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Change in snow leopard predation on livestock after revival of wild prey in the Trans-Himalaya

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Human–wildlife conflict arising from livestock-losses to large carnivores is an important challenge faced by conservation. Theory of prey–predator interactions suggests that revival of wild prey populations can reduce predator's dependence on livestock in multiple-use landscapes. We explore whether 10-years of conservation efforts to revive wild prey could reduce snow leopard's *Panthera uncia* consumption of livestock in the coupled human-and-natural Trans-Himalayan ecosystem of northern India. Starting in 2001, concerted conservation efforts at one site (intervention) attempted recovery of wild-prey populations by creating livestock-free reserves, accompanied with other incentives (e.g. insurance, vigilant herding). Another site, 50 km away, was monitored as status quo without any interventions. Prey remains in snow leopard scats were examined periodically at five-year intervals between 2002 and 2012 to determine any temporal shift in diet at both sites to evaluate the effectiveness of conservation interventions. Consumption of livestock increased at the status quo site, while it decreased at the intervention-site. At the intervention-site, livestock-consumption reduced during 2002–2007 (by 17%, $p = 0.06$); this effect was sustained during the next five-year interval, and it was accompanied by a persistent increase in wild prey populations. Here we also noted increased predator populations, likely due to immigration into the study area. Despite the increase in the predator population, there was no increase in livestock-consumption. In contrast, under status quo, dependence on livestock increased during both five-year intervals (by 7%, $p = 0.08$, and by 16%, $p = 0.01$, respectively). These contrasts between the trajectories of the two sites suggest that livestock-loss can potentially be reduced through the revival of wild prey. Further, accommodating counter-factual scenarios may be an important step to infer whether conservation efforts achieve their targets, or not.

Keywords: arid ecosystems, diet analysis, human–wildlife conflict, *Panthera*, predator, rangeland

Mitigation of human–wildlife conflicts has emerged as an important dimension of global conservation efforts. Conflicts can arise when wild animals have a negative impact on goods and services valued by humans, and are especially relevant for large-bodied carnivores which kill livestock (Weber and Rabinowitz 1996, Redpath et al. 2013, Eklund et al. 2017, Suryawanshi et al. 2017, Bagchi 2019, Krafte Holland et al. 2018). Predator–prey interactions at this interface between humans and carnivores are particularly damaging for regions with under-developed economies (Singh and Bagchi 2013), and there is strong resistance toward predators even in regions with developed economies (Berger 2006). Such predator–prey interactions are of great concern throughout central Asian highlands where pastoralism is the predominant land-use (Mishra et al. 2010).

In the Trans-Himalaya of northern India, predator–prey interactions involve a feedback between snow leopards *Panthera uncia*, status of the wild prey and livestock production that supports human livelihoods (Fig. 1). High livestock densities restrict the distribution and abundance of wild ungulates, such as ibex *Capra sibirica* (Bagchi et al. 2004) and bharal *Pseudois nayaur* (Mishra et al. 2004), which are important prey throughout much of the snow leopard's range in Central Asia (Lyngdoh et al. 2014). Negative effects of livestock on wild prey arise from forage competition (Bagchi et al. 2004, Mishra et al. 2004). This has demographic consequences, since young:female ratio for wild ungulates is nearly halved under high livestock density when compared against areas with low or moderate livestock density (Mishra et al. 2004). Competition from livestock ultimately leads to poorer demographic performance in wild ungulates – lower birth rate, lower survival of newborn or both (Mishra et al. 2004).

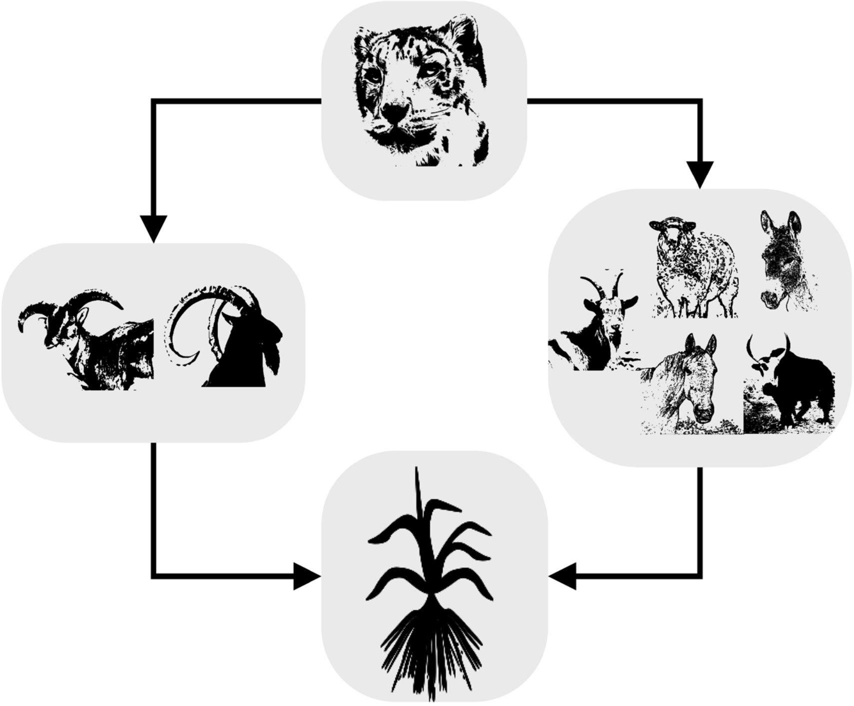

Figure 1. Conceptual diagram of the interactions between predator (snow leopard), wild prey (bharal and ibex), livestock (goat, sheep, horse, donkey and yak–cattle) and forage in Spiti region of Trans-Himalaya. Under high livestock density, forage-competition can limit the distribution and abundance of wild prey. This, in turn, increases snow leopards' dependence on livestock, and initiates human–wildlife conflict.

Efforts to reduce livestock-loss from carnivores have frequently included measures such as improved husbandry, strengthening corrals or pens and financial compensation (Namgail et al. 2007a, Lee et al. 2017). There are historical precedents that attempted to resolve the conflict by eradicating carnivores (Treves et al. 2016, Krafte Holland et al. 2018). Bounties on wolf *Canis lupus* in North America and Europe, Tasmanian tiger *Thylacinus cynocephalus* in Australia, wild dog *Lycaon pictus* in Africa, are examples of such antithesis for conservation (Paddle 2002). In many contemporary scenarios, predators are controlled at sites designated for livestock-production, but they receive protection elsewhere (Reynolds and Tapper 1996, Treves et al. 2016). Contemporary interventions also include livestock protection and financial compensation; these may reduce livestock loss and influence human perceptions of the conflict although they may not necessarily overcome the problem of predator's dependence on livestock (Mishra et al. 2003). Attempts at the recovery of wild prey can reduce livestock-loss by addressing the underlying prey–predator interactions (Mishra et al. 2003, 2010, 2016). These expectations are grounded in the theory of prey–predator interactions involving spatial patchiness, and source–sink dynamics that yield meta-populations (Bagchi 2019), as well as potential for apparent competition between prey-types (Holt 1977). But, there is scant evidence to assess their effectiveness (Treves et al. 2016, Eklund et al. 2017, Krafte Holland et al. 2018).

Here we explore whether 10-years of conservation efforts to revive wild prey populations (Mishra et al. 2003, 2010, 2016, 2017) could also reduce snow leopard's dependence on livestock in the Trans-Himalayan ecosystem. One key aspect was establishing livestock-free reserves to facilitate the recovery of wild prey (Mishra et al. 2016). Although the livestock-free reserves made up a small part of the overall landscape, they were expected to improve forage availability for the wild prey and assist over-wintering survival of newborns, eventually yielding a positive numerical response in prey populations and consequently reduce predator's dependence on livestock (Mishra et al. 2016). We explore these anticipated outcomes of revival of wild prey in the Trans-Himalaya, by documenting change in carnivore diets at five-year intervals between 2002 and 2012.

We compare trends at two matched-paired study sites (Table 1) – one where conservation efforts were implemented (i.e. intervention site; Kibber) and another site without any intervention (i.e. status quo site; Pin Valley). This study design where an intervention is paired with status quo affords an important opportunity to evaluate the effectiveness of conservation efforts (Ferraro and Pattanayak 2006, Ferraro 2009, Eklund et al. 2017). Quantitative empirical evidence of the impact of conservation interventions, over a wide range of biodiversity issues, is alleged to be weak when compared to other fields of societal importance (e.g. health, education, poverty, etc.). A major lacuna in conservation practice has been a historical inability to fully address counter-factual scenarios. As a consequence, it remains difficult to assess the outcomes from conservation efforts, as one cannot determine whether 'conservation interventions work better than no interventions at all' (Ferraro and Pattanayak 2006, Ferraro 2009, Eklund et al. 2017). Therefore, despite many studies, there is little evidence that conservation interventions can actually reduce livestock-loss from carnivores (Eklund et al. 2017). Empirical contrasts between the results of conservation actions against an appropriate status quo sce-

Table 1. Comparison of various features between the two study sites, Pin Valley and Kibber which served as status quo and intervention-site, respectively.

Description	Pin Valley	Kibber
Location	32°N, 78°E	32.5°N, 79°E
Altitude* (m, mean ± SD)	4590 ± 518	4741 ± 459
Altitude* (m, min., median, max.)	Min: 4183, Median: 4620, Max: 5001	Min: 4336, Median: 4679, Max: 4997
Highest nearby peak	Kangla Tarbo 1 (6315 m)	Cho Cho Kang Nilda (6303 m)
Vegetated area*	58.9% of pixels	56.2% of pixels
Precipitation* (mm year^{-1}, mean ± SD)	317 ± 42	237 ± 17
Max temperature* (°C, annual mean ± SD)	8.4 ± 0.4	6.8 ± 0.4
Min temperature* (°C, annual mean ± SD)	−3.7 ± 0.3	−5.6 ± 0.3
No. of settlements	11	6
No. of large settlements	4	3
Largest settlement	70 households	70 households
Smallest settlement	1 household	2 households
Estimated human population	600–800	700–800
Herded livestock	cattle, yak–cattle hybrids, goat, sheep, donkey	cattle, yak–cattle hybrids, goat, sheep, donkey
Free ranging livestock	yak, horse	yak, horse

* Altitude information is from NASA Aster-GDEM database (<www.asterweb.jpl.nasa.gov>); vegetated area calculated from MODIS 250 m resolution NDVI data for 2002–2012 (<www.modis.gsfc.nasa.gov>); precipitation information from CRU database of University of East Anglia (<www.cru.uea.ac.uk/>).

nario are important (Kleiman et al. 2000, Pullin and Knight 2009), as these can highlight whether the revival of natural prey can ameliorate livestock losses.

Methods

Study design

Snow leopard is the major predator in Spiti region of Indian Trans-Himalaya, where two areas are important for its conservation (see map in Supplementary material Appendix 1 Fig. A1) – Pin Valley National Park, and Kibber Wildlife Sanctuary (Mishra et al. 2003, 2016, 2017, Bagchi and Mishra 2006, Ghoshal et al. 2019). These served as status quo and intervention sites, respectively. In Kibber (intervention-site), a 5 km^2 area was strategically designated free of livestock-use in 2001, and this was subsequently expanded to include another 15 km^2 by 2004. No such set-asides were created in Pin Valley, and it remained as status quo.

Though livestock-free reserves were smaller than typical home-ranges of the predator, they were expected to have a positive influence on the prey populations (Mishra et al. 2003, 2010). Since set-asides were strategically located in regions known to be important wintering and calving grounds for bharal, they initiated a positive response in wild prey population size (Mishra et al. 2016). The reserves were expected to reduce the intensity of forage competition from livestock, and improve demographic performance of wild prey by facilitating survival of newborns, with eventual spill-over into adjacent unreserved areas (Mishra et al. 2004, 2010). After livestock use of reserves is curtailed, one expects the wild prey population to be determined by carrying capacity and the effect of predation by snow leopards. If their birth rate exceeds mortality, and emigration exceeds immigration, then, the reserves function as a net source of wild prey that spill-over into adjacent open areas which are sinks. Although size of livestock-free reserves can be considerably smaller than typical home-ranges of snow leopards, they can still be consequential at the landscape-scale (Mishra et al. 2010, 2016, 2017). In the open areas, wild prey abundance is determined by carrying capacity, competition and predation. But, they do not go extinct unless births and immigration are exceeded by mortality and emigration. So, even though demographic performance can be compromised due to livestock (Mishra et al. 2004), wild prey in the open areas can benefit if there is sufficient immigration from the reserves. With net spill-over from the livestock-free reserves, it is possible to offset the net reduction of wild prey in the larger open landscape, and thereby ultimately reduce snow leopard's dependence on livestock.

Additional features of the conservation efforts at Kibber included insurance against livestock-loss to offset the financial burden, compensation to the local villages against loss of grazing (i.e. a lease for reserved pastures), and incentives for vigilant herding (see further details in Mishra et al. 2003, 2010, 2017). At both sites, livestock consist of goat, sheep, horse, donkey, yak (a native but domesticated species) and cattle, including yak–cattle hybrids (Table 1). The main wild prey are ibex and bharal; birds (e.g. Himalayan snowcock *Tetraogallus himalayensis*) and lagomorphs (e.g. woolly hare *Lepus oiostolus*, Royle's pika *Ochotona roylei*) are minor prey.

Contrasts between intervention and status quo invariably require assessments at a landscape scale, where two sites are compared as a matched-pair (Andam et al. 2008, Ferraro 2009, Nelson and Chomitz 2011). Kibber and Pin Valley were fairly similar in a number of aspects (Table 1) and were judged suitable to be treated as matched-pairs to compare trends over time (Allen et al. 2017). Strengths and weaknesses of such landscape-level comparisons are well-known (Allen et al. 2017, Barley and Meeuwig 2017). There is a long history of landscape-level comparative assessments for biodiversity concerns (Allen et al. 2017, Barley and Meeuwig 2017), when alternatives do not exist. For e.g. well-known whole-lake experiments that began in the 1970s (Schindler 1974, Schindler et al. 2008) have provided compelling evidence for mechanisms of eutrophication and have paved the way for landmark environmental laws and regulations. In these studies, a lake (intervention) was compared to another matched-pair lake (status quo), and our approach is similar where we compare temporal trends in Kibber (intervention) against those in Pin Valley (status quo).

Data collection

We monitored wild prey populations at both sites. We conducted annual censuses over approximately 100–120 km^2 each at both sites (see map in Supplementary material Appendix 1 Fig. A1) in early-spring when animals are restricted to relatively low-lying snow-free areas (Suryawanshi et al. 2012). Fixed trails were surveyed, and animals foraging in low-lying and snow-free areas were counted from vantage positions along the trails. Conspicuous nature of animal aggregations during snow-melt would enable a large fraction of their population to be counted. Through much of winter, ibex and bharal feed on low-quality forage by digging craters in the snow, and this is energetically very expensive. They seek snow-free patches with fresh spring foliage and form seasonal aggregations where they can be counted from vantage points along trails. In open mountainous landscapes, total counts are thought to be a reliable alternative to other census methods (Singh and Milner-Gulland 2011, Suryawanshi et al. 2012, Moullec et al. 2017). In parallel, livestock were censused through door-to-door counts in villages whose herds graze in the study areas (Singh et al. 2015).

During this decade, we identified several sampling locations to monitor snow leopards' use of the study area and recorded indirect signs such as scrapes, sprays and scats. At the beginning of the experiment, snow leopards' dependence on livestock was estimated by reconstructing their diet from scats collected in these areas in 2002 (Bagchi and Mishra 2006). We repeated this analysis at five-year intervals in 2007 and in 2012. Changes in snow leopard diet, alongside any changes in wild prey populations, would represent the effects of the conservation intervention. Scats were collected from high-ridges and rocky outcrops, aided by signs of predator identity such as scrapes and scent marks, physical characteristics such as shape and size, and subsequent genetic screening. Field-collected scats are a random sample from different individuals using the study area; they represent the average of predator's diet across the landscape and may not represent individual preferences.

Data analysis

We analyzed undigested prey remains in these scats (i.e. hairs, feathers) to estimate the relative contribution of different prey types to predators' diet (Bagchi and Mishra 2006, Weiskopf et al. 2016). Differences in cuticular and medullary patterns in the hair of the prey were used for identification using a reference library. Scat analysis is considered a reliable method to estimate diets of large carnivores (Klare et al. 2011, Williams et al. 2011). We considered the number of scats produced by predators to be related to the body size of prey consumed and accounted for the variation in numbers of field-collectable scats when the prey differ in their body size (Chakrabarti et al. 2016). This allometric relationship has a number of advantages compared to previous formulations, and was implemented as: $y = a - b\left(e^{c(x/z)}\right)$, where y is the number of field-collectible scats; a, b and c are constants; x is prey body size, and z is predator body size. Data from 95 scats in 2002 were included in our analysis (44 scats from Kibber and 51 from Pin Valley, Bagchi and Mishra 2006). We analyzed 126 scats in 2007 (59 from Kibber, and 67 from Pin Valley), and 114 scats in 2012 (53 from Kibber, and 61 from Pin valley). To assess the adequacy of sample sizes (number of scats examined), we noted the cumulative frequency of prey items in ten randomly chosen scats at a time, and repeated this iteratively until all scats were included (Bagchi and Mishra 2006). This showed that a sample of 40 scats is required to reliably estimate of the relative contribution of the different prey in predators' diet (Supplementary material Appendix 2 Fig. A2). We converted relative biomass of the different ungulate prey in diet to the relative numbers killed using their average body sizes (Chakrabarti et al. 2016, Weiskopf et al. 2016).

We used 100 re-sampling bootstrap iterations of scats to estimate mean and variation in frequency of occurrence of prey items, and their contribution to predator diet (Klare et al. 2011, Williams et al. 2011). We compared differences in the relative contribution of wild prey vis-à-vis livestock across years at Kibber and Pin Valley using 1000 randomized iterations with $\alpha = 0.1$, i.e. against 90% confidence intervals. In this way, if the confidence interval of one group does not include the mean of another group, then the two groups are inferred to be different from each other. Level of statistical significance, i.e. p-value, is obtained from the 1000 iterations (Williams et al. 2011). From this, we inferred whether 1) contribution of wild prey changed over time at each site, and 2) whether the trends were different between the two sites.

Since diet data contain multiple variables (many prey species), we used multivariate analysis to aid their visualization and interpretation. First, we summarized the bootstrapped diet composition data using nonmetric multidimensional scaling (NMDS) over two axes, for all years and both sites using Euclidean distance. NMDS is a distance-based ordination tool (Legendre and Legendre 1998) which represents the difference between samples that belong to unique groups, i.e. diet at each site and in each year. Next, we checked whether diet composition changed with time at each site using redundancy analysis (RDA). RDA combines ordination and regression (Legendre and Legendre 1998) for a set of multivariate response variables (i.e. diet composition) to partition variance explained by different predictor variables (i.e. site and year). RDA can be used to test hypothesis over main-effects an interactions between different predictor variables. This approach can be more informative than univariate indices for diet-selectivity, diet-breadth, etc. In our RDA model, we evaluated the support for the site × year interaction-term. If this model received strong support (i.e. variance explained, and model AIC), then it would imply that change in diet over time differed between the sites. Otherwise, it would imply both sites experienced similar trajectories. All analyses were done in R ver. 3.5.3 (<www.r-project.org>). Scat data for 2002 are from Bagchi and Mishra (2006), and these were re-analyzed using allometric conversion alongside data from 2007 to 2012 (Chakrabarti et al. 2016).

Predator identity

Misidentification in predator's identity from scat, due to the presence of co-predators, can introduce bias in estimating diets (Weiskopf et al. 2016). We relied on several facts and precautions as lines of evidence in order to reduce or eliminate any potential bias. First, large-bodied co-predators such as the wolf are known to be very rare in the study area, and this was verified by a separate study using camera-traps (Sharma et al. 2015). In 23 remotely-triggered camera traps deployed in Kibber (intervention-site) between June and October 2007 (n = 2645 trap days, see map in Supplementary material Appendix 1 Fig. A1), we recorded a total of 38 captures which were identified as three individual snow leopards (Supplementary material Appendix 3 Fig. A3). Similarly, in six trap locations in Kibber (intervention-site) between October 2011 and March 2012 (n = 742 traps days), we recorded a total of 40 captures, which were identified as five individual snow leopards (Supplementary material Appendix 3 Fig. A4). Contemporaneous studies found evidence (from the genetic identity of individuals from scats) of at least two snow leopards using the area surveyed in Pin Valley (Suryawanshi et al. 2017), but ad-hoc sightings suggest there might be at least three individuals. During this period, over the general landscape (30 camera traps total, n = 4314 trap days total) there were no captures of wolves, and only four instances of village dogs (see Sharma et al. 2015 for full details of camera-trapping data and analysis).

Second, we measured the size of scats from 2012; these were within the known range for snow leopard scats, and were larger than those of other species, such as red fox *Vulpes vulpes* (Anwar et al. 2011): overall diameter 2.2 ± 0.3 cm SD; 2.3 ± 0.3 cm SD for Pin valley; 2.2 ± 0.3 cm SD for Kibber.

Third, we used DNA-based molecular determination of predator identity on 100 scats from 2012 (details in Supplementary material Appendix 4). Of these 72 tested positive for snow leopard DNA, while the remaining were judged too degraded for genetic analysis and inference (Supplementary material Appendix 4 Fig. A5). We did not attempt to identify individual snow leopards with DNA obtained from scats.

Finally, the mathematical properties of diet-estimation (Chakrabarti et al. 2016) suggest that any remnant bias after the above precautions is likely to have minimal impact on overall interpretation. Recall that the allometric scaling (Chakrabarti et al. 2016) is implemented as $y = a - b\left(e^{c(x/z)}\right)$, where y is the number of field-collectible scats; a, b and c are constants; x is prey body size, and z is predator body size. Now, sensitivity of y to differences in prey body size is given by $\frac{\partial y}{\partial x} = -\left[\frac{bce^{1/z}}{z}\right]e^{-cx}$. And, sensitivity of y to differences in predator body size is given by $\frac{\partial y}{\partial z} = -x\left[\frac{bce^{1/z}}{z^2}\right]e^{-cx}$. In this way, $\frac{\partial y}{\partial z}$ is a source of error in the estimated diet profile when predator's identity is uncertain, and it can be evaluated mathematically. Now, the sensitivity to prey-size for a given predator, and sensitivity to predator size for a given prey, are differentially influenced by x and z. In formal terms, we have $\frac{\partial y}{\partial x} \propto e^{-cx}\frac{e^{1/z}}{z}$, but $\frac{\partial y}{\partial z} \propto xe^{-cx}\frac{e^{1/z}}{z^2}$. From this difference, it follows that the estimated value of y for snow leopard (typically ~40–45 kg) and a co-predator (e.g. wolf; typically ~32–38 kg) will differ substantially only when they consume small sized prey ($x \ll z$). But, the estimated value of y for both predators will be nearly identical when they consume large prey ($x \geq z$). So, there is a chance of miscalculation and bias when small prey (rodents and lagomorphs) are the overwhelming feature in scats. But, we found this was not the case, as large prey (ungulates) were most common in scats. This is consistent with previous reports which found that snow leopards mainly kill ungulate prey, both wild and livestock (Weiskopf et al. 2016). Collectively, these four lines of evidence indicate that any confusion due to predator identity was likely to be low in our study, and unlikely to impact the broad inference.

Results

Abundance of livestock and wild prey

Among the livestock, in both Pin Valley and Kibber, goat–sheep and yak–cattle were most numerous (Fig. 2). Overall, horses were more abundant in Pin Valley than in Kibber (Fig. 2). Over time, there were noticeable changes in livestock herd-composition at both sites. There was a decline in the relative abundance of goat–sheep (Fig. 2). But, total livestock biomass did not vary appreciably due to changes in the larger-bodied livestock as well (Fig. 2). In Pin Valley, ibex was the lone wild ungulate, and its population fluctuated around 180–200 individuals (Fig. 2). In Kibber, bharal were more abundant than ibex (Fig. 2). Bharal population increased from less than 200 to more than 450 individuals; the smaller ibex population varied between 20 and 40 individuals (Fig. 2).

Predators' dependence on livestock

Six wild prey and five livestock types were identified in the scats (Fig. 3). Prey species could be identified in 317 scats (94.6%). Vegetation was seen in 27 scats (8.0%), while 35 scats (10.4%) had remains of unidentified prey. Majority of scats (230 scats, 68.6%) contained a single prey item, and 60 scats (17.9%) contained more than one prey. In Pin Valley, ibex was the most frequently recorded prey item; in Kibber it was bharal (Fig. 3).

Trends in predator diet in Pin valley under status quo (increasing dependence on livestock) were in the opposite direction compared to trends under conservation interventions at Kibber (decreasing dependence on livestock, Fig. 4–6). In Pin Valley (status quo), ibex and horse were the major constituents of predator diet (Fig. 4). In Kibber (intervention-site), although bharal was a major constituent, predator diet was more varied, with substantial contributions from the other prey (Fig. 4). Patterns in relative number of ungulate prey killed reflected these changes in biomass contribution to diet (Fig. 5). In brief, bharal kills increased in Kibber, whereas ibex kills declined in Pin Valley (Fig. 5).

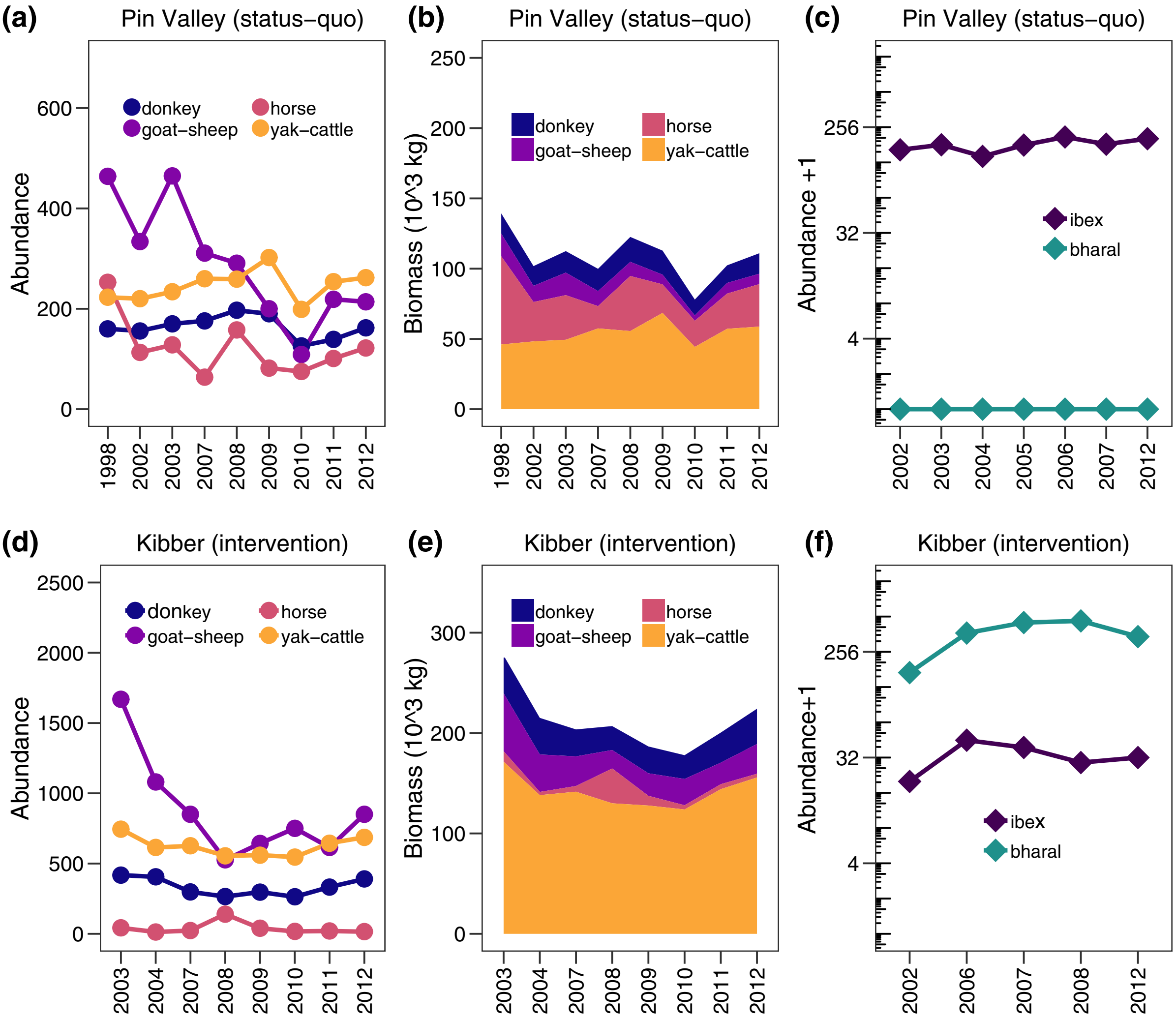

Figure 2. Trends in animal census over time in two regions of Spiti, northern India. In 2001, conservation interventions were implemented in Kibber (intervention), and Pin Valley served as status quo. Over the next decade, small-bodied livestock (goat, sheep) declined at both sites. But appreciable increase in wild prey were documented only in Kibber. (Data sources include Bagchi et al. 2004, Mishra et al. 2004, Singh et al. 2015.) For clarity, (c) and (f) are shown using log(2) scale.

In Kibber, total wild prey contribution in 2002 was 58% (±7% SD), and it increased to 64 ± 4% in 2007 ($p = 0.06$, 1000 randomizations), but did not show further change in 2012 (61 ± 6%, $p = 0.53$, Fig. 6). Average relative change in wild prey contribution in Kibber was +17% and +3% during these successive time intervals. In Pin Valley, wild prey contribution declined from 71 ± 6% in 2002 to 68 ± 4% in 2007 ($p = 0.08$). It declined further to 64 ± 6% in 2012 ($p = 0.01$, Fig. 6). The average relative change in wild prey contribution in Pin Valley was −7% and −16% during these successive time intervals. Seen together, recovery of wild prey coincided with reduced consumption of livestock in Kibber (intervention), but it increased in Pin Valley (status quo).

Change in predator diet composition

NMDS analysis (stress = 0.11), for two ordination axes, are summarized for different prey (Fig. 7a), and for diets at each site over time (Fig. 7b–c). Patterns suggest that over time, predator diet in Pin Valley shifted away from ibex, and towards livestock. But, in Kibber, predator diet shifted away from livestock and towards bharal. RDA revealed a significant site × time interaction ($F_{1,590} = 338.3$, $p < 0.001$, $\Delta AIC = 346$ relative to null) and explained 88% of variation in diet composition. This supports that trajectories of diet shift were different at the two sites (Fig. 7b–c).

Discussion

Our primary result is that dependence on livestock intensified under status quo, whereas it was partially ameliorated under conservation interventions that comprised of livestock-free reserves, insurance and related incentives. This result can offer an opportunity to discuss the effectiveness of conservation interventions to achieve biodiversity targets when matched against an appropriate counterfactual scenario. They also show that long-term monitoring, commensurate with the time-scale of underlying ecological processes, is needed to determine outcomes. For example, a five-year interval, 2002–2007, would perhaps reach a different conclusion than a 10-year interval (2002–2012). Creation of small

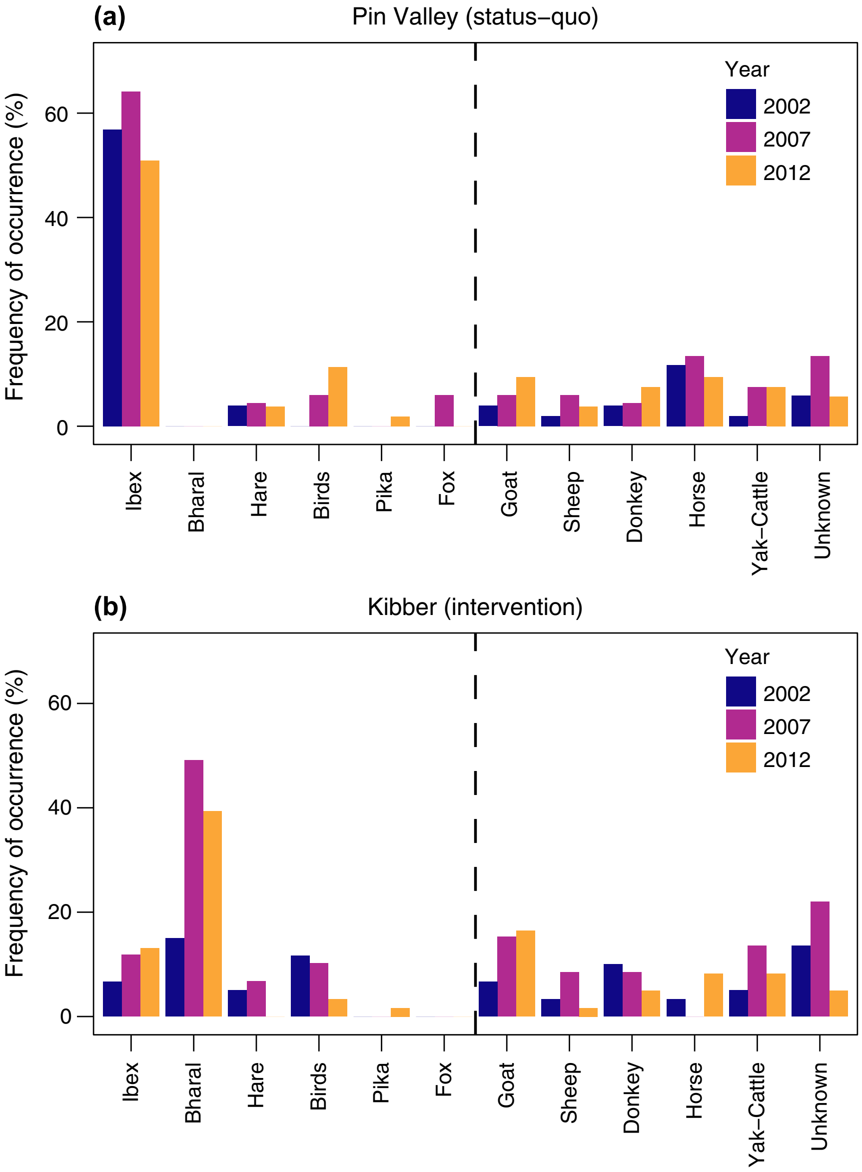

Figure 3. Summary of frequency of occurrence of different prey species in carnivore scats in two regions of Spiti, northern India. Kibber was the site for conservation intervention starting in 2001, and Pin Valley was site for status quo. The dashed lines separate the wild prey species from the livestock. Data for 2002 are from Bagchi and Mishra (2006).

village-reserves free of livestock did coincide with an increase in wild ungulates in Kibber. This was followed by a decline in predators' dependence on livestock (i.e. prey-switching, Khorozyan et al. 2015). In contrast, the consumption of livestock increased over time under status quo. Overall, changes documented after conservation interventions in wild prey and predator diets were in the anticipated direction. These trends may imply conservation success as livestock-loss could be controlled, and below we evaluate confounding effects of background socio-economic factors in influencing the observed patterns over the duration of our study.

Response of prey and predators to the conservation interventions

One key result is the large and persistent increase in wild prey population at Kibber (Mishra et al. 2016), chiefly bharal, but also ibex (Fig. 2), whereas there was no clear trend at Pin Valley. Experimental livestock-free reserves could relax forage competition for bharal and ibex, and can explain this population-level response through mechanisms such as improved forage availability for wild-prey and improved survival of their newborns (Mishra et al. 2003, 2010).

Predator diet data suggest that livestock-dependence was more severe in Kibber than in Pin Valley at the beginning of our study (in 2002, Fig. 4–6). Over the next decade, during the course of our study, livestock-dependence reduced in Kibber (Fig. 4–6). The direction of diet shift was towards bharal and away from livestock (Fig. 7). In comparison, livestock-dependence steadily increased in Pin Valley under status quo (Fig. 4–6). This shift was away from ibex, and towards livestock (Fig. 7). So, one can infer that conservation interventions may address biodiversity objectives better than status quo (Kleiman et al. 2000, Ferraro and Pattanayak 2006, Ferraro 2009, Pullin and Knight 2009).

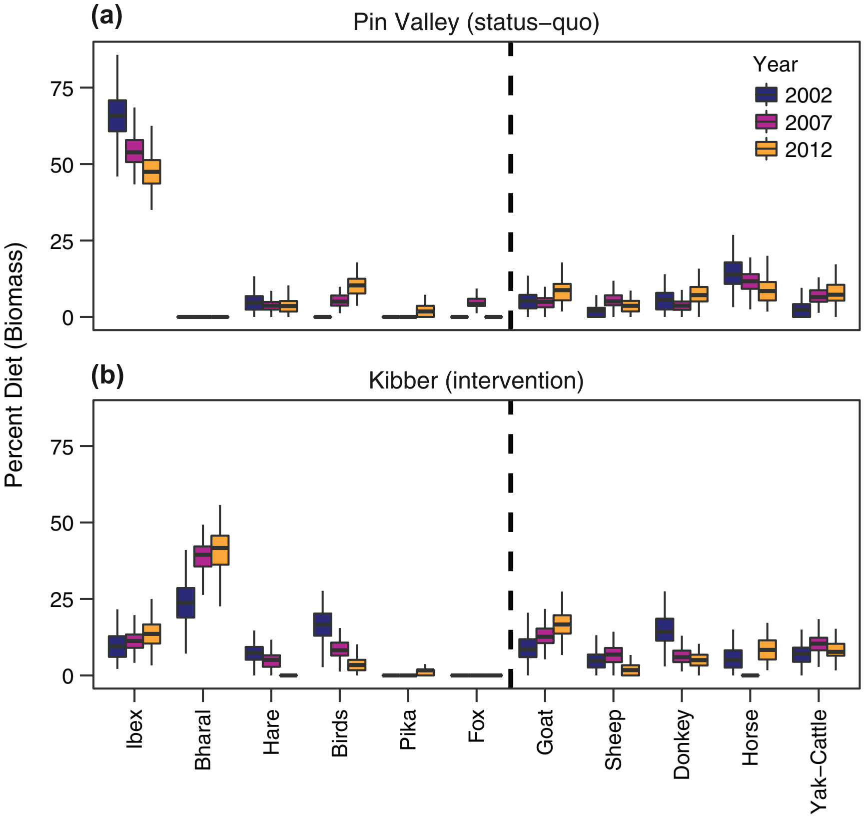

Figure 4. Contributions of different prey species to predator diets calculated from scats using allometry of differences in prey body size. Conservation intervention began in 2001 in Kibber, and Pin Valley was site for status quo. Boxplots represent median and interquartile range based on 100 resampling iterations. The dashed line separates the wild prey from the livestock. Data for 2002 are from Bagchi and Mishra (2006).

However, despite sustained improvements in wild prey populations in Kibber (Fig. 2), livestock-dependence did not continue to decline further at the end of our study (Fig. 4–6). This can be explained by changes in predator population – most likely through immigration into the study area (i.e. numerical response, Suryawanshi et al. 2017). In 2007, three individuals were recorded in camera-traps, whereas this had increased to five individuals by 2011–2012 (Supplementary material Appendix 3 Fig. A3, A4). Effectively, a change from 3 to 5 individuals in the area sampled in Kibber (100–120 km^2), amounts to a relatively steep increase in predator density (overall average density of snow leopard across its geographic range is around 1 individual every 100–200 km^2, Sharma et al. 2015). Contemporaneous studies found at least two individual snow leopard in Pin Valley based on genetic identification of individuals (Suryawanshi et al. 2017), and there might be little scope for similar numerical response at the status quo site. So, dependence on livestock did not worsen despite an apparent increase in the number of predators that use the study site. The peaked response in wild prey abundance, with moderate reduction towards the end of the study (Fig. 2), is also consistent with an increase in predation pressure on bharal. While gains due to reduction in snow leopard dependence on livestock during 2002–2007 were not improved upon during 2007–2012, we also find that despite a likely increase in snow leopard numbers, there was no worsening in terms of livestock-consumption.

Potential confounding effects and alternative explanations

The conservation interventions also overlap with a period of unprecedented socio-economic transition in the Trans-Himalaya and neighbouring highlands (Singh et al. 2015), as agro-pastoral economies gradually shift away from traditional subsistence-based livelihoods toward greater integration with external market influences (Namgail et al. 2007b, Singh et al. 2015). Alongside increase in wild prey at Kibber, we also documented a decline in small-bodied livestock (goat–sheep, Fig. 2). Such decline in goat–sheep holdings over the past 3–4 decades is a general feature of the larger Trans-Himalayan landscape, and was also seen in Pin valley. This may be related to a suite of social and economic factors that were unlikely to be influenced by the conservation efforts (Namgail et al. 2007b, Singh et al. 2015). So, the increase in bharal populations could reflect a reduction in goat–sheep which is independent of the conservation efforts. But, one should not dismiss the potential link between the increase in wild prey and the conservation interventions (Mishra et al. 2016), since there was no major change in ibex populations in Pin Valley even though goat–sheep declined at this site as well. Similarly, reduction in livestock loss could reflect more vigilant herding (Mishra et al. 2003), and the outcome from this cannot be readily distinguished from that of change in wild prey availability. As a counter-argument,

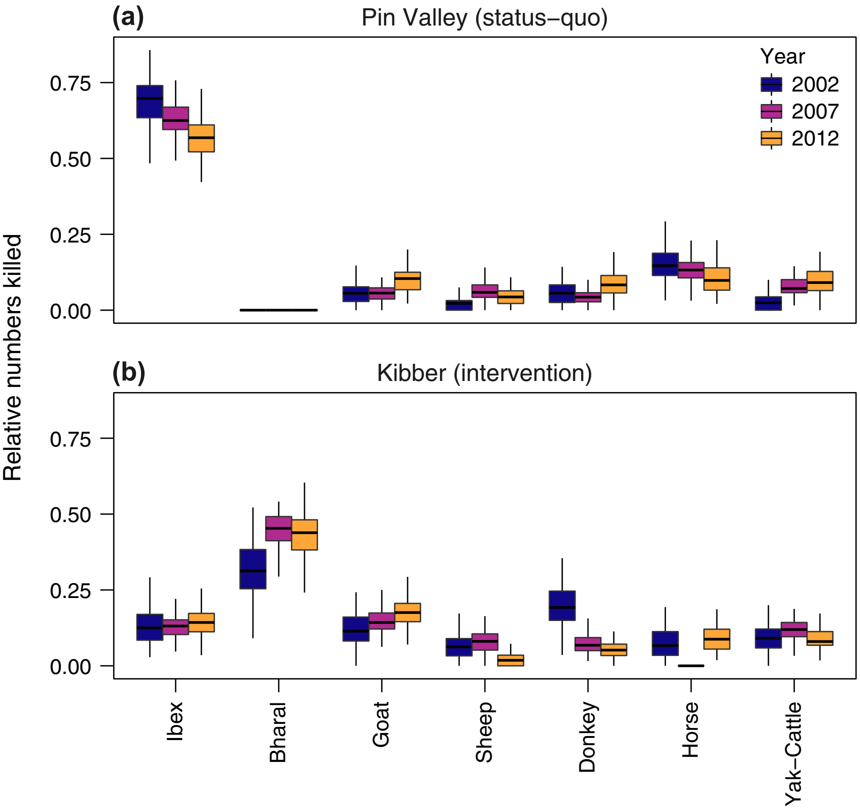

Figure 5. Representation of diet patterns in Fig. 4 as relative number of animals killed for the different ungulate prey. From 2001, Kibber was the site for conservation interventions and Pin Valley was site for status quo. Boxplots represent median and interquartile range based on 100 resampling iterations. Data for 2002 are from Bagchi and Mishra (2006).

since the conservation interventions included insurance against livestock losses, it could potentially lead to erosion of husbandry practices (Lee et al. 2017). Given a safety provisioned by insurance, villagers may have become complacent in guarding their herds. In this way, the lack of improvement in livestock-loss during the latter half of our study could reflect complacent husbandry in Kibber (Fig. 5, 6). Once again, the counterfactual scenario at Pin Valley may offer some clarity. In Pin Valley, livestock-loss increased despite absence of insurance (Fig. 5, 6). Thus, the observed contrasts between intervention and status quo sites affords inference on the effectiveness of the conservation interventions, and help to distinguish them from potential confounding effects.

Reflections on evaluation of conservation interventions

Invariably, conservation interventions are embedded within a shifting socio-economic matrix; often the outcome of conservation cannot be fully distinguished from social change. In our study, social changes: background changes in livestock holdings and perhaps also in husbandry – may appear to obstruct clear lines of inference. However, their influence may not be so overwhelming that they could nullify ecological interpretations of predator–prey interactions altogether. Background social factors may have likely accentuated the trajectories of change in wild prey population that were initiated through livestock-free reserves. The reverse seems less plausible as the goat–sheep were already on a decline

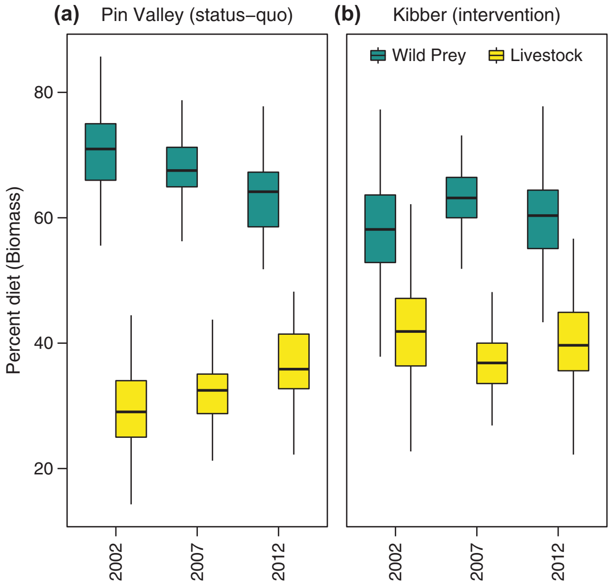

Figure 6. Combined contributions of the different wild prey and domestic livestock to predator diet, aggregated as two categories. Kibber was the site for conservation intervention starting in 2001, and Pin Valley was site for status quo. Predator diet was estimated from prey remains in scats. Plots show median and interquartile range based on 100 resampling iterations. Data for 2002 are from Bagchi and Mishra (2006).

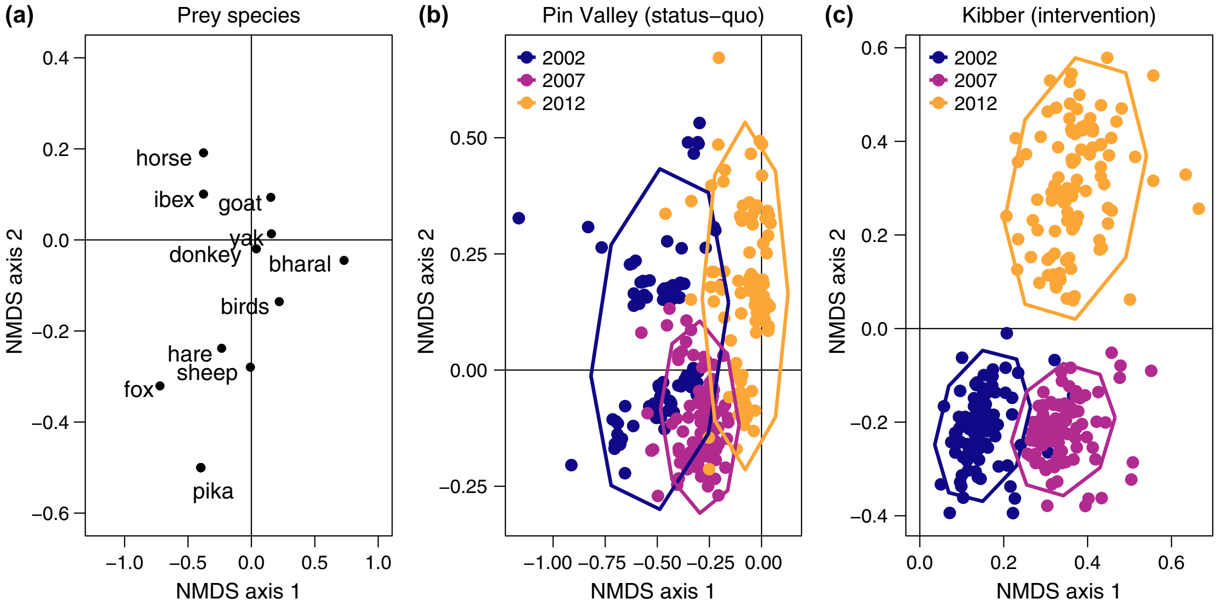

Figure 7. Representation of predator's diet composition through ordination. Kibber was the site for conservation intervention starting in 2001, and Pin Valley was site for status quo. Ordination scores with NMDS for different prey species are shown in (a). Ordination scores for diet in Pin Valley (b) and Kibber (c) are shown for the different years. The polygons accommodate 90% of datapoints. In Pin Valley, the patterns indicate a diet shift away from ibex, and towards livestock over time, based on analysis of prey remains in scats. But, in Kibber, diet shifted away from livestock and towards bharal.

at least two decades before the conservation interventions were implemented (Singh et al. 2015). Similar considerations have appeared in other studies: e.g. the number of bear–human interactions declined shortly after conservation interventions in New York, USA. But, this coincided with a season of bountiful fruiting in the forest, whereby bears were less likely to seek food in urban neighbourhoods (Gore et al. 2008).

Nevertheless, a favourable change in predator numbers can be an alternative indicator of conservation success, albeit one that could affect our initial premise of reducing livestock-loss from predation (Khorozyan et al. 2015, Suryawanshi et al. 2017). Unless inter-related and sometimes counterintuitive aspects of such feedbacks are accounted in a conservation strategy, it may remain problematic to judge whether they are effective, or not. Here, we find that it may not be possible to eliminate livestock losses completely, despite improvements in wild prey availability. So, accompanying measures, such as compensation and insurance (Mishra et al. 2003), should feature alongside primary attempts to reduce losses as a multi-pronged strategy (Mishra et al. 2017). Admittedly, our quasi-experimental approach with landscape comparisons (Barley and Meeuwig 2017) does not create true treatment/control conditions (Allen et al. 2017). Yet, the results can afford discussion on whether the change in predator diets was a consequence of the conservation interventions, or not (Ferraro and Pattanayak 2006, Ferraro 2009, Eklund et al. 2017). Accommodating feedback due to conservation interventions into planning, as highlighted by our results, can prove valuable. We conclude that it is timely and important to include a broader discussion on the effects of conservation practice on conservation outcomes into ongoing narratives on achieving biodiversity targets.

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Supplementary material (available online as Appendix wlb-00583 at <www.wildlifebiology.org/appendix/wlb.00583>). Appendix 1–5.