



## Supplementary ungulate feeding affects movement behavior of brown bears

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### Abstract

Food availability plays a key role in animal movements. Anthropogenic provisioning of food to wildlife is a common practice of unprecedented magnitude worldwide and is of increasing conservation concern. Ungulate supplementary feeding is widespread in game management; however its effects on non-target species have received little attention. Here, we investigate how ungulate feeding affects the movement behavior of a non-target species, the brown bear (*Ursus arctos*). We tracked bear movements in the Northeastern Carpathians (1500 km<sup>2</sup>) and inventoried 212 ungulate feeding sites. We analyzed encounter rates of nine GPS-collared bears with ungulate feeding sites (1658 km, n = 49 tracks) and compared them with the corresponding encounter rate of simulated tracks. We also estimated the encounter rate with feeding sites using snow-tracking of unknown bears (232 km, n = 40 tracks). GPS-tracked bears encountered feeding sites three times more frequently (mean  $\pm$  SE =  $0.154 \pm 0.022$  per km travelled) than would be expected if they were moving randomly ( $0.054 \pm 0.0010$  per km random walk). The rate was even higher for snow-tracked bears, which visited on average  $0.926 \pm 0.271$  feeding sites per kilometer travelled. This suggests a link between the winter activity of some individuals and their frequent use of feeding sites. Bears seemed to rely on spatial memory and patrol known sites, independent of whether food was available at the feeding sites. This alteration of the natural behavior of species with behavioral flexibility, such as brown bears, could be interpreted as a sign of environmental degradation. Our results demonstrate an important effect of ungulate feeding on the movement ecology of non-target species. We warn of the impacts of this practice on species and ecosystems and highlight the need to preserve natural movement behaviors and urgently reevaluate management practices involving food provisioning to wildlife.

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### Introduction

One of the main reasons animals move is to exploit the spatio-temporal variation in food resources. Food availabil-

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ity has, therefore, an important and direct effect on animal movements on fine (e.g. local foraging paths) and broad scales (e.g. long-distance migration, Polis, Anderson, & Holt 1997; Mueller et al. 2008; Jones et al. 2014; Teitelbaum et al. 2015). Alterations of the spatio-temporal distribution of food resources, together with habitat loss and fragmentation, over-exploitation and climate change, are some of the main reasons for recent changes in the movement ecology of a number of species (Nathan et al. 2008; Wilcove & Wikelski 2008; Jones et al. 2014; Seebacher & Post 2015). Some of these alterations in resource availability are due to the anthropogenic provisioning of food, an issue of increasing concern in wildlife ecology and conservation. Humans have not only increased the amount of food available to wildlife (30–40% of all food produced in the world is wasted; Oro, Genovart, Tavecchia, Fowler, & Martínez-Abraín 2013), but also its predictability in time and space. These anthropogenic food subsidies have important consequences for both species and ecosystems, including alterations of social behavior, interactions, reproductive performance, activity patterns, trophic cascades and pathogen transmission (Robb, McDonald, Chamberlain, & Bearhop 2008; Selva, Berezowska-Cnota, & Elguero-Claramunt 2014; Sorensen, van Beest, & Brook 2014).

One important source of anthropogenic provisioning of food is intentional supplementary feeding of wildlife. Supplementary feeding is a widespread practice, particularly for ungulates in the northern hemisphere, where it is still an important tool for game management (Putman & Staines 2004; Apollonio, Andersen, & Putman 2010; Jones et al. 2014; Selva et al. 2014). Despite its ubiquity and magnitude, the ecological effects of this practice and its effect on animal movements are just beginning to be investigated. The empirical evidence available, though limited, shows that supplementary feeding can alter the migration and seasonal movement patterns of ungulates (Jones et al. 2014). However, ungulate supplementary feeding is non-selective and its effects could go far beyond ungulates themselves (Selva et al. 2014). How the provisioning of food for ungulates affects the movements of non-target species is largely unexplored. Here, we aim to investigate the relationship between supplementary food and the movement behavior of non-target species. In particular, we examine how ungulate supplementary feeding sites of ungulates affect movement of brown bears (*Ursus arctos*).

Ungulate supplementary feeding occurs in many areas where brown bears are present in Europe and in six of the ten European populations (Bautista et al. 2017). Brown bears are omnivorous and track the seasonality in natural food availability, but also exploit anthropogenic food whenever available (Bojarska & Selva 2012; Kavčič, Adamič, Kaczensky, Krofel, & Jerina 2013; Schindler et al. 2013). Additionally, bears wander over large home ranges, have high nutritional demands, and spent much of their time foraging. We tracked bear movements in the Carpathian Mountains and tested whether supplementary feeding sites for ungulates affected the movement behavior of bears.

## Material and methods

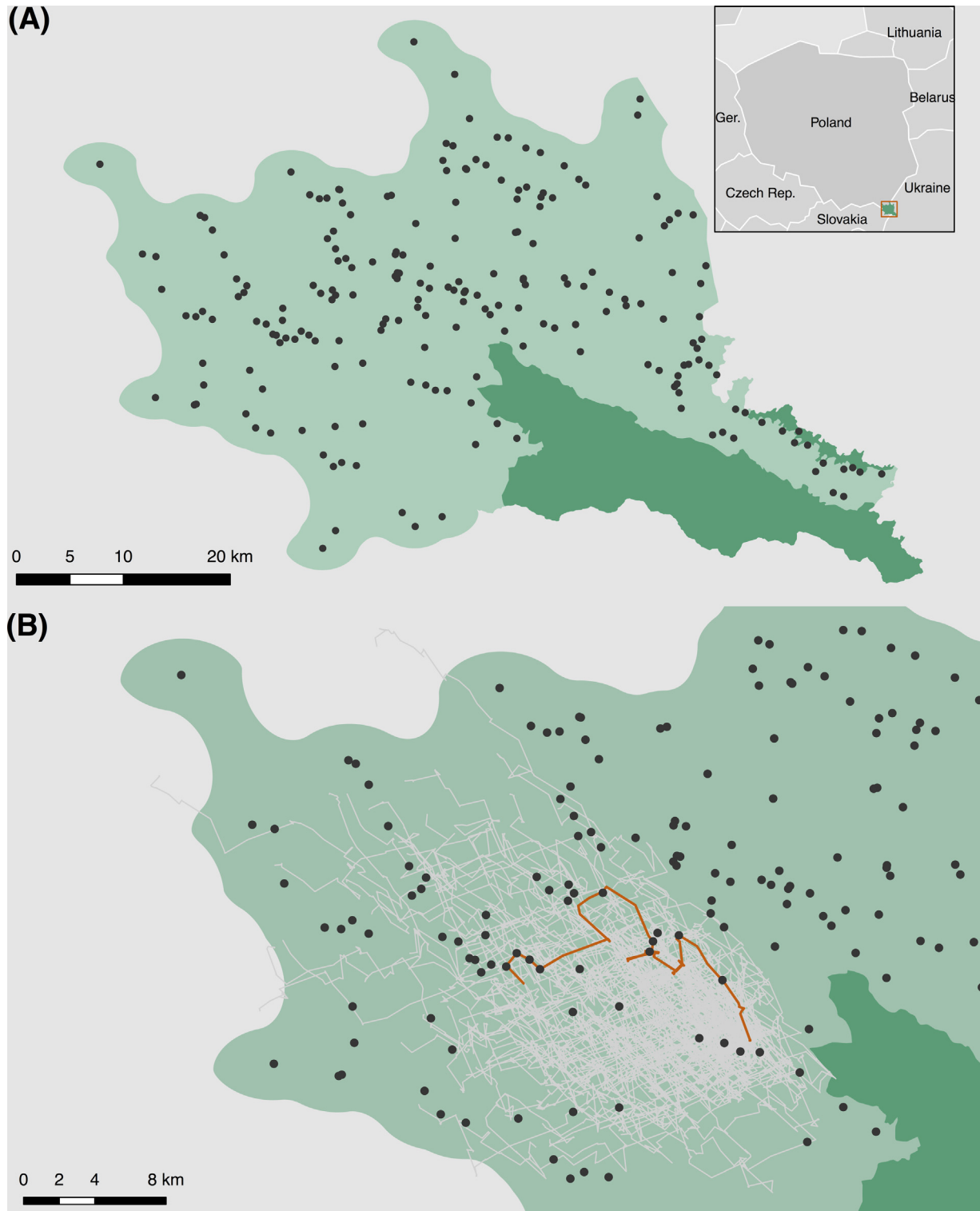
### Study area

The study area was located in the Northeastern part of the Carpathian Mountains, in SE Poland and neighboring areas in Slovakia (Fig. 1, 1500 km<sup>2</sup>). The area is characterized by gentle slopes (maximum altitude 1350 m a.s.l.) and dominated by beech (*Fagus sylvatica*) and fir (*Abies alba*). The forest is intertwined with meadows and valleys, particularly in the lower parts of the mountains. The whole area represents a suitable habitat for brown bear occurrence, reproduction and movement (Fernández, Selva, Yuste, Okarma, & Jakubiec 2012; Ziółkowska et al. 2016). The climate is continental; snow cover can persist for three months. The vertebrate community includes five ungulate species (red deer, *Cervus elaphus*; roe deer, *Capreolus capreolus*; wild boar, *Sus scrofa*; European bison, *Bison bonasus*; and moose, *Alces alces*, this last quite rare), and three species of large carnivores (brown bear, wolf, *Canis lupus*; and Eurasian lynx, *Lynx lynx*). Brown bears inhabiting the area are estimated at 46–61 individuals and belong to the eastern Carpathian subpopulation (Selva, Zwijacz-Kozica, Sergiel, Olszańska, & Zięba 2011). Most individuals, particularly males, are transboundary, and the population is shared with neighbor countries (Slovakia and Ukraine). The brown bear has been a protected species in Poland since 1952 (Selva et al. 2011).

Most of the area is managed by the Polish State Forest Holding for timber extraction and game hunting, except the Bieszczady National Park, a protected area (Fig. 1, 290 km<sup>2</sup>). In the commercially managed part, supplementary feeding of ungulates, mostly for red deer, bison and wild boar, is regularly conducted, usually at the same locations for decades (feeding sites hereafter). Feeding of game animals in Poland is compulsory by law in periods of low food availability and to decrease damages to crops and forestry; however, it is completely unregulated in terms of amount and type of food, as well as when and where to feed. As a result, ungulate feeding is conducted practically year round, but most intensively from the end of summer to the beginning of spring. These feeding sites usually consist of a glade inside the forest where supplementary food (corn, beetroots, fodder, grain) is thrown on the ground in the proximity of hunting towers. This is a generalized practice in Europe (Apollonio et al. 2010). Numerous target and non-target species use this ungulate supplementary food (Selva et al. 2014).

### Inventory of ungulate feeding sites

We conducted an inventory of feeding sites in 2010 through interviews with managers from the State Forest Holding and hunting clubs, and subsequent field inspections. This inventory was completed with information on the location of feeding sites compiled since 2008 during other field activities



**Fig. 1.** (A) Study area in the Polish Northeastern Carpathians. Ungulate feeding sites are shown as black points and the protected area (Bieszczady National Park) without feeding sites is in dark green. (B) Example of a five-day GPS track (orange line) of a brown bear and 100 simulated movement paths (grey lines) in relation to ungulate feeding sites. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Fig. 1). We visited and marked the locations of all feeding sites with GPS units.

### Analysis of bear movement data

We analyzed 49 tracks of brown bear movement, each of which lasted 5 days and had relocation data at 30-minute intervals. These tracks corresponded to nine brown bears (6 males, 3 females) surveyed in 2008–2009 and 2014–2015. Bears in the first study period had GPS-fixes at 30-min intervals only during five days in the beginning of each month. For each individual, tracks were separated by 23–27 days in time, i.e. we took one track per bear and month. Bears were trapped in box or Aldrich traps, immobilized and fitted with GPS-GSM collars (Lotek Wireless Inc., Vectronic Aerospace GmbH). Collars were equipped with a drop-off system. Captures took place in spring and autumn. We followed the biomedical protocols by Arnemo, Evans, and Fahlman (2011) during capture and handling.

We excluded those tracks where >50% of the locations were outside the study area (e.g. in Slovakia or Ukraine). We used only the portions of bear paths within the study area because we could only calculate encounter rates where the locations of feeding sites were known. Periods when GPS-tracked bears were denning and, thus, inactive, were excluded. For each track we calculated encounter rates with the feeding sites based on the number of times a bear entered a 200-m buffer zone around a feeding site, as determined by the bear locations. We choose a 200-m buffer because that buffer is large enough to consider bears which obtained food at feeding sites and consumed the food (e.g. beetroots) little farther under cover, as we have observed in the field. On the other hand, this buffer is sufficiently small to minimize the risk of false positives, given the average distance covered by bears between consecutive 30-min locations (182 m, Zedrosser, Steyaert, Brunberg, Swenson, & Kindberg 2013; 323 m, this study).

Observations of bears active in winter or non-denning are not rare in the study area. We also snow-tracked unmarked bears in 2010–2012 from December through March and registered their visits to feeding sites. In these years we did not have GPS-tracked bears. In 2008–2009 and 2014–2015, the only GPS-tracked bears in winter were two pregnant females that spent all winter in the den. Information about the location of bears active in winter was obtained from the State Forest game managers, local people and during our field observations. For the snow-tracking data, we calculated encounter rates for each track in the same way as for the GPS data. If a snow-track began within 200 m of a feeding site, we clipped it so that it began as soon as the bear left the 200-m buffer zone, thus excluding the portion of the track starting at the feeding site. This method provided a conservative estimate of encounter rates. We only included snow-tracks that were longer than 500 m.

To test whether bears encounter feeding sites more frequently than would be expected by chance, we created 100 simulations of each of the 49 GPS-tracks by randomly drawing (with replacement) pairs of distances and turning angles from the corresponding original track (Fig. 1). We used the `angefun` function in R (R Development Core Team 2014) to calculate distances and turn angles from the distributions present in the original GPS tracks. Each random track featured the same starting position and the same number of (simulated) relocations as the corresponding original track (Fig. 1). If simulated tracks exited the study area, we clipped them so that they contained only points within the study area (as we did for actual tracks). We calculated the random encounter rate as the median of each set of simulated paths and calculated the difference between original encounter rates and the random encounter rate of the corresponding simulated paths. We used a linear mixed model to test whether the difference between the random and original encounter rates was significantly different from zero. The model incorporated bear identity as a random intercept.

### Results

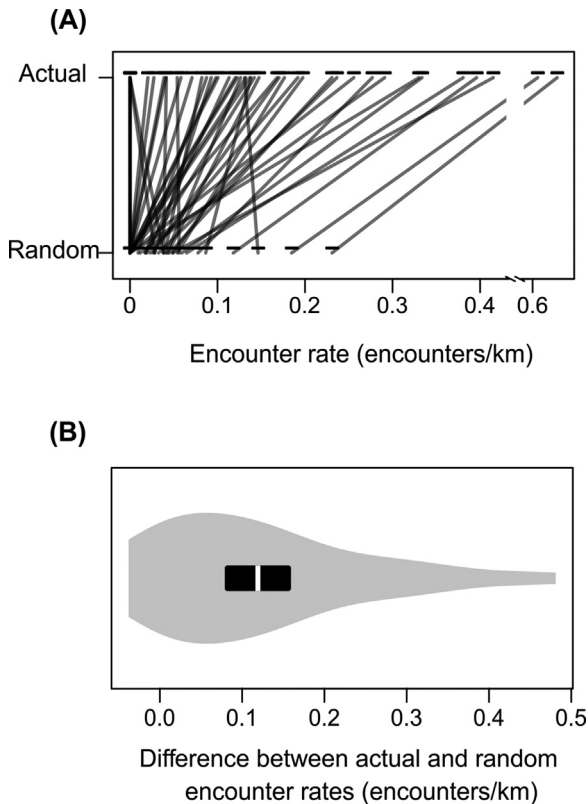
A total of 212 ungulate feeding sites were inventoried in the managed part of the study area (ca 1500 km<sup>2</sup>, Fig. 1). The mean nearest neighbor distance among feeding sites was 1291 (±68.8 m SE); the density of feeding sites was 14 sites per 100 km<sup>2</sup>. Overall, we analyzed 1658 km of bear movements obtained from telemetry and counted 204 bear encounters with ungulate supplementary feeding sites in 49 five-day tracks (Fig. 2). On average, bears visited 0.154 (±0.022 SE) feeding sites for each kilometer travelled (Table 1, see Appendix A in Supplementary material). GPS-tracked bears encountered feeding sites three times more frequently than would be expected if they were moving randomly with respect to the feeding sites (random encounter rate = 0.054 ± 0.010 SE sites/km, modeled difference = 0.119 sites/km, 95% CI = (0.081, 0.156),  $p < 0.001$ ). Along 232 km of snow-tracking, bears encountered ungulate feeding sites much more frequently than did GPS-tracked bears: on average 0.926 (±1.271 SE) feeding sites per kilometer travelled (Table 1).

### Discussion

Our results reveal an important role of ungulate feeding sites in the movements of a non-target species, such as the brown bear. Supplementary feeding has been shown to reduce home range size and to alter the migration patterns, local distribution and habitat selection of ungulates, the target group (see Table 2 for a review of studies). This study provides evidence that ungulate supplementary feeding also affects the movement ecology of non-target species.

**Table 1.** Summary statistics (mean  $\pm$  SE) of brown bear movements in the Northeastern Carpathians, Poland, in relation to ungulate supplementary feeding sites as derived from GPS tracks of collared bears, corresponding simulated tracks and snow-tracking of unknown bears.

	Simulated tracks	GPS-tracks	Snow-tracks
No. tracks	4900	49	40
Track length (km)	34.202 $\pm$ 3.037	34.202 $\pm$ 3.037	5.948 $\pm$ 0.928
Encounter rate (feeding sites/km travelled)	0.054 $\pm$ 0.010	0.154 $\pm$ 0.022	0.926 $\pm$ 0.271
Distance travelled between feeding sites (km)	62.605 $\pm$ 17.109	10.108 $\pm$ 1.553	2.453 $\pm$ 0.528
Number of feeding sites visited per day	0.228 $\pm$ 0.116	0.833 $\pm$ 0.098	NA



**Fig. 2.** Encounter rates (no. ungulate feeding sites visited by brown bears per km travelled in the Northeastern Carpathians, Poland) calculated from actual and simulated data. (A) Each of the 49 GPS tracks is connected to the median of its corresponding 100 simulations of that track. (B) Violin plot of the difference in encounter rates between actual and simulated data. The central boxplot shows the parameter estimate (white line) and 95% confidence interval (black box) for a model predicting the difference between actual and random encounter rates.

The quantity, distribution and predictability of food resources are among the main factors that explain space use by vertebrates (e.g. Polis et al. 1997; Newsome et al. 2014). Ungulate supplementary feeding is highly predictable in space and time. This predictability tends to increase particularly in Europe and North America, where wildlife feeding is not any longer limited to emergency situations but turning into regular feeding, usually at the same locations and year-round (Mysterud 2010; Selva et al. 2014). It has become

increasingly popular; in the USA alone, ca.  $2.8 \times 10^{12}$  t of bait are offered to big game each year (Oro et al. 2013). In our study area, some Forest Districts provided up to 2.5 t/km<sup>2</sup> per hunting season in some years (data from Regional Directorate of the State Forest in Krosno). The density of feeding sites we found (14 per 100 km<sup>2</sup>) is similar to that of areas with intensive supplementary feeding practices (16–34 feeding sites/100 km<sup>2</sup>, Kavčič et al. 2015). Steyaert et al. (2014) investigated resource selection by brown bears in Slovenia, where they are intentionally and intensively fed for hunting, and found that bears selected for feeding sites. Our results suggest that, along with the recently-addressed effects of hunting on target species behavior (e.g. Ordiz et al. 2012), the changes in foraging movements of target and non-target species are an additional effect of game management to be seriously considered.

The alteration of food resource availability through ungulate supplementary feeding had a clear impact on brown bear foraging movements. Except for one long-distance disperser bear, all data used in the analyses were from tracks of resident bears, which may suggest that bears' spatial memory was important (Fagan et al. 2013) and that they were probably patrolling known sites to evaluate whether food was available. We lack exact information on when and how much food was provided because ungulate feeding in the study area is unregulated and each site is managed independently and at the discretion of the corresponding game manager. However, field observations during snow-tracking and inspections of GPS locations of collared bears showed that bears also visited sites when no food was available, supporting the notion that bears may regularly patrol feeding sites. In experimental studies with other bear species, captive animals visited depleted feeders, which suggests a strategy of searching at the memorized locations (Tarou 2003; Zamisch & Vonk 2012).

The impact of ungulate feeding sites on bear movements was higher for the snow-tracking data compared to telemetry data. Winter is a period of low food availability for bears, when they usually den and decrease activity, but it is also a period of intensive ungulate feeding. We conducted bear snow-tracking in all winter months, from December through March, which indicates bear activity throughout all winter. The fact that snow-tracked bears encountered feeding sites more frequently than GPS-tracked bears may also suggest individual differences and that those bears using

**Table 2.** Summary of the literature review on the documented effects of ungulate supplementary feeding on species movements.

Species	Location	Documented effects	References
Brown bear <i>Ursus arctos</i>	Carpathian Mountains, Poland	Regular patrolling of feeding sites Alteration of movement behavior, particularly in winter	This study
Red deer <i>Cervus elaphus</i>	Rocky Mountains, Western Wyoming, USA	Shorter migration distance and higher use of stopovers Later arrivals at and earlier departures from summer ranges Change of migration pattern and seasonal range use	Jones et al. (2014)
Moose <i>Alces alces</i>	Southeastern Norway	Feeding station users made twice longer mean daily distances	Mathisen, Milner, van Beest, and Skarpe (2014)
Red deer <i>Cervus elaphus</i>	Dinaric Mountains, Slovenia	Reduction in annual home range size	Jerina (2012)
Moose <i>Alces alces</i>	Southern Norway	No effect on home range size	van Beest, Rivrud, Loe, Milner, and Mysterud (2011)
Moose <i>Alces alces</i>	Northern Scandinavia	The vicinity of feeding sites (up to 200 m) was more used at the end of migration No effect at early migration Alteration of local distribution patterns	Sahlsten et al. (2010)
Moose <i>Alces alces</i>	Southern Norway	Individual differences in the use of feeding stations Space use concentrated around feeding sites for feeding-site users Change in habitat selection	van Beest, Loe, Mysterud, and Milner (2010)
White-tailed deer <i>Odocoileus virginianus</i>	Texas rangeland, USA	Fed deer had larger home ranges than unfed deer Most deer locations (>99%) within 1.5 km of feeding sites Little effect on deer spatial dynamics	Webb, Hewitt, Marquardt, and Hellickson (2008)
Mule deer <i>Odocoileus hemionus</i>	Mountains in Northern Utah, USA	Fed deer migrated later in spring than non-fed deer Fed deer spent more time on winter range than non-fed deer Alteration of migration behavior	Peterson and Messmer (2007)
White-tailed deer <i>Odocoileus virginianus</i>	Texas rangeland, USA	No alteration of female home range size, but reduction in their 50% core area Males in areas without supplementary feeding have larger home range sizes Alteration of the use of space within the home range	Cooper, Owens, Cooper, and Ginnett (2006)
Red deer <i>Cervus elaphus</i>	Alps, Italy	Winter locations of migratory deer closer to feeding stations than for stationary deer Higher overlap between home ranges of migratory and stationary deer in winter Increase in red deer concentrations in small areas during winter	Luccarini, Mauri, Ciuti, Lamberti, and Apollonio (2006)
White-tailed deer <i>Odocoileus virginianus</i>	Suburban areas, Connecticut, USA	Deer with temporary bait sites inside their home ranges but outside their original core areas, shifted core areas closer to bait sites No effect on home range and core-area size	Kilpatrick and Stober (2002)
Roe deer <i>Capreolus capreolus</i>	Sweden	Concentration around feeding sites and smaller home range and core areas compared with winters when natural food was available, in one study area Alteration of home range use	Guillet, Bergström, and Cederlund (1996)

supplementary foods were not denning and/or were more active in winter. Whether some bears are not denning due to the availability of supplementary foods or whether these bears are visiting feeding sites because they are not denning is an open question. It is known that abundant food resources in late autumn-winter are associated with longer bear activity and later den entry, while weather conditions seem to be more important for den emergence (Van Daele, Barnes, & Smith 1990; Pigeon, Stenhouse, & Côté 2016). Although the increased activity of bears in winter can also be related to increasingly milder winters in the study area, our results suggest that supplementary feeding is a factor that may affect bears' winter ecology. Recent studies in areas with intensive supplementary feeding support an increased use of feeding sites by bears during the denning period (Štofik et al. 2016; Krofel, Špacapan, & Jerina 2017).

Artificial feeding of wildlife may increase fidelity of animals to the places with supplementary foods and change their behavior through "domestication", halt population range expansion, and diminish long-distance migration and dispersal, a phenomenon which is vanishing worldwide (Mysterud 2010; Caro & Sherman 2012; Jones et al. 2014). The continued loss of long-distance movement behaviors and routes has been mostly linked to habitat fragmentation (Caro & Sherman 2012). However, human provisioning of food may have an increasingly important role in the movement ecology of a range of species, from those that show behavioral plasticity, like bears (e.g. Cozzi et al. 2016), to less plastic species, like vultures or ungulates (Oro et al. 2013, Table 2). This raises the question of how to preserve species beyond numbers. The brown bear is a good example, as it is the most abundant large carnivore in Europe and is expanding in a human-dominated landscape (Chapron et al. 2014). Artificial feeding may enhance bear numbers and fitness, but also promote non-natural behaviors, like non-denning and extreme sedentarism, or the establishment of distinct behavioral types within a population (sedentary vs migratory; Cozzi et al. 2016). These changes in behavior may be also an indicator of environmental degradation (Boydston, Kapheim, Watts, Szykman, & Holekamp 2003). Conservation targets should move from a strict focus on species numbers and distribution and start considering the preservation of natural behaviors. Not only is it important how many bears we want to preserve in a given population, but also which type of bears we aim to have (i.e. their functional role in the ecosystems). The preservation of behavioral diversity is pointed out as a worthy conservation goal to adapt to ongoing and future environmental changes (Caro & Sherman 2012).

Moving is a fundamental part of the life of any animal. How, why and where animals move may have far-reaching consequences at individual, population and ecosystem levels (Nathan et al. 2008). Alterations in movements are associated with a cascade of subsequent changes, e.g. in diet, reproduction, interactions and associated processes such as disease transmission, seed dispersal and indirect effects on co-occurring species. Human-provided food affects abundance,

food habits, life-history, sociality and space use of mammals (Newsome et al. 2014). Given the magnitude of supplementary feeding of wildlife worldwide, it is important to gain further understanding of the impact of human-provided food on movement ecology and subsequent consequences for species and ecosystems (Robb et al. 2008; Oro et al. 2013; Newsome et al. 2014; Selva et al. 2014; Sorensen et al. 2014).

## Conclusions

Wildlife feeding is aimed at drawing animals away from undesired places to avoid conflicts (diversionary feeding), at improving population viability or densities (supplementary feeding) and at concentrating animals to facilitate their observation (recreational feeding) or hunting (game baiting). Independent of the goals and whether the food is provided intentionally or unintentionally, from an ecological perspective, these practices and their effects are rather similar. In the case of brown bears, food is intentionally provided for conflict mitigation, for trophy hunting and for recreational viewing; in all cases ecological and behavioral effects have been documented (Kavčič et al. 2013; Steyaert et al. 2014; Fortin et al. 2016; Štofik et al. 2016; Krofel et al. 2017). Our study adds to this recent scientific evidence supporting the need to ban, limit or modify the practice of artificial feeding in brown bear areas (e.g. using hay as ungulate food instead of corn, grain, beetroots or other potential bear foods). As a first step, managers should stop increasing the amount of food provided to ungulates, a trend which is observed in numerous areas, and start progressively to reduce it. Well known is the abrupt stop of bear feeding in Yellowstone in 1970s, which brought a high increase in movements and annual home ranges, but also high bear mortality in the following years (Blanchard & Knight 1991; Mattson & Reid, 1991). More than 30 years after dump closure, and following an initial population decline, the Yellowstone bear population has increased in numbers and expanded in range (e.g. Doak & Cutler 2014).

There is an urgent need for environmental policies that adequately address the problems associated with the access of bears and other wildlife to artificial food (Newsome et al. 2014). Our study points out the effects of ungulate supplementary feeding on movement of a non-target carnivore species and highlights the need to preserve natural behaviors and to reevaluate the practice of food provisioning to wildlife.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baec.2017.09.007>.

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