



Behavioral correlates of supplementary feeding of wildlife: Can general conclusions be drawn?

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Abstract

Supplementary feeding is a common, but controversial, tool in wildlife management, because it can benefit both humans and wildlife (e.g., increased wildlife densities), but has certain downsides (e.g., increased disease transmission). For species that are often involved in human-wildlife conflicts, two opposing paradigms with respect to supplementary feeding exist, i.e., (i) that supplementary feeding is efficient to lure animals away from undesired places (i.e., diversionary feeding; hypothesis 1), and (ii) that supplementary feeding stimulates ‘nuisance’ behavior (i.e., increased tolerance for humans and selection for human facilities; hypothesis 2). We formulated an alternative hypothesis (hypothesis 3); i.e., that behavioral variation among individuals dilutes population-wide, general patterns with respect to supplementary feeding. Based on GPS relocation data and resource selection functions, we show that neither of the two opposing management paradigms (hypothesis 1 and 2) hold in a particularly ‘conflict rich’ species, the brown bear (*Ursus arctos*), because individual variation in selection behavior with respect to supplementary feeding diluted population-wide patterns (hypothesis 3), even under very different environmental contexts (Sweden vs. Slovenia; i.e., different human and bear population density, history and intensity of supplementary feeding, topography, etc.). Our results emphasize that individual variation is an important component of behavioral ecology and should be considered in wildlife management and conservation.

Zusammenfassung

Ergänzende Fütterungen sind ein häufiges, aber umstrittenes Mittel beim Management von Wildtieren, weil sie sowohl dem Menschen als auch den Wildtieren nützen können (z.B. durch erhöhte Siedlungsdichten der Wildtiere), aber es gibt auch Nachteile (z.B. erleichterte Übertragung von Krankheiten). Bei Arten, die häufig mit dem Menschen in Konflikt geraten, gibt es zwei entgegengesetzte Ansichten: (i) dass sich mit Fütterungen Tiere effektiv von unerwünschten Plätzen weglocken lassen

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(ablenkende Fütterung; Hypothese 1) und (ii) dass Fütterungen Problemverhalten anregt (zunehmende Toleranz gegenüber dem Menschen und Aufsuchen von menschlichen Einrichtungen; Hypothese 2). Wir formulierten eine alternative Hypothese (Hypothese 3), die besagt, dass die Variabilität im Individualverhalten allgemeine, die Population umfassende Verhaltensmuster hinsichtlich der Fütterungen abschwächt. Mithilfe von GPS-Lokalisation und Ressourcenauswahl-Funktionen zeigen wir für den „konfliktreichen“ Braunbären (*Ursus arctos*), dass keins der entgegengesetzten Managementmodelle (Hypothesen 1 und 2) zutrifft. Der Grund ist, dass individuelle Variation im Auswahlverhalten bezüglich der Fütterungen populationsweite Reaktionsmuster abschwächte (Hypothese 3) und dies sogar in stark unterschiedlichen Umweltkontexten (Schweden und Slowenien, d.h., bei unterschiedlichen Bären- und Bevölkerungsdichten, unterschiedlicher Geschichte und Intensität der Fütterung, Topographie usw.). Unsere Ergebnisse unterstreichen, dass individuelle Variation eine wichtige Komponente der Verhaltensökologie ist und beim Wildtiermanagement und -schutz berücksichtigt werden sollte.

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Introduction

Supplementary foods are provided to wildlife wherever humans and wildlife coexist (Beckmann & Berger 2003), either intentionally for management or recreational purposes, or unintentionally, for example as garbage. Supplementary feeding can influence wildlife behavior (e.g., movement patterns, reproductive strategies), demography (e.g., population growth), and life history (e.g., reproduction), and may alter community structures (e.g., species diversity) (Boutin 1990; Robb, McDonald, Chamberlain, & Bearhop 2008). These potential influences can be applied to wildlife management and conservation. For example, supplementary feeding is used to increase the productivity and density of wildlife populations (Boutin 1990), or to support the recovery of endangered species, such as the kakapo (*Strigops habroptilus*) (Clout, Elliott, & Robertson 2002), or the Iberian lynx (*Lynx pardinus*) (López-Bao, Rodríguez, & Palomares 2008). Supplementary feeding is often used to redistribute wildlife populations (i.e., diversionary feeding) to reduce forest damage (Ziegler & Russell 2004) or traffic collisions (Rea 2003). Supplementary feeding is also applied for recreational and hunting purposes, i.e., to attract elusive species to specific places for observation or harvest (i.e., baiting) (Bischof, Fujita, Zedrosser, Söderberg, & Swenson 2008) or to improve trophy size (e.g., antlers in Cervidae) (Putman & Staines 2004).

However, supplementary feeding can also have undesired effects on wildlife and habitats (Boutin 1990; Robb et al. 2008), and is therefore considered as a controversial practice (Putman & Staines 2004). Undesired potential effects include elevated risk for disease transmission or parasite burdens (Putman & Staines 2004), altered sex ratios (Clout et al. 2002), potential risks to human health (Kavčič, Adamič, Kaczensky, Krofel, & Jerina 2013), concerns about selective harvest at bait sites (e.g. when certain sex and age classes make disproportionate use of bait sites) (Bischof et al. 2008), increased interspecific predation (Cortés-Avizanda,

Carrete, Serrano, & Donazar 2009), and habitat degradation (Putman & Staines 2004). An additional concern is that animals may relate supplementary feeding with humans (i.e., become food-conditioned) and lose their ‘normal’ wariness (i.e., habituation) towards people (Woodroffe, Thirgood, & Rabinowitz 2005). Animals with increased tolerance towards humans may become a ‘nuisance’, and can—dependent on the species—be a threat to human safety. Such species include elephants (O’Connell-Rodwell, Rodwell, Rice, & Hart 2000), bears (Elfström, Zedrosser, Støen, & Swenson 2014), felids (Saberwal, Gibbs, Chellam, & Johnsingh 1994), and canids (Orams 2002). The potential to condition animals on certain foods and/or habituate them to humans also highlights the fact that supplementary feeding may cut both ways as a management tool, and raises the question: does supplementary feeding facilitate nuisance behavior, or can it efficiently redistribute wildlife in relation to humans?

Here, we test if and how selection for supplementary feeding correlates with management efficacy (i.e., diversionary feeding) and potential nuisance behavior in a ‘conflict-rich’ species, the brown bear (*Ursus arctos*). Brown bears are large omnivorous opportunists and are often perceived as a ‘problem species’ because they sometimes damage property and kill livestock, and occasionally attack and kill people (Elfström, Zedrosser, Støen, et al. 2014). Supplementary feeding is commonly used as a wildlife management tool, for example to bait animals for hunting purpose (i.e., population regulation) (Bischof et al. 2008), or to lure animals away from undesired places (i.e., diversionary feeding) (Elfström, Zedrosser, Støen, et al. 2014). However, supplementary feeding is also generally presumed to stimulate ‘nuisance’ behavior in bears (Herrero, Smith, DeBruyn, Gunther, & Matt 2005; Elfström, Zedrosser, Støen, et al. 2014). The dichotomous perceptions among wildlife biologists, managers, and the general public on the functionality of supplementary feeding is hotly debated, and can lead to opposing management approaches. For example,

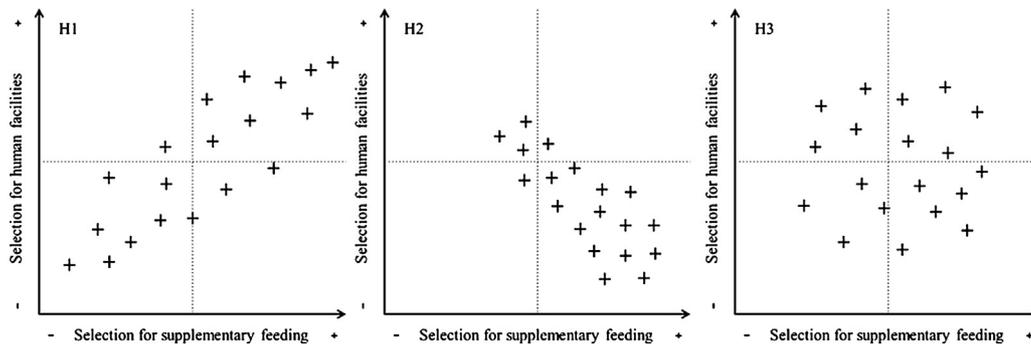


Fig. 1. Conceptual representation the three hypotheses to evaluate behavioral correlates between the selection for supplementary feeding and the selection for human facilities in brown bears. Hypothesis 1 (H1) predicts that bears generally select for supplementary feeding and select against human facilities. H2 predicts that selection for supplementary feeding sites is positively correlated with selection for human facilities. H3 postulates that the variance in selection for supplementary feeding is not associated with selection for human facilities, and that variance in selection for supplementary feeding sites is mostly explained by variation in behavior among and within individuals.

supplementary feeding brown bears is strongly discouraged in several countries, regions, or national parks (e.g., Scandinavia, Yellowstone National Park, Denali National Park, etc.), whereas legally mandated (e.g., Slovenia until 2004, Croatia), or recommended in others (Craighead, Sumner, & Mitchell 1995; Robbins, Schwartz, & Felicetti 2004; Kavčič et al. 2013).

We formulated three hypotheses to address our general objective. Hypothesis 1 postulates that diversionary feeding efficiently mitigates conflicts between bears and humans, and predicts that (a) selection for supplementary feeding sites correlates negatively with selection for human facilities and (b) that the majority of bears select for supplementary feeding sites (Fig. 1). Hypothesis 2 postulates that supplementary feeding stimulates potential nuisance behavior, and predicts that selection for supplementary feeding sites correlates positively with selection for human facilities (Fig. 1). Because individual behavioral differences are common among mammals (Wolf & Weissing 2012), hypothesis 3 postulates that individual variance in behavior dilutes population-wide selection patterns, and predicts that selection for supplementary feeding sites does not correlate with selection for human facilities (Fig. 1). We tested our hypotheses in two brown bear populations (i.e., Sweden and Slovenia) with very different environments (density of bears, humans, and supplementary feeding sites) to control for contingencies and to reveal generalities in behavioral correlates in relation to supplementary feeding. Because human-bear conflicts are often suggested to correlate with the annual variation in the availability of natural foods (low availability \sim high conflict rates) (Mattson, Blanchard, & Knight 1992), we also test the importance of annual variation in supplementary feeding site selection. Because more dominant sex and age classes can dominate supplementary feeding sites (Craighead et al. 1995), we also evaluated a potential effect of reproductive status (i.e., a combination of sex and age classes, and presence or absence of young) on supplementary feeding site selection.

Material and methods

Study areas

The Swedish study area encompassed approximately 13,000 km² of intensively managed boreal forest in south-central Sweden (61°N, 15°E). The human population density (4.1 – 7.1 inhabitants/km²) is one of the lowest within the European brown bear range, and the bear population density is approximately 30 bears/1000 km² (Bellemain, Swenson, Tallmon, Brunberg, & Taberlet 2005). Supplementary feeding was extensively used to bait bears for hunting until 2001, when it was banned. We were granted permission to maintain two experimental supplementary feeding sites between 2008 and 2012, which were restocked weekly with 5 kg of game meat or fish, 5 kg of corn, 5 kg of sugar beet pulp, and 5 l of molasses (Zedrosser, Steyaert, Brunberg, Swenson, & Kindberg 2013). Approximately 1.5% of all harvested bears in Sweden are considered problem bears. Problem bears are generally younger than non-problem bears in Sweden, and the occurrence of problem bears is not related to body condition in bears (i.e., and proxy for food availability) or bear population density (Elfström, Zedrosser, Jerina, et al. 2014).

The Slovenian study area encompassed approximately 3800 km² of extensively managed forest in south-central Slovenia (45°N, 14°E). The human population density averages 54 inhabitants/km², and the bear population can locally reach extremely high densities (>400 bears/1000 km²). Supplementary feeding sites occur at densities of 1/400 – 700 ha and have been maintained with continuous supplies of large amounts (annual average: 70 – 280 kg/km²) of predominantly corn and carrion for several decades in some areas (Kavčič et al. 2013). About 14% of all harvested bears in Slovenia are considered problem bears. As in Sweden, however, Slovenian problem bears are generally younger than non-problem bears, and the incidence of problem bears is not related to body condition or bear population density (Elfström, Zedrosser, Jerina, et al. 2014).

GPS-relocation data

We captured and equipped brown bears with Global Positioning System collars (GPS; Vectronic Aerospace GmbH) by aerial darting with an immobilization drug from a helicopter between 2008 and 2012 in Sweden, and using Aldrich foot snares (Margo Supplies Ltd.) and darting with an immobilization drug from the ground between 2005 and 2012 in Slovenia. The Swedish bears were monitored on a 30-min GPS relocation schedule, whereas we monitored Slovenian bears on an hourly basis. For details on capture and handling, refer to [Arnemo et al. \(2011\)](#) and [Jerina, Krofel, Stergar, & Videmsek \(2012\)](#). We classified bears into adult males (males ≥ 5 years), lone females (≥ 5 years, without young), family groups (females with young), subadult males (< 5 years), and subadult females (< 5 years without young).

Statistical analysis

We used resource selection functions (RSFs) to quantify the behavior of individual bears with respect to a fixed set of landscape variables that are considered important in animal resource selection, including bears (i.e., normalized difference vegetation index, forest vs. nonforest, terrain ruggedness, and distance to supplementary feeding sites, settlements, single houses, and roads) ([Martin et al., 2010](#); [Steyaert, Kindberg, Swenson, & Zedrosser 2013](#)). Refer to Appendix A for details on the spatial data. The GPS relocations and a set of random point represent ‘use’ and ‘availability’ of resources, respectively, and served as the response variable in logistic regression models. We sampled use/availability in a 1:1 ratio, and within the annual 100% minimum convex polygon of each bear-year that overlapped at least one supplementary feeding site outside the denning period. The parameter estimates (β) and standard errors (SE) for each landscape variable included in the model reveal if variables are selected for, selected against, or are relatively unimportant in an individual’s resource selection (i.e., behavioral responses) ([Boyce, Vernier, Nielsen, & Schmiegelow 2002](#)). We multiplied the parameter estimates of the ‘distance to’ variables with -1 to facilitate interpretation; such that positive values indicated selection, whereas negative values indicated avoidance. We used the parameter estimates generated by the individual RSFs to evaluate the relationship between supplementary feeding site selection (i.e., the response variable), selection for landscape variables, as well as bear-year specific data (i.e., bear ID, year, and reproductive status) with linear mixed-effect regression models ([Dingemans & Dochtermann 2013](#)). We included ‘bear ID’ as a random factor. We used akaike information criteria differences (ΔAIC_c) and weights (AIC_{cw}) to select the most parsimonious model among seven candidates defined *a priori* ([Table 1](#)). We considered models with ΔAIC_c values > 4 as inconclusive ([Burnham, Anderson, & Huyvaert 2011](#)). We validated the most parsimonious models by plotting the

model residuals versus the fitted values to evaluate potential heteroskedasticity ([Zuur, Ieno, Walker, Saveliev, & Smith 2009](#)). We used R 2.15.0 for all statistical analyses ([R Development Core Team 2013](#)).

Results

We obtained relocation data and behavioral estimates from 24 and 33 bears in Sweden and Slovenia, respectively ([Table 2](#)). We removed behavioral responses to roads from the Slovenian dataset in the second step, because of collinearity with settlements ($r = -0.67$) ([Table 1](#)).

The most parsimonious model was the ‘null’ model for both Sweden and Slovenia ($AIC_{cw} = 1$). Individual bear variance explained 33% and 43% of the total variance in supplementary feeding site selection in Sweden ($1.59/4.91 \times 10^{-8}$) and Slovenia ($1.96/4.75 \times 10^{-7}$), respectively. All other candidate models were inconclusive (ΔAIC_c values > 54.4 , [Table 1](#)). Bears in Slovenia generally selected for supplementary feeding sites ($\beta = 0.589 \times 10^{-3}$; 95% bootstrapped confidence limits $0.484 - 0.896 \times 10^{-3}$); whereas Swedish bears generally did not select for or against supplementary feeding sites ($\mu = 0.045 \times 10^{-3}$; $-0.013 - 0.105 \times 10^{-3}$). No heteroskedasticity was apparent in the model residuals.

Discussion

We found that individual behavior best explained the strength and direction of selection for supplementary feeding sites (hypothesis 3), and suggest that variation in individual behavior dilutes population-wide patterns related to supplementary feeding site selection. Selection for supplementary feeding sites was not related to reproductive state, year, and selection for human facilities in both Sweden and Slovenia ([Fig. 2](#)). This indicates that diversionary feeding has only low conflict-mitigation potential (hypothesis 1), and that supplementary feeding generally is unlikely to cause nuisance behavior (hypothesis 1) in brown bears. Our results are consistent in both countries, although bears in Slovenia generally selected for supplementary feeding sites whereas Swedish bears did not.

Supplementary feeding is common in wildlife management and conservation, and has received considerable attention in the literature ([Putman & Staines 2004](#); [Robb et al. 2008](#)). However, the importance of individual behavior with respect to supplementary feeding has been largely omitted in research ([Boutin 1990](#)). Ecological research (including studies on supplementary feeding) typically focuses on population-wide generalities in behavior or demography, and rarely on the individual level ([Boutin 1990](#); [Dingemans & Dochtermann 2013](#)). However, the importance of behavioral types (for example shy vs. not shy), individual behavior, and suites of correlated behaviors (i.e., behavioral syndromes)

Table 1. Model selection diagnostics for five candidate linear mixed-effect regression models to determine the relationship between selection behavior for supplementary feeding sites, year, and reproductive status (Status), and selection for environmental characteristics (TRI = terrain ruggedness index, forest/non-forest, NDVI = Normalized Difference Vegetation Index, and distance to Settlements, Houses, and Roads) of GPS-marked brown bears in Sweden (2008 – 2012) and Slovenia (2005 – 2010). We included ‘Bear ID’ as a random factor in all candidate models. ΔAIC_c and AIC_{cw} indicate second-order corrected Akaike’s Information Criteria differences and weights, respectively. \checkmark indicates the inclusion of a certain model term in a candidate model. Distance to roads was never included in the Slovenian candidate model, because of collinearity with distance to settlements. Bear ID was always included as a random factor on the intercept.

Candidate model	Model term										ΔAIC_c	AIC_{cw}
		NDVI	TRI	Forest	Year	Status	Distance to:			Bear ID		
							Settlements	Houses	Roads			
Sweden	All inclusive	\checkmark	202.77	0.0								
	Human				\checkmark		\checkmark	\checkmark	\checkmark	\checkmark	78.11	0.0
	Terrain	\checkmark	\checkmark	\checkmark	\checkmark					\checkmark	142.35	0.0
	Bear				\checkmark	\checkmark				\checkmark	132.71	0.0
	Status					\checkmark				\checkmark	54.40	0.0
	Year				\checkmark					\checkmark	77.02	0.0
	Null									\checkmark	0	1.0
Slovenia	All inclusive	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark		\checkmark	\checkmark	243.43	0.0
	Human				\checkmark		\checkmark	\checkmark		\checkmark	87.10	0.0
	Terrain	\checkmark	\checkmark	\checkmark	\checkmark					\checkmark	139.26	0.0
	Bear				\checkmark	\checkmark				\checkmark	162.95	0.0
	Status					\checkmark				\checkmark	78.11	0.0
	Year				\checkmark					\checkmark	81.43	0.0
	Null									\checkmark	0	1.0

Table 2. Descriptive statistics of bear relocation data in Sweden and Slovenia as used in this study.

	Slovenia	Sweden
N_{bears}	33	24
$N_{females}$	18	10
N_{males}	15	14
$N_{bear\ years}$	43	54
$N_{relocations} (\mu \pm SE)$	2162 \pm 2089	3547 \pm 1177
$N_{relocations} (range)$	221 – 6903	153 – 5351
Study period	2005 – 2010	2008 – 2012

are becoming more prevalent in ecology and evolution (Dingemanse & Dochtermann 2013). We suggest that there is considerable variation among individuals and selection strategies regarding selection for supplementary feeding sites, i.e., some individuals select strongly for supplementary feeding sites, whereas other do not. This selection may be correlated (positively or negatively) with the selection for human facilities by certain individuals, but not for others. This does not rule out that supplementary feeding may trigger nuisance behavior in certain individuals; or, on the other hand, that supplementary feeding may indeed be efficient to lure certain individuals away from human facilities. We stress, however, that (i) the absence of a general relationship between selection for supplementary feeding sites and human facilities does not warrant the use of supplementary

feeding as an efficient management tool *in general*, and (ii) that the presumption that supplementary feeding *generally* causes nuisance behavior does not necessarily hold.

Supplementary feeding game species has a long tradition in Slovenia (>100 years in certain areas), and bears have year-round access to large amounts of high energy supplementary feed (i.e., an annual average of 70 – 280 kg/km², predominantly corn). Kavčič et al. (2011) estimated that Slovenian bears obtain approximately 35% of their annual energy requirements from supplementary feeding. Jerina, Jonozovič, Krofel, & Skrbinišek (2013) suggested that such long-term and intensive supplementary feeding can increase an area’s carrying capacity, which can explain the extremely high local bear densities in Slovenia (>40 bears/100 km²) compared to other European (e.g. Italian Alps, 3 bears/100 km²; Slovakian Carpathians, 5 – 11/100 km²; Romania: 9/100 km²) (Swenson, Gerstl, Dahle, & Zedrosser 2000; Rigg & Adamec 2007; Groff, Dlpiaz, Rizzoli, & Zanghellini 2012) and interior North American population averages (<5 bears/100 km²) (Hilderbrand, Schwartz, Robbins, Jacoby, Hanley et al. 1999). Our result that Slovenian bears generally selected for supplementary feeding sites whereas Swedish bears did not, suggests that long-term and intensive supplementary feeding can condition bears to such predictable food resources. However, food conditioning does not necessarily result in nuisance behavior (Elfström, Zedrosser, Støen, et al. 2014). A similar situation arose in the Greater Yellowstone Ecosystem, in which grizzly bears were conditioned to large-scaled

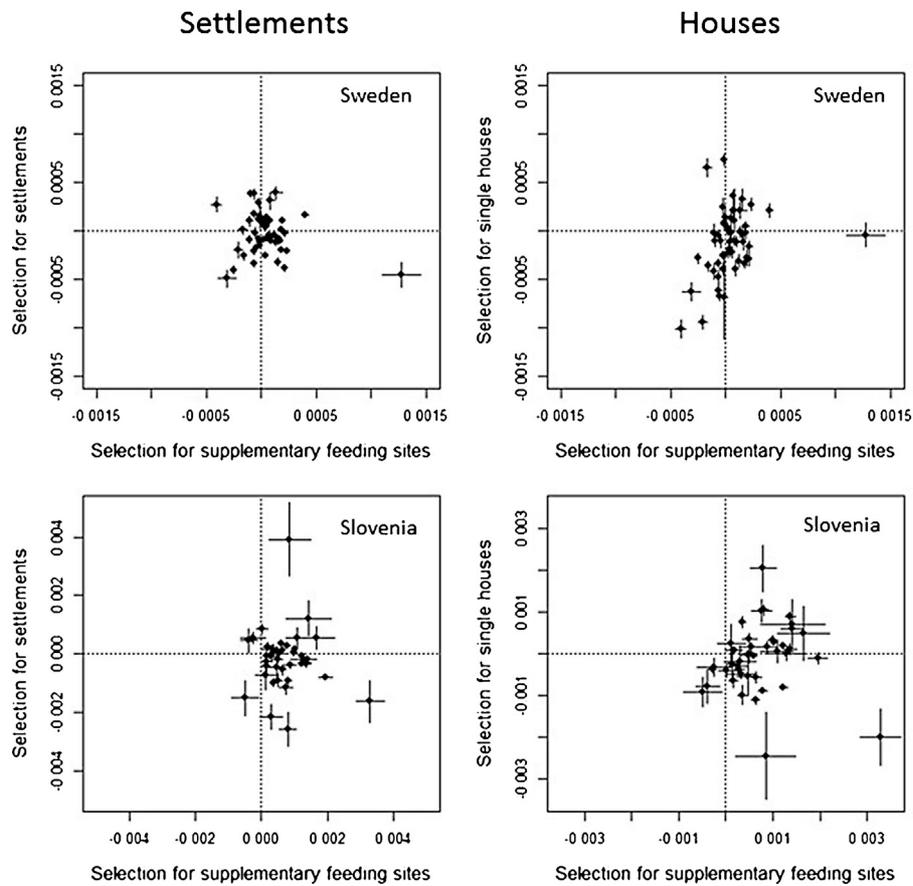


Fig. 2. Relationship between bait site selection and selection for settlements and houses by GPS-marked brown bears in Sweden (2008 – 2012) and Slovenia (2005 – 2010). Coefficients of determination (r^2) indicate the strength of the relationships. Measures of selection (β) were estimated with individual-based resource selection functions. Dashed lines indicate $\beta=0$. Whiskers indicate one standard error around the parameter estimates. Selection for human facilities was not included in the most parsimonious models for both countries.

open pit garbage dumps that were maintained for several decades. These open pit garbage facilitated a larger bear population than the system in fact could hold. Sudden closure of these dump sites in the 1970s resulted in a population decline through increased mortality and dispersal, and reduced reproductive rates (Craighead et al. 1995).

Because supplementary feeding can increase population densities (Boutin 1990), it has also the potential to positively feed-back on human-wildlife conflict rates (Woodroffe et al. 2005). In Slovenia, a dense bear population, coexisting with a relatively dense and dispersed human population probably results in high human-bear conflict rates ($\sim 14\%$ of all harvested bears are considered problem bears). The Swedish bear population, on the other hand, has a relatively low density, coexists with a low density and centralized human population; which probably results in lower conflict rates as compared to Slovenia ($\sim 1.5\%$ of all harvested bears are considered problem bears). We suggest supplementary feeding bears may increase human-wildlife conflict rates, but by increasing population densities rather than that supplementary feeding would stimulate nuisance behavior.

There appears to be no consensus among researchers whether or not supplementary feeding can mitigate conflict (i.e., diversionary feeding and/or to facilitate efficient harvest), or stimulate nuisance behavior. For example, in black bears, some authors argue that diversionary feeding can be efficient (Ziegler & Russell 2004), without stimulating nuisance behavior (Rogers 2011), whereas others advocate the opposite; i.e. that supplementary feeding should not be practiced, because it results in problem behavior (Herrero 1985; Inglis 1992; Herrero et al. 2005). The efficacy of supplementary feeding as a management tool has also been questioned for other species (e.g., wild boar (*Sus scrofa*) (Geisser, Reyer, & Krausman 2004), moose (*Alces alces*) (Rea 2003), red deer (*Cervus elaphus*) (Putman & Staines 2004), and may depend on e.g., natural food availability, habitat quality, supplementary feeding intensity and history, spatial scale, etc. We suggest that in other systems without apparent general supplementary feeding-related behavior, individual behavioral strategies may dilute general population-wide patterns with respect to supplementary feeding.

Conclusions

We found that variability among individuals was the single most important factor explaining the strength of selection for supplementary feeding sites by brown bears in Sweden and Slovenia, two environmental extremes in terms of human density, bear density, and history and intensity of supplementary feeding. Non-explanatory model components included year and reproductive status, and the individual-based selection coefficients for terrain ruggedness, NDVI, and forested vs. non-forested habitat. In addition, selection for supplementary feeding sites was unrelated to selection for settlements, buildings, and roads. Our results imply that selection for supplementary feeding sites did not generally stimulate nuisance behavior in bears, nor that supplementary feeding is an efficient tool to keep bears away from people. We stress that individual variation in behavioral strategies can dilute population-wide behavioral patterns. We suggest that managing supplementary feeding sites can have direct but nonetheless unexpected effects on a population (e.g., increased densities and potential conflict rates; or population declines after reducing supplementary feeding), and our results add to the growing body of evidence that individual variance is an important component of behavioral ecology and should be considered in wildlife management and conservation.

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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.baae.2014.10.002>.

References

- Arnemo, J. M., Evans, A., Fahlman, Å., Ahlqvist, P., Andrén, H., Brunberg, S., et al. (2011). *Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx*. Evenstad, Norway: Hedmark University College.
- Beckmann, J. P., & Berger, J. (2003). *Rapid ecological and behavioural changes in carnivores: The responses of black bears (Ursus americanus) to altered food*. *Journal of Zoology*, *261*, 207–212.
- Bellemain, E., Swenson, J. E., Tallmon, D., Brunberg, S., & Taberlet, P. (2005). *Estimating population size of elusive animals with DNA from hunter-collected feces: Four methods for brown bears*. *Conservation Biology*, *19*, 150–161.
- 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*. *Journal of Wildlife Management*, *72*, 79–88.
- Boutin, S. (1990). *Food supplementation experiments with terrestrial vertebrates: Patterns, problems, and the future*. *Canadian Journal of Zoology*, *68*, 203–220.
- Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. A. (2002). *Evaluating resource selection functions*. *Ecological Modelling*, *157*, 281–300.
- Burnham, K., Anderson, D., & Huyvaert, K. (2011). *AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons*. *Behavioral Ecology and Sociobiology*, *65*, 23–35.
- Clout, M. N., Elliott, G. P., & Robertson, B. C. (2002). *Effects of supplementary feeding on the offspring sex ratio of kakapo: A dilemma for the conservation of a polygynous parrot*. *Biological Conservation*, *107*, 13–18.
- Cortés-Avizanda, A., Carrete, M., Serrano, D., & Donázar, J. A. (2009). *Carcasses increase the probability of predation of ground-nesting birds: A caveat regarding the conservation value of vulture restaurants*. *Animal Conservation*, *12*, 85–88.
- Craighead, J. J., Sumner, J. S., & Mitchell, J. A. (1995). *The grizzly bears of Yellowstone: Their ecology in the Yellowstone ecosystem, 1959 – 1992*. Washington D.C: Island Press.
- Dingemans, N. J., & Dochtermann, N. A. (2013). *Quantifying individual variation in behaviour: Mixed-effect modelling approaches*. *Journal of Animal Ecology*, *82*, 39–54.
- Elfström, M., Zedrosser, A., Jerina, K., Støen, O.-G., Kindberg, J., Budic, L., et al. (2014). *Does despotic behavior or food search explain the occurrence of problem brown bears in Europe? The Journal of Wildlife Management*, *78*, 881–893.
- 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*. *Mammal Review*, *44*, 5–18.
- Geisser, H., Reyer, H.-U., & Krausman. (2004). *Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars*. *Journal of Wildlife Management*, *68*, 939–946.
- Groff, C., Dlpiaz, D., Rizzoli, R., & Zanghellini, P. (2012). *Bear report of the forestry and wildlife department of the autonomous province of Trento*. Trento.
- Herrero, S. (1985). *Bear attacks: Their causes and avoidance*. Piscataway, New Jersey: Winchester Press.
- Herrero, S., Smith, T., DeBruyn, T. D., Gunther, K., & Matt, C. A. (2005). *Brown bear habituation to people: Safety, risks, and benefits*. *Wildlife Society Bulletin*, *33*, 362–373.
- Hilderbrand, G. V., Schwartz, C. C., Robbins, C. T., Jacoby, M. E., Hanley, T. A., Arthur, S. M., et al. (1999). *The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears*. *Canadian Journal of Zoology*, *77*, 132–138.
- Inglis, J. E. (1992). *An analysis of human-black bear conflicts in Algonquin Provincial Park, Ontario (1973 – 1990)*.

- 11th Eastern Black Bear Workshop* (pp. 108 – 123). Waterville Valley, NH.
- Jerina, K., Krofel, M., Stergar, M., & Videmsek, U. (2012). *Factors affecting bear habituation to humans: A GPS telemetry study*. Ljubljana: University of Ljubljana, Biotechnical Faculty (Final report – summary for users)
- Jerina, K., Jonozovič, M., Krofel, M., & Skrbinšek, T. (2013). Range and local population densities of brown bear *Ursus arctos* in Slovenia. *European Journal of Wildlife Research*, *59*, 459–467.
- Kavčič, I., Adamič, M., Kaczensky, P., Krofel, M., & Jerina, K. (2013). Supplemental feeding with carrion is not reducing brown bear depredations on sheep in Slovenia. *Ursus*, 111–119.
- Kavčič, I., Adamič, M., Krofel, M., Jerina, K., & Kaczensky, P. (2011). Brown bear food habits in human dominated landscapes of Slovenia: Importance of intensive long-term supplemental feeding. *Proceedings of the 20th international conference on bear research and management* (pp. 162 – 163). Ottawa.
- López-Bao, J. V., Rodríguez, A., & Palomares, F. (2008). Behavioural response of a trophic specialist, the Iberian lynx, to supplementary food: Patterns of food use and implications for conservation. *Biological Conservation*, *141*, 1857–1867.
- Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allainé, D., & Swenson, J. E. (2010). Coping with human disturbance: Spatial and temporal tactics of the brown bear (*Ursus arctos*). *Canadian Journal of Zoology*, *88*, 875–883.
- Mattson, D. J., Blanchard, B. M., & Knight, R. R. (1992). Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *The Journal of Wildlife Management*, *56*, 432–442.
- O'Connell-Rodwell, C. E., Rodwell, T., Rice, M., & Hart, L. A. (2000). Living with the modern conservation paradigm: Can agricultural communities co-exist with elephants? A five-year case study in East Caprivi, Namibia. *Biological Conservation*, *93*, 381–391.
- Orams, M. B. (2002). Feeding wildlife as a tourism attraction: A review of issues and impacts. *Tourism Management*, *23*, 281–293.
- Putman, R. J., & Staines, B. W. (2004). Supplemental winter feeding of wild red deer *Cervus elaphus* in Europe and North America: Justifications, feeding practice and effectiveness. *Mammal Review*, *34*, 285–306.
- R Development Core Team. (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL (<http://www.R-project.org/>).
- Rea, R. V. (2003). Modifying roadside vegetation management practices to reduce vehicular collisions with moose *Alces alces*. *Wildlife Biology*, *9*, 81–91.
- Rigg, R., & Adamec, M. (2007). *Status, ecology and management of the brown bear (Ursus arctos) in Slovakia*. Liptovský Hrádok: Slovak Wildlife Society.
- Robb, G. N., McDonald, R. A., Chamberlain, D. E., & Bearhop, S. (2008). Food for thought: Supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment*, *6*, 476–484.
- Robbins, C. T., Schwartz, C. C., & Felicetti, L. A. (2004). Nutritional ecology of ursids: a review of newer methods and management implications. *Ursus*, *15*, 161–171.
- Rogers, L. L. (2011). Does diversionary feeding create nuisance bears and jeopardize public safety? *Human – Wildlife Interactions*, *5*, 287–295.
- Saberwal, V. K., Gibbs, J. P., Chellam, R., & Johnsingh, A. J. T. (1994). Lion-human conflict in the Gir forest, India. *Conservation Biology*, *8*, 501–507.
- Steyaert, S. M. J. G., Kindberg, J., Swenson, J. E., & Zedrosser, A. (2013). Male reproductive strategy explains spatiotemporal segregation in brown bears. *Journal of Animal Ecology*, *82*, 836–845.
- Swenson, J. E., Gerstl, N., Dahle, B., & Zedrosser, A. (2000). *Action plan for the conservation of the brown bear (Ursus arctos) in Europe Council of Europe*. Strasbourg.
- Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology and Evolution*, *27*, 452–461.
- Woodroffe, R., Thirgood, S., & Rabinowitz, A. (2005). *People and wildlife: Conflict or co-existence?* Cambridge: Cambridge University Press.
- Zedrosser, A., Steyaert, S. M. J. G., Brunberg, S., Swenson, J. E., & Kindberg, J. (2013). The effects of baiting for hunting purposes on brown bears and their behavior. *Report number 2013-3 from the Scandinavian Brown Bear Research Project*.
- Ziegeltrum, G. J., & Russell. (2004). Efficacy of black bear supplemental feeding to reduce conifer damage in western Washington. *Journal of Wildlife Management*, *68*, 470–474.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.

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