



A meta-analysis of ungulate predation and prey selection by the brown bear *Ursus arctos* in Eurasia

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Abstract

At the biogeographic scale, spatial variation in diets may reflect not only the ecological flexibility of carnivore feeding habits, but also evolutionary adaptations of different populations within a species. We described the large-scale pattern in brown bear *Ursus arctos* predation on ungulates, its selectivity for ungulate species, and its relative role in ungulate mortality. We collated data from 63 studies in Europe and Asia and analyzed them in relation to annual temperature. Ungulate meat makes up, on average, 8.7% of brown bear diets, with European bears feeding on ungulates more (mean 10.5%) than Asiatic bears (6.8%). In Europe (but not in Asia), the percentage share of ungulates in bear diet was negatively related to the mean annual temperature. Northern populations of Asian bears consumed less ungulate meat than the respective populations in Europe, because of the widespread occurrence of Siberian pine *Pinus sibirica* and dwarf Siberian pine *Pinus pumila*, which produce relatively large, protein-rich seeds. In both continents, ungulates peak in the diet of bears in spring. Brown bears' preference for 10 species of ungulates increased with body mass of prey. The bear significantly preferred preying upon moose *Alces alces* throughout its range. Bears were the most important predator of moose and caused, on average, 23% of total natural mortality in moose populations. Brown bear preference for moose and its dominant role in moose mortality suggest an evolutionary predator–prey relationship between these two species. Brown bears illustrate that even an apparently omnivorous predator can prefer one prey species.

Keywords Biogeographical variation · Carnivory · Annual temperature · Seasonal variation in diet · Prey preferences · Ungulate mortality

Introduction

Plasticity in predator feeding habits is an essential factor in the relative roles of top-down versus bottom-up forces in shaping the abundance of herbivorous mammals (Jędrzejewska and

Jędrzejewski 1998). At the scale of local populations, variation in dietary (functional) and numerical responses of predators to changes in prey abundance, theoretically places carnivore species on a gradient from specialist to generalist (Holling 1959; Andersson and Erlinge 1977), with presumed different consequences for their impact on prey numbers and population dynamics (Sinclair 1989; Messier 1995; Jędrzejewska and Jędrzejewski 1998). However, reviews of prey preferences of large predators to date have only revealed one “generalist” predator—the spotted hyaena *Crocuta crocuta* (Hayward 2006). At the biogeographic scale, such as the continental range of a species, spatial variation in diets may reflect not only the ecological flexibility of carnivore feeding habits, but also evolutionary adaptations of different populations within a species (e.g., Arctic fox *Alopex lagopus*, Dalén et al. 2005; European wolves *Canis lupus*, Jędrzejewski et al. 2012; Canadian wolves, Stronen et al. 2014).

Local population-level, temporal variation in carnivore diet and predator impact on prey populations has received great

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attention in ecological studies. However, the biogeographic-scale variation has rarely been studied, although meta-analyses of data on several species of carnivores have been published (e.g., Eurasian lynx *Lynx lynx*, Jędrzejewski et al. 1993; badger *Meles meles*, Goszczyński et al. 2000; pine marten *Martes martes*, Zalewski 2004; dhole *Cyon alpinus*, Hayward et al. 2014). Recent findings show that top-down forces (predation by large carnivores) have a greater effect on ungulate population density in less productive habitats (e.g., European roe deer *Capreolus capreolus*; Melis et al. 2009). Therefore, our understanding of the mechanisms that mediate top-down (predation impact) and bottom-up interactive effects in food resources has been improved. These interactions arise from large-scale variation in predator ecology and/or compensatory abilities of prey populations.

The brown bear *Ursus arctos* is a suitable species for studying the variation in the carnivory level at the global scale. Although omnivorous, brown bears are accomplished predators and scavengers, and consume meat whenever it is available. Their diets are diverse, and important components can include plant material (Mattson et al. 1991; Rode et al. 2001), honey (Kalaber et al. 1994), fungi (Mattson et al. 2002b), earthworms (Mattson et al. 2002a), ants (Makarov 1987; Swenson et al. 1999; Grosse et al. 2003), marine and landlocked salmon (Kistchinskii 1972; Seryodkin and Paczkowski 2004, 2006; Mowat and Heard 2006), small mammals (Aichun et al. 2006), large ungulates (Case and Stevenson 1991; Mattson 1997; Reynolds et al. 2002), other bear species (Boyd and Heger 2000), and even other apex predators (tigers *Panthera tigris*; Seredin et al. 2004). Livestock also provide food, through both predation and scavenging (Hell 1990; Frackowiak and Gula 1992).

When hunting for ungulates, brown bears kill prey by attacking the head and neck (Cole 1972; Hamer and Herrero 1991), and then begin feeding on the rump and viscera (Clevenger et al. 1994). Brown bears kill far more neonate and yearling ungulates than adults (White et al. 2001; Zager and Beecham 2006). They detect prey neonates by smell and then locate them with circuitous searches that can lead to the calf fleeing (Hamer and Herrero 1991). Such hunts can last over 2 h and cover distances of up to 11 km (Haglund 1968). Alternatively, bears may charge into herds several times in an apparent attempt to separate calves from their mothers (French and French 1990). However, brown bears are capable of killing ungulates as large as adult American bison *Bison bison* and European bison *Bison bonasus* (Karcov 1903; Mattson 1997).

There are genuine evolutionary benefits to carnivory for bears as the amount of meat in the diet is directly related to fitness via its influence on nutritional state and body size (Hilderbrand et al. 1999a), skull size (Mowat and Heard 2006), and ultimately litter size and population density (Reynolds and Garner 1987; Hilderbrand et al. 1999b). Despite these benefits, the amount of meat in the diet of brown

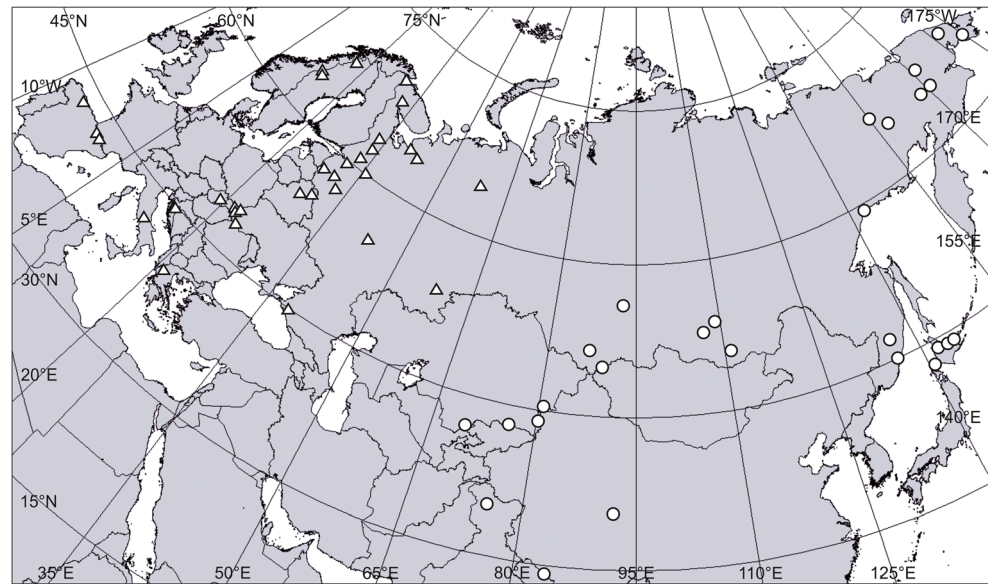
bears from Yellowstone National Park, USA, did not predict the rate of population increase (Pease and Mattson 1999). The timing of meat consumption also affects fat storage and muscle mass accumulation (Hilderbrand et al. 1999a; Rode et al. 2001). However, the brown bear is relatively poorly adapted to cursorial predation (Van Valkenburgh 1985) and strict carnivory (Van Valkenburgh 1989). Nonetheless, reviews from North America reveal that bear predation was consistently the most important mortality source accounting for up to > 90% of deaths of radio-collared neonatal ungulates, with bear predation being most important for moose *Alces alces* calves (see review in Zager and Beecham 2006).

Most investigations of bear–prey relationships deal with single species systems, focus on the prey rather than the bears, and/or are restricted to individual ecosystems (Mattson 1997). Here, we aim to review the quantitative data from the Eurasian range of brown bears to determine (1) the percentage share of ungulate meat (hunted and scavenged) in brown bear diet and its seasonal variation; (2) bear selectivity while hunting for individual ungulate species; and (3) the relative role of brown bear predation among other natural agents of mortality in ungulates. Taking advantage of the fact that brown bear is a well-studied Palaearctic mammal in terms of diet composition, we aimed at comparing the large-scale variation in brown bear feeding on ungulates with the environmental (climatic) conditions. We suppose that the percentage share of meat in bear diet is larger in colder regions of Eurasia and in colder seasons (early spring) than in southern areas and during summer. Although opportunistic, we hypothesize that brown bear prefer/select moose over other ungulate species across large spatial scales.

Methods

A review of the literature was conducted using web-based databases (Web of Science, Google Scholar), the reference lists of papers, and an extensive search of the Russian-language literature held at the library of Mammal Research Institute, Polish Academy of Sciences (Białowieża, Poland). Our keyword searches of these sources included “*Ursus arctos*” AND “diet” / “forag*” / “predat*” in English or “brown bear” and “predation” in Russian. We focused on “terrestrial” populations of bears and did not include those that heavily relied on marine or landlocked fish. In total, our literature search resulted in quantitative data from 63 studies (with at least one of the above parameters) conducted in 17 countries on two continents (Fig. 1, Table 1, full list of locations, types of data, and sources in Appendix S1 in Supporting Information). Several studies could not be incorporated into this review due to fears of repetition with other data sets (Vereschagin 1974; Filonov 1980).

Fig. 1 Location of studies on brown bear *Ursus arctos* diet used in this review. Triangles—Europe, circles—Asia. List of data and sources in Appendix S1 in Supporting Information



Data on the role of ungulate meat in brown bear diet were obtained by analysis of scats and/or stomach contents in most studies, and were expressed as percentage of occurrence or weight of prey remains in scats, or percentage of prey biomass consumed. In all cases, where original data on diet composition summed to 100%, the numbers reported in the original papers were taken for meta-analysis. The percentages of occurrence of prey in scats usually sum to > 100%, as that measure shows in what percentage of all analyzed scats a given prey species or type was found (comp. Jędrzejewska and Jędrzejewski 1998: p. 182). Thus, we recalculated those data in a way that all reported items formed 100%. Most of the studies contained data concerning the percentage share of wild ungulate in the bear diet. However, in several localities, brown bear fed also on domestic animals, e.g., in Greece (Paralikiadis et al. 2010) or in Poland (Frackowiak and Gula 1992). In these cases, the domestic ungulates were included in the percentage share of all ungulates consumed by bears. In reviewing the seasonal variation in brown bears feeding on ungulates, we followed the division into seasons (spring, summer, and

autumn) given in the original papers. Winter period was not taken into consideration, as in majority of locations bears were inactive in winter (hibernation).

Several of the studies used were conducted over a long term, which provided temporally separated estimates of predation variables to be calculated because prey abundance changed over time. Others provided detailed information on bear prey and their abundance in different study regions. Such partitioning has been used previously in the study of carnivore ecology (see Creel and Creel 2002). We do not believe that autocorrelation exists by using data from the same area at different levels of prey abundance, as one of the fundamental rules of whether a species is captured and killed is the probability of it coming in contact with the predator, which varies with prey density (Hayward et al. 2012).

The analysis of brown bear hunting preferences for ungulate species was based on studies that were conducted in areas with two or more coexisting species of ungulates, and provided information on both the species structure of ungulate community and the relative percentage share of each species among ungulates killed by bears (Table 1, Appendix S1). Prey preferences were calculated using Jacobs' (1974) variation of Ivlev's selectivity index (D):

$$D = \frac{r-p}{r+p-2rp} \quad (1)$$

where r is the proportion of a given species in the total number of ungulates killed by bears, and p is the proportion of that species in the ungulate community of a site. Jacobs' index ranges from -1 (complete avoidance) to 1 (maximum positive selection) (Jacobs 1974). Jacobs' indices were calculated for the main prey species at each site.

Table 1 Number of studies on the Eurasian brown bear *Ursus arctos* used for meta-analysis in this paper. Full list of localities and sources in Appendix S1 in Supporting Information

Parameter	Number of studies with a given parameter		
	Europe	Asia	Total
Ungulate meat in diet (%)	24	23	47
Seasonal variation in feeding on ungulates	16	18	34
Prey preferences (selectivity index)	8	2	10
Role of bear predation in ungulate mortality	10	7	17
Studies with at least one parameter	33	30	63

In an attempt to assess the role of brown bear predation in the total natural mortality of ungulates, we sought studies that were focused on ungulate populations and their mortality factors. The majority of data originated from long-term inventories of ungulate carcasses in protected areas of Eurasia. In those surveys, causes of deaths were assessed visually (comp. Okarma et al. 1995). For all data points with described bear diet, we determined geographic coordinates and mean annual temperature from the WorldClim – Global Climate Data (Hijmans et al. 2005). We used linear regression analysis to test for relationship between the percentage of ungulates in the diet of brown bears and mean annual temperature separately for European and Asian populations. We did not include latitude as an additional explanatory variable because of the significant correlation between latitude and mean annual temperature (Europe: $N = 24$, $R = -0.86$, $P < 0.001$; Asia: $N = 23$, $R = -0.80$, $P < 0.001$). We decided to use only mean annual temperature, as it is likely to have a direct ecological meaning for bears through changing availability of food resources and affecting the physical condition of potential ungulate (comp. Boertje et al. 1988, Mowat and Heard 2006, Bojarska and Selva 2012). For both data sets (European and Asian), the applied variograms did not show significant spatial autocorrelation in model residuals. Kruskal–Wallis ANOVA was used to test for seasonal and intercontinental differences in diet. Relationships between Ivlev's selectivity index and ungulate body mass were tested by linear regression models. The relative roles of bear predation in ungulate mortality were compared with non-parametric Kruskal–Wallis ANOVA and Mann–Whitney tests. All means are presented along with standard errors.

Results

Ungulate meat makes up, on average, 8.7% of brown bear diets in Eurasia (SE 1.5, range 0–28.4, $N = 47$). However, bears from Europe and Asia differ significantly in this respect, with European bears eating more ungulates (mean 10.5%, SE 1.9, range 0–33) than Asiatic bears (mean 6.8%, SE 2.4, range 0–51; Kruskal–Wallis ANOVA in pairwise comparisons; $H = 6.47$, $P = 0.011$).

In Europe, the percentage share of ungulates in brown bear diet was negatively related to the mean annual temperature of the study site (Fig. 2). Temperature explained 31% of the observed variation in Europe ($R^2 = 0.31$, $P = 0.005$). In Asia, no relationship between brown bear foraging on ungulates and annual temperature was found (Fig. 2).

Part of the intercontinental differences in overall contribution of ungulates to brown bear diet may come from an uneven spatial distribution of the studied localities: warmer regions were sampled in Europe than in Asia (see Figs. 1 and 2). Thus, we compared the values within the common range of

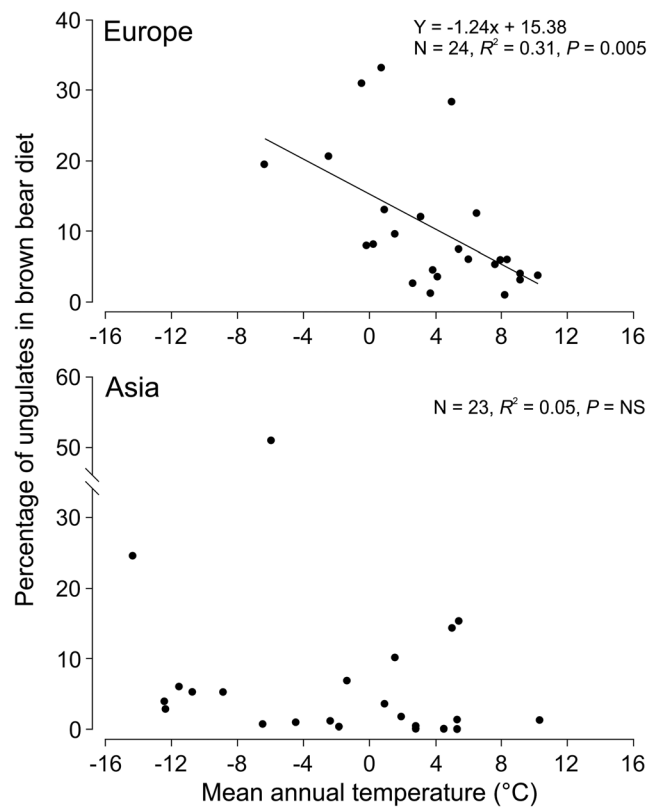


Fig. 2 Relationship between the percentage share of ungulates in the diet of brown bears and mean annual temperature in Europe and Asia

temperature: from -6.5 to 10.3 °C. Again, the percentage share of ungulates in bear diet in Europe was significantly higher than that in Asia (Kruskal–Wallis ANOVA, $H = 7.505$, $P = 0.006$).

In 34 studies, information on seasonal (spring, summer, and autumn) variation in brown bear diet was available. In Eurasia, ungulates contributed, on average, 15.4% to food consumed in spring (SE 3.2, range 0–72), 5.0% in summer (SE 1.6, range 0–37), and 5.4% in autumn (SE 1.2, range 0–29), and the differences among seasons were significant (Friedman's ANOVA, $\chi^2_{(33,2)} = 19.45$, $P = 0.0001$). However, the pattern of seasonal variation in ungulate consumption by bears varied between continents (Fig. 3). If we take spring means as reference values (= 1) in each continent, summer averages reach levels of 0.24 in Asia and 0.37 in Europe. The largest intercontinental differences appeared in the mean values for autumn, which were 0.55 in Asia and only 0.28 of the respective spring values in Europe (Fig. 3). In other words, Asiatic bears consumed less ungulates in summer, whereas European bears fed less on ungulates in both summer and autumn.

The 10 species of ungulates studied ranged in mean body mass from 10 to 295 kg. Brown bears' prey preference for these species increased with prey size (Table 2, Fig. 4). Small ungulates (< 60 kg) were always killed less often than expected from their percentage share in the ungulate

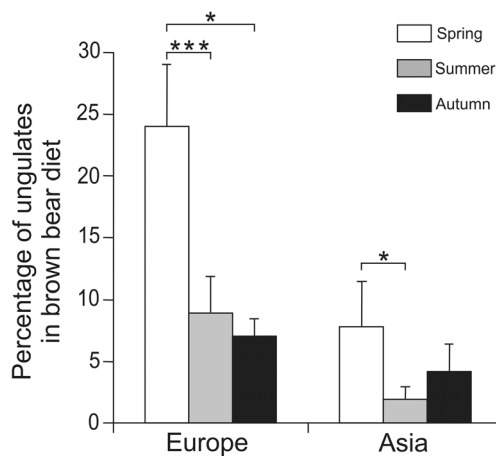


Fig. 3 Seasonal variation in the percentage share of ungulate meat in bear diet (mean \pm SE) based on 16 studies in Europe and 18 in Asia. Differences between seasons significant at: *** $P < 0.001$, * $P < 0.05$ (Friedman's ANOVA)

community. Selection of medium-sized (60–130 kg) species by bears was most variable, ranging from strong avoidance to clear positive selection. Only the two largest species—European bison and moose—were consistently positively selected by bears and these were eaten more often than expected from their relative abundance in the local ungulate communities (Table 2, Fig. 4).

We looked at the importance of brown bear predation in the total predation-caused mortality of ungulates in Eurasia. Generally, predation by all species of large carnivores was the most important cause of natural mortality in roe deer (mean 64% of death, range 32–100%), moose (61.5%, range 21.5–86%), and red deer (60.5%, range 28–93%) (Fig. 5). In wild boar, predation was responsible for an average of one third of deaths (35%, range 12–66%). The contribution of brown bear to the total predation-caused mortality was largest in moose (37%, range 10–90%), which allowed us to estimate that at the Eurasian scale, bears caused, on average, 23% of total mortality in moose populations. Bears' significance as

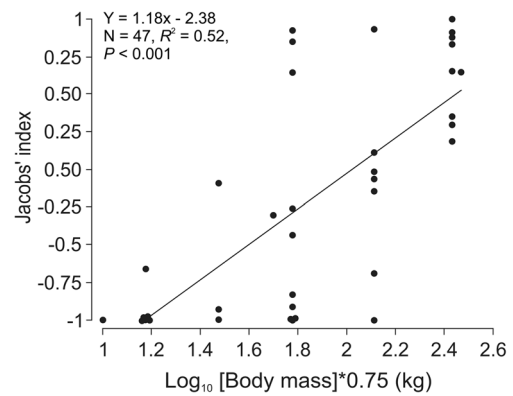


Fig. 4 Brown bear selection of ungulate prey, calculated as Jacobs' selectivity index D (see "Methods") in relation to prey body mass (log transformed). Each point = one study. Open circles denote moose. See Table 2 for the list of species

predators was markedly smaller in other ungulates (Fig. 5) and translated into 7% of total natural mortality in wild boar, 4% in red deer, and 1% in roe deer. It must be kept in mind that those estimates regard only localities where ungulate populations coexist with brown bears.

Discussion

Diverse diets of a carnivore as large as brown bear have long intrigued researchers. Some suggested that "The grizzly is a carnivore that cannot capture enough prey for subsistence" (Murie 1981 p. 135). Others emphasized that "Although well known as carnivores and not capable of digesting plant fiber, grizzly bears [...] are entirely vegetarian in some ecosystems" (Rode et al. 2001; p. 62). However, it was also noted that "Very large bears will have difficulty meeting their energy requirements on vegetation diet" (Rode et al. 2001; p. 62). On the other hand, recent studies have shown that in Sweden, bilberry crops determined body weights of female

Table 2 Prey preferences of brown bears in Eurasia calculated by Jacobs' index D (see "Methods" which varies from -1 (complete avoidance of a species), to 0 (random utilization), to 1 (the strongest positive selection). Body mass of ungulate species (in kilograms) is based on $\frac{3}{4}$ of adult female body mass to account for young and juveniles preyed upon following earlier prey preference studies (Hayward 2006; Hayward et al. 2006a, b, c). Roe deer includes both *Capreolus capreolus* and *C. sibirica*

Species	Body mass (kg)	N studies	Jacobs' index D	
			Mean \pm SE	(min–max)
European bison <i>Bison bonasus</i>	295	1	0.650	–
Moose <i>Alces alces</i>	270	8	0.637 \pm 0.112	(0.183, 1)
Red deer <i>Cervus elaphus</i>	130	7	-0.124 ± 0.233	(-1 , 0.934)
Wild boar <i>Sus scrofa</i>	60	8	-0.138 ± 0.292	(-1 , 0.927)
Reindeer <i>Rangifer tarandus</i>	60	2	-0.955 ± 0.044	(-1 , -0.911)
Caucasian ibex <i>Capra caucasica</i>	50	1	-0.302	–
Sika deer <i>Cervus nippon</i>	30	2	-0.546 ± 0.454	(-1 , -0.092)
Chamois <i>Rupicapra rupicapra</i>	30	1	-0.931	–
Roe deer <i>Capreolus</i> sp.	15	7	-0.952 ± 0.048	(-1 , -0.661)
Musk deer <i>Moschus moschiferus</i>	10	2	-1 ± 0	(-1 , -1)

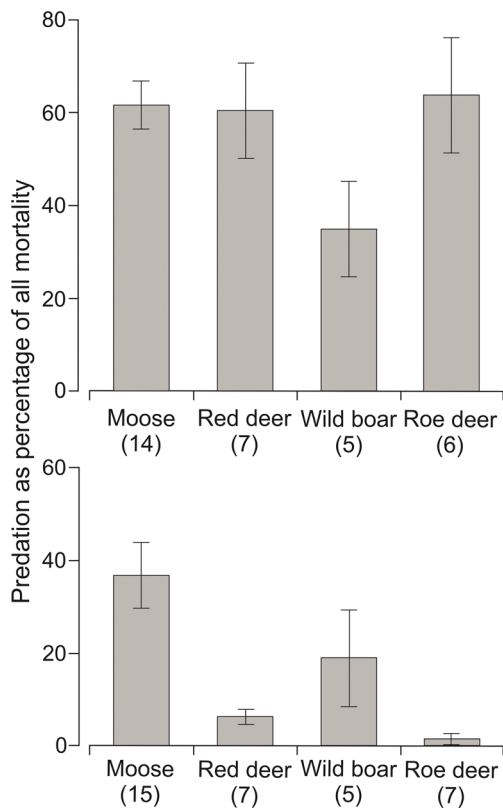


Fig. 5 Upper panel: the mean (\pm SE) percentage of the total natural mortality events in five species of Eurasian ungulates attributed to predation. Lower panel: the mean (\pm SE) percentage of predation-caused mortality attributed to brown bear. Numbers below the *x*-axis denote sample sizes (*N* studies). Roe deer includes both *Capreolus capreolus* and *C. sibirica*

bears in autumn and spring weights of yearlings and thus affected the reproductive success of bears (Hertel et al. 2018).

Many authors have suggested that brown bears are more predatory and have a greater proportion of ungulate meat in their diets the further north they exist (Danilov 1983; Krechmar 1995; Persson et al. 2001). By taking a continental perspective, we provided a statistical test for this assertion. We found a clear latitudinal pattern in Europe: the proportion of ungulates in bear diets generally increased with cooler annual temperatures and as we mentioned earlier, the mean annual temperature of the study sites correlated with latitude. The same gradient of the increasing south-to-north carnivory in European bears was earlier reported by Vulla et al. (2009) based on six studies ranging from Slovenia to Norway. Also, a large-scale study of grizzly bear diet (based on stable isotope ratios in hair) across western North America provided evidence for the latitudinal gradient in bears' carnivory (Mowat and Heard 2006). Using the data of Mowat and Heard (2006, Table 3 in pp. 484–486), we calculated that the proportion of terrestrial meat in bear diet increased significantly with latitude between 48° and 69° N (meat = $-0.5277 + 0.0126$ latitude, $n = 81$, $R^2 = 0.174$, $P = 0.0001$).

As shown in our meta-analysis, Asian bears ate less ungulates and their consumption of ungulate meat did not increase towards the north into harsher climate. The most likely reason for that is the widespread occurrence of two tree species, Siberian pine *Pinus sibirica* and dwarf Siberian pine *Pinus pumila*, both of which produce relatively large, highly nutritious and protein-rich seeds (Hytteborn et al. 2005). In their Eurasian range, brown bears feed on large, heavy seeds of trees wherever available, and such seeds are especially important in autumn-early winter as they allow for rapid weight gain (seeds of *Castanea*, *Fagus*, *Quercus* in Spain, Naves et al. 2006, and *Fagus* in southern Poland, Frackowiak and Gula 1992). However, in Europe, no tree species producing large seeds occur in the boreal forest zone. In Central and Eastern Asia, forests with Siberian pine occur from northern Mongolia up to 65° N, and shrubs of dwarf Siberian pine reach beyond the northern tree line, up to 70° N (Richardson 1998). In mainland Siberia, the seeds of either of the two species are prime food resource to brown bears (over 60% in autumn diet, near the Baikal Lake, Chernikin 1978; and 77% in the extreme north-eastern Siberia, Krechmar 1995).

The latitudinal gradient in brown bear feeding on ungulates is driven by mean annual temperature via the extended period of snow cover in northern latitudes. Deep snow prevents the utilization of alternative foods and makes predation and scavenging increasingly optimal (Bojarska and Selva 2012). On this basis, we would predict interannual variation in the amount of ungulate meat in brown bear diet to be related to the period of snow cover each year. Similarly, extended periods of snow cover in spring probably result in increased predation rates by brown bears, due to the scarcity of alternative foods and the vulnerability of prey (Boertje et al. 1988).

Ungulate predation generally peaks after bears emerge from hibernation (Mattson et al. 1991; Linnell et al. 1995; Seryodkin et al. 2004). This corresponds to the time that post-winter carrion is present, surviving ungulates are in poorer condition before fresh plant growth appears (McLellan and Hovey 1995), predatory bears are better able to negotiate the frozen snow crust than their prey (Danilov 1983; Zager and Beecham 2006).

Our meta-analysis of the seasonality of bear consumption of ungulates in Eurasia is supported by additional data that covered spring only or was otherwise not suitable for analysis. In the Lapland Reserve, Russia, 76.9% of moose were killed by bears in spring, and in northern Karelia, 57.8% of moose predation events occurred in spring (Danilov 1983). Sika deer *Cervus nippon* were most frequently killed by brown bears in spring in Hokkaido, Japan, and only comprised a minimal proportion of the diet for the remainder of the year (Sato

et al. 2005). Bears that do not hibernate are reported to be exceedingly predatory (Kalaber et al. 1994).

Numerous authors contend that brown bears are non-selective or purely opportunistic predators (Krechmar 1995). However, our continental-scale analysis showed the opposite. First, in Europe, brown bears rarely prey on ungulates at southern latitudes, where communities of ungulates comprise up to several species (e.g., Okarma 1995) and their crude biomass is higher (e.g., Jędrzejewski et al. 2007), but rather in the north, where one or two species of ungulates coexist. Secondly, in Eurasia, brown bears' preference for meat increased with the body size of its prey. A similar linear relationship between prey preference and body mass has also been observed in the large carnivores of Africa and Asia—the African lion *Panthera leo* and tiger *P. tigris* (Hayward and Kerley 2005; Hayward et al. 2012). Endangered European bison, occurring in small and isolated populations (Kraśnińska et al. 2013), plays a marginal role as a food resource to brown bears in contemporary European environments. Moose has a large Holarctic range, which extensively overlaps with the range of brown bears in Europe, Asia, and North America. Eurasian brown bears showed a notable preference for moose. This selectivity, along with the bears' dominant role in moose natural mortality, suggest an evolutionary predator–prey relationships between these two species. In Eurasia, very close predator–prey relationships have been identified for wolf–red deer and Eurasian lynx–roe deer (Jędrzejewski et al. 2011), both of these predators are, however, strictly carnivorous.

Our findings on the large-scale biogeographic pattern in brown bear consumption of ungulates have implications for future studies on both extinct and extant species. Nutritional ecology of living species, as determined by stable isotopes, is often considered a reference point for estimating the palaeodiets of extinct species (e.g., Hilderbrand et al. 1996). Our study suggests that also in the case of extinct species that used to occupy vast geographic ranges, their nutritional ecology would be location-dependent and might show great variation among sites (see discussion on cave bears *Ursus speleaus* in: Bocherens 1998; Hilderbrand et al. 1998). Brown bears are one of the best-studied mammals in terms of phylogeography (review in: Davison et al. 2011). Therefore, it would be interesting to compare the variation in bear feeding on ungulates with the respective pattern of its dental morphology and genetic diversification at global scale.

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