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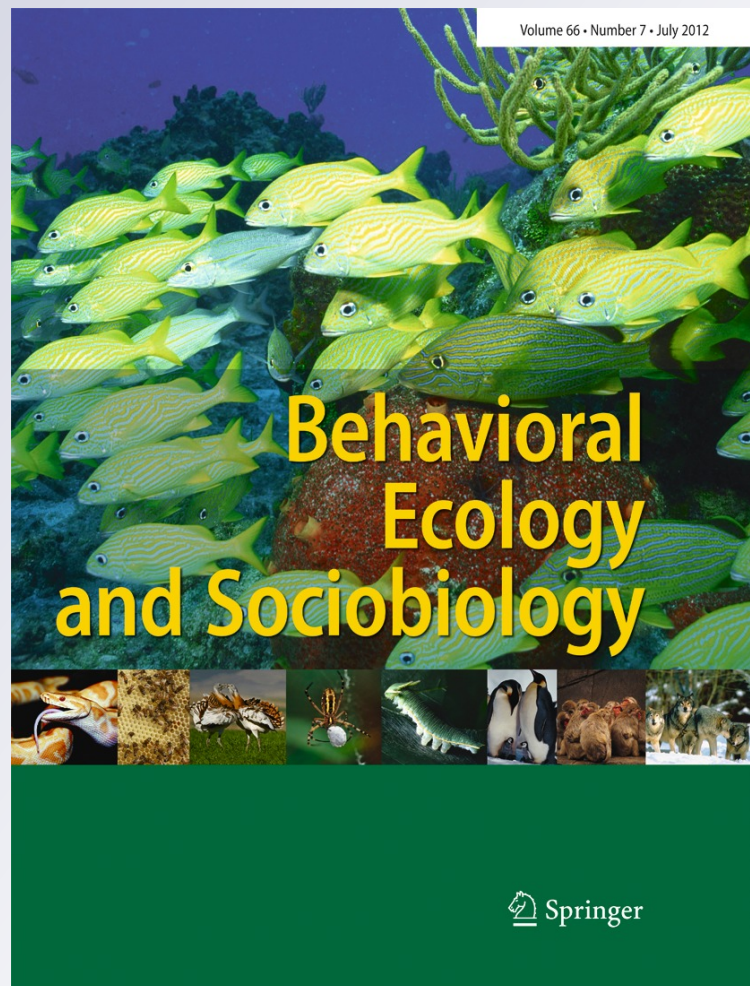
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The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators

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Abstract Scavenging is an important but poorly understood ecological process. Dominant scavengers can impose a selection pressure that alters the predator's fitness, morphology, behavior, and ecology. Interactions between ursids, likely the most important dominant scavengers in the Holarctic region, and solitary felids, which are characterized by long feeding times, provide a good opportunity for studying the effects of kleptoparasitism by dominant scavengers. We analyzed the effects of scavenging by brown bears *Ursus arctos* on Eurasian lynx *Lynx lynx* and predator's response to kleptoparasitism in a European temperate forest ecosystem. Bears found 32 % of lynx prey remains and 15 % of all biomass of large prey killed by lynx was lost to bears. In response, lynx increased their kill rate by 23 % but were able to compensate for only 59 % of the losses. The frequency of bear scavenging was strongly dependent on bear activity patterns and was highest during the lynx pregnancy and lactation period, when up to half of lynx kills were usurped by bears. We suggest that ursid scavenging, by promoting the hunting of smaller prey, may have played an important role in the evolution of the *Lynx* genus as well

as other predators in the Holarctic. Our study indicates that prey loss to dominant scavengers is a widespread phenomenon among felids worldwide, including forest habitats. We highlight several implications of scavenging that could considerably improve our understanding of the ecology of vertebrate communities and the evolution of predators as well as benefit the future management and conservation of endangered predators.

Keywords Competition · Interspecific interactions · Kleptoparasitism · *Lynx lynx* · Temperate forest · *Ursus arctos*

Introduction

Carrion use by facultative scavengers is a key ecological process that has a strong influence on food webs (DeVault et al. 2003; Wilson and Wolkovich 2011). Nevertheless, scavenging is still poorly understood and it is also considerably more prevalent than widely assumed (Wilson and Wolkovich 2011). Scavenging includes feeding on the remains of prey killed by predators. This interaction, known as kleptoparasitism, or food stealing, is a ubiquitous and widespread phenomenon, both taxonomically and across ecosystems (Iyengar 2008). Although it has been frequently recorded in mammals (Creel et al. 2001; Ballard et al. 2003), extensive quantitative studies are rare (Iyengar 2008). Available studies suggest that scavenging may affect the prey selection (Jędrzejewski et al. 1993; Hebblewhite and Smith 2010), hunting behavior (Caro 1994), social systems (Cooper 1991; Vucetich et al. 2004), and evolution of predators (Iyengar 2008). In certain situations, scavenging may even represent a threat to endangered predators (Carbone et al. 1997; Gorman et al. 1998).

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Besides group size, body size is an important factor in determining the outcome of interspecific interactions among predators and scavengers (Palomares and Caro 1999; van der Meer et al. 2011). Large, dominant scavengers that can easily usurp food resources could have a large impact on predators. It has been suggested that kleptoparasitism by dominant scavengers can greatly affect the fitness of subordinate species, and over evolutionary time spans, dominant competitors can impose a selection pressure that alters the subordinate's morphology, behavior, and ecology (Creel et al. 2001; Stankowich et al. 2011). As the largest terrestrial scavengers, bears are potentially one of the most important mammalian kleptoparasites in the Holarctic region. Bears have an acute sense of smell, and many species of ursids readily use mammalian carcasses when available (Mattson 1997; Derocher et al. 2002; Herrero 2002; Ballard et al. 2003). Because of their large size, bears can almost always displace predators from their kills (Mattson 1997; Murphy et al. 1998). It has often been speculated that scavenging by bears could greatly affect the prey utilization and kill rates of predators (e.g., Wilton 1986; Ballard et al. 2003; Krofel and Kos 2010). Nevertheless, and despite the wealth of studies on large carnivore ecology in Europe and North America, empirical data on the effects of bear scavenging are rare (e.g., Murphy et al. 1998).

Solitary felids that hunt large prey provide a good opportunity for studying the effects of scavenging on predators because of their prolonged consumption process (Stander et al. 1997; Jobin et al. 2000), which theoretically makes predators more susceptible to scavengers (Stillman et al. 1997). Most felids can defend their kill when confronted with small and mid-sized scavengers (Palomares and Caro 1999; Jobin et al. 2000), but they are defenseless against confrontations with larger scavengers such as bears. Eurasian lynx (*Lynx lynx*), which is the largest member of its genus, is a specialized predator of small ungulates and has a feeding time lasting several days for each kill (Breitenmoser and Breitenmoser-Würsten 2008). Its distribution range originally overlapped extensively with that of the brown bear (*Ursus arctos*), and the two species have coexisted for over 400,000 years in some areas (Kurtén 1968; Werdelin 1981). Yet, interactions between these two large carnivores remain poorly understood. In this study, we analyzed the effects of scavenging by brown bears on an endangered population of Eurasian lynx in a temperate forest ecosystem in the Dinaric Mountains of Slovenia and Croatia, where the two species still coexist.

We determined the proportion of lynx kills found by bears and quantified the amount of biomass lost to scavenging bears. In addition, we tested whether lynx respond to scavenging by increasing hunting effort and estimated the extent to which lynx are able to compensate for the losses by increasing their kill rate. We also monitored movement of

bears throughout the year to determine if, and to what extent, the frequency of kleptoparasitic interactions depends on bear activity patterns. The results are discussed in the context of evolutionary implications for solitary predators influenced by dominant scavengers. We also review studies on the effects of dominant scavengers on felids and draw attention to the importance of scavenging for the conservation of endangered predators, and the understanding of how vertebrate communities function.

Materials and methods

Study area

The study was conducted in the northern part of the Dinaric Mountains in Slovenia and Croatia (45°24'–45°47'N and 14°15'–14°50'E; Central and Southeastern Europe) in mixed temperate forests dominated by fir and beech associations (Omphalodo-Fagetum s. lat.). The altitudes range from approximately 168 m to the peak of Mount Snežnik at 1,796 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 1,400–3,500 mm. According to analysis of lynx scats and kill remains, the main prey in the area is European roe deer (*Capreolus capreolus*), and the most important alternative prey edible dormouse (*Glis glis*), representing 79 % and 7 % of biomass consumed by lynx, respectively (Krofel et al. 2011). During our study, roe deer represented 95 % of ungulates killed by lynx; other recorded ungulate prey species included red deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*), and livestock. The average density of brown bears in most of the lynx range in Slovenia is estimated at 12 bears/100 km² (K. Jerina et al., unpublished data).

Fieldwork

We used snow-tracking and location cluster analysis of telemetry data (Merrill et al. 2010) to locate carcasses of ungulates killed by lynx. 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). We usually visited these kill sites the day after lynx abandoned the kill (median—4.5 days after the kill), but on some occasions we arrived earlier to install the video system at the kill site. Only carcasses of roe deer were included in this study. We excluded from further analysis 9 % of the roe deer carcasses for which the presence of potential scavengers could not be determined (because only small parts of the carcass or hair were found, with no other signs of the

presence of scavengers) or the carcass was too old. Because the absence of a carcass could have been due to its removal by bears, we believe that our estimate of the effects of bear scavenging on lynx is conservative. To gain a better understanding of the effects of bear kleptoparasitism, we also excluded kills that were used by other large scavengers during lynx consumption (gray wolves *Canis lupus* or wild boars *Sus scrofa*) or removed by people. Some kills were also monitored by an automatic digital video system with an infra-red light and automatic picture analyzer mounted at least 2 m high on a tree (e.g., see video clip in Online Resource 1). The video recordings did not indicate that the presence of the video system affected the behavior of lynx or any of the scavengers.

Lynx predation, lynx prey consumption, and seasonal differences in bear movements were studied using telemetry. In the period 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 (Krofel et al. 2010). GPS collars were scheduled to attempt seven to eight GPS fixes per day for lynx and 12–24 fixes per day for bears. Bears were captured and monitored throughout the year for an average of 257 days, while most of the lynx were captured during winter and monitored for an average of 166 days. Sample sizes for lynx were therefore lower for autumn.

Data analysis

To estimate changes in lynx kill rate and the amount of biomass lost to scavenging bears, we further analyzed data on prey killed by lynx equipped with telemetry collars. For analysis, we distinguished between kills that were visited by bears and those showing no signs of bear presence. For each prey item, we calculated the feeding time and search time. We defined the feeding time as the period between when the prey was killed and when lynx abandoned the kill. We used feeding time as a measure of lynx food intake per kill. The search time was defined as the period between the abandonment of current prey item and the next kill. The timing of these events was estimated to 0.5-day precision. The kill rate was defined as the number of ungulates killed per unit time and was calculated from the average time between consecutive kills (feeding time+search time). In six cases, females with kittens fed at the same kill. None of the prey remains were found by bears in these cases. Due to the higher consumption rate of multiple lynx, we made a correction based on the age and number of kittens and data provided by Jobin et al. (2000). The only case when two adult lynx were feeding from the same kill during breeding period was not included in the analysis.

We estimated lynx biomass consumption (or biomass lost to bears) from the number of days lynx had (not) fed on a kill, multiplied by the average ingested biomass per feeding day (3.3 kg/day) provided by Jobin et al. (2000) for lynx originating from the same population as the lynx in our study area. Data on average energetic requirements (2 kg/day) were also obtained from Jobin et al. (2000) and used in the calculations of the importance of these losses for lynx. Because the data were not normally distributed and a series of standard transformations failed to transform these data to a normal distribution, we used non-parametric Wilcoxon rank sum test to test differences in feeding times, search times, and kill rate between lynx kills found by bears and kills showing no signs of bear presence.

To analyze monthly differences in the proportion of lynx kills found by bears, we grouped data for each month except the months between August and December, which were pooled into one group to achieve a sensible sample size (min. 5 units) for further analyses. The proportion of kills found by bears was correlated with bear movement for each period. Bear movements were calculated from 89,917 GPS bear locations by measuring the average straight-line distance between consecutive GPS locations taken 1 h apart.

Results

We found 104 lynx kills in the period 1996–2012 of which 83 roe deer carcasses were used for further analysis. For 50 kills, lynx feeding and predation were monitored by telemetry, and 11 of these were also monitored by video surveillance for a total of 1104 h.

Bears usurped 30 % (25 of 83) of lynx kills, including 27 % (three of 11) of those monitored by video surveillance. After bears scavenged the kills, the only parts of the carcasses that remained were pieces of bone and skin, and nothing was left over that could have been consumed by lynx. In all three cases of kleptoparasitism recorded on video, bears consumed the entire carcass in a single night (e.g., see Online Resource 1).

The proportion of lynx kills found by bears changed with the seasons and was highest in late spring and early summer (Fig. 1). Based on these seasonal differences, the predicted proportion of all lynx kills found by bears throughout the year was 32 %. The proportion of lynx kills found by bears was closely correlated with monthly bear movements ($r=0.885$, $P=0.003$, $n=8$; Fig. 1).

Mean feeding time (\pm SD) was 47 % shorter for kills that were found by bears compared with kills showing no signs of bear presence (2.3 ± 1.3 days and 4.4 ± 1.4 days, respectively; $W=444$, $P<0.0001$, $n=46$; Fig. 2a). This difference corresponds to 6.7 kg of ingested biomass per kill or 3.3 times the average daily requirement for lynx. Based on our

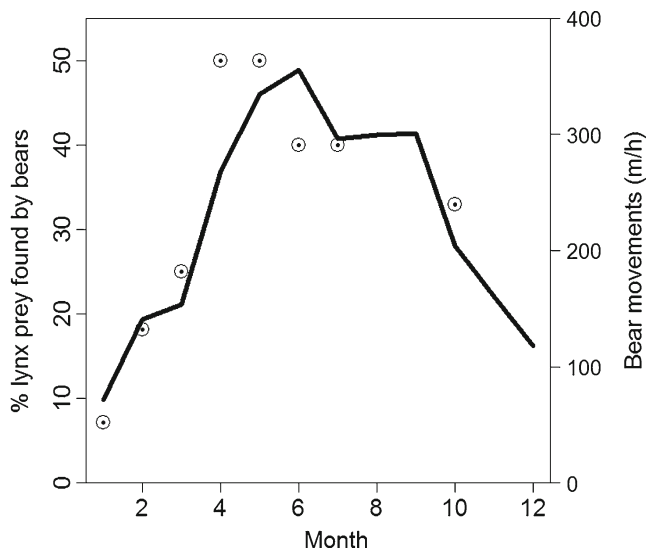


Fig. 1 Proportion of Eurasian lynx kills found by brown bears ($n=82$; line) and mean moving rate of bears ($n=89,917$ GPS locations; points) in different months in the Dinaric Mountains (Slovenia and Croatia). Because of the small sample size of monitored kills from August to December, data for the proportion of kills found by bears were grouped for this time period

data on the proportion of kills found by bears, the total annual losses for lynx due to bear scavenging amounts to 14.9 % of all biomass of deer killed by lynx, assuming lynx do not compensate by increasing kill rate.

Lynx search times after kills were usurped by bears and after kills with no signs of bear presence were similar (4.1 ± 3.7 days and 3.9 ± 3.1 days, respectively; $W=189$, $P=0.98$, $n=45$; Fig. 2b). Thus, the increase in kill rate was only due to shorter feeding times (one deer killed per 6.6 ± 4.3 days for kills found by bears and 8.1 ± 3.9 days for kills with no bear signs; $W=226$, $P=0.17$, $n=43$; Fig. 2c). However, because of the relatively long time needed to kill new prey (3.9 days on average), lynx were able to use this extra time to compensate for only 59 % of the losses. Thus, there was a net loss of 6.1 % of all biomass from the deer killed by lynx, which corresponds to 39 kg of consumable biomass per year.

Discussion

We have shown that brown bears find about one third of deer killed by lynx and that scavenging by bears considerably affects the prey utilization of Eurasian lynx. The large amount of edible biomass lost indicates that bear scavenging represents a substantial energetic loss for lynx. Lynx did not respond by increasing hunting efficiency after bears displaced them from their kills (search time remained the same), but, because feeding times were shorter for kills usurped by bears, lynx had extra time (2.1 days on average)

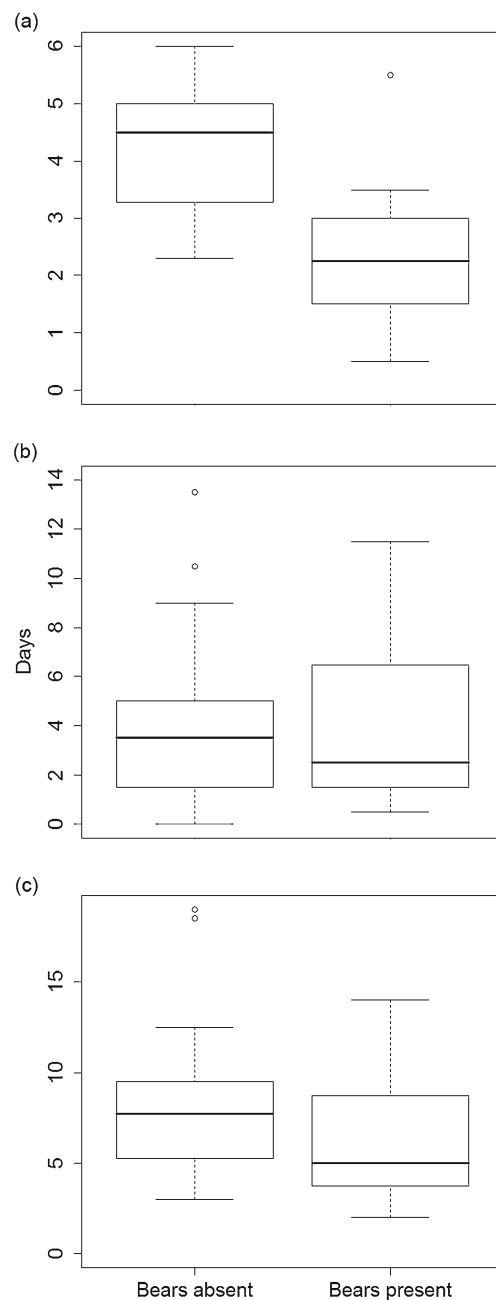


Fig. 2 Comparison of Eurasian lynx feeding times (a), subsequent search times (b), and interval between kills (c) in relation to the presence of brown bears at lynx kill sites in the Dinaric Mountains (Slovenia and Croatia). Box plots show median (bold horizontal lines), interquartile range (box), range up to 1.5 times interquartile range (bars), and outliers beyond 1.5 times interquartile range (circles)

for hunting. However, because of the long search times needed to capture the next prey item, lynx were only able to compensate for 59 % of the losses by increasing their kill rate. Consequently, lynx still lost approximately 39 kg of consumable biomass annually. It should also be noted that the increase in kill rate comes with additional costs to lynx, such as increased energetic expenditure and increased risk

of injuries, which can be an important mortality factor for solitary felids hunting large prey in forest habitats (Ross et al. 1995). Thus, the total cost of bear scavenging to lynx is probably even higher.

Most facultative scavengers use carrion more frequently during winter (Jędrzejewska and Jędrzejewski 1998; Selva et al. 2005). We observed a different pattern for brown bears, with the highest frequency of scavenging between April and July. Kleptoparasitism was strongly correlated with bear activity patterns, with the peak in scavenging coinciding with periods of high movement rates. Increased movement in late spring and early summer is partly connected with bear mating, as males and estrous females actively search for mating partners at this time (Dahle and Swenson 2003; Krofel et al. 2010). However, we also observed increased movement during this period among non-mating bears (K. Jerina and M. Krofel, unpublished data), indicating that other reasons also seem to be important. Our results confirm previous observations that the activity of scavengers can affect the extent of kleptoparasitism (van der Meer et al. 2011). In bears, this observed specific seasonal behavioral pattern probably leads to even more negative effects for the host because lynx sustains the highest losses to scavenging in the late gestation and the lactation period, before kittens start following the mother to feed on kills. During this time, up to 50 % of lynx kills were lost to bears. Energy requirements are higher for females in the late gestation and lactation periods, and it has been shown that food availability affects reproductive success in Eurasian lynx (Jędrzejewska and Jędrzejewski 1998; Nilsen et al. 2012).

Beside breeding females, we can also expect bear scavenging to have larger effects on subadult lynx because they have the longest feeding times. Thus, bear kleptoparasitism could have the most pronounced effects on the lynx population through decreasing lynx reproduction and recruitment. This could be an important additional constraint for populations that are already threatened by human-related factors (e.g., poaching, vehicle collisions, depleted prey base) or/and by inbreeding, as is also the case for the Dinaric lynx population (von Arx et al. 2004).

Beside predators, dominant scavengers such as bears probably also affect other members of scavenger guilds. Because bears consume carcasses so rapidly, areas with high bear density could see the availability of large carcasses decrease to the extent that scavenger community structure is affected. On the other hand, prey remains left behind by predators represent an important food source for competitively dominant scavengers. For bears, these remains may be especially important in spring, when little other food is available and their energy stores are depleted after hibernation. It is therefore not surprising that this period coincided with higher use of lynx kills.

In general, kleptoparasitism intensity increases with scavenger density (Stillman et al. 1997; van der Meer et al. 2011; but see Creel et al. 2001). At the northern edge of the brown bear distribution range in Europe, where bear densities are relatively low, Mattisson et al. (2011) rarely documented bear scavenging on monitored carcasses. The frequency of scavenging was considerably higher in our case, where the higher bear densities are probably more similar to those in most other parts of the brown bear distribution range. Similarly, Hebblewhite and Smith (2010) reported that practically all recorded wolf kills were usurped by bears in a part of Yellowstone National Park with very high grizzly bear densities. It is therefore reasonable to assume that future bear management, through changes in bear densities and consequent impacts on scavenging frequency, would affect Eurasian lynx, although a direct connection between bear densities and the extent of lynx losses has yet to be confirmed. Increase in bear scavenging could also occur with shortening of the bear denning period, which is predicted with future climate change (Pigeon 2011).

In our case, the brown bear was by far the most important dominant scavenger for lynx, but we expect that similar principles also apply to other dominant scavengers such as wild boar and gray wolf, which were recorded at 4 % and 1 % of lynx kills, respectively. Wild boar, in particular, could be an important scavenger for lynx since it can reach very high densities in some regions. An effect similar to that of scavenging by dominant scavengers also occurs when people remove fresh kill remains, and such human kleptoparasitism seems to be relatively common in some parts of the lynx range (Krofel et al. 2008). Scavenging by smaller scavengers differs importantly from that by dominant scavengers because the predator can usually continue feeding after scavenging and can defend its prey, although subordinate scavengers can still sometimes remove considerable amounts of biomass (Vucetich et al. 2004; Mattisson et al. 2011).

It is generally assumed that kleptoparasitism is more intense in open habitats (Creel et al. 2001), but this study and other recent research have shown that scavenging on the kills of predators is also prevalent in forest ecosystems (Selva et al. 2003, 2005; Krofel 2011; Mattisson et al. 2011). Although the number of studies is still rather limited, especially for forest habitats, a review of available papers suggests that prey loss to dominant scavengers might be a general pattern among felids in different habitats throughout the world (Table 1).

Some studies have pointed out that kleptoparasitism can be a major driving force in the evolution of the morphology and behavior of subordinate competitors (Iyengar 2008). Our results indicate that bears may be one of the most important scavengers in temperate forests and that bear scavenging plays a more important role in vertebrate

Table 1 Frequency of scavenging and estimated biomass lost to dominant scavengers by felids

Host	Scavenger(s)	Study area	Habitat	Proportion of kills found by scavenger	Proportion of kills usurped by scavenger	Estimated biomass lost
<i>Acinonyx jubatus</i>	<i>Crocuta crocuta</i> , <i>Panthera leo</i>	Kruger, South Africa ^a	Open savannah	12 %	12 %	–
	<i>Crocuta crocuta</i> , <i>Panthera leo</i>	Mala Mala, South Africa ^b	Woodland–open savannah	10 %	10 %	–
	<i>Crocuta crocuta</i>	Serengeti, Tanzania ^c	Open grassland	12 %	9 %	9.2 %
	<i>Panthera leo</i>			2 %	2 %	–
	<i>Panthera leo</i>	Kwandwe, South Africa ^d	Open–bush savannah	3 %	3 %	–
<i>Panthera leo</i>	<i>Crocuta crocuta</i>	Chobe, Botswana ^e	Open grassland	79 %	16 %	8.6 %
	<i>Crocuta crocuta</i>	Etosha, Namibia ^f	Open grassland–woodland	–	0 %	–
<i>Panthera pardus</i>	<i>Crocuta crocuta</i>	Kruger, South Africa ^g	Open–bush savannah	52 %	–	–
	<i>Crocuta crocuta</i> , <i>Lycaon pictus</i> , <i>Panthera leo</i> , <i>Panthera pardus</i>	Kalahari, NE Namibia ^h	Woodland–shrub savannah	12 %	3 %	–
<i>Puma concolor</i>	<i>Canis lupus</i>	Banff, Canada ⁱ	Mixed forest–grassland	27 %	11 %	–
	<i>Ursus arctos</i> , <i>Ursus americanus</i>	Glacier, USA ^j	Montane forest–grassland	15 %	7 %	– ^o
	<i>Ursus arctos</i> , <i>Ursus americanus</i>	Yellowstone, USA ^j	Montane forest–grassland	33 %	12 %	–
<i>Lynx lynx</i>	<i>Sus scrofa</i>	Białowieża, Poland ^k	Mixed temperate forest	40 %	–	“about 10 %”
	<i>Ursus arctos</i>	Sarek, Sweden ^l	Boreal forest–tundra	2 %	–	–
	<i>Ursus arctos</i>	Dinaric Mts., Slovenia and Croatia ^m	Mixed temperate forest	32 %	32 %	14.9 %
	<i>Sus scrofa</i>			4 %	2 %	–
	<i>Homo sapiens</i>	SE Norway ⁿ	Boreal forest–agricultural land	14 %	1 %	–

^a Mills et al. 2004^b G.T. Randloff, unpublished data (cited in Mills et al. 2004)^c Caro 1994 and Hunter et al. 2007^d Bissett and Bernard 2007^e Cooper 1991^f Trinkel and Katsberg 2005^g Bailey 1993^h Stander et al. 1997ⁱ Kortello et al. 2007^j Murphy et al. 1998^k Jędrzejewski et al. 1993 and Jędrzejewska and Jędrzejewski 1998^l Mattisson et al. 2011^m This study and M. Krofel, unpublished dataⁿ Krofel et al. 2008^o The authors estimated biomass lost to bears by cougars at 0.64 kg/day; however, the amount of edible biomass of prey killed by cougars is not given

communities than previously thought. We believe that scavenging by brown bears may have been an especially important factor in shaping prey selection for the smallest ungulate species available (smaller prey decreases feeding time and therefore the possibility of prey remains being found by bears) and consequent morphological and

behavioral adaptations during the evolution of Eurasian lynx, which, for the most part, took place in sympatry with brown bears. It is also noteworthy that in the Dinaric Mountains, diet analysis showed considerably higher use of rodents by Eurasian lynx compared with studies done in areas without or with low density bear populations and that

the use of small prey in the Dinaric Mountains was highest in females and subadults, i.e., groups predicted to be most affected by bear scavenging, and during periods of higher bear activity (Krofel et al. 2011).

Furthermore, we suggest that ursids could have also been important in the evolution of other predators, including other lynx species. Like Eurasian lynx, Iberian lynx (*Lynx pardinus*), Canadian lynx (*Lynx canadensis*), and bobcat (*Lynx rufus*) descended from a larger and more robust ancestor named *Lynx issiodorensis* (Kurtén 1978; Werdelin 1981). During evolution, which took place in sympatry with several bear species, all of the three smaller modern lynx species considerably decreased in size and became specialized for hunting lagomorphs and other small prey. It has been suggested that this was a response to competition from larger felids (Werdelin 1981). Given our results, we suggest that bear kleptoparasitism, by promoting the hunting of smaller prey, may have also played an important role in the evolution of the *Lynx* genus as well as other large and mid-sized predators in the Holarctic.

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Ethical standards The work complies with the current laws of the country in which they were performed. Procedures involving handling of lynx and bears were permitted by the Slovenian Environmental Agency (permissions no. 35601-45/2006-6 and 35601-167/2008-4).

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