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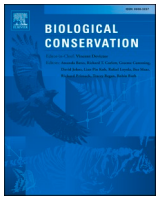

Policy analysis

Does artificial feeding affect large carnivore behaviours? The case study of brown bears in a hunted and tourist exploited subpopulation

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ABSTRACT

Artificial food supplementation of wildlife is an increasing practice for species conservation, as well as for hunting and viewing tourism. Yet, our understanding of the implications of wildlife supplementary feeding is still very limited. Concerns have been raised over the potential negative impact of artificial feeding, but the effects of this practice on animal movements and rhythms of activity are just beginning to be investigated. Here, with the aim of studying whether the artificial feeding of brown bears may affect their behaviour, we analysed (1) the probability and intensity of feeding site use at different temporal scales, (2) how the use of artificial feeding sites is related to the bear's age and sex, main periods of the bear's annual cycle (i.e. mating and hyperphagia) and characteristics of the feeding sites, and (3) how the use of artificial feeding may be affecting bear movement patterns. We analysed the movements of 71 radio-collared brown bears in southern-central Finland and western Russian Karelia. Artificial feeding sites had several effects on brown bears in boreal habitats. The probability of a feeding site being used was positively correlated to the stability of this food resource over time, whereas sexes and bear classes (subadults, adults and females with cubs) did not show significant differences in the use of feeding sites, which were visited predominantly at night and slightly more during hyperphagia. The probability of using an artificial feeding site affected the daily net distance only (bears using feeding sites: 3.5 ± 4.5 km, range: 0–29 km; bears not using feeding sites: 4.4 ± 4.9 km, range: 0–47 km). Those brown bears using artificial feeding more intensively moved shorter distances at a lower speed within smaller home ranges compared to bears that used this food sources less. Highly predictable and continuously available anthropogenic food may therefore have substantial impacts on brown bear movement patterns, ecology and health. The recorded changes in movement patterns support the evidence that artificial feeding may have important implications for bear ecology and conservation.

1. Introduction

Food supplementation of wildlife, i.e. the intentional provision of natural and/or non-natural foods to animals, is an increasing practice in species management and conservation, which is broadly applied and affects a wide range of species (Dubois and Fraser, 2013; Ewen et al., 2014; Murray et al., 2016; Selva et al., 2014; Steyaert et al., 2014; Tryjanowski et al., 2017; van Beeck Calkoen et al., 2020; Walpole, 2001). For example, supplementary feeding has been considered necessary because: (a) the distribution and availability of natural food might limit threatened populations (Ewen et al., 2014; Thierry et al., 2020); (b) there is a hypothesised benefit to providing safe food sources, free of veterinary drugs or poisons (Oro et al., 2013); (c) it might aid recovery of hunted populations (Delibes-Mateos et al., 2009) or (d) it may prevent damages in forestry and agriculture (Arnold et al., 2018; Borowski et al., 2019; Selva et al., 2014). But artificial feeding is also widely used to support human leisure activities, by both the hunting and ecotourism industries (Orams, 2002; Penteriani et al., 2017; Prinz et al.,

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2020; Steyaert et al., 2014), e.g.: (a) to maintain a high quality of trophy animals and a high density of animals for hunting, as well as to attract them to shooting spots (Selva et al., 2014); and (b) to increase the likelihood of wildlife observations as a touristic attraction (Orams, 2002; Penteriani et al., 2017; Prinz et al., 2020; Selva et al., 2014).

However, despite the ubiquity and magnitude of artificial feeding practices, our understanding of the ecological, behavioural, physiological and conservation implications of wildlife supplementary feeding is still very limited (Dubois and Fraser, 2013; Penteriani et al., 2017; Selva et al., 2014), and the range of potential motivations justifying the use or non-use of supplementary feeding is creating divergent opinions among managers (Ewen et al., 2014; Mysterud et al., 2019; Tryjanowski et al., 2017; van Beeck Calkoen et al., 2020; Walpole, 2001). The expected benefits of providing supplementary food is often not carefully evaluated and previous studies have demonstrated that artificial feeding may negatively affect both the population it is intended to help (Dunkley and Cattet, 2003; Ewen et al., 2014; Felton et al., 2017; Milner et al., 2014) and animal communities surrounding feeding spots. Indeed, food subsidies may redistribute and aggregate local predators, increasing the top-down effect of predation on alternative prey (Candler et al., 2019; Oja et al., 2015; Selva et al., 2014), and/or affect many non-target species, which could have several ecological and management-relevant effects, together with potentially undesired consequences such as disruption of animal cycles, e.g. hibernation (Bojarska et al., 2019; Candler et al., 2019; Fležar et al., 2019; Krofel et al., 2017; Krofel and Jerina, 2016; Manning and Baltzer, 2011). Additionally, supplemental feeding may (Candler et al., 2019; Dunkley and Cattet, 2003; Felton et al., 2017; Milner et al., 2014; Murray et al., 2016): (a) increase the risk of pathogen transmission by increasing contact rates between hosts and promoting pathogen accumulation at and around feeding sites; (b) be a source of immunosuppressive contaminants; and (c) increase wildlife stress, rates of injury and/or malnutrition. Actually, human-provided food has the potential to alter the overall dietary quality and hormonal patterns linked to seasonal nutritional requirements (Sergiel et al., 2020). Artificial feeding in forest ecosystems also has the potential to favour the expansion of non-native plant species (Jaroszewicz et al., 2017). Together with health effects, there is also a wide variety of negative impacts on wildlife that can occur as a result of artificial feeding for touristic purposes, e.g. alteration of natural behaviour patterns, dependency on anthropogenic food resources and habituation to humans, and an increase in animal aggression towards humans (Dubois and Fraser, 2013; Dunkley and Cattet, 2003; Orams, 2002; Penteriani et al., 2017; Steyaert et al., 2014; Walpole, 2001).

Among the species targeted by artificial feeding, bears are among the most common in the world, especially brown bears *Ursus arctos* (Penteriani et al., 2017; Penteriani and Melletti, 2020). Bears are generally fed to move individuals away from undesired locations (e.g. diversionary feeding; Garshelis et al., 2017; Ziegltrum, 2004), bait them for hunting and/or attract them close to bear viewing sites (e.g. Kirby et al., 2017; Massé et al., 2014). Brown bears are omnivorous opportunists that feed on a variety of food sources, including anthropogenic foods (Bojarska and Selva, 2012), and artificial feeding is commonly used to bait them for hunting (Bischof et al., 2008; Kavčič et al., 2015; Steyaert et al., 2014) and diversionary feeding purposes (Elfström et al., 2014; Garshelis et al., 2017; Kavčič et al., 2015), as well as for bear viewing (Penteriani et al., 2018, 2017). Since the beginning of the last decade, concerns have been raised over the potential impact of brown bear artificial feeding in Europe (Kojola and Heikkinen, 2012; Morales-González et al., 2020; Penteriani et al., 2018, 2017, 2010; Steyaert et al., 2014; Štofík et al., 2016). However, despite the ubiquity and magnitude of this practice (artificial feeding is practiced in at least 57% of European bear viewing sites; Penteriani et al., 2017), the effects of artificial feeding on bear movements and rhythms of activity are just beginning to be investigated (Bojarska et al., 2019; Selva et al., 2017; Todorov et al., 2020), as is also occurring in other artificially fed species (Ossi et al., 2017). Because how, why and where animals move may have important consequences at the individual and population levels (Nathan et al., 2008), alterations in movements due to anthropogenic sources of food may be associated with changes in food habits, reproduction, intra- and interspecific interactions and space use (Cozzi et al., 2016; Newsome et al., 2015; Penteriani et al., 2018; Selva et al., 2017).

Here, we aim to study whether brown bear artificial feeding for leisure purposes, mainly bear viewing, are affecting individual behaviours. Food at Karelian feeding sites for brown bears is delivered every evening, in the front of the blinds that are in use by people in the following night (author's personal data). Before mad cow syndrome dead cows were commonly used as bait, but nowadays the most important baits are dog food pellets and remnants from the salmon fillet factories, which require daily refills. Nowadays, the replenishing of feeding site cannot occur before evening, otherwise seagulls and ravens would consume pellets and salmon before bears start to be active.

First, we studied temporal patterns of artificial feeding use, i.e. the probability and intensity of feeding site use at different temporal scales (yearly, seasonal and daily temporal scales), and whether the use of artificial feedings is influenced by the internal features of individuals (i.e. age and sex), the main periods of the bear's annual cycle (i.e. mating and hyperphagia) and the characteristics of the feeding sites (i.e. number of available artificial feedings and time they remained opened). Second, we studied whether the use of artificial feeding may affect brown bear movement patterns. Because human activities can impact environmental predictability and, therefore, animal movement (Riotte-Lambert and Matthiopoulos, 2020), prolonged and stable sources of food, such as feeding sites, have the potential to determine the emergence of movement patterns other than those related to the use of natural resources only. One of the most significant properties of anthropogenic food maintained consistently over time is its fairly high predictability, more reliable for feeding individuals than intermittent natural food resources (Tryjanowski et al., 2017).

2. Materials and methods

2.1. Study area

The movements of our radio-collared brown bears covered most of southern and central Finland (220,000 km^2) and also encompassed a part of Russian Karelia (160,000 km^2; Fig. 1), and ranged from 61.69°N to 66.56°N. The topography is relatively smooth with elevation ranging from 100 to 576 m a.s.l. Both regions are largely dominated by highly managed boreal forest (Ahti et al., 1968; Hagen et al., 2015). About 86% of the land area is covered by forests, where the main tree species are Scots pine *Pinus sylvestris*, Norway spruce *Picea abies* and various birches (*Betula* spp.). The terrain is also characterized by the presence of lakes and peat bogs. Human settlements and high-traffic roads are scarce, but isolated houses and low-traffic roads are widespread in the study area. Tourism around wildlife, especially brown bear and other large carnivores, has developed in the 2010–2020 decade in eastern Finland (Kojola and Heikkinen, 2012; Penteriani et al., 2017, 2010), where (a) bear-watching tourism is expected to increase, mainly by means of present enterprises expanding their activities (Eskelinen, 2009; Penteriani et al., 2017), and (b) ca. 4000 visitors arrived annually to observe bears at the Finnish-Russian border at the beginning of the last decade (Kojola and Heikkinen, 2012). However, intensity and patterns of artificial feeding were similar during the whole study period (author's unpublished data) and, thus, we are confident that artificial feeding did not influence results and how the data from before 2010 relate to the situation after the development of tourism.

2.2. Data collection, bear capture and artificial feeding sites

From 2002 to 2013, 71 brown bears (i.e. 115 total captures as some individuals were captured several times; 2002: n = 9; 2003: n = 6; 2004: n = 13; 2005: n = 7; 2006: n = 6; 2007: n = 7; 2008: n = 7; 2009: n = 9;

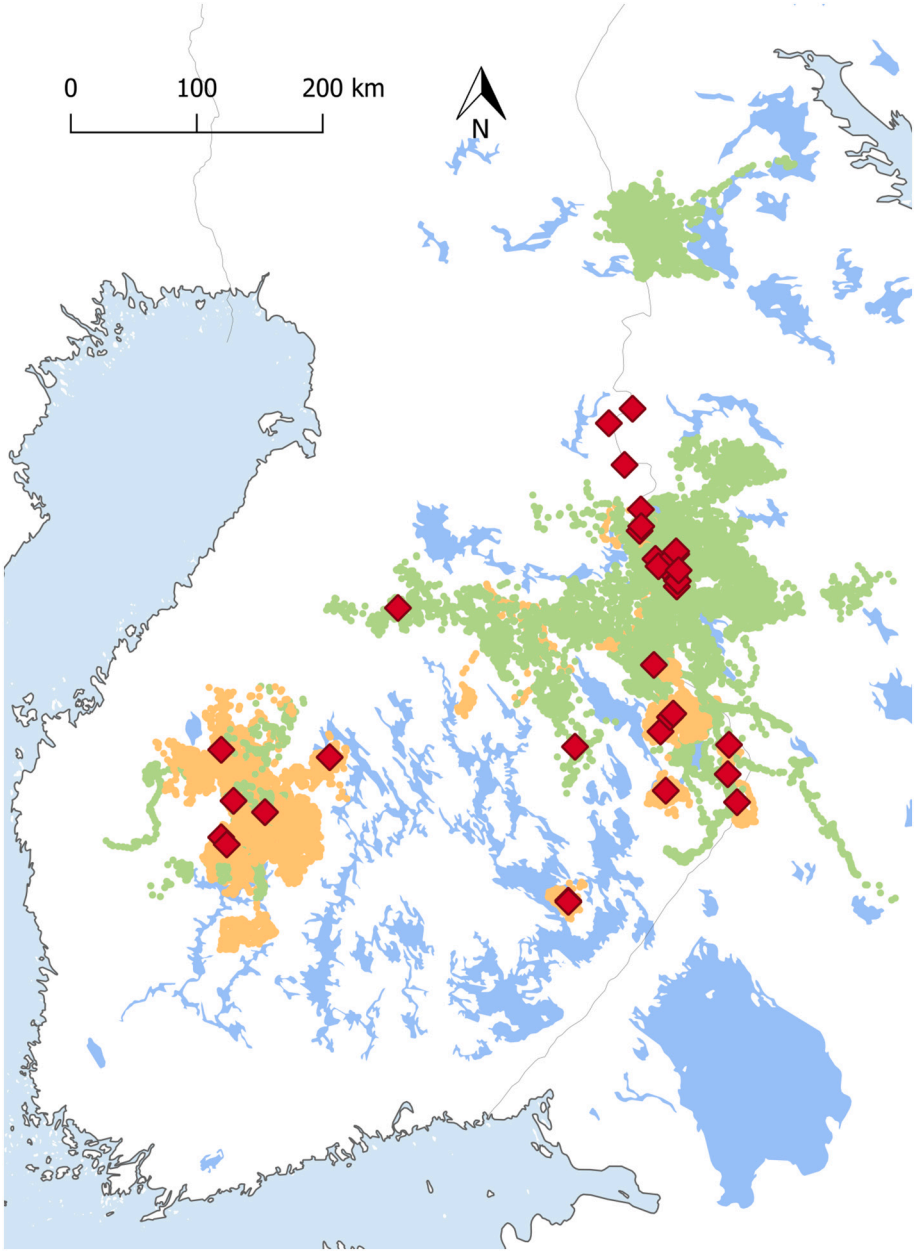


Fig. 1. Distribution of GPS locations (2002—2015) of 42 brown bear males (green), 24 females (orange) and artificial feeding sites (red diamonds) across south-eastern Finland and Russian Karelia. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2010: n = 17; 2011: n = 16; 2012: n = 15; 2013: n = 3) were captured from spring until they entered the winter den. Due to changes in bear physiology and body fat levels, sedative doses were adjusted according to the season of capture, and bears were darted from blinds built at temporary baits. Immobilisation drugs and dosages followed the protocol by Jalanka and Roeken (1990). The tranquilizer contained a mix of medetomidine (50 μg/kg) and ketamine (2 mg/kg), with their proportion adjusted according to the size of the bear (Jalanka and Roeken, 1990). Usually in late summer–early autumn, the spring dosage is increased by 25–50%, and longer needles are used due to increased body fat (Arnemo et al., 2007). Bears were sexed, weighed and a first premolar removed for age determination via cementum annuli counts (Craighead et al., 1970). Permission to capture and handle bears was issued by the County Veterinarian of Oulu, and by the Regional State Administrative Agency of Lahti (Finland). Individuals were fitted with a collar that carried a single 1.5 kg global positioning system (GPS) transmitter (Televilt, Lindesberg, Sweden; Vectronic Airspace, Berlin, Germany). The weight of the collars was less than 1.0–2.0% of the bodyweight of adult females (mean ± SD = 124.6 ± 27.5 kg) and 0.5–1.0% of adult males (mean ± SD = 212 ± 61.4 kg). For subadults, the collars were adjusted to allow individuals to grow and increase in body size, and we used cotton belt so that collars would drop-off before a subadult bear would grow too much to start having problems. Brown bears were categorized as subadult when they were ˂4 years old. Collars had a pre-programmed drop off mechanism with an average battery life of one year. The drop-off worked well for 40% of collars. When the mechanism did not work due to technical defects, the bear was recaptured and the collar was removed. All collars were removed before the end of the project in 2014. The GPS collars were calibrated to continuously track brown bears, collecting one location every 2 h (n = 74,723 locations, denning period excluded; mean number of locations per individual ± SD = 1966.6 ± 1833.3; mean number of tracking days per individual ± SD = 696 ± 670 days, range = 68–3562 days). Signals from the satellite transmitters were recorded by the ARGOS satellite system

(www.cls.fr). We recorded the positional dilution of precision (PDOP) value for all 3-D fixes and the horizontal dilution of precision for 2-D fixes. Following the method developed by D'Eon et al. (2002), we excluded all 2-D fixes. Although this data screening method reduces the data set (i.e. n = 68,943 locations), it allows removing large location errors (Bjørneraas et al., 2010). Thirty known artificial feeding sites of our study area were included in the analyses. On average, 11.1 ± 1.8 feeding sites (range = 7–13) were active per year (until bears started hibernating), and they were rather equally supplied in the mating and hyperphagia periods. Average distance between active artificial feeding sites was 187.6 ± 116.4 km, ranging from less than 1 km to 415.2 km.

2.3. Variable extraction

We considered the following nine parameters: (1) age (i.e. subadults, single adults and females with cubs); (2) sex; (3) season (i.e. mating vs. hyperphagia seasons); (4) year; (5) number of active artificial feeding sites per year; (6) number of years that the feeding site nearest to the bear's location was active; (7) influence of a feeding site, i.e., a binomial variable showing if the bear visited or not a feeding site (one location within 500 m of a feeding site) at least once per day; (8) the percentage of bear locations within 500 m of a feeding site in a day, which is the sum of the locations inside a 500 m buffer zone around feeding sites divided by the total number of locations recorded on a daily scale, and (9) the time of day (i.e. dawn from 1 h before to 1 h after sunrise; daylight from 1 h after sunrise to 1 h before sunset; dusk from 1 h before to 1 h after sunset; and night from 1 h after sunset to 1 h before sunrise). The sex and age descriptions specified above allow the internal state of the individual to be assessed. The mating season lasts for about three months from den exit to the 31st of July (Dahle and Swenson, 2003a; Spady et al., 2007), and the period of hyperphagia begins the 1st of August and terminates at the end of October when bears enter the den (Ordiz et al., 2017). Lastly, we obtained daily brown bear trajectories by using the *adehabitat* package (version 0.4.15) for R software (Calenge, 2006). We estimated the following two movement parameters at a daily scale: (1) net distance, i.e. distance travelled between initial position and final position each day; and (2) average daily speed, which is the mean of the step distance (distance between two relocations) divided by the time interval between consecutive locations. To deal with missing fixes we took 4-hour interval and assumed that bears moved in a straight line (but we allowed only 1 missing value per day). Finally, we also estimated the size of the home range at a daily scale per individual (n = 4244 daily home ranges, after removing individuals with less than 15 days of data) using the minimum convex polygon (MCP) method (Dahle and Swenson, 2003b; Mohr, 1947). MCP was chosen over the kernel estimator because it is applicable with less than 30 locations (Seaman et al., 1999). To set the limits of the home range, we used isopleths values of 95% density.

2.4. Statistical analyses

2.4.1. Probability of use of artificial feeding sites

We built two sets of Generalized Linear Mixed Models (GLMMs), both including the probability that a bear visited a feeding site at least once in a day as a binomial response variable (i.e. 1 = when the percentage of locations within 500 m of the feeding site is higher or equal to 1, or 0 = when the percentage of locations within 500 m of the feeding site is equal to 0). In the first set of models, we included year, season, age, sex and characteristics of the feeding site as explanatory variables. In the second set of models, we included time of day together with age and sex as explanatory variables.

2.4.2. Intensity of use of artificial feeding sites

To explore the intensity of use of artificial feeding sites for those bears that visited a feeding site at least once in a day, we built a set of models which included the number of locations within 500 m of the feeding site as the response variable, i.e. [(number of bear locations within 500 m around a feeding site / total number of locations per day) * 100]. Specifically, we used GLMMs with Poisson distribution, and included year, season, internal features of individuals and characteristics of the artificial feedings as explanatory variables. Because the total number of locations recorded varied across days and bears, we included the total number of locations per bear per day as an offset in the models following Ferrari and Comelli (2016) and Wagenius et al. (2012).

2.4.3. Does the use of artificial feeding sites influence movement patterns?

To assess whether movement patterns are influenced by the use of artificial feeding sites, we first built a set of GLMMs with Gamma distribution for each movement parameter (i.e. daily net distance, daily mean speed and daily home range size). Each set of models included one of the above-mentioned variables as a response variable, and the probability of using artificial feeding sites as an explanatory variable. Second, by considering only those bears that visited a feeding site at least once a day, we built a second set of GLMMs with Gamma distribution for each movement parameter, and the intensity of use of artificial feeding sites as an explanatory variable. Whereas the aim of the first set of models is to assess whether movements are affected by the probability of using a feeding site (i.e. if a bear uses or not feeding sites), the second one aims to assess if and how movements are affected by the intensity with which bears use feeding sites (excluding those bears that never use feeding sites).

In all sets of models, to take into account the differences in behaviour between brown bears, we included the individual as a random factor. For analysis of the probability and intensity of use of artificial feeding sites, we constructed a set of competing models that included all possible combinations of predictor variables, from the simplest null model (intercept model only) to a complete model that included all landscape parameters. The best competing model or set of models was chosen based on Akaike's information criterion (AICc). Models with a ΔAICc below 2 were considered as equally competitive. Values of ΔAICc and weighted AICc, indicating the probability that the model selected was the best among the competing candidates (Table 1), were calculated as well. Parameter coefficients and the relative importance value (RIV) of each explanatory variable were generated by employing model averaging on the 95% confidence set (Burnham and Anderson, 2002). Models were run in R v. 3.5.1 statistical software (R Foundation for Statistical Computing, 2018) using the lme4 package (Bates et al., 2015). Model generation and model averaging were performed using the MuMIn package (Barton, 2018).

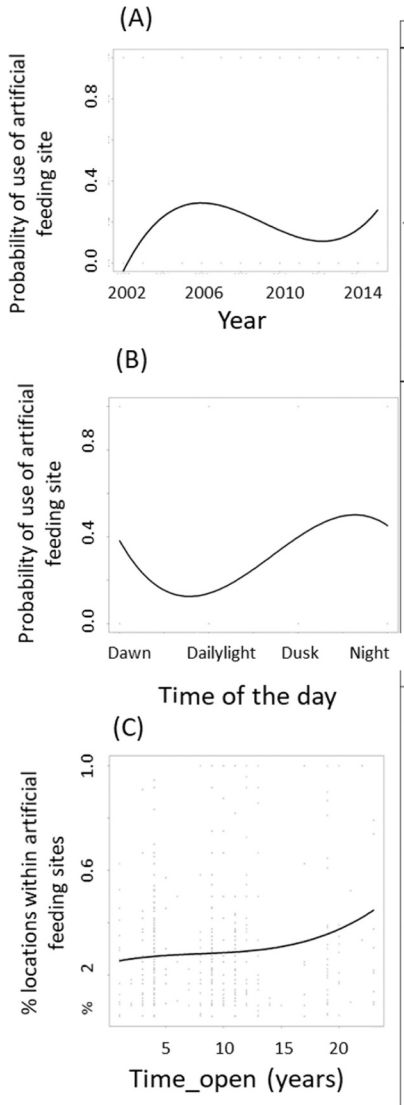
3. Results

Out of a total of 1210 days of male tracking, males visited a feeding site at least once 218 days (18.0%), whereas females visited feeding sites 443 days (13.7%, n = 3223 days of tracking). The frequency of days spent at feeding stations was almost the same for subadults (16.3% of days, n = 1505 days of tracking) and adults (15.3% of days, n = 1826 days of tracking), and slightly less for females with cubs (12.3% of days, n = 1102 days of tracking; Fig. 2). Finally, for all bears, feeding sites were visited a total of 325 days during the mating period (13.8%, n = 2362 days of tracking) compared to 336 days during hyperphagia (16.2%, n = 2071 days of tracking).

3.1. Probability and intensity of use of artificial feeding sites

We found that the probability of a brown bear visiting a feeding site was influenced by some external factors, but not by any of the internal factors that we took into account in our analyses. The most parsimonious model included the year and season, as well as the time that the feeding site nearest to the bear's location was active. Specifically, the probability that brown bears visited feeding sites increased (Table 1): (1) over the years (Table 1; panel A), with the probability of a brown bear visiting a

Table 1
Model-averaged coefficients, AICc, ΔAICc, weighted AICc and RIV values for the probability (at yearly, seasonal and daily scales) and intensity (at yearly and seasonal scales) of use of artificial feeding sites against age and sex, and characteristics of the feeding sites (i.e. number of active feeding sites: Nfeed_site; and time (i.e. years) the feeding sites were active: Time_open), depending on the model. Competitive models are ordered from the highest to the lowest AICc value (best model). Panels A–C are graphical examples of some variables influencing the probability and intensity of use of feeding sites.



Dependent variable	Competing models		AICc	ΔAICc	Weighted AICc
Probability of use of the artificial feeding sites (yearly and seasonal temporal scales)	Age + NFeed_site + Time_open + Year + Season		2836.34	1.81	0.12
	Age + Time_open + Year + Season		**2834.53**	**0.00**	**0.28**
	Explanatory variables	Model-averaged coefficients and relative importance values			
		β	SE	CI	RIV
	Intercept	-3.30	0.67	-4.61;-1.98	
	Time_open	**0.25**	**0.08**	**0.09;0.40**	**0.99**
	Year	**0.37**	**0.15**	**0.08;0.66**	**0.91**
	Season	**0.22**	**0.11**	**0.00;0.43**	**0.74**
	NFeed_site	0.08	0.12	-0.15;0.33	0.34
	Adults	-0.44	0.47	-1.35;0.48	0.79
	Females w/cubs	-0.75	0.45	-1.62;0.12	0.79
	Sex	-0.03	0.98	-1.96;1.90	0.25
Probability of use of the artificial feeding sites (daily temporal scales)	Age + Sex + Time of the day		12063.77	1.95	0.27
	Age + Time of the day		**12061.82**	**0.00**	**0.73**
	Explanatory variables	Model-averaged coefficients and relative importance values			
		β	SE	CI	RIV
	Intercept	-0.33	0.26	-0.84;0.17	
	Adults	**-0.81**	**0.26**	**-1.32;-0.30**	**1.00**
	Females w/cubs	-0.30	0.25	-0.79;0.19	1.00
	Daylight/Night	**-1.43**	**0.08**	**-1.58;-1.27**	**1.00**
	Night/Dusk	0.10	0.10	-0.09;0.28	1.00
	Night/Night	**0.43**	**0.08**	**0.28;0.59**	**1.00**
	Sex	0.08	0.35	-0.61;0.77	0.27
Intensity of use of the artificial feeding sites (yearly and seasonal temporal scales)	Age + Time_open + Season		3511.13	1.81	0.04
	Age + Time_open + Year		3510.91	1.59	0.05
	Age + NFeed_site + Time_open + Year + Season		3510.82	1.50	0.05
	Age + Time_open + Year + Season		3510.50	1.18	0.06
	Age + NFeed_site + Time_open		3509.80	0.48	0.09
	Age + NFeed_site + Time_open + Season		**3509.32**	**0.00**	**0.11**
	Explanatory variables	Model-averaged coefficients and relative importance values			
		β	SE	CI	RIV
	Intercept	-1.18	0.15	-1.58;-1.15	
	Time_open	**0.08**	**0.04**	**0.01;0.16**	**0.80**
	Year	-0.06	0.06	-0.17;0.06	0.37
	Season	0.08	0.05	-0.01; 0.16	0.61
	NFeed_site	-0.05	0.03	-0.12;0.01	0.58
	Adults	-0.26	0.16	-0.58; 0.06	0.83
	Females w/cubs	-0.10	0.16	-0.41;0.21	0.83
	Sex	0.04	0.15	-0.32;0.34	0.25

feeding site being higher when the latter was opened for several years in a row; and (2) during the hyperphagia period. The probability of a brown bear visiting a feeding site increased from 0.14 to 0.18 depending on the time the feeding site was active (from 1 to 25 years); that is, the longer the duration of feeding site activity over the years, the higher the probability of receiving a visit from a bear. We also found that the probability of a brown bear visiting a feeding site was influenced by the time of day, being higher at night (Table 1; panel B) for all bear classes (Fig. 2). However, no spatial overlap occurred between the radio-collared females with cubs and adult males, which used different feeding sites (Fig. 3). In addition, we also found that the intensity of use of feeding sites was higher when the feeding site was open several years in a row (Tables 1; panel C).

3.2. The use of artificial feeding sites influences movement patterns

The use of artificial feedings influenced some movement patterns. On one hand, the probability of using an artificial feeding site affected the daily net distance only (bears using feeding sites: 3.5 ± 4.5 km, range: 0–29 km; bears not using feeding sites: 4.4 ± 4.9 km, range: 0–47 km). Specifically, bears moved shorter daily net distances when the probability of visiting artificial feeding sites was high (β = −0.22, CI = −0.332; −0.113). On the other hand, the intensity of use of feeding sites influenced net distance (β = −0.01, CI = −0.024; −0.016; Fig. 4A), average daily speed (β = −0.01, CI = −0.013; −0.010; Fig. 4B) and daily home range size (β = −0.02, CI = −0.029; −0.020; Fig. 4C). That is, bears moved shorter distances, at a lower speed, and within smaller home ranges when the intensity of use of feeding sites increased.

4. Discussion

Brown bears in boreal habitats are sensitive to the presence of artificial feeding sites within their home ranges. On one hand, both the probability of a particular feeding site being used and the intensity of its use were positively correlated to the stability of this food resource over time. This is probably due to individual spatial memory and learning,

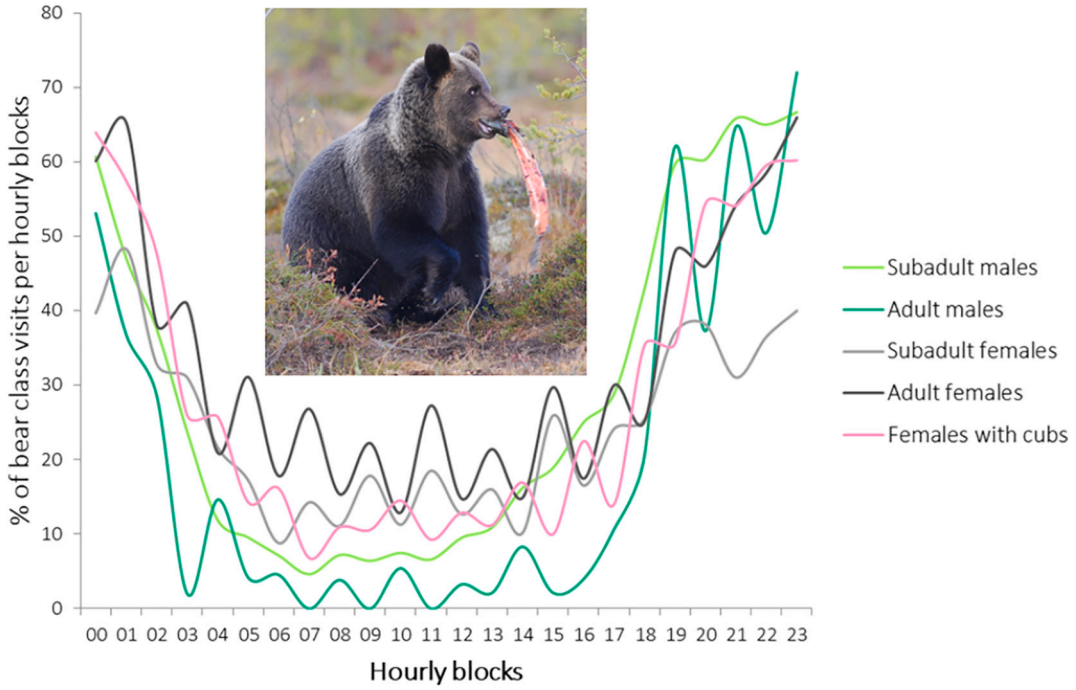


Fig. 2. All bear classes, i.e. adults, subadults and females with cubs, visited the feeding sites with the same crepuscular and nocturnal patterns, with visits during the day being rare (brown bear picture: V. Penteriani).

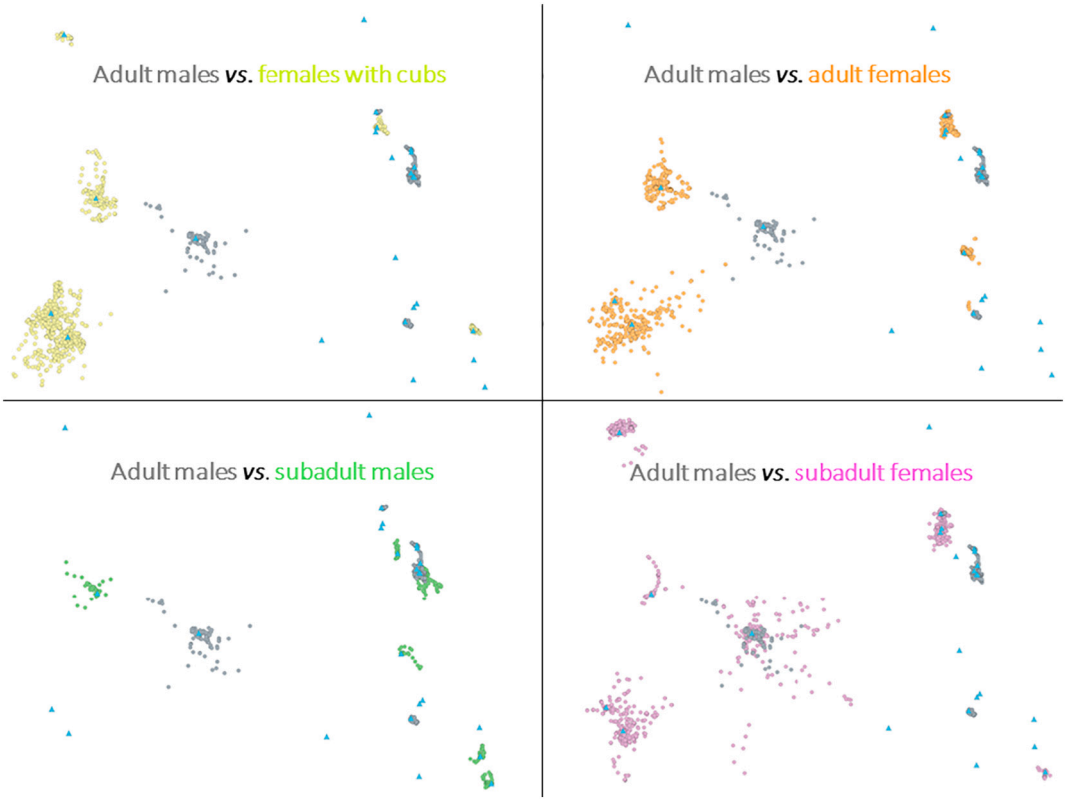


Fig. 3. Spatial overlaps of the different classes of radio-collared bears (n = 71 individuals) at feeding sites. Radio-collared females with cubs and adult males do not overlap. Light blue triangles represent feeding sites. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

which are advantageous in environments with a relatively high level of resource predictability (Fagan et al., 2013; Mery, 2013; Riotte-Lambert and Matthiopoulos, 2020), as artificial feeding sites are. On the other hand, the use of feeding sites was not clearly related to sex, age class or reproductive status (subadults, adults and females with cubs). Feeding sites were visited predominately at night (twilight included) and slightly

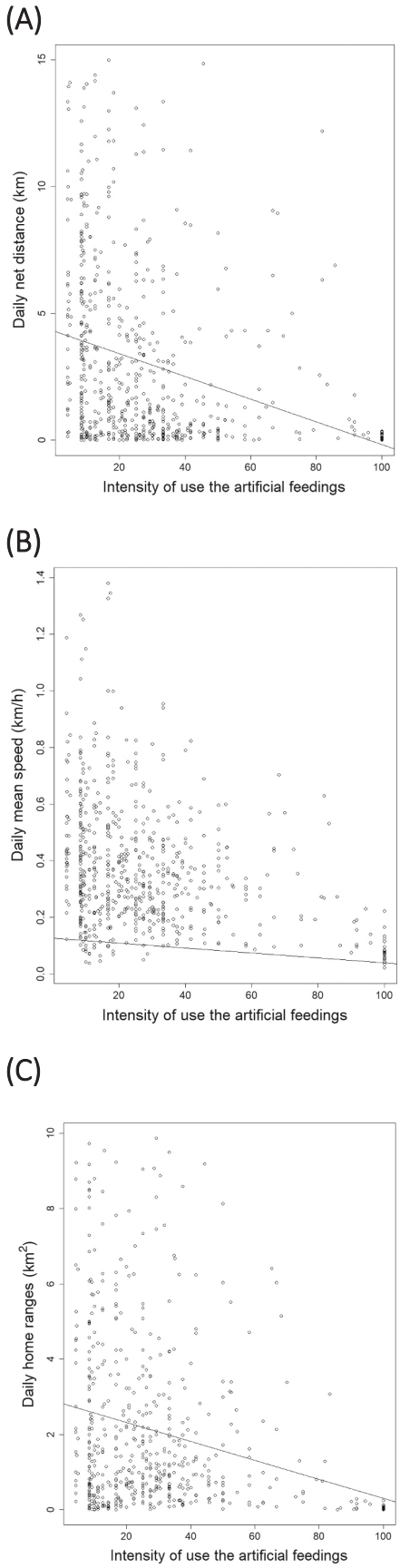


Fig. 4. Effects of the intensity of use of artificial feeding sites on daily net distance, speed and home range sizes.

more during hyperphagia.

Brown bears using garbage dumps in northeast Turkey were also observed to increase visitation rates during hyperphagia (Cozzi et al., 2016). Given the importance of storing fat during hyperphagia, foraging is the main activity of brown bears during this season (González-Bernardo et al., 2020; Swenson et al., 2020). This may contribute to explaining the more intense use of feeding sites during the brown bears' hyperphagia period, when the nutritional impact of feeding sites should be higher than in other periods. During hyperphagia, bears must consume large amounts of food and they may need to make large displacements in order to find sufficient high-energy foods to build up large fat reserves before hibernation (Swenson et al., 2020). By staying close to the feeding sites, fed bears in our study area should not need to travel long distances or move quickly in order to find food, probably indicating that they are meeting a relevant part of their energetic demands at the feeding sites during hyperphagia (Massé et al., 2014). Yet, the relatively low visitation rates throughout the year, i.e. feeding sites were visited 13.8% and 16.2% of the days during the mating and hyperphagia periods, respectively, might reveal that Karelian brown bears are not strictly dependent on artificial feeding, probably due to abundant local natural food resources (e.g. wild berries are available onwards late July, author's unpublished data). If during hyperphagia, which is crucial for successful bear hibernation and cub production (Farley and Robbins, 1995; González-Bernardo et al., 2020; López-Alfaro et al., 2013), brown bears invest a large proportion of time in security (primarily nocturnal foraging to avoid humans and conspecific aggression), this might reduce time for foraging and imply high foraging costs (Brown and Kotler, 2004). However, we cannot discard the possibility that intraspecific competition might have also contributed to reduce bear visitation rates to artificial feeding sites. Compared to the densities reported in other parts of Europe (e.g. 14 artificial feeding sites/100 km^2 in Bieszczady Mountains in Poland; Bojarska et al., 2019), it seems that artificial feeding site density in our study area is low. This would increase chances that intraspecific competition for food at these sites could be an important factor contributing to low visitation rates at the individual level.

Artificial feeding caused brown bears to move short distances at a low speed within small home ranges when they increased the intensity of use of feeding sites. Generally, individuals that travel quickly and over long distances may exploit local resources less thoroughly and need more energy for movement, but they can potentially encounter higher quality resource patches by moving more. In fact, individuals with greater displacements may encounter and cross more habitat patches per day than individuals with shorter displacement distances (Hertel et al., 2019). But this possibility, which can occur in animals depending on natural resources only, is probably less important when part of the diet is composed of predictable and continuously renewed resources, as in the case of artificial feeding sites. Actually, at a within-resource-patch scale, as a response to environmental predictability (i.e. continuous resource availability at given spatial localities), many animals use an area-restricted search (also called 'intensive search') strategy by adopting a more tortuous path or reducing speed when moving in a profitable area (Benhamou, 1994). These restricted patterns of movements are typical of moving organisms faced with constancy over time and space, which involves fixed, nondepletable (or immediately renewable) and nonmoving resources (Riotte-Lambert and Matthiopoulos, 2020). This tendency of artificially fed brown bears to restrict their movements (as also observed in North American brown bears *Ursus arctos horribilis*; Blanchard and Knight, 1991) might be revealing an increase in fidelity to places with supplementary foods that, as an end result, may provoke changes in bear behaviour through 'domestication', reduce population range expansion and diminish long-distance displacements (Cozzi et al., 2016; Selva et al., 2017).

Large carnivores, such as brown bears, have shown to alter their behaviour to reduce encounters with humans by becoming more nocturnal (Ordiz et al., 2014, 2011). Legal hunting, which takes place

during the day, is the most important cause of mortality for brown bears in Scandinavia, e.g. >80% of bear deaths in Sweden between 1984 and 2006 (Bischof et al., 2009). Thus, nocturnal habits help bears to avoid encounters with people in general and, more specifically, to reduce mortality risk in areas where human activities like hunting are practiced. This might help explain the prevalently nocturnal patterns of feeding site visitations and the influence of artificial feeding on space use and movements of bears recorded for the Karelian subpopulation, an explanation that has been proposed for brown bears moving in landscapes characterized by high densities of artificial feeding sites for hunting purposes in both Slovenia (Jerina et al., 2012) and Sweden (Zedrosser et al., 2013). Indeed, the distribution of visits within a 24-hour period showed a clear bimodal pattern, with most visits registered during the early morning and evening hours, and the fewest visits being registered during the middle of the day. But, since brown bear general activity patterns frequently show bimodal activity with peaks around evening and morning, and lowest activity in midday (Swenson et al., 2020), this behaviour cannot be entirely attributed to the presence of artificial feeding sites and risk of hunting mortality.

In contrast to previous studies, we also observed that subadults, adults and females with cubs visited artificial feeding sites predominantly between sunset and sunrise (Fig. 2). Thus, there was no apparent temporal avoidance to reduce intraspecific conflicts between, for example, adult males and subadults or females with cubs to avoid the risks of infanticide, and no avoidance of risky dominance hierarchies among different bear classes (Jerina, 2012; Penteriani et al., 2018, 2017; Steyaert et al., 2012; Zedrosser et al., 2013). To our knowledge, this is the first record of the apparent lack of avoidance mechanisms of females with cubs and subadults towards potentially aggressive adult males at feeding sites and, more generally, at sources of anthropogenic food. We suggest that this might be due to the schedule of daily food replenishing of Karelian artificial feeding sites, i.e. primarily in late afternoon (author's unpublished data). This means that most of the food is available from sunset to sunrise only, whereas the amount of food is irrelevant during the day. Thus, if bear classes at risk of adult male aggression want to find food there, they need to run the risk of visiting artificial feeding sites at a decreasing rate from sunset to sunrise, as Karelian radio-collared bears effectively did (Fig. 2). Such a human-induced pattern of largely nocturnal bear visits to artificial feeding sites has the potential to trap females with cubs and subadults in a possibly highly risky time bracket when feeding. An effective way to avoid such a problem would be to require the people/companies that manage artificial feeding sites for bears: (a) to include in their feeding schedule at least one replenishment of feeding sites a little after sunrise, thus offering subadults and females with cubs the opportunity to choose a safer visitation time, as reported in other areas (Jerina et al., 2012; Zedrosser et al., 2013); (b) use foods that cannot be quickly reduced by seagulls and ravens coming to exploit these resources after sunrise; and/or (c) placing food in boxes with heavy lids or/and on raised platforms could further prevent birds or ungulates feeding (Fležar et al., 2019).

Even if we cannot radio-collar all the bears using each feeding site, the absence of any spatial overlap between marked females with cubs and adult males might indicate that females with cubs may use a mechanism of spatial avoidance (Steyaert et al., 2012) by predominantly using those feeding sites that are not used by adult males (Fig. 3). This possibility is also consistent with the patterns of spatial overlap recorded for subadults (both males and females), which largely overlap with adult males (Fig. 3). However, we cannot discard the influence of an additional, not mutually exclusive effect on artificial feeding site visitation patterns, i.e. the relatively low bear densities in Finland compared to other parts of Europe where artificial feeding is practiced, which might enable bears to easily avoid dangerous conspecifics spatially.

Highly predictable and continuously available anthropogenic food has substantial ecological impacts on movement patterns in another ursid, the American black bear *Ursus americanus*, for which the practice of baiting for hunting purposes is widespread in North America. In fact, as we detected in brown bears, fed bears showed reduced annual and seasonal home ranges and decrease movement rates, especially in autumn and during the daytime in all seasons (Massé et al., 2014). But artificial feeding does not only affect bear species. For example, analogous home range contractions have been reported for the red deer *Cervus elaphus*, potentially leading to increased disease transmission and intra- and interspecific (sympatric wild and domestic ungulates, respectively) competition due to the high deer densities around feeding sites. And this collateral effect of artificial feeding can result in the exact opposite of what was intended by managers, i.e. increase deer trophy value to hunters and reduce forest damages (Jerina, 2012).

Because frequenting artificial feeding sites modifies individual behaviour, thus affecting the overall energy budget of bears, and artificial feeding has the potential to produce several collateral negative effects on bear ecology, behaviour and health (Kavčič et al., 2015; Penteriani et al., 2018, 2017; Skuban et al., 2016), the recorded changes in movement patterns add more weight to the evidence that artificial feeding may have important but overlooked implications for bear ecology and management. Thus, managers should focus on minimizing human-induced behaviours in large carnivores that might cause fitness disadvantages for the affected individuals and as a result have the potential to distress the ecosystems in which large carnivores play key ecological roles (Ordiz et al., 2014). Though some displacements of bears due to the presence of feeding sites can occur with minimal nutritional effects, when estimating the impacts of artificial feeding on local bear populations we should always consider local factors such as the carrying capacity of the area relative to the existing bear population, annual availability and distance of alternative food resources, as well as the distance and energy needed to move to alternative food sources. Indeed, potential detrimental effects on fed bears may be strictly dependent on local conditions and change as a function of the bear population and landscape features. Thus, every area should be regarded as a separate case and the suitability and location of brown bear feeding should be evaluated on the basis of the conservation status of the bear population, bear behaviour and local density, year-to-year availability of food resources and their use, as well as anthropogenic activities that may interact with bears (Morales-González et al., 2020).

CRediT authorship contribution statement

Vincenzo Penteriani: conceptualization, methodology, resources, writing- original draft preparation, supervision, funding acquisition; **Cindy Lamamy**: methodology, formal analysis, writing- original draft preparation; **Ilpo Kojola**: conceptualization, investigation, resources, writing - review & editing, supervision, project administration, funding acquisition; **Samuli Heikkinen**: investigation, resources, writing - review & editing, project administration, funding acquisition; **Giulia Bombieri**: methodology, formal analysis, writing - review & editing; **María del Mar Delgado**: methodology, formal analysis, writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their actions in North Western Europe. Ann. Bot. Fenn. 5, 169–211.

Arnemo, J.M., Fahlman, Å., Ahlqvist, P., Brunberg, S., Segerström, P., Swenson, J.E., 2007. Biomedical Protocol for Free-ranging Brown Bears (Ursus arctos) in Scandinavia, pp. 113–124. https://doi.org/10.13140/RG.2.1.2637.1684.

Arnold, J.M., Gerhardt, P., Steyaert, S.M.J.G., Hochbichler, E., Hackländer, K., 2018. Diversionary feeding can reduce red deer habitat selection pressure on vulnerable forest stands, but is not a panacea for red deer damage. For. Ecol. Manag. 407, 166–173. https://doi.org/10.1016/j.foreco.2017.10.050.

Barton, K., 2018. Package 'MuMIn': multi-model inference. Available at: http://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Benhamou, S., 1994. Spatial memory and searching efficiency. Anim. Behav. 47, 1423–1433.

Bischof, R., Fujita, R., Zedrosser, A., Söderberg, A., Swenson, J.E., 2008. Hunting patterns, ban on baiting, and harvest demographics of brown bears in Sweden. J. Wildl. Manag. 72, 79–88.

Bischof, R., Swenson, J.E., Yoccoz, N.G., Mysterud, A., Gimenez, O., 2009. The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. J. Anim. Ecol. 78, 656–665. https://doi.org/10.1111/j.

Bjørneraas, K., Van Moorter, B., Rolandsen, C.M., Herfindal, I., 2010. Screening global positioning system location data for errors using animal movement characteristics 74, 1361–1366. https://doi.org/10.2193/2009-405.

Blanchard, B.M., Knight, R.R., 1991. Movements of Yellowstone grizzly bears. Biol. Conserv. 58, 41–67.

Bojarska, K., Selva, N., 2012. Spatial patterns in brown bear Ursus arctos diet: the role of geographical and environmental factors. Mamm. Rev. 42, 120–143. https://doi.org/10.1111/j.1365-2907.2011.00192.x.

Bojarska, K., Drobniak, S., Jakubiec, Z., Zyśk-Gorczyńska, E., 2019. Winter insomnia: how weather conditions and supplementary feeding affect the brown bear activity in a long-term study. Glob. Ecol. Conserv. 16, e00523 https://doi.org/10.1016/j.gecco.2019.e00523 (Contents).

Borowski, Z., Bałazy, R., Ciesielski, M., Korzeniewski, K., 2019. Does winter supplementary feeding affect deer damage in a forest ecosystem? A field test in areas with different levels of deer pressure. Pest Manag. Sci. 75, 893–899. https://doi.org/10.1002/ps.5131.

Brown, J., Kotler, B., 2004. Hazardous duty pay and the foraging cost of predation. Ecol. Lett. 7, 999–1014.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, Berlin.

Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017.

Candler, E.M., Severud, W.J., Bump, J.K., 2019. Who takes the bait? Nontarget species use of bear hunter bait sites. Human-Wildlife Interact. 13, 98–110. https://doi.org/10.26076/49xm-fx57.

Cozzi, G., Chynoweth, M., Kusak, J., Çoban, E., Çoban, A., Ozgul, A., Şekercioğlu, H., 2016. Anthropogenic food resources foster the coexistence of distinct life history strategies: year-round sedentary and migratory brown bears. J. Zool. 300, 142–150. https://doi.org/10.1111/jzo.12365.

Craighead, J.J., Craighead, F.C., McCutchen, H.E., 1970. Age determination of grizzly bears from fourth premolar tooth sections. J. Wildl. Manag. 34, 353. https://doi.org/10.2307/3799022.

Dahle, B., Swenson, J.E., 2003a. Seasonal range size in relation to reproductive strategies in brown bears Ursus arctos. J. Anim. Ecol. 72, 660–667.

Dahle, Bjørn, Swenson, J.E., 2003b. Home ranges in adult Scandinavian brown bears (Ursus arctos): effect of mass, sex, reproductive category, population density and habitat type. J. Zool. 260, 329–335. https://doi.org/10.1017/S0952836903003753.

Delibes-Mateos, M., Ferreras, P., Villafuerte, R., 2009. European rabbit population trends and associated factors: a review of the situation in the Iberian Peninsula. Mamm. Rev. 39, 124–140.

D'Eon, R.G., Serrouya, R., Smith, G., Kochanny, C.O., 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildl. Soc. Bull. 30, 430–439.

Dubois, S., Fraser, D., 2013. A framework to evaluate wildlife feeding in research, wildlife management, tourism and recreation. Animals 3, 978–994.

Dunkley, L., Cattet, M.R.L., 2003. A Comprehensive Review of the Ecological and Human Social Effects of Artificial Feeding and Baiting of Wildlife. Newsletters & Publications, Canadian Cooperative Wildlife Health Centre.

Elfström, M., Zedrosser, A., Støen, O.G., Swenson, J.E., 2014. Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. Mamm. Rev. 44, 5–18. https://doi.org/10.1111/j.1365-2907.2012.00223.x.

Eskelinen, P., 2009. Finnish brown bear watching tourism entrepreneurship in numbers. In: Riista- ja kalatalous – Selvityksiä, p. 15 (Helsinki, in Finnish).

Ewen, J.G., Walker, L., Canessa, S., Groombridge, J.J., 2014. Improving supplementary feeding in species conservation. Conserv. Biol. 29, 341–349. https://doi.org/10.1111/cobi.12410.

Fagan, W.F., Lewis, M.A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U.E., Tang, W., Papastamatiou, Y.P., Forester, J., Mueller, T., 2013. Spatial memory and animal movement. Ecol. Lett. 16, 1316–1329. https://doi.org/10.1111/ele.12165.

Farley, S.D., Robbins, C.T., 1995. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Can. J. Zool. 73, 2216–2222.

Felton, A.M., Felton, A., Cromsigt, J.P.G.M., Edenius, L., Malmsten, J., Wam, H.K., 2017. Interactions between ungulates, forests, and supplementary feeding: the role of nutritional balancing in determining outcomes. Mammal Res. 62, 1–7. https://doi.org/10.1007/s13364-016-0301-1.

Ferrari, A., Comelli, M., 2016. A comparison of methods for the analysis of binomial clustered outcomes in behavioral research. J. Neurosci. Methods 274, 131–140. https://doi.org/10.1016/j.jneumeth.2016.10.005.

Fležar, U., Costa, B., Bordjan, D., Jerina, K., Krofel, M., 2019. Free food for everyone: artificial feeding of brown bears provides food for many non-target species. Eur. J. Wildl. Res. 65, 1. https://doi.org/10.1007/s10344-018-1237-3.

Garshelis, D.L., Baruch-Mordo, S., Bryant, A., Gunther, K.A., Jerina, K., 2017. Is diversionary feeding an effective tool for reducing human–bear conflicts? Case studies from North America and Europe. Ursus 28, 31–55. https://doi.org/10.2192/ursu-d-16-00019.1.

González-Bernardo, E., Russo, L., Valderrábano, E., Fernández-González, A., Penteriani, V., 2020. Denning in brown bears. Ecol. Evol. 10, 6844–6862.

Hagen, S.B., Kopatz, A., Aspi, J., Kojola, I., Geir Eiken, H., 2015. Evidence of rapid change in genetic structure and diversity during range expansion in a recovering large terrestrial carnivore. Proc. R. Soc. B Biol. Sci. 282, 13–16. https://doi.org/10.1098/rspb.2015.0092.

Hertel, A.G., Leclerc, M., Warren, D., Pelletier, F., Zedrosser, A., Mueller, T., 2019. Don't poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife. Anim. Behav. 147, 91–104. https://doi.org/10.1016/j.anbehav.2018.11.008.

Jalanka, H.H., Roeken, B.O., 1990. The use of medetomidine, medetomidine-ketamine combinations, and atipamezole in nondomestic mammals: a review. J. Zoo Wildl. Med. 21, 259–282.

Jaroszewicz, B., Kwiecień, K., Czortek, P., Olech, W., Pirożnikow, E., 2017. Winter supplementary feeding influences forest soil seed banks and vegetation. Appl. Veg. Sci. 20, 683–691. https://doi.org/10.1111/avsc.12319.

Jerina, K., 2012. Roads and supplemental feeding affect home-range size of Slovenian red deer more than natural factors. J. Mammal. 93, 1139–1148. https://doi.org/10.1644/11-mamm-a-136.1.

Jerina, K., Krofel, M., Stergar, M., Videmšek, U., 2012. Factors Affecting Brown Bear Habituation to Humans: A GPS Telemetry Study. University of Ljubljana, Biotechnical Faculty, Department of Forestry and Renewable Forest Resources, Večna pot 83, SI-1000 Ljubljana.

Kavčič, I., Adamič, M., Kaczensky, P., Krofel, M., Kobal, M., Jerina, K., 2015. Fast food bears: brown bear diet in a human-dominated landscape with intensive supplemental feeding. Wildlife Biol. 21, 1–8. https://doi.org/10.2981/wlb.00013.

Kirby, R., Macfarland, D.M., Pauli, J.N., 2017. Consumption of intentional food subsidies by a hunted carnivore. J. Wildl. Manag. 81, 1161–1169. https://doi.org/10.1002/jwmg.21304.

Kojola, I., Heikkinen, S., 2012. Problem brown bears *Ursus arctos* in Finland in relation to bear feeding for tourism purposes and the density of bears and humans. Wildlife Biol. 18, 258–263. https://doi.org/10.2981/11-052.

Krofel, M., Jerina, K., 2016. Mind the cat: conservation management of a protected dominant scavenger indirectly affects an endangered apex predator. Biol. Conserv. 197, 40–46. https://doi.org/10.1016/j.biocon.2016.02.019.

Krofel, M., Špacapan, M., Jerina, K., 2017. Winter sleep with room service: denning behaviour of brown bears with access to anthropogenic food. J. Zool. 302, 8–14. https://doi.org/10.1111/jzo.12421.

López-Alfaro, C., Robbins, C.T., Zedrosser, A., Nielsen, S.E., 2013. Energetics of hibernation and reproductive trade-offs in brown bears. Ecol. Model. 270, 1–10. https://doi.org/10.1016/j.ecolmodel.2013.09.002.

Manning, J.L., Baltzer, J.L., 2011. Impacts of black bear baiting on Acadian forest dynamics - an indirect edge effect? For. Ecol. Manag. 262, 838–844. https://doi.org/10.1016/j.foreco.2011.05.017.

Massé, S., Dussault, Christian, Dussault, Claude, Ibarzabal, J., 2014. How artificial feeding for tourism-watching modifies black bear space use and habitat selection. J. Wildl. Manag. 78, 1228–1238. https://doi.org/10.1002/jwmg.778.

Mery, F., 2013. Natural variation in learning and memory. Curr. Opin. Neurobiol. 23, 52–56.

Milner, J.M., Van Beest, F.M., Schmidt, K.T., Brook, R.K., Storaas, T., 2014. To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. J. Wildl. Manag. 78, 1322–1334. https://doi.org/10.1002/jwmg.798.

Mohr, C.O., 1947. Table of equivalent populations of north American small mammals. Am. Midl. Nat. 37, 223–249.

Morales-González, A., Ruiz-Villar, H., Ordiz, A., Penteriani, V., 2020. Large carnivores living alongside humans: brown bears in human-modified landscapes. Glob. Ecol. Conserv. 22, e00937 https://doi.org/10.1016/j.gecco.2020.e00937.

Murray, M.H., Becker, D.J., Hall, R.J., Hernandez, S.M., 2016. Wildlife health and supplemental feeding: a review and management recommendations. Biol. Conserv. 204, 163–174. https://doi.org/10.1016/j.biocon.2016.10.034.

Mysterud, A., Viljugrein, H., Solberg, E.J., Rolandsen, C.M., 2019. Legal regulation of supplementary cervid feeding facing chronic wasting disease. J. Wildl. Manag. 83, 1667–1675. https://doi.org/10.1002/jwmg.21746.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. Proc. Natl. Acad. Sci. 105, 19052–19059. https://doi.org/10.1073/pnas.0800375105.

Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J., Dickman, C.R., 2015. The ecological effects of providing resource subsidies to predators. Glob. Ecol. Biogeogr. 24, 1–11. https://doi.org/10.1111/geb.12236.

Oja, R., Zilmer, K., Valdmann, H., 2015. Spatiotemporal effects of supplementary feeding of wild boar (Sus scrofa) on artificial ground nest depredation. PLoS One 10, 1–11. https://doi.org/10.1371/journal.pone.0135254.

Orams, M.B., 2002. Feeding wildlife as a tourism atraction: a review of issues and impacts. Tour. Manag. 23, 281–293.

Ordiz, A., Støen, O.G., Delibes, M., Swenson, J.E., 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia 166, 59–67. https://doi.org/10.1007/s00442-011-1920-5.

Ordiz, A., Kindberg, J., Sæbø, S., Swenson, J.E., Støen, O.G., 2014. Brown bear circadian behavior reveals human environmental encroachment. Biol. Conserv. 173, 1–9. https://doi.org/10.1016/j.biocon.2014.03.006.

Ordiz, A., Saebø, S., Kindberg, J., Swenson, J.E., Støen, O.-G., 2017. Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation? Anim. Conserv. 20, 51–60. https://doi.org/10.1111/acv.12284.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S., Martínez-Abrain, A., 2013. Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett. 16, 1501–1514.

Ossi, F., Gaillard, J.M., Hebblewhite, M., Morellet, N., Ranc, N., Sandfort, R., Kroeschel, M., Kjellander, P., Mysterud, A., Linnell, J.D.C., Heurich, M., Soennichsen, L., Sustr, P., Berger, A., Rocca, M., Urbano, F., Cagnacci, F., 2017. Plastic response by a small cervid to supplemental feeding in winter across a wide environmental gradient. Ecosphere 8, e01629. https://doi.org/10.1002/ecs2.1629.

Penteriani, V., Melletti, M. (Eds.), 2020. Bears of the World: Ecology, Conservation and Management. Cambridge University Press, UK.

Penteriani, V., Delgado, M.M., Melletti, M., 2010. Don't feed the bears! Oryx 44, 169–170. https://doi.org/10.1017/S003060530003194X.

Penteriani, V., López-Bao, J.V., Bettega, C., Dalerum, F., Delgado, M. del M., Jerina, K., Kojola, I., Krofel, M., Ordiz, A., 2017. Consequences of brown bear viewing tourism: a review. Biol. Conserv. 206, 169–180. https://doi.org/10.1016/j.biocon.2016.12.035.

Penteriani, V., Delgado, M.D.M., Krofel, M., Jerina, K., Ordiz, A., Dalerum, F., Zarzo-Arias, A., Bombieri, G., 2018. Evolutionary and ecological traps for brown bears Ursus arctos in human-modified landscapes. Mamm. Rev. 48, 180–193. https://doi.org/10.1111/mam.12123.

Prinz, N., Story, R., Lyon, S., Ferse, S.C.A., Bejarano, S., 2020. To feed or not to feed? Coral reef fish responses to artificial feeding and stakeholder perceptions in the Aitutaki Lagoon, Cook Islands. Front. Mar. Sci. 7, 1–16. https://doi.org/10.3389/fmars.2020.00145.

R Foundation for Statistical Computing, 2018. R: A Language and Environment for Statistical Computing.

Riotte-Lambert, L., Matthiopoulos, J., 2020. Environmental predictability as a cause and consequence of animal movement. Trends Ecol. Evol. 35, 163–174. https://doi.org/10.1016/j.tree.2019.09.009.

Seaman, D.E., Millspaugh, Joshua J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., Gitzen, R.A., 1999. Effects of sample size on kernel home range estimates. J. Wildl. Manag. 63, 739–747.

Selva, N., Berezowska-Cnota, T., Elguero-Claramunt, I., 2014. Unforeseen effects of supplementary feeding: ungulate baiting sites as hotspots for ground-nest predation. PLoS One 9, e90740. https://doi.org/10.1371/journal.pone.0090740.

Selva, N., Teitelbaum, C.S., Sergiel, A., Zwijacz-Kozica, T., Zięba, F., Bojarska, K., Mueller, T., 2017. Supplementary ungulate feeding affects movement behavior of brown bears. Basic Appl. Ecol. 24, 68–76. https://doi.org/10.1016/j.baae.2017.09.007.

Sergiel, A., Barja, I., Navarro-Castilla, Á., Zwijacz-Kozica, T., Selva, N., 2020. Losing seasonal patterns in a hibernating omnivore? Diet quality proxies and faecal cortisol metabolites in brown bears in areas with and without artificial feeding. PLoS One 15, 1–16. https://doi.org/10.1371/journal.pone.0242341.

Skuban, M., Findo, S., Kajba, M., 2016. Human impacts on bear feeding habits and habitat selection in the Poľana Mountains. Slovakia. Eur. J. Wildl. Res. 62, 353–364. https://doi.org/10.1007/s10344-016-1009-x.

Spady, T.J., Lindburg, D.G., Durrant, B.S., 2007. Evolution of reproductive seasonality in bears. Mamm. Rev. 37, 21–53. https://doi.org/10.1111/j.1365-2907.2007.00096.x.

Steyaert, S.M.J.G., Endrestøl, A., Hackländer, K., Swenson, J.E., Zedrosser, A., 2012. The mating system of the brown bear Ursus arctos. Mamm. Rev. 42, 12–34. https://doi.org/10.1111/j.1365-2907.2011.00184.x.

Steyaert, S.M.J.G., Kindberg, J., Jerina, K., Krofel, M., Stergar, M., Swenson, J.E., Zedrosser, A., 2014. Behavioral correlates of supplementary feeding of wildlife: can general conclusions be drawn? Basic Appl. Ecol. 15, 669–676.

Štofík, J., Merganič, J., Merganičová, K., Bučko, J., Saniga, M., 2016. Brown bear winter feeding ecology in the area with supplementary feeding - Eastern Carpathians (Slovakia). Polish J. Ecol. 64, 277–288. https://doi.org/10.3161/15052249PJE2016.64.2.011.

Swenson, J.E., Ambarlı, H., Arnemo, J.M., Baskin, L., Danilov, P.I., Delibes, M., Elfström, M., Evans, A.L., Groff, C., Hertel, A., Huber, D., Jerina, K., Alexandros, A., Kindberg, J., Kojola, I., Krofel, M., Kusak, J., Mertzanis, G., Ordiz, A., Mano, T., Mario, M., Palazón, S., Parchizadeh, J., Penteriani, Vincenzo, Quenette, Y., Sergiel, A., Selva, N., Seryodkin, I., Støen, G., Konstantin, F., Skuban, M., Steyaert, S.M.J.G., 2020. Brown bear (Ursus arctos Linnaeus, 1758). In: Penteriani, V., Melletti, M. (Eds.), Bears of the World: Ecology, Conservation and Management. Cambridge University Press, UK, Cambridge, UK.

Thierry, A.M., De Bouillane De Lacoste, N., Ulvund, K., Andersen, R., MeÅs, R., Eide, N. E., Landa, A., 2020. Use of supplementary feeding dispensers by Arctic foxes in Norway. J. Wildl. Manag. 84, 622–635. https://doi.org/10.1002/jwmg.21831.

Todorov, V.R., Zlatanova, D.P., Valchinkova, K.V., 2020. Home range, mobility and hibernation of Brown bears (Ursus arctos, Ursidae) in areas with supplementary feeding. Nat. Conserv. Res. 5, 1–15.

Tryjanowski, P., Panek, M., Karg, J., Szumacher-Strabel, M., Cieślak, A., Ciach, M., 2017. Long-term changes in the quantity and quality of supplementary feeding of wildlife: are influenced by game managers? Folia Zool. 66, 248–253. https://doi.org/10.25225/fozo.v66.i4.a6.2017.

van Beeck Calkoen, S.T.S., Mühlbauer, L., Andrén, H., Apollonio, M., Balčiauskas, L., Belotti, E., Carranza, J., Cottam, J., Filli, F., Gatiso, T.T., Hetherington, D., Karamanlidis, A.A., Krofel, M., Kuehl, H.S., Linnell, J.D.C., Müller, J., Ozolins, J., Premier, J., Ranc, N., Schmidt, K., Zlatanova, D., Bachmann, M., Fonseca, C., Lonescu, O., Nyman, M., Šprem, N., Sunde, P., Tannik, M., Heurich, M., 2020. Ungulate management in European national parks: why a more integrated European policy is needed. J. Environ. Manag. 260, 110068. https://doi.org/10.1016/j.jenvman.2020.110068.

Wagenius, S., Dykstra, A.B., Ridley, C.E., Shaw, R.G., 2012. Seedling recruitment in the long-lived perennial, Echinacea angustifolia: a 10-year experiment. Restor. Ecol. 20, 352–359. https://doi.org/10.1111/j.1526-100X.2011.00775.x.

Walpole, M.J., 2001. Feeding dragons in Komodo National Park: a tourism tool with conservation complications. Anim. Conserv. 4, 67–73. https://doi.org/10.1017/S136794300100107X.

Zedrosser, A., Steyaert, S.M.J.G., Brunberg, S., Swenson, J., Kindberg, J., 2013. The effects of baiting for hunting purposes on brown bears and their behaviour. Skandinaviska Björnprojektet.

Ziegltrum, G., 2004. Efficacy of black bear supplemental feeding to reduce conifer damage in Western Washington. J. Wildl. Manag. 68, 470–474. https://doi.org/10.2193/0022-541x(2004)068[0470:eobbsf]2.0.co;2.