Mind the cat: Conservation management of a protected dominant scavenger indirectly affects an endangered apex predator

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ABSTRACT

Interspecific interactions are among the key factors influencing the structure of animal communities and have high relevance for conservation. However, managers, conservationists and decision-makers rarely consider the potential side-effects of single-species carnivore management for the conservation of other carnivores. We studied how management of protected brown bears (*Ursus arctos*) affected interspecific interactions with an endangered apex predator, the Eurasian lynx (*Lynx lynx*) in Slovenia. Due to large body size and superb olfactory abilities, bears are one of the most important dominant scavengers and regularly usurp kills from other large predators, a process known as kleptoparasitism. At the same time, bears throughout the world are usually actively managed through zone-specific culling regimes, supplemental feeding, and translocations. This can considerably alter bear densities and activity patterns and in turn influence interactions among carnivores. Overall, we observed that bear scavenging pressure resulted in substantial energetic losses for Eurasian lynx. The probability of lynx losing kills to bears ranged from 8 to 74% and strongly depended on local bear densities and monthly bear movement rates. Kleptoparasitic interaction intensity differed almost 3-fold between different bear management zones. Furthermore, the presence of a bear feeding site increased the odds of lynx losing kills by 5-fold compared to areas > 1000 m from these sites. We suggest that existing bear-feeding regimes should be reconsidered in order to reduce unwanted side-effects of this controversial practice on endangered apex predators. We also call attention to the importance of considering impacts of interspecific interactions in wildlife management and conservation.

1. Introduction

Interspecific interactions have profound effects on ecosystem function and community structure (Begon et al., 2006). Understanding the underlying mechanisms that influence interspecific interactions is increasingly an important aspect of animal conservation (Creel et al., 2001; Moleón et al., 2014). Despite the potential to alter entire communities, wildlife managers rarely consider possible negative side-effects of management decisions on interspecific interactions (Linnell and Strand, 2000; Ordiz et al., 2013; Selva et al., 2014). More empirical knowledge is needed for better conservation and management that accounts for interactions across multiple levels of ecosystems (Lozano et al., 2013; Périquet et al., 2015). This is particularly true for strongly interacting species, such as large mammalian carnivores due to their cascading effects on numerous species and terrestrial ecosystems worldwide (Estes et al., 2011; Ripple et al., 2014).

Researchers are increasingly concerned about unwanted or unexpected impacts of specific management actions involving large carnivores. For example, hunting increases infanticide in African lions

(*Panthera leo*; Loveridge et al., 2007; Whitman et al., 2004) and brown bears (*Ursus arctos*; Gosselin et al., 2015; Swenson et al., 1997), decreases pack stability in wolves (*Canis* spp.) and increases their hybridization with domestic dogs (Moura et al., 2014; Rutledge et al., 2010). For cougars (*Puma concolor*) and African lions, hunting changes their distribution and movement patterns (Davidson et al., 2011; Maletzke et al., 2014). Hunting also changes brown bear activity and foraging behaviour (Ordiz et al., 2012). Changes in abundance, sociality, foraging, spatial distribution and movement patterns have also been reported as a consequence of carnivores exploiting readily available human-provided foods (Newsome et al., 2015; Oro et al., 2013). On the other hand, much less is known about the effects of these measures beyond the managed species (Périquet et al., 2015). Consequently, carnivore management programmes rarely consider the indirect effects on other apex predators via changes in interspecific interactions.

Interspecific interactions among carnivores frequently occur at kill sites (Atwood and Gese, 2008). The stealing of kills or kleptoparasitism is recognized as an important part of large carnivore ecology with the potential to change entire ecological communities (Allen et al., 2014). High levels of kleptoparasitism can directly threaten predators (Carbone et al., 1997; Gorman et al., 1998). Kleptoparasitic interactions among bears and solitary felids provide an opportunity to study these

interactions. Solitary felids that kill large prey are characterized by a prolonged consumption process of their kills (Jobin et al., 2000; Stander et al., 1997) and are regularly exposed to kleptoparasitism in their ranges worldwide (Krofel et al., 2012a). As the largest terrestrial scavengers with superb olfactory abilities, bears are one of the most important dominant scavengers and kleptoparasites in the Holarctic region (Allen et al., 2014; Krofel et al., 2012a; Murphy et al., 1998). At the same time, ursids are often actively managed either through hunting and management removals (Kaczensky et al., 2013; Nielsen et al., 2004) or, in case of endangered populations, through reintroductions (Clark et al., 2002). In addition, bear movements, local densities, diet and other life history traits can be greatly altered through human-caused changes of habitat and food availability (Apps et al., 2004; Güthlin et al., 2011; Kavčič et al., 2015; Penteriani et al., 2010). However, it is poorly understood how management of dominant scavengers like bears affect their interactions with other predators.

Our research focuses on how management of protected brown bears in Slovenia influences interspecific interactions with a sympatric apex predator, the Eurasian lynx (*Lynx lynx*). The highly endangered Dinaric lynx population is impacted by kleptoparasitism from brown bears, through substantial energetic losses and potential reduction in reproductive success. On average, bears usurpe one third of lynx kills and despite increasing their kill rate, lynx are not able to fully compensate the losses (Krofel et al., 2012a). These kleptoparasitic interactions were highest during the bear mating season and lowest in the denning period (Krofel et al., 2012a). Brown bears in the region are intensively managed through a zoning system of culling and supplemental feeding, which was shown to considerably alter bear distribution, local densities, diet and activity patterns (Jerina and Adamič, 2008; Jerina et al., 2013; Kavčič et al., 2015; Steyaert et al., 2014). We speculated that these management actions could influence interactions between bears and the lynx (Krofel et al., 2012a). Here we tested this hypothesis. We predicted that the proportion of lynx kills usurped by bears would cumulatively increase with: 1) higher local bear densities, 2) higher bear movement rates, and 3) proximity to bear feeding sites.

2. Material and methods

2.1. Study area and study species

The study was conducted in the Northern Dinaric Mountain Range in Slovenia (45°25′–45°47′N, 14°15′–14°50′E) in mixed temperate forests dominated by fir and beech (Omphalodo-Fagetum s. lat.). The altitudes range from 200 m to the peak of Mount Snežnik at 1796 m. The climate is a mix of influences from the Alps, the Mediterranean sea and the Pannonia basin with annual temperature averaging 5–8 °C, ranging from average maximum of 32 °C to a minimum of −20 °C, and average annual precipitation of 1400–3500 mm.

The study area encompasses the north-western part of the transboundary Alps-Dinaric–Pindos brown bear population. Here bears are under strong influence of various human activities and management measures, which created a large gradient in bear densities. Bears were nearly extirpated in the late 19th century, but since the 1940s, their numbers and distribution increased due to conservation measures, including establishment of the Core Bear Protective Area (CBPA) of 3500 km^2 within the Dinaric Range in 1966, where bear hunting was strictly regulated (Simonič, 1994). In contrast, bears outside this area (mostly dispersing individuals) experienced higher harvest rates and consequently bear densities there have remained low (Jerina and Adamič, 2008; Krofel et al., 2010). Currently, bears are present in approximately half of the country, although the majority (95%) of bears are concentrated in 19% of Slovenian territory. The average density of brown bears in most of the lynx range in Slovenia is estimated at 12 bears/100 km^2, with local densities exceeding 40 bears/100 km^2 (Jerina et al., 2013).

Today the most important bear management practices are hunting and supplemental feeding. In Slovenia, 75% of bear mortality is human-caused (Jerina and Krofel, 2012) and 20% of the brown bear population is removed annually through legal hunting (Krofel et al., 2012b). Supplemental feeding in the central part of the CBPA is intensive, with high-energy supplemental food, especially corn, available to bears year-round and in high quantities (on average, 12,500 kg/100 km^2 annually) at numerous feeding sites. Supplemental food represents 34% of dietary energy content ingested by bears in this area (Kavčič et al., 2015). Locally intensive supplemental feeding likely increases carrying capacity and may result in some of the highest recorded densities and reproduction rates of brown bears worldwide (Jerina et al., 2013; Kavčič et al., 2015; Reding, 2015). It has also been observed that intensive supplemental feeding affects habitat use of bears in Slovenia (Jerina et al., 2012) and likely shortens bear denning periods by as much as 20% compared to areas without supplemental feeding; currently average denning period for bears in Slovenia lasts 75 days (Krofel et al., 2013a).

Eurasian lynx are the largest felid in Europe and along with the grey wolf (*Canis lupus*), the main predator of wild ungulates on the continent (Jedrzejewski et al., 2011). In most of Europe, lynx specialize in hunting European roe deer (*Capreolus capreolus*), which they typically consume in a course of several days (Breitenmoser and Breitenmoser-Würsten, 2008). Lynx in Slovenia are part of the Dinaric lynx population, one of the most threatened populations in Europe (Kaczensky et al., 2013; Sindičić et al., 2013). The population is rapidly declining in Slovenia with estimated 15–25 residential animals (Kos et al., 2012). In the study area, lynx hunt mainly wild ungulates, which together represent 88% of biomass consumed (Krofel et al., 2011). Roe deer is the main prey species (79% of consumed biomass), with edible dormouse (*Glis glis*) and red deer (*Cervus elaphus*) as important alternative prey, each representing approximately 7% of consumed biomass.

2.2. Locating kills and telemetry

We measured lynx predation, lynx prey consumption, and bear movements using telemetry. During 2005–2011, eight lynx (five females and three males) and 33 bears (14 females and 19 males) were captured and equipped with telemetry collars (five lynx and all bears with GPS–VHF collars and three lynx with VHF collars) using standard protocols (see Krofel et al. (2013b) and Jerina et al. (2012) for details on capture and immobilization of lynx and bear, respectively). GPS collars were scheduled to attempt 7–8 GPS fixes per day for lynx and 12–24 fixes per day for bears.

We used snow-tracking and GPS location cluster analysis of lynx telemetry data to locate kill sites with prey remains of ungulates killed by lynx (see Krofel et al., 2013b for details). At each kill site we checked for signs of bear presence (footprints, hair, scat, or characteristic signs of consumption — e.g. large broken bones or crushed skull) or monitored the carcass consumption with the use of automatic infra-red video cameras with motion detectors (Fig. 1; Krofel et al., 2012a). Only carcasses of roe deer, the main lynx prey, were included in this study. Kleptoparasitic interaction (i.e. kill being found by bears) was noted only when bears usurped the kill during the time while lynx were still feeding on them. Lynx pin the study area fed on roe deer for 4.4 days on average if kills were not usurped by bears (Krofel et al., 2012a). We typically visited the kill sites the day after lynx abandoned the kill site (median time of visit: 4.5 days after the kill was made), but on some occasions (n = 13) we arrived earlier to install the video system at the kill site. When a kill site was too old to reliably asses it, these data was not included in the analysis.

2.3. Analysing effects of bear densities, movement rates and supplemental feeding sites

For each lynx kill site we determined the local bear density. We used raster map of local bear population densities in Slovenia with 1 km^2 resolution, which was produced using voting classifications method based
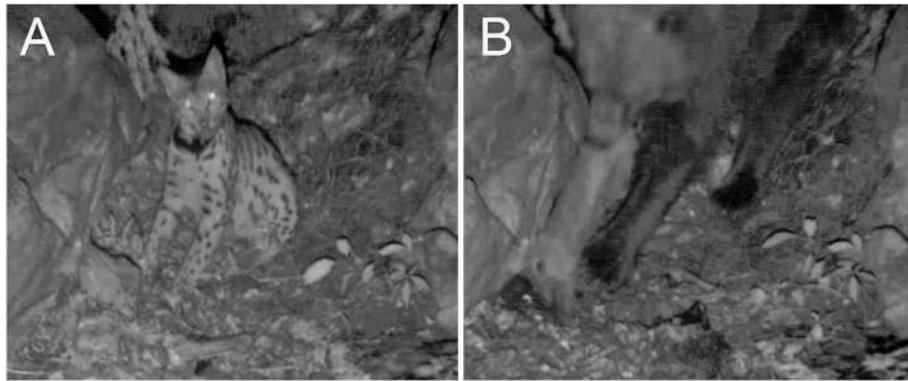
Fig. 1. Still photographs from a video showing a female Eurasian lynx feeding on a roe deer she killed (A) and a brown bear usurping the kill (B).

on GPS telemetry data, records of bear removals, systematic and opportunistic direct observations and signs of bear presence, and non-invasive genetic samples (Jerina et al., 2013). Data for estimating bear densities was obtained in the same period as lynx kill site monitoring. Since precise data on local bear densities were available only for Slovenia, we excluded kill sites located in neighbouring Croatia from the analysis.

Frequency of the lynx–bear kleptoparasitic interactions changes seasonally and is strongly correlated ($r = 0.89$) with the bear daily movement rate (Krofel et al., 2012a). We used bear telemetry data to calculate average daily movements (i.e. sum of linear distances between consecutive GPS locations; Jerina et al., 2012) for each month of the year. We attributed the corresponding bear movement rate to each lynx kill site according to the month when the predation event occurred.

Based on local bear densities and month-specific movement rates we also created a new variable, index of total path walked daily by all bears around given kill site in given month (total bear path length), which represents an interaction (product) of both variables. This interaction (product) could be understood as a proxy for probability of a kill being randomly found by bears and could be biologically meaningfully interpreted already without the main effects of both variables. Thus we used it in the models also without the main effects of variables.

To analyse effects of supplemental feeding on the kleptoparasitic interactions, we measured distance from each lynx kill site to the nearest bear feeding site. Because effects of feeding sites on bear space use are markedly non-linear (close to feeding sites the space use of bears steeply decreases with distance to the feeding site, but at greater distances effects are not detected anymore; Jerina et al., 2012), we categorized this variable into three classes (<500 m, 500–1000 m, and >1000 m from the feeding site) and thus include it in the analysis as a factor.

Bear finding a lynx kill was regarded as a binary event (i.e. bear either finds the remains or not) and we used generalised linear mixed models (GLMM; binomial error and a logit link function) with bear finding the lynx kill as a dependent variable, local bear density, monthly bear movement rate, and total bear path length as independent covariates, and distance to the closest bear feeding site as a factor. In addition, we included lynx ID as a random factor in all GLMMs. We calculated all possible models and explored structure of all candidate models with ΔAICc scores ≤2 and used them for model averaging to obtain robust parameter estimates (Burnham and Anderson, 2002). For easier interpretation of the results, we also produced correlation matrix for the relationships among the predictor variables and dependent variable (Appendix B) and calculated odd ratios (change in predicted probability of a lynx kill being found by bears) for changes in values of each independent variable from the first to the last decile, while values of the other variables remained constant. To demonstrate relative importance of the results we also calculated probabilities for kill being found by bears for various combinations of independent variables' values (for the first and the last deciles), as well as for different bear management zones.

Supplemental feeding affects density and spatial distribution of bears on different scales. On a large scale, supplemental feeding likely increases carrying capacity for bears since it represents one of the main food sources (Kavčič et al., 2015). In addition, it affects bear densities on a local scale, where preferential habitat use has been observed in the vicinity of feeding sites (Jerina et al., 2012). However, this may in part be a consequence of local hunters placing feeding sites in more suitable habitats for bears, where bear densities would be high regardless of supplemental feeding. To account for this, we also used a more conservative approach to analyse effects of feeding sites. We first produced weighted averaged GLMM in a similar manner as described above, but without including the variable "distance to the feeding site" (conservative GLMM; Appendix A). Thus all explained variances connected with the bear densities, including variance potentially resulting from hunters placing feeding sites in more suitable habitats for bears (which might otherwise be attributed to the effect of supplemental feeding), was allocated to the variable "local bear density". Next, we calculated predicted probabilities of kleptoparasitic event for each lynx kill site from the conservative GLMM and subtracted them from observed values (whether the kleptoparasitic event took place or not). Thus we obtained residual values from the conservative GLMM, which range from −1 to 1 and where negative values indicate that actual probability of kleptoparasitism was overestimated and vice versa. If presence of a feeding site affected the probability of kleptoparasitism, the residual values should decrease with the distance to the feeding site. Due to non-linear effects of feeding sites on bear habitat use (see above), we used rank non-parametric correlation to test for relationships between residual values and distance to the nearest feeding site. We also visually inspected the residuals by dividing them in five classes (each containing the same sample size) in respect to the distance to the closest feeding site and for each class calculated average residual values and CI (for $p = 95\%$).

3. Results

We found 117 lynx kill sites among which 81 were suitable for further analysis. The probability of a lynx kill being usurped by bears was affected by local bear density, bear movement rates for a given month, their interaction (total bear path length), and distance to the nearest bear feeding site (Table 1, Figs. 2 and 3). The best model explaining the probability of kleptoparasitism included distance to the feeding site and total bear path length (Nagelkerke $R^2 = 0.27$). Four additional candidate models with combinations of local bear density, movement rate, total bear path length, and distance to the feeding site had ΔAICc scores ≤2 (Table 1). Total bear path length and distance to the feeding site were included in four out of five models and bear density and movement rate in two models. Bivariate correlation analyses revealed significant correlations between dependant variable (event of kleptoparasitism) and all independent variables ($r_{min} = 0.229$, $p < 0.05$; Appendix B).

Table 1
Parameter estimates and test statistics for the best generalised linear mixed models (ΔAICc ≤2) explaining probability of bear kleptoparasitism on lynx kills. Distance 0–500 m from the nearest feeding site served as a contrast (estimate = 0) for the remaining levels of that variable. Ω_i = model Akaike's weights; [a] refers to change from the first to the last decile of the variable.

Model	Variable	Estimate	SE (β)	Odd ratio[a]	ΔAICc	Ω_i	Nagelkerke R^2
1	Total bear path length	0.93	0.33	12.0	0	0.36	0.27
	Distance to the feeding site						
	500–1000 m	−1.00	0.86	0.37			
	>1000 m	−1.57	0.69	0.21			
2	Total bear path length	0.88	0.29	10.5	1.3	0.19	0.19
3	Bear movement rate	0.77	0.33	8.3	1.5	0.17	0.28
	Bear density	0.56	0.31	4.1			
	Distance to the feeding site						
	500–1000 m	−1.05	0.89	0.35			
	>1000 m	−1.62	0.74	0.20			
4	Total bear path length	0.76	0.44	7.6	1.7	0.15	0.28
	Bear movement rate	0.25	0.45	2.0			
	Distance to the feeding site						
	500–1000 m	−1.07	0.88	0.34			
	>1000 m	−1.70	0.74	0.18			
5	Total bear path length	0.96	0.44	13.0	2.0	0.13	0.27
	Bear density	0.05	0.41	1.1			
	Distance to feeding place						
	500–1000 m	−1.02	0.87	0.36			
	>1000 m	−1.60	0.74	0.20			
Average model	Total bear path length	0.88	0.35	10.5			0.26
	Bear density	0.56	0.31	4.1			
	Bear movement rate	0.52	0.47	4.2			
	Distance to the feeding site						
	500–1000 m	−1.03	0.87	0.36			
	>1000 m	−1.61	0.72	0.20			

Local bear densities at kill sites ranged from 0.2 to 38.6 bears/ 100 km^2 (mean 16.9 bears/100 km^2). Localities of lynx kills usurped by bears had on average 36% higher bear densities (mean: 21.0, CI: 18.1–23.9, n = 20) compared to lynx kill sites not found by bears (mean: 15.5, CI: 13.3–17.7, n = 61; Mann–Whitney U = 307.5; $p < 0.0001$).

Across the combinations of months and bear densities (while keeping the variable supplemental feeding at fixed value), the predicted probability of kleptoparasitism ranged from 8% (the lowest decile of bear densities and month with the lowest bear movement rate) to 74% (the highest decile of bear densities and month with the highest movement rate; Table 1, Average model). Inside the CBPA (average density 14.0 bears/100 km^2) the predicted probability of kleptoparasitism was 2.75-fold higher compared to the bear distribution range outside this management zone (average density 0.6 bears/100 km^2; Table 1, Model 3).

The odds of kleptoparasitism increased 4-times from areas with the lowest to the highest decile of bear densities (i.e. 8 and 28 bears/ 100 km^2, respectively; Table 1, Model 3), 8.3-times from the lowest to the highest decile of bear movement rate (1.7 and 8 km/day, respectively; Table 1, Model 3), 10.5-times from the lowest to the highest decile of total bear path length values (Table 1, Average model) and 5-times from far (>1000 m) to close (<500 m) distance to the nearest bear feeding site (Table 1, Average model).

Very similar results were obtained with a more conservative approach, when distance to the nearest bear feeding site was analysed separately, based on the residual values from the GLMM model without distance to the feeding sites (conservative GLMM; Appendix A). Probability of kleptoparasitism (residual values) decreased with distance from the feeding site (Spearman Rank Order Correlation r = −0.321, n = 81, p = 0.004), but the effects were detected only until distances were approximately 1 km from the nearest feeding site (Fig. 4). Effects of bear density, movement rate and total bear path length remained similar in the conservative GLMM (see Appendix A for exact values).

4. Discussion

In a large part of the bear distribution range, bear densities, habitat use, and movement patterns are under strong influence of management measures (Apps et al., 2004; Gosselin et al., 2015; Kavčič et al., 2015). Because bears regularly interact with other species in the ecosystem, bear management can induce cascading effects. In Slovenia, management-induced perturbations of the brown bear population affected the endangered Dinaric population of Eurasian lynx by modulating interactions between these two keystone carnivores.

The probability of lynx losing its kill to a scavenging bear was related to the local bear density and bear movement rates. The importance of the interaction between both parameters indicates that they both act multiplicatively and thus create considerable spatial and seasonal variation in interaction intensity. In our study area, the predicted probability of lynx kill being lost to bears ranged from 8 to 74% for combinations
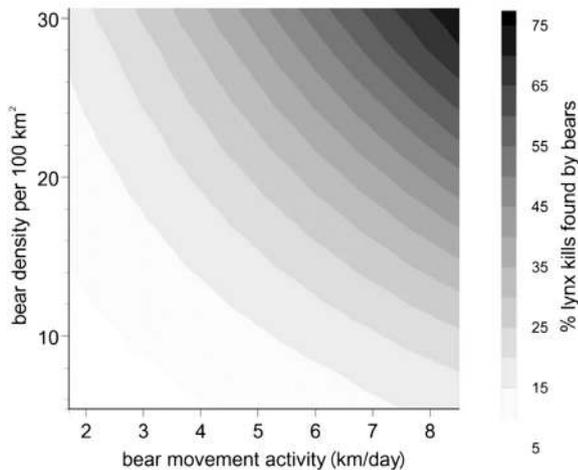

Fig. 2. Proportion of lynx kills usurped by bears during the time when carcass was still being used by lynx in relation to the local (1 km^2) bear density and average monthly bear movement rate within the range observed in the Dinaric Mountains in Slovenia.
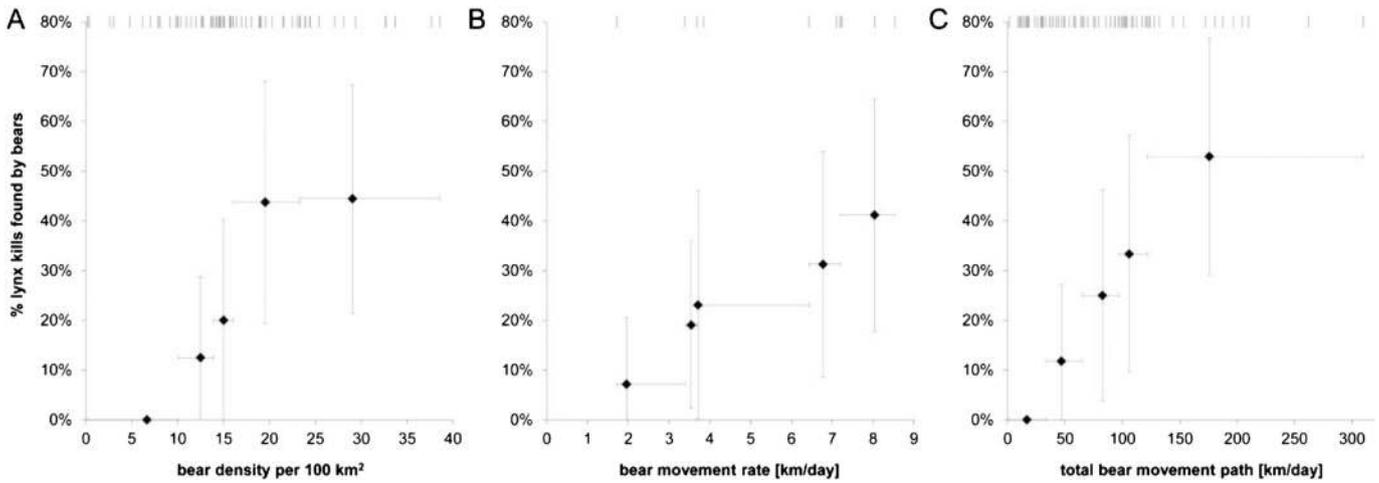
Fig. 3. Proportion of lynx kills usurped by bears during the time when carcass was still being used by lynx in relation to the local (1 km²) bear density (A), average monthly bear movement rate (B), and interaction (product) between bear density and movement rate (total bear path length; C). Vertical bars indicate confidence intervals ($p = 0.95$), horizontal bars indicate limits of given class (each containing equal sample size), and lines on top indicate sample distribution in the gradient of independent variable.

of months and lynx distribution range. These results provide strong support that by affecting bear densities, managers indirectly influence the amount of food that lynx lose due to bear kleptoparasitism. In Slovenia, bear densities have been strongly regulated by zone-specific hunting regimes for many decades and about 20% of the population is culled annually (Krofel et al., 2012b). At the same time, the supplemental feeding in the CBPA zone provides 34% of the total dietary energy content ingested by bears, which is believed to be the reason for one of the highest observed concentrations and reproductive rates for brown bears worldwide (Kavčič et al., 2015). Zone-specific bear management thus created remarkably varied conditions for lynx regarding their interactions with bears. For example, for a lynx living inside the CBPA the predicted probability of losing kill to a bear is almost 3-fold higher compared to a lynx living in the bear distribution range outside this management zone.
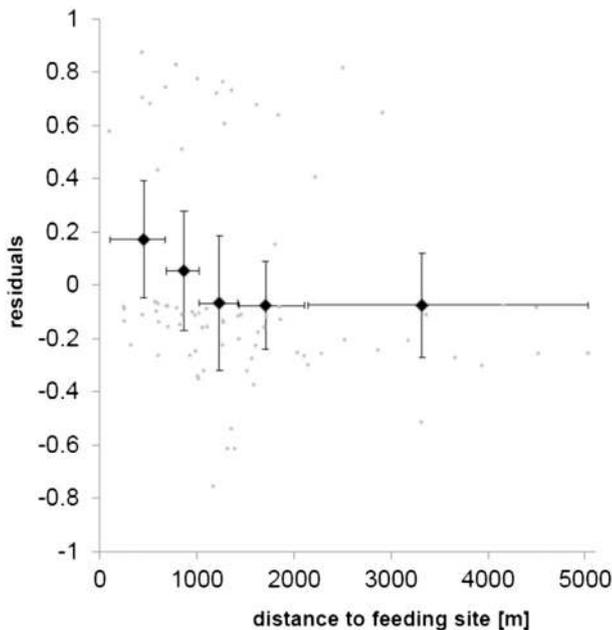

Fig. 4. Residual values from the generalised linear mixed model explaining probability of bear kleptoparasitism on lynx kills in relation to distance from the nearest bear feeding site. Vertical bars indicate standard deviation and horizontal bars limits of each class.

Furthermore, we observed that supplemental feeding of bears modulated bear–lynx interactions even beyond the effects on local bear densities. When controlling for bear densities at 1 km² scale, the presence of bear feeding sites locally increased odds for kleptoparasitism 5-fold. This probably reflects changes in the use of space by bears induced by supplemental feeding, which has already been observed in a bear telemetry study (Jerina et al., 2012). The strongest effects of feeding site presence were detected only up to a 675 m radius (Fig. 4). However, when the high density of these sites is considered (on average one feeding site per every 2.7 km²), a substantial (45%) part of the CBPA is thus affected. Therefore, by avoiding the vicinity of bear feeding sites, lynx could substantially reduce its vulnerability to kleptoparasitism. Further research will be needed to test whether lynx actually adjust their hunting efforts in respect to the distribution of the bear feeding sites and local bear densities. Elsewhere, for example, it has been observed that cheetahs (*Acinonyx jubatus*) avoid hunting in areas with higher densities of lions, which regularly usurp cheetah kills (Cooper et al., 2007).

In addition to affecting local bear densities and space use, supplemental feeding could affect lynx-bear interactions through its impact on bear movement rates, which had a similar importance as bear density in our study. On one hand, the presence of abundant human-provided food can reduce the amount of daily activity of bears (Beckmann and Berger, 2003), which would decrease the probability of kleptoparasitism. On the other hand, overall annual movement activity in bears is strongly affected by the length of the denning period, which can last over 7 months for brown bears (Manchi and Swenson, 2005) and it has been shown that availability of human-provided food reduces the time period bears spend in a den (Beckmann and Berger, 2003). Compared to the neighbouring region in Italy, where no supplemental feeding is practised, bears in Slovenia were observed to shorten their denning period by 20% (Kavčič et al., 2015; Krofel et al., 2013a).

Pigeon (2011) showed that climate change caused a shortening of the bear denning period in Alberta. The strong connection between bear movement activity and interaction intensity observed in our study thus indicates the possible effect of predicted future climate change on interspecific interactions among large carnivores. Similarly, since the bear denning period generally increases towards northern regions (Manchi and Swenson, 2005), we expect that potential for kleptoparasitism decreases with latitude. At the same time, bear densities are typically substantially lower in northern regions (Jerina et al., 2013). A combination of lower densities and a longer denning period probably best explains why the frequency of lynx–bear kleptoparasitic interactions in Sweden (Mattisson et al., 2011) is 94% lower compared to our study area.

4.1. Conservation and management implications

Human-caused perturbations of interspecific interactions between Eurasian lynx and brown bears could have important implications for lynx conservation and management of its prey. Apex predators are thought to often function close to physiological energetic limits (Gorman et al., 1998; but see Scantlebury et al., 2014). Thus, additional energetic pressure due to increased prey losses, which can be substantial in the case of Eurasian lynx, in combination with higher risk of injuries due to increased hunting rate, could have demographic effects on lynx populations (Krofel et al., 2012a). This may be especially important for threatened populations, which already suffer from other serious threats, such as inbreeding and poaching in the case of the Dinaric population (Sindičić et al., 2013).

We suggest that including the effects of kleptoparasitism in conservation actions for Eurasian lynx populations coexisting with bears where bear densities are high (e.g. Dinaric, Balkan, and Carpathian lynx populations) could benefit lynx recovery programmes. For example, when funds for conservation are limited, more effort could be focused on areas with lower bear densities (given that there are no differences in other threats), where there is a better chance of preserving at least part of the predator population. A similar recommendation can be used when planning reintroduction of a potentially vulnerable carnivore.

In response to kleptoparasitism, lynx in Slovenia compensate losses by increasing their kill rate by 23% (Krofel et al., 2012a). We suggest that wildlife managers should take into account scavenger-driven cascading effects in predator–prey interactions and appropriately adjust management of prey species when needed.

Since scavenging is an important natural process, we believe that it would be unwise to attempt to prevent this interaction (e.g. by radical culling of dominant scavengers), as this would contradict the general premise of nature conservation, which strives to preserve the ecological integrity of ecosystems and their processes (Ray et al., 2013; Ripple et al., 2014). Moreover, dominant scavengers like bears are often protected and threatened themselves. However, we do urge managers and conservationists to pay attention not to artificially increase local scavenger densities without considering indirect effects of management measures on apex predators and other species directly or indirectly affected by dominant scavengers. Several conservation initiatives already led to overpopulation of some large carnivores, especially when populations were confined to small reserves (Hayward et al., 2007). Even more common are superabundant scavenger communities due to human-provided foods, which can create local high concentrations of facultative scavengers (Cortes-Avizanda et al., 2009; Selva et al., 2014). The observed impact of bear supplementary feeding on endangered Eurasian lynx population in Slovenia provides another caution against uncritical promoting of supplementary feeding practices. In the case of Slovenia we recommend that bear feeding intensity should be reduced, which could be achieved by gradual reduction in the number of feeding sites or the amount of food provided per site, especially in the season of increased kleptoparasitic interactions and during the bear denning period.

Since bears throughout the world are actively managed through hunting, reintroductions, and supplemental feeding or baiting (Clark et al., 2002; Kaczensky et al., 2013; Kavčič et al., 2013), effects similar to those observed in our study could be expected also for other predators and scavengers that co-exist with healthy bear populations, such as cougars in North America, tigers (*Panthera tigris*) and leopards (*Panthera pardus*) in Asia, and wolves throughout the Holarctic. In addition to bears, other dominant scavengers can also importantly affect apex predators (Cooper, 1991; Gorman et al., 1998; Jedrzejewska and Jedrzejewski, 1998), indicating a general need for wildlife managers to broaden their focus from single-species management to community- or ecosystem-focused approach and include evaluation of potential cascading effects of their management plans into decision-making processes, especially when managing dominant scavengers, apex predators, and other strongly interacting species.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.02.019.

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Appendix A: Mind the cat: Conservation management of protected dominant scavenger indirectly affects an endangered apex predator

Miha Krofel, Klemen Jerina

Table A.1: Parameter estimates and test statistics for the average generalised linear mixed model explaining probability of bear kleptoparasitism on lynx prey with excluded effects of distance to the closest bear feeding site ("conservative GLMM"). [a] for change from the first to the last decile of the variable.

Model	Variable	Estimate	$SE (\beta)$	Odd ratio[a]
Average model	Total bear path length	0.83	0.33	9.3
	Bear density	0.52	0.41	3.8
	Bear movement rate	0.58	0.30	5.1

Appendix B: Mind the cat: Conservation management of protected dominant scavenger indirectly affects an endangered apex predator

Miha Krofel, Klemen Jerina

Values of the continuous variables (bear movement rate, bear density, and total bear path length) were non-normally distributed, one variable was ordinal (distance to the nearest feeding site) and one variable was binary (event of kleptoparasitism). To construct correlation matrix we used: Spearman's rho (for pairs of continuous variables), point-biserial correlation (for pairs of binary and continuous variables) and Kendall's tau b correlation (for pairs of binary and ordinal variables).

Table B.1: Correlation matrix for the relationships among the dependent variable (event of kleptoparasitism) and predictor variables. * correlation is significant at the 0.05 level (2-tailed). ** correlation is significant at the 0.01 level (2-tailed).

	Bear movement rate	Bear density	Total bear path length	Distance to the feeding place	Event of kleptoparasitism
Bear movement rate	1.000	0.225*	0.793**	0.142	0.229*
Bear density	0.225*	1.000	0.707**	-0.130	0.314**
Total bear path length	0.793**	0.707**	1.000	0.025	0.340**
Distance to the feeding place	0.142	-0.130	0.025	1.000	-0.437**
Event of kleptoparasitism	0.229*	0.314**	0.340**	-0.437**	1.000