the surveys were carried out along trails, and the consecutive spatial replicates were likely to be non-independent, we fitted a model that accounts for spatial correlation among detections (Hines et al., 2010). The parameters estimated include ψ – probability of species present in the site, p_t – probability of detection in a replicate conditional on presence in site, θ^0 and θ^1 – probability of replicate-level presence conditional on signs being absent or present in the previous replicate, respectively. We chose ecological and anthropogenic covariates that were most likely to influence leopard occurrence and detection, and used a combination of singular and additive effects of these covariates to model ψ and p_t (Table 1). All covariates were standardized and tested for collinearity prior to analyses; covariate pairs that were highly correlated (Pearson's correlation $r > |0.7|$) were not used in the same model. Analysis was implemented in program PRESENCE v11.9 (Hines, 2006); model selection, ranking and fit was based on Akaike Information Criterion (Burnham and Anderson, 2002).

2.2.2. Patterns of livestock/human attacks

We used a multi-state occupancy modeling framework to examine patterns of leopard attacks on livestock and humans (MacKenzie et al., 2009). The detection matrix for this modeling approach was generated based on information collected through questionnaire surveys, and classified as '0'– non-detection of leopards in the previous 12 months, '1'– detection of leopards only, with no attacks, and '2'– detection of leopard attacks on livestock or people. The corresponding parameters estimated were ψ_p – probability of leopard presence in a site (with no attacks); ψ_a – probability of attack by leopard in a site; p_{pp} – probability of detecting leopard presence in a site; p_{aa} – probability of detecting leopard attack in a site; p_{pa} – probability of detecting only leopard presence but there may be leopard attack in the site. A combination of ground-based and remotely sensed covariates were used to model ψ_a and the number of interviews per site (survey effort) was used as a covariate for estimating detection probability (Table 1). We retained an intercept-only formulation for ψ_p to avoid issues of over-fitting.

2.3. Assessing leopard diet profile

We collected leopard scats during indirect sign surveys for assessing dietary patterns of leopards in the landscape, and to gauge their dependence on wild versus non-wild prey. All scats (deposited post-monsoon and remained intact for ~ one month period) were collected and species identity was confirmed based on presence of secondary signs such as scrape marks and pugmarks. We assigned a unique specimen number to each scat and recorded ancillary information like geographic coordinates, secondary signs, substrate condition, scat condition, and date and time of collection. We washed all scats thoroughly using a mesh-sieve to remove any soil substrate and foreign matter, sun-dried and stored the samples for further examination. We identified prey species primarily on the basis of the hair content in the

Table 1
 Descriptions of ecological, social and landscape covariates used to model probabilities of leopard occupancy (ψ), detectability (p_t), and probabilities of livestock/human attacks by leopards (ψ_a) in the Kamha–Pench forest landscape; *a priori* predictions for the direction of influence, and data sources.

Covariates	Parameters	Covariate description	Direction of influence	Source
Forest cover (fcov)	ψ, p_t	Land-cover vegetation classes collectively considered as ‘forests’. Area under forest cover computed for each site.	+	Indian Institute of Remote Sensing, Govt. of India
Langur abundance (lgr)	ψ	Hanuman langur <i>Semnopithecus entellus</i> is principal arboreal prey for leopards. Relative abundance calculated for each site as ratio of number of replicates with signs of langur to total number of surveyed replicates.	+	Data collected during field surveys
Medium-sized prey abundance (npr)	ψ, p_t	Chital, Axis axis, wild pig <i>Sus scrofa</i> , muntjac <i>Muntiacus muntjak</i> and four-horned antelope <i>Tetracerus quadricornis</i> are principal ungulate prey for leopards. Relative abundance calculated for each site as ratio of number of replicates with signs of any of the four prey species to total number of surveyed replicates.	+	Data collected during field surveys
Anthropogenic disturbance (dist)	ψ, ψ_a, p_t	Areas with high livestock movement indicate disturbed habitats. Frequency of livestock signs calculated for each site as ratio of replicates with livestock signs to total number of surveyed replicates.	- for occupancy; + / - for depredation	Data collected during field surveys
Settlement size (sett)	ψ, ψ_a	Total area under human settlements calculated for each site.	- for occupancy; + / - for depredation	Indian Institute of Remote Sensing, Govt. of India
Cattle holding (catl)	ψ_a	Average number of cattle per household calculated for each site.	+	Questionnaire surveys of households
Goat holding (goat)	ψ_a	Average number of goats per household calculated for each site.	+	Questionnaire surveys of households
Dog abundance (dogs)	ψ, ψ_a	Relative abundance calculated for each site as ratio of number of replicates with signs of dogs to total number of surveyed replicates.	+	Data collected during field surveys
Occupancy (occp)	ψ_a	Probability of leopard occurrence for each site.	+ / -	Estimates derived from distribution analysis

scats. We also found bone fragments, hooves of ungulates, paw skin of primates, quills, claws, and teeth in scat samples, which allowed for reliable species identification during physical examination. Scat samples were processed following methods described in Mukherjee et al. (1994), Karanth and Sunquist (1995) and Athreya et al. (2014); prey species were identified based on cuticle and medullary patterns (Bahuguna, 2010), and reference slides of hair samples available at the Centre for Wildlife Studies, Bengaluru. For each wild and non-wild prey species, we first calculated the frequency of occurrence in scats. Average weights for prey species were derived from Hayward et al. (2006). We then applied the non-linear correction factor described in Chakrabarti et al. (2016) to calculate relative prey biomass consumed and the relative number of prey individuals consumed by leopards.

2.4. Alternate scenarios of prey availability

We considered three hypothetical alternate scenarios for leopard prey consumption whereby wild prey biomass consumed was reduced by 25%, 50% and 75%. The three cases represent plausible future situations where prey populations would decline because of habitat loss, subsistence hunting, or, lethal control (culling) by wildlife managers to reduce crop damage by wild herbivores. Our aim was to envision tentative conditions where leopards would continue to persist at current population levels, but wild prey numbers would decline. We therefore assume that (1) leopard population does not change with decline in prey population, and (2) leopard diet would shift to domestic livestock. We retained the total biomass consumed by leopards to be constant and proportionally increased the consumption of domestic livestock and free-ranging dogs (Table S1). This allowed us to generate relative numbers of wild and non-wild prey species consumed under the three alternate scenarios.

3. Results

3.1. Prey abundance and land cover determine leopard distribution

Leopard signs were detected in 60 of the 128 grid-cells. The best-fit model for detectability indicated that detection of signs was negatively influenced by anthropogenic disturbance [β (SE) = -1.04 (0.76); Table S1]. Since a single model did not receive full support from the data (based on AIC weights and ranks), we model-averaged across all candidate covariate models to obtain the final estimate of occupancy (ψ ; Table S2). Average probability of leopard occupancy in the landscape was ψ (SE) = 0.8 (0.01), with relatively high replicate-level detectability p_t (SE) = 0.58 (0.02). We found that forest cover and prey abundance had a positive effect on leopard occurrence, while the size of human settlements had a negative influence (Fig. 2, Table 2).

3.2. Socio-ecological factors influence livestock/human attacks

Among the 675 residents interviewed, 89% were able to correctly identify the leopard from photographs. Average cattle holding was 3.9 cattle per household and average goat holding was 1.5 goats per household. Livestock/human attacks were reported from 71 sites (during the previous 12 months). As with the distribution analysis in the previous step, no single model received full support from the data, and we averaged across all candidate models (Table S3). Average probability of leopard occurrence with no attacks was ψ_p (SE) = 0.08 (0.006) and probability of attacks was ψ_a (SE) = 0.84 (0.01). Site-wise estimates of attack probabilities are mapped in Fig. 3. We found that site level cattle-holding and leopard occupancy (estimated in the previous step) positively influenced probabilities of attacks, while anthropogenic disturbance had a negative effect (Table 3).

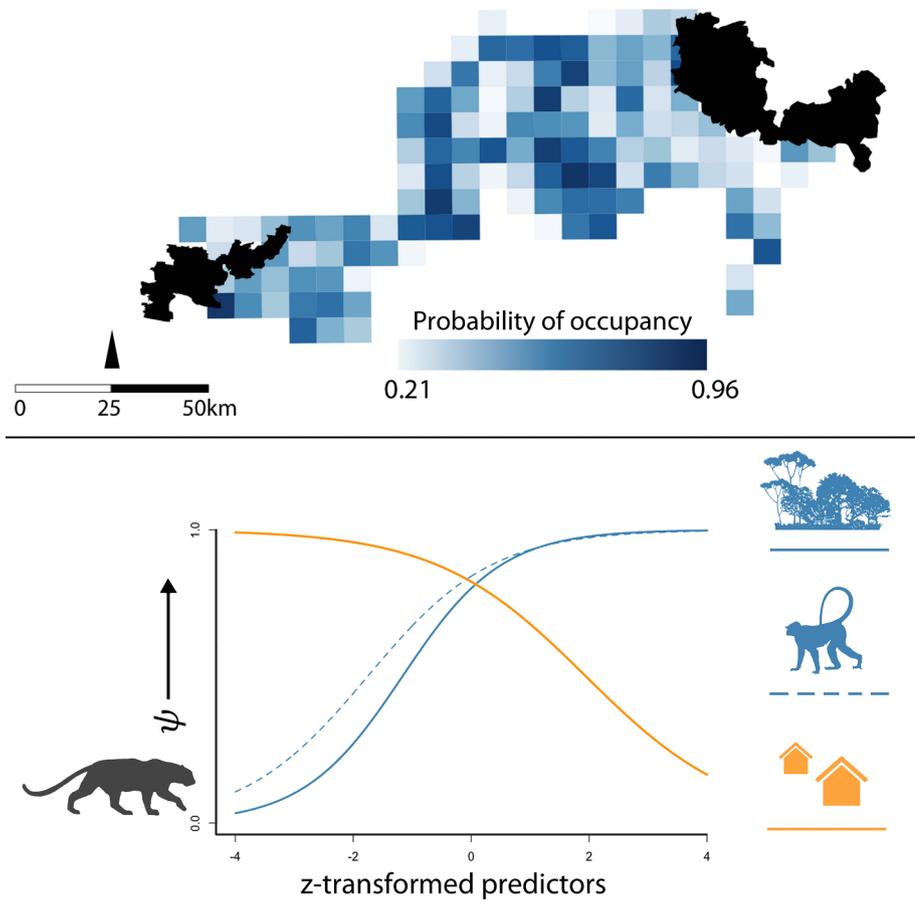


Fig. 2. Top panel: Site-wise estimates of leopard occupancy probabilities based on sign surveys across 128 sites in the Kanha–Pench forest landscape, 2015–2016. Bottom panel: Leopard occupancy shown as a function of forest cover, langur abundance and area of human settlements. Estimates of occupancy for the three trend lines are based on models with singular effects of the three covariates.

3.3. Wild prey dominates leopard diet

A total of 253 leopard scats were analysed to examine leopard diet composition. In all, 16 prey species were consumed by leopards, including human remains which were found in one scat sample. Hanuman langur (*Semnopithecus entellus*) was the most frequently encountered species in the scats, with the highest number of individuals consumed. However, the highest relative biomass consumed was that of chital (*Axis axis*) (Table 4). Nearly 90% of leopard diet was composed of primates and wild ungulate herbivores; non-wild prey (domestic livestock and dogs) accounted for less than 3% of total biomass consumed by leopards. Results from diet analysis somewhat mirrored results from distribution patterns, where wild prey (medium-sized ungulates and primates) had a positive effect on leopard occurrence (Fig. 4).

3.4. Alternate ecological scenario

Based on the three hypothetical scenarios that were considered, a decline in wild prey abundance (and therefore, biomass in leopard diet) resulted in corresponding increase in relative biomass of domestic livestock and free-ranging dogs in leopard diet, and changes in the relative numbers for all prey species consumed (Fig. 5; Table S4). With a 25% decrease in wild prey biomass (to 68% of the diet), the contribution of domestic livestock to leopard diet increased from 3% to 21%. At half the current wild prey levels, domestic livestock would constitute nearly 40% of leopard diet. Finally, if wild prey biomass decreased to one-fourth the current estimate, 60% of predicted leopard diet comprised of cattle and goats. In terms of relative numbers consumed, the estimate for cattle and goats increased from 0.1 and 0.2 (current) to 4 and 9 individuals, signifying a proportional increase of 39% and 44%, respectively.

Table 2

Estimated β -coefficients (standard errors in parentheses) for covariates influencing probabilities of leopard occupancy (ψ) in the Kanha–Pench forest landscape, 2015–2016. Here, θ^0 and θ^1 are spatial dependence parameters and p_i is the probability of detection. Values indicate magnitude and direction of covariate influence on leopard occupancy probability based on sign surveys. Estimates are from the top five models ($\Delta AIC < 2$).

Model	fcov	mpr	lgr	dist	sett	dogs
ψ (fcov), $\theta^0(\cdot)$, $\theta^1(\cdot)$, $p_i(\text{dist})$	1.19 (0.84)	–	–	–	–	–
ψ (fcov + mpr), $\theta^0(\cdot)$, $\theta^1(\cdot)$, $p_i(\text{dist})$	4.81 (3.29)	0.42 (0.90)	–	–	–	–
ψ (lgr), $\theta^0(\cdot)$, $\theta^1(\cdot)$, $p_i(\text{dist})$	–	–	0.95 (0.51)	–	–	–
ψ (fcov + dist), $\theta^0(\cdot)$, $\theta^1(\cdot)$, $p_i(\text{dist})$	5.66 (4.03)	–	–	–0.19 (1.17)	–	–
ψ (lgr + sett), $\theta^0(\cdot)$, $\theta^1(\cdot)$, $p_i(\text{dist})$	–	–	0.90 (0.60)	–	–0.61 (0.51)	–
ψ (fcov + dogs), $\theta^0(\cdot)$, $\theta^1(\cdot)$, $p_i(\text{dist})$	1.24 (0.75)	–	–	–	–	0.48 (0.84)

fcov – forest cover; mpr – abundance of medium-sized ungulate prey; lgr – abundance of langur; dist – anthropogenic disturbance; sett – size of human settlements; dogs – abundance of free-ranging dogs.

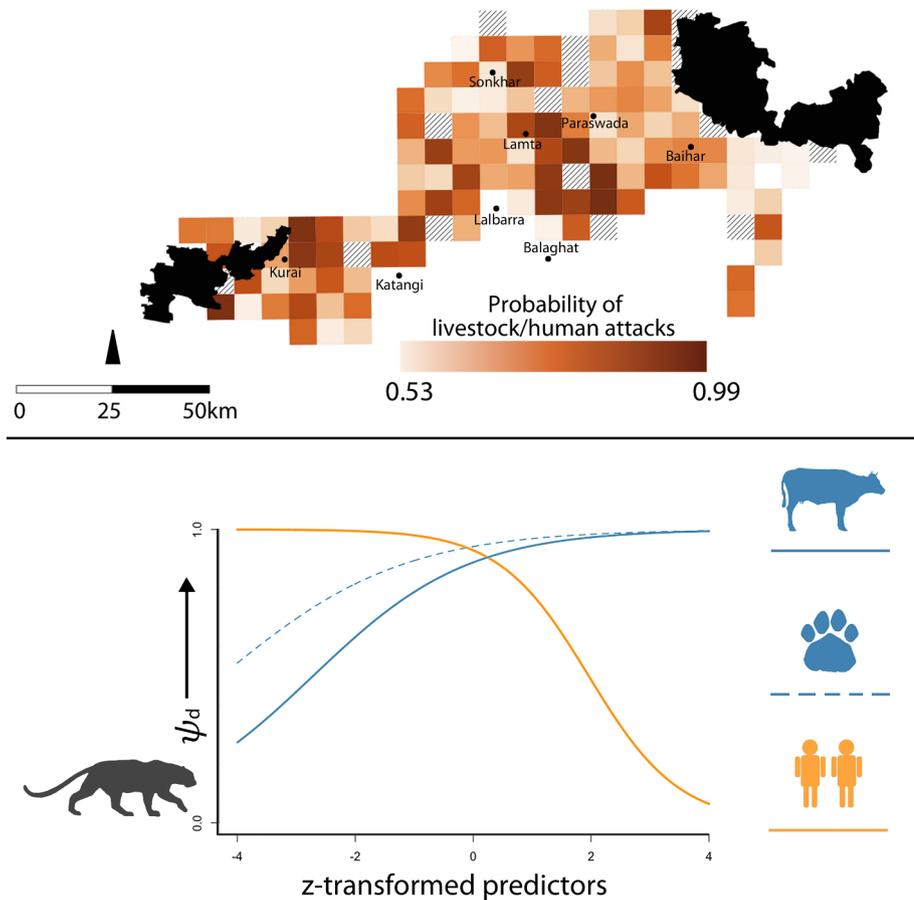


Fig. 3. Top panel: Site-wise estimates of probabilities of livestock/human attacks by leopards. Estimates are based on interview surveys across 112 sites in the Kanha–Pench forest landscape, 2015–2016; 16 sites that did not contain villages or households, or those that were not sampled because of survey design restrictions have been clipped out. Points denote locations of major towns. Bottom panel: Probability of livestock/human attacks by leopards shown as a function of average cattle-holding by locals, leopard occupancy (based on sign surveys), and anthropogenic disturbance. Estimates of attack probabilities for the three trend lines are based on models with singular effects of the three covariates.

4. Discussion

Human-carnivore interactions are complex, and have ecological, social, economic, and political implications. Examining interdisciplinarity in studies of human-lion interactions, [Montgomery et al. \(2018\)](#) highlight five essential components for assessing and understanding people-prey-predator systems. Our study adheres to these components in that we examined (1) the carnivore dimension – diet profile and ecological attributes of leopard presence, (2) livestock dimension – spatial patterns of livestock abundance/availability, both, within forests and household-level ownership, (3) wild prey dimension – relative abundance of wild prey vis-à-vis distribution of leopards (4) human dimension – losses to local residents in terms of livestock depredation and attacks on humans, and (5) environmental dimension – landscape features that influence leopard distribution and depredation patterns.

Table 3

Estimated β -coefficients (standard errors in parentheses) for covariates influencing probabilities of livestock/human attacks by leopards (ψ_a) in the Kanha–Pench forest landscape, 2015–2016. Here, ψ_p is the probability of leopard presence with no human/livestock attacks, and p_{pp} , p_{pa} and p_{aa} are detection parameters. Values presented indicate the magnitude and direction covariate influence, based on questionnaire surveys. Estimates are from the top five models (based on AIC ranks and weights).

Model	dist	catl	occp	goat	dogs
$\psi_p(\cdot), \psi_a(\text{dist} + \text{catl}), p_{pp}(\text{ints}), p_{pa}(\cdot), p_{aa}(\text{ints})$	-1.55 (0.94)	1.38 (0.82)	-	-	-
$\psi_p(\cdot), \psi_a(\text{dist} + \text{catl} + \text{occp}), p_{pp}(\text{ints}), p_{pa}(\cdot), p_{aa}(\text{ints})$	-1.60 (1.05)	1.68 (1.02)	0.39 (0.37)	-	-
$\psi_p(\cdot), \psi_a(\text{dist} + \text{catl} + \text{goat}), p_{pp}(\text{ints}), p_{pa}(\cdot), p_{aa}(\text{ints})$	-1.62 (1.02)	1.63 (0.90)	-	-0.36 (0.42)	-
$\psi_p(\cdot), \psi_a(\text{dist}), p_{pp}(\text{ints}), p_{pa}(\cdot), p_{aa}(\text{ints})$	-1.31 (0.92)	-	-	-	-
$\psi_p(\cdot), \psi_a(\text{dist} + \text{catl} + \text{occp} + \text{goat} + \text{dogs}), p_{pp}(\text{ints}), p_{pa}(\cdot), p_{aa}(\text{ints})$	-1.58 (1.06)	1.67 (1.03)	0.39 (0.38)	-	-0.02 (0.28)

dist – anthropogenic disturbance; catl – cattle-holding by local residents; occp – leopard occupancy; goat – goat-holding by local residents; dogs – abundance of free-ranging dogs; ints – number of interviews per site.

4.1. Role of wild prey in leopard diet

Large felids generally prefer wild prey to domestic livestock, resorting to the latter only when wild prey populations decline or become otherwise unavailable. In Botswana, for example, [Valeix et al. \(2012\)](#) found that lions with access to livestock still preferentially preyed on wild ungulates, except in the migratory season when wild prey were not locally available. Similarly, leopards in Iran showed different levels of avoidance towards large and medium-sized domestic stock, given adequate availability of wild prey ([Ghoddousi et al., 2016](#)). But carnivore-wild prey-livestock interplay can be far more complex. For instance, snow leopard attacks on livestock in the Trans-Himalayas intensified with increase in wild prey densities ([Suryawanshi et al., 2017](#)). In such cases, high abundance of wild prey may not necessarily subsidize the share of livestock in carnivore diet. While there may be location-specific peculiarities, or individual-level behavioral nuances

Table 4

Diet profile of leopards based on analysis of scats ($n = 253$) in the Kanha–Pench forest landscape, 2015–2016. Frequency of prey occurrence (A), average prey weight (X; calculated as $\frac{3}{4}$ weight of adult females for each prey species, based on Hayward et al., 2006), prey biomass consumed (Y; derived using correction factor described in Chakrabarti et al., 2016), relative biomass consumed by leopards (D) and relative number of individuals consumed (E).

Species	A (%)	X (kg)	Y (kg/scat)	D (%)	E
Hanuman langur <i>Semnopithecus entellus</i>	34.87	7	1.04	25.72	41.17
Chital <i>Axis axis</i>	23.37	30	1.86	30.77	11.49
Nilgai <i>Boselaphus tragocamelus</i>	8.81	135	2.17	13.54	1.12
Muntjac <i>Muntiacus muntjak</i>	7.28	14	1.41	7.26	5.81
Black-naped hare <i>Lepus nigricollis</i>	5.75	1.5	0.63	2.58	19.29
Wild pig <i>Sus scrofa</i>	5.36	47	2.05	7.79	1.86
Civet spp.	4.21	3	0.76	2.26	8.45
Rhesus macaque <i>Macaca radiata</i>	3.45	6.5	1.01	2.47	4.25
Mongoose spp.	1.53	2	0.68	0.73	4.12
Indian porcupine <i>Hystrix indica</i>	1.15	8	1.1	0.9	1.26
Sambar <i>Rusa unicolor</i>	1.15	200	2.17	1.77	0.1
Domestic cattle <i>Bos taurus</i>	1.15	200	2.17	1.77	0.1
Blackbuck <i>Antelope cervicapra</i>	0.77	28	1.82	0.99	0.4
Domestic dog <i>Canis familiaris</i>	0.38	18	1.56	0.42	0.26
Goat <i>Capra aegagrus</i>	0.38	25	1.76	0.48	0.21
Human <i>Homo sapiens</i>	0.38	60	2.11	0.57	0.11

(e.g., see Blecha et al., 2018 for pumas), the aforementioned preference for wild prey appears to be common for large felids across the world (Khorozyan et al., 2015). To our knowledge, only two studies in India have examined leopard diet outside protected reserves (Athreya et al., 2014; Kshetry et al., 2018). In both cases, leopards mostly consumed non-wild prey, likely because of very low wild prey densities – below a critical threshold (see Khorozyan et al., 2015). On the contrary, we found that leopards predominantly consumed wild prey (97% of consumed biomass) despite widespread presence and high densities of domestic livestock in the region. This could perhaps be attributed to higher wild prey availability in our study system in comparison to other human-dominated landscapes.

Interestingly, the langur – an arboreal prey species – constituted a large part of leopard diet (26% of consumed biomass), although the region supports several medium-sized ungulate species (preferred by leopards elsewhere across their range; Hayward et al., 2006). We suspect this is because the Kanha–Pench forest landscape is a multi-carnivore system, where tiger, dhole and wolf may compete with leopards for ungulate prey. Being the only semi-arboreal carnivore in the guild, leopards have perhaps fully exploited this exclusive niche. Similar

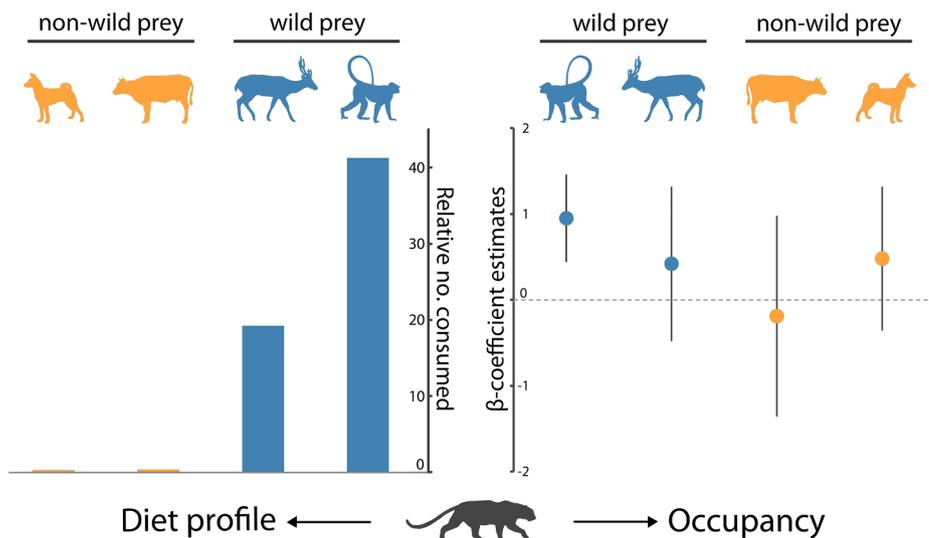


Fig. 4. Comparison between relative number of prey individuals consumed by leopards (based on diet analysis) and covariate effects of prey (means and corresponding standard errors) on spatial probabilities of leopard occupancy. Wild prey includes langur and medium-sized ungulate herbivores (chital, muntjac and wild pig for diet; chital, muntjac, wild pig and four-horned antelope for occupancy). Domestic prey includes livestock (cattle and goat) and free-ranging dogs.

segregation in dietary niche has been documented from other multi-carnivore systems with sub-optimal prey densities, where socially dominant co-predators compel leopards into changing their prey preference (Bhattarai and Kindlmann, 2012; Thinley et al., 2018). We do submit however that our assessment includes a key caveat – we identified leopard scats in the field based on morphological features and secondary signs. Studies that have compared ocular versus genetic identification of species from scats have documented a range of error rates between the two methods (see Morin et al., 2016). Most (> 90%) scats in our study were not fresh enough to allow for application of genetic analysis. Using genetics for species identification may have minimized (but not eliminated) these error rates. While we took extreme caution in conservatively assigning species identification in the field, we do not discount potential misidentification of scats, albeit in very few cases.

4.2. Consequences of land cover change and prey depletion for leopards

Vegetation cover is an important ecological requirement for large carnivores, particularly for ambush predators like leopards (Karanth and Sunquist, 2000; Jacobson et al., 2016). In spite of their versatility, leopards do need either natural vegetation cover (Athreya et al., 2015), or, structurally similar crop cover (Athreya et al., 2013). Our results support previous studies in that forest cover positively influenced leopard presence in our study area. Occupancy probability was also lower in sites with larger settlements, indicating that at the landscape scale, leopards still avoided human presence. Results from diet analysis mirrored spatial determinants of leopard distribution to a considerable extent. Livestock activity did not influence leopard presence, nor did cattle/goat appear to be common prey in leopard diet. In some regions of India, free-ranging dogs are primary prey species for leopards (Athreya et al., 2014, 2015). There was some spatial overlap between leopards and dogs in our study site, but this did not translate to appreciable levels of dog depredation by leopards (Fig. 4). Reduction in forest cover could reduce wild prey populations, or, increase chances of them foraging into farmlands to forage on cultivated crops. Considered together, our results indicate that either scenario could bear negative consequences for leopards. Concurrent degradation of forests in the Kanha–Pench landscape for commercial use and infrastructure development (Habib et al., 2016) may severely distort the balance between predators, wild prey and domestic stock.

4.3. Social attributes impact livestock/human attacks by leopards

Spatial risk maps of livestock depredation can be important

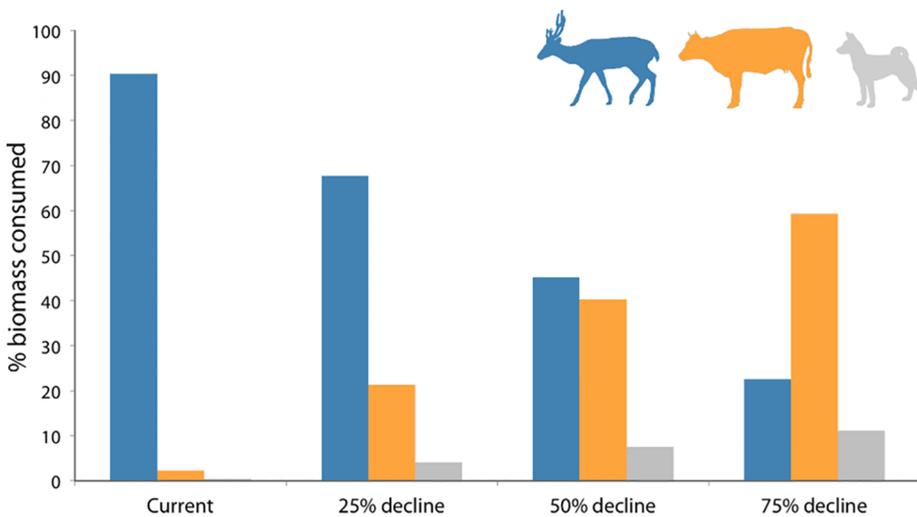


Fig. 5. Relative biomass of prey consumed by leopards under four alternate scenarios. Current numbers are based on results from this study. Alternate hypothetical cases represent scenarios where wild prey biomass consumed by leopards reduces by 25%, 50% and 75%, and is substituted by non-wild prey. Wild prey here includes hanuman langur, chital, nilgai, muntjac, wild pig, rhesus macaque, sambar and blackbuck; non-wild prey includes domestic livestock (cattle and goats), and free-ranging dogs.

resources for determining areas to allocate funds and implementing mitigation measures (Treves and Rabenhorst, 2017). Our treatment of spatial risk differs from most studies in certain aspects. First, we make clear distinction between perceived and realized conflict between humans and leopards (Suryawanshi et al., 2013; Miller et al., 2016). The questions posed during interview surveys did not directly pertain to depredation by leopards. Rather, we recorded total livestock mortalities and their causal factors, and used only leopard-related losses in our analysis. Second, we delineate leopard presence in human areas as probabilistic states of ‘presence with no attacks’ (8% of sites) and ‘presence with attacks’ (84% of sites), thereby accounting for plausible non-negative interactions between humans and leopards. Third, we recognize that surveys of human-carnivore interactions based on data generated opportunistically or under participatory basis include biases arising from unequal sampling effort. Data from government or management records also entail issues of underreporting, and hence, potential non-detection of depredation events (Karanth et al., 2012; Goswami et al., 2015). Such concerns are important because they could alter interpretation of observed depredation patterns or trends. Our application of occupancy models addresses these biases to produce a more realistic spatial map of depredation risks.

Leopard distribution (based on sign surveys) was positively associated with depredation patterns (based on interview surveys), lending certain credence to people’s self-reported data on leopard presence. Depredation of livestock by large felids could potentially be influenced by a combination of landscape features and livestock holding/management factors (Michalski et al., 2006). Livestock presence and activity within forest habitats can be a source of anthropogenic disturbance for large carnivores (Karanth et al., 2011; Srivathsa et al., 2014; Puri et al., 2015). Not only do livestock directly compete with wild prey for forage, but they also reduce the overall available habitat for carnivore presence and movement (Soofi et al., 2018). Sites with high risk of attacks were those with low livestock activity, suggesting that attacks generally happened in relatively undisturbed sites, or in smaller settlements amidst fragmented forests. This corroborates observations in Nepal, where forest fragmentation was a key determinant of human-leopard conflict (Acharya et al., 2016). We also found that size of cattle-holdings by local residents determined leopard attacks, i.e., depredation was higher in sites with larger holdings. Overall probability of livestock attack by leopards was high ($\psi_a = 0.84$), but depredation-related loss accounted for less than 1% of total livestock losses (57% was attributed to disease, 25% to predation by other carnivores, 12% due to injury/accident/old age; M. Puri unpublished results). Based on our findings, we posit that (1) building more secure shelters could further reduce livestock depredation by leopards, (2)

easing the compensation process would allow more people to avail government assistance in case of depredation events, and (3) providing general veterinary care in depredation-prone villages would reduce the overall livestock losses, and thereby benefit local communities.

4.4. Economic benefits of sharing space with leopards

Wild herbivores can inflict severe damage to crops. Economic loss associated with crop damage is estimated to range between 99 and 566 USD per household annually across various locations in India (Karanth and Surendra, 2018). From 2010 to 2012, the government of Madhya Pradesh provided an annual average compensation of over 56,400 USD for a total of 3302 cases of crop loss (Karanth et al., 2018). In our study landscape, primates (langur and macaque), and medium- and large-sized ungulates are responsible for most crop-raiding incidents (Karanth et al., 2012). In some regions, the Indian government is exploring lethal methods such as culling of wild herbivores to alleviate financial losses from crop damage. In the absence of quantitative, reliable and periodic estimates of herbivore populations in human-use landscapes, such policies can be detrimental to the ecological balance in shared spaces. Leopards are highly adaptable and will continue to persist in disturbed or human-modified landscapes. But unscientific population control of wild herbivores may coerce leopards into resorting to domestic animals as primary prey (Fig. 5). Although leopard-related deaths account for a very small percentage of total livestock deaths annually, people still incur a loss of 50–750 USD per individual animal, depending on the type and breed of livestock. From 2010 to 2012, the State government spent over 285,000 USD on average per year for a total of 11,814 reported cases of livestock depredation (Karanth et al., 2018). Maintaining current leopard and wild prey populations can therefore confer economic benefits by offsetting financial losses of crop-raiding (by ungulates) and livestock depredation (by leopards). It is important to note, however, that the number of crop loss cases here represents only a small proportion of the actual cases. Most crop loss incidents remain unreported due to procedural complexities and insufficient monetary compensation. We also recorded seven cases of attacks on humans (four of which led to human deaths). Management efforts should therefore be targeted towards ensuring safety of people’s lives, prompt dispensation of State-mandated monetary compensation in response to human injury/death, and thereby foster non-negative attitudes towards carnivore conservation.

4.5. Conclusion

Large carnivores across the world provide a range of ecosystem

services that are beneficial to humans (O'Bryan et al., 2018). But the potential economic benefits of conserving large carnivores continue to remain undervalued. For example, Prowse et al. (2015) predict that top-down predatory control imposed by dingoes could mediate the balance between kangaroo (wild prey) and domestic livestock, thereby benefiting pastoralists. Similarly, mesocarnivores in South Africa perhaps benefit agriculturists through biological control of rodent pests (Williams et al., 2018). Leopards may be tolerated in many places within India, but are also among the most persecuted large carnivores. Management inaction, or uninformed interventions (such as physical removals and translocations; Athreya et al., 2011), are common because the ecological role of leopards in shared spaces is not fully understood. Our study shows that leopards can persist in such landscapes with relatively little damage to people's property, so long as adequate cover and wild ungulate/arboreal prey are available. Management of leopards, and large carnivores in general, would benefit from understanding the complex ecological and economic services they provide, particularly accounting for their adaptations in altered trophic structures and in shared, human-modified landscapes.

Author contributions

MP and AS conceived the ideas; MP, AS, KKK and NSK designed the survey methodology; MP and IP collected the data; MP and AS analysed the data; MP and AS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data accessibility

The raw data supporting the conclusions of this manuscript has been made available at [figshare.com](https://doi.org/10.6084/m9.figshare.7235036). The DOI for the data is <https://doi.org/10.6084/m9.figshare.7235036>.

Appendix A. Supplementary data

Tables S1, S2 and S3 show comparisons of models used for estimating detection probability, leopard occupancy probability, and livestock/human attack probability, respectively. Table S4 contains estimates of prey biomass consumed by leopards in four alternate scenarios of prey availability. Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2019.105931>.

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