



Do Scandinavian brown bears approach settlements to obtain high-quality food?



Marcus Elfström^{a,*}, Marie L. Davey^{a,b}, Andreas Zedrosser^{c,d}, Martin Müller^d, Marta De Barba^e, Ole-Gunnar Støen^a, Christian Miquel^e, Pierre Taberlet^e, Klaus Hackländer^d, Jon E. Swenson^{a,f}

^a Department of Natural Resources and Management, Norwegian University of Life Sciences, POB. 5003, NO-1432 Ås, Norway

^b Microbial Evolution Research Group (MERG), Department of Biology, University of Oslo, POB 1066 Blindern, NO-0316 Oslo, Norway

^c Faculty of Arts and Sciences, Department of Environmental and Health Studies, Telemark University College, NO-3800 Bø i Telemark, Norway

^d Institute for Wildlife Biology and Game Management, University of Natural Resources and Life Sciences, AT-1180 Vienna, Austria

^e Laboratoire d'Ecologie Alpine, CNRS UMR 5553, Université Joseph Fourier, BP 53, FR-38041 Grenoble cedex 9, France

^f Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

ARTICLE INFO

Article history:

Received 30 May 2014

Received in revised form 2 August 2014

Accepted 4 August 2014

Available online 30 August 2014

Keywords:

Carnivores

Despotic

Diet

DNA metabarcoding

Food conditioning

Near-infrared spectroscopy

ABSTRACT

Large carnivores that approach human settlements are usually considered a threat to human property and safety. The prevailing paradigm, that such 'problem' animals approach settlements in search of food, ignores their social organization. Based on feces, we compared the diet of individual brown bears (*Ursus arctos*) in Sweden in relation to settlements. Nutritive quality was quantified using near-infrared spectroscopy, and food items were identified using a DNA metabarcoding approach. We analyzed the diet of 21 bears during 36 visits near (<150 m) settlements, and the corresponding diet when the same bears were in remote areas (>600 m from settlements; constituting 95% of bears' habitat use). The food-search hypothesis predicted a different and higher-quality diet when an individual was close to settlements than when in a remote area. Less than 1.9% of the variation in diet was associated with location, giving no support for the food-search hypothesis. However, females with yearlings had $5.1\% \pm 2.9$ (SE) lower fecal protein content than adult males. In addition, females with young (cubs-of-the-year or yearlings) exploited slaughter remains less often than other bears. This suggests that the diet of predation-vulnerable bears may have been affected by despotic behavior of dominant conspecifics. We provide evidence against the paradigm that food search explained the occurrence of brown bears near settlements and suggest that predation-vulnerable bears may use habitation as a human shield without being food conditioned. Management authorities should consider this knowledge when dealing with large carnivores near settlements.

© 2014 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/3.0/>).

1. Introduction

Several large carnivore species have increased in numbers and range in some areas in recent decades (Linnell et al., 2001). Although they generally avoid human activity and settlements (Woodroffe and Ginsberg, 1998; Frid and Dill, 2002), large carnivores do sometimes occur close to settlements. They are then often considered 'problematic', both because people fear them (Johansson et al., 2012) and because they may damage property

or injure humans (Woodroffe and Ginsberg, 1998). In many areas, mesopredators, such as Eurasian badgers (*Meles meles*) and red fox (*Vulpes vulpes*), utilize human-derived foods near settlements (Goszczyński et al., 2000; Bino et al., 2010). Several authors have proposed that also large carnivores, such as brown bears (*Ursus arctos*), approach settlements in search of food, which can result in food conditioning, i.e. associating people with easily accessible and attractive foods (McCullough, 1982; Gunther et al., 2004). Thus, if some bears gain access to high-quality foods near settlements (Hobson et al., 2000), this may explain why these individuals tolerate the disturbance associated with human activity and approach settlements.

The distribution of brown bears in a landscape is affected by food availability, anthropogenic disturbances, and intraspecific interactions, such as aggression or predation from dominant conspecifics (Steyaert et al., 2013a,b). This suggests that the distribution of

* Corresponding author.

E-mail addresses: marcus.elfstrom@nmbu.no (M. Elfström), marie.louise.davey@unis.no (M.L. Davey), andreas.zedrosser@hit.no (A. Zedrosser), mueller.martin@posteo.de (M. Müller), marta.debarba@gmail.com (M. De Barba), ole.stoen@nmbu.no (O.-G. Støen), christian.miquel@ujf-grenoble.fr (C. Miquel), pierre.taberlet@ujf-grenoble.fr (P. Taberlet), klaus.hacklaender@boku.ac.at (K. Hackländer), jon.swenson@nmbu.no (J.E. Swenson).

individuals in bear populations follows a despotic pattern, where human settlements may supply food resources and may function as refuges for smaller/subdominant bears that are avoiding interference competition and aggression (Elfström et al., 2014a). Subadults and females with dependent offspring seem to exploit habitats with lower diet quality than adult males (Mattson et al., 1987, 1992; Wielgus and Bunnell, 1994; Ben-David et al., 2004; Steyaert et al., 2013b). Smaller bears have lower nutritional requirements than larger bears (Welch et al., 1997; Rode et al., 2001). Thus, large adult males may require more abundant or higher quality-foods due to their larger size (Robbins et al., 2004). Yet, it is subadults and females with offspring that most often occur near people (Kaczensky et al., 2006; Rode et al., 2006; Schwartz et al., 2006; Hristienko and McDonald 2007; Elfström et al., 2014b). Adult males more often are found in remote areas (Mattson et al., 1987, 1992; Gibeau et al., 2002; Nellemann et al., 2007; Steyaert et al., 2013a). If bears occur near settlements because they are food conditioned, this may be viewed as an ‘unnatural’ behavior and increase people’s fear of bears. However, the type of bears occurring near settlements is better explained by their despotic behavior than searching for food and, thus, food conditioning is not a prerequisite for bear occurrence near settlements (Elfström et al., 2014a).

Avoidance of settlements by predators creates refuges for several prey species, i.e. the human shield theory (Berger, 2007; Barber et al., 2009). Settlements may function as human shields for moose (*Alces alces*) against brown bears and wolves (*Canis lupus*) (Berger, 2007; Rogala et al., 2011), for roe deer (*Capreolus capreolus*) against lynx (*Lynx lynx*) (Basille et al., 2009), and for American black bears (*Ursus americanus*) against brown bears (MacHutchon et al., 1998; Schwartz et al., 2010).

We evaluated brown bear movements in relation to settlements and analyzed their fecal nutritive constituents using near-infrared reflectance spectroscopy (NIRS) (Cen and He, 2007; Steyaert et al., 2012) and diet composition by identifying short fecal DNA sequences, i.e. DNA metabarcoding (Valentini et al., 2009; Taberlet et al., 2012; De Barba et al., 2014). Our objective was to investigate the diet of individual bears feeding near settlements and in remote areas. If bears gain a nutritional advantage by using areas close to settlements, the food-search hypothesis predicts that they would have a different diet and consume foods with higher nutritive value when near settlements than in remote areas (Hobson et al., 2000; Hopkins et al., 2012). Alternatively, if bears use areas close to settlements to avoid intraspecific aggression, or because they are naïve (i.e. lack experience with people), diet composition or quality should be similar near settlements and in remote areas.

2. Material and methods

2.1. Study area

Our ~12,000 km² study area was situated in south-central Sweden (~61°N, 15°E) (Dahle and Swenson, 2003). More than 80% of the area consists of intensively managed boreal forest, dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*); the remaining area is mainly covered by bogs or lakes (Moe et al., 2007). The forest floor is dominated by lichens, heather (*Calluna vulgaris*), bilberry (*Vaccinium myrtillus*), cowberry (*V. vitis-idaea*) and crowberry (*Empetrum hermaphroditum*) (Swenson et al., 1999). Elevations range between 200 and 1000 m a.s.l., and 90% of the area lies below the timberline (~750 m) (Dahle and Swenson, 2003). The area is sparsely populated, with few settlements and isolated houses (Martin et al., 2010). There are six towns, ranging from 3000 to 11,000 inhabitants, and two large tourist resorts with cabins (Nellemann et al., 2007). Human presence is most pronounced during summer and fall, and mainly related to hunting

and berry picking (Ordiz et al., 2011). Brown bear population density is about 30 individuals per 1000 km² (Bellemain et al., 2005) and the population is intensively hunted from 21 August until 15 October (Bischof et al., 2009).

2.2. Study design

We studied brown bear diet using fecal remains found at GPS-collar locations between 1 May and 1 October 2010 in three areas defined in relation to distance to human settlements. We monitored 49 bears equipped with GPS/GSM-collars scheduled to obtain locations at 10- or 30-min intervals (VECTRONIC Aerospace GmbH, Berlin, Germany). All capture and handling of bears were approved by the appropriate Swedish Ethical Committee (Uppsala Djurförsöksetiska Nämnd). See Arnemo et al., (2011) for details about capturing and handling of bears. Bears were categorized according to their sex, age, and reproductive status. Males ≥ 5 years of age were defined as adult males and males ≤ 4 years and nulliparous females as subadults. After having given birth, females were categorized as lone parous females, females with cubs-of-the-year, or females with dependent 1–2-year old offspring (Dahle and Swenson, 2003; Zedrosser et al., 2007).

We used ArcGIS 9.2 (Environmental Systems Research Institute, Inc., Redlands, California) for spatial analyses. We defined settlements as inhabited building(s) with registered garbage collection. Bear-proof garbage bins are not used in this area. The County Administrative Boards of Dalarna and Gävleborg provided digital maps (GSD Fastighetskartan) of buildings (D nr 501-6993-09 and 09910-2009). Registers of garbage collection were provided by the municipalities of Ljusdal, Mora, Orsa, Ovanåker, Rättvik and Älvdalen, and four garbage disposal companies. We defined three areas in relation to bear movements: a settlement visit, a remote area and prior to a settlement visit.

A settlement visit (SV) was defined as a bear occurring within a 150-m radius of a settlement for a minimum of two consecutive relocations. Minimum SV duration was the time elapsed between the first and last location <150 m from a settlement. The 150-m cut-off around settlements likely excluded unknown bear movements between consecutive locations exceeding the maximum recommended distance of 450 m between garbage bins and residential houses, based on decisions by the Swedish Environmental Supreme Court (cases M 7725-05 and M 583-06). Bears in our study area have an upper range of movement, i.e. 3rd quartile, of 600 m per 30 min when active (Moe et al., 2007), thus the maximum distance from a settlement and back between two consecutive GPS locations separated by a maximum of 30 min corresponds to ~300 m. We collected SV samples from all bed sites starting ≥ 1 h after the first GPS location <150 m from a settlement, and until 24 h after the first GPS location >150 m from the settlement. Thus, we sampled feces deposited during a minimum of 24 h after a bear entered a settlement, which overlaps reported gut retention times of 6 and 14.5 h for captive Scandinavian brown bears on berry and meat diets, respectively (Elfström et al., 2013), i.e. diets with different fiber content and digestibility (Pritchard and Robbins, 1990).

A remote area (RA) was defined as >600 m from any settlements, and corresponded to 95% of the habitat used by GPS-collared bears in our study area during 2006–2009. We randomly selected two bed sites from the same individual to sample RA fecal remains >48 h after a bear visited a settlement, and only after all GPS locations had been in RAs for >24 h.

We analyzed fecal samples defecated in the 24-h period prior to a settlement visit (PSV). The PSV samples were collected from two randomly selected bed sites only when the bear had not been located <150 m from a settlement for >48 h before SV occurred and independently of bear use in RA.

We sampled feces only from bed sites, identified as clusters of ≥ 2 GPS locations < 20 m apart and used by the bear ≥ 60 min. We collected a ca. 1 cm^3 sample from all feces found within 5 m of bed sites, mixed all samples, and preserved ca. 1 cm^3 in 1 sample per bed site in ethyl alcohol for diet composition analysis. We only sampled the feces found closest to the bed for diet quality analysis. We estimated the maximum time period elapsed from first GPS location by a bear at a cluster until fecal sampling, because it may affect the fecal nutritive constituents (Steyaert et al., 2012). Details for nutritive sampling procedure, treatment and analysis are described in Steyaert et al. (2012).

2.3. Diet composition identification

We amplified DNA metabarcoding regions for plants, vertebrates, and invertebrates by polymerase chain reaction (PCR) in two multiplexed reactions using universal primers for the targeted taxonomic groups (De Barba et al., 2014). DNA processing and identification of unique taxa are described in Appendix A. Taxa identified as nonnative species that may have been incorrectly identified were kept in our analyses to avoid removing potential dietary differences in relation to settlements.

2.4. Diet quality quantification

We quantified the nutritive quality of fecal remains using NIRS (Cen and He, 2007), which has been reported as an accurate technique to evaluate diet based on fecal remains for the brown bear (Steyaert et al., 2012). We have described the preparation of fecal nutritive samples and NIRS processing in Appendix B.

3. Statistics

3.1. Diet composition; model selection and validation

All statistical analyses were carried out in R 2.15.0 (R Development Core Team, 2011). We compared the occurrence of each dietary item identified in $\geq 25\%$ of all fecal remains by area (prior-to-settlement-visit, settlement visit, remote area) and bear category (subadult, female with cubs-of-the-year, female with 1–2-year-old offspring, adult male, lone parous female), using separate binomial generalized linear mixed-effect models (GLMM) for each dietary item in the package ‘lme4’ (Bates and Maechler, 2010). We constructed two *a priori* candidate GLMMs for each dietary item (fecal presence/absence), one intercept only and one with area and bear category as fixed factors, with bear identity included as a random effect in both models. We evaluated the most parsimonious GLMM to explain the occurrence of diet items, based on Akaike’s Information Criteria scores for small sample sizes (AIC_c) and AIC_c weights (AIC_cw) (Akaike, 1973; Burnham and Anderson, 2002).

3.2. Diet quality; model selection and validation

We constructed three identical candidate sets, each containing eight *a priori* linear mixed-effect models (LMM) (defined in Tables A.3, A.5 and A.6), to explain the variation in fecal crude fat (CFA), crude protein (CP), and acid detergent lignin/neutral detergent fiber (ADL/NDF) separately. We used the following fixed factors: area (prior-to-settlement-visit, settlement visit, remote area), duration of settlement visits (in min), bear category (subadult, female with cubs-of-the-year, female with 1–2-year-old offspring, adult male, lone parous female), field exposure time (in min), Julian date, and included bear identity as a random effect. We evaluated the most parsimonious LMM to explain variation in each

fecal nutritive constitute, based on AIC_c and AIC_cw (Akaike, 1973; Burnham and Anderson, 2002). We used the package ‘lme4’ (Bates and Maechler, 2010) for statistical modeling and generated β and its 95% highest posterior density interval (HPD) for the fixed effects of the LMM with a Markov Chain Monte Carlo (MCMC) algorithm using 1,000 simulations, using the package ‘LMERConvenienceFunctions’ (Tremblay, 2011). We controlled for outliers with Cleveland dotplots, and for multicollinearity with variance inflation factors (Zuur et al., 2009).

3.3. Diet composition and quality combined; model selection and validation

We compared diet composition using both Global Nonmetric Multidimensional Scaling (Kruskal, 1964a,b; Minchin 1987) and Detrended Correspondence Analysis (DCA) (Hill, 1979; Hill and Gauch, 1980) ordination methods (see Appendix C). We interpreted similar results from the two methods (Table A.1) and the absence of visual artefacts as a strong indication of a reliable gradient structure (Økland, 1996). The *envfit* function in package ‘vegan’ was used to fit Julian date, duration of settlement visits, CFA, ADL/NDF and CP as vectors to each DCA (Hill, 1979; Hill and Gauch, 1980; Oksanen et al., 2011) ordination, as well as bear identity, bear category, and area (prior-to-settlement-visit, settlement visit, remote area) as factors, using 999 random permutations. We used partial canonical correspondence analysis (CCA) (ter Braak, 1986) to further investigate the effect of settlement visits. The hypothesis that settlement visits did not explain significant variation in the data set was tested against the one-tailed alternative (greater than) by conducting 999 permutations of the variable area (prior-to-settlement-visit, settlement visit, remote area), and examining the variation in the dataset remaining after the effects of bear identity and Julian date had been partialled out.

4. Results

We analyzed 120 fecal samples (28 prior-to-settlement-visits, 51 settlement visits and 41 remote areas) for diet quality associated with 36 visits to settlements, from 21 individuals (33 samples from 5 adult males, 14 from 3 females with cubs-of-the-year, 11 from 3 females with 1–2-year-old offspring, 37 from 2 lone parous females, and 25 from 9 subadults). One female with cubs-of-the-year lost her offspring and therefore also was included as a lone parous female. Among the females with 1–2-year-old offspring, there were 8 samples from females with 1-year-old offspring and 3 from females with 2-year-old offspring. For the diet composition analysis, we recovered a complete dietary profile for 106 fecal samples. The median number of feces per bed site was 1 (1st and 3rd quartile: 1 and 2). The median duration of a settlement visit was 30 (1st and 3rd quartile: 10 and 230) min.

4.1. Diet composition

We detected 228 dietary items based on genetic barcoding: 140 plants, 62 invertebrates, and 26 vertebrates (Table A.2). Common, expected dietary items were detected in high frequencies, including berries (*V. vitis-idaea*, *V. myrtillus*, *Empetrum* sp., *Rubus idaeus*), mammalian prey (*A. alces*), and insects (*Formica* and *Camponotus* ant species). In addition, a number of presumed settlement-associated items were detected, such as cereals (*Avena* sp., *Hordeum vulgare*, *Triticum aestivum*), domestic animals (*Bos* sp., *Ovis* sp., *Sus scrofa*), and nonnative plant species (e.g. *Musineon vaginatum*, *Areca triandra*).

GLMMs that included area and bear category were not more parsimonious than intercept-only models to capture the presences

of dietary items, with the exceptions of *S. scrofa* and one unknown species of the Tribe Poeae (intercept-only GLMM: $\Delta AIC_c = 12.87$, $AIC_{cW} = 0.00$, and $\Delta AIC_c = 8.68$, $AIC_{cW} = 0.01$, respectively, Table 1). Bears had a higher frequency of *S. scrofa* in their feces during prior-to-settlement-visits than settlement visits ($\beta = -1.5$, $SE = 0.6$, $z = -2.8$, $P = 0.006$) and in remote areas ($\beta = -1.5$, $SE = 0.6$, $z = -2.5$, $P = 0.011$), but the frequencies were similar between settlement visits and remote areas ($\beta = 0.0$, $SE = 0.5$, $z = 0.1$, $P = 0.924$). Females with cubs-of-the-year and lone parous females had a higher fecal frequency of one unknown species of Poeae than adult males ($\beta = 3.6$, $SE = 1.0$, $z = 3.7$, $P < 0.000$, and $\beta = 1.4$, $SE = 0.7$, $z = 2.1$, $P = 0.038$, respectively). We found no other significant differences in dietary items among areas and bear categories (Table 1). However, when combining females with young (i.e. females with cubs-of-the-year and with 1–2-year-old offspring) and comparing them with other bears, and thus increasing the sample sizes within the two categories, we found that females with young had a lower fecal frequency of *S. scrofa* ($\beta = -1.8$, $SE = 0.7$, $z = -2.5$, $P = 0.012$) than other categories of bears. The intercept-only GLMM was not supported regarding fecal presence of *S. scrofa*, when ranked

against the candidate GLMM with only one fixed factor; separating bears into groups with and without the company of young ($\Delta AIC_c = 6.84$, $AIC_{cW} = 0.03$).

4.2. Diet quality

Bear category was included in the LMM with highest support to explain variation in fecal CP among bears ($\Delta AIC_c = 0.00$, $AIC_{cW} = 0.98$, Table A.3). Females with 1–2-year-old offspring had $\beta = -5.05\% \pm 2.89$ (SE) lower fecal CP than adult males ($P = 0.024$). No other differences were found among bear categories (Table A.4). Fecal CP decreased during the season (i.e. Julian day $\beta = -0.08\% \pm 0.01$ (SE), $P = 0.001$, Table A.4). Area was not included in the LMM with the highest support to explain variation in fecal CP among bears (Table A.3). Our models were not successful in capturing variation in fecal CFA and ADL/NDF, because the intercept models were ranked as the most parsimonious LMMs, ($\Delta AIC_c = 0.00$, $AIC_{cW} = 0.92$, and $\Delta AIC_c = 0.00$, $AIC_{cW} = 1.00$, Tables A.5 and A.6, respectively). Descriptive fecal estimates for CP, CFA and ADL/NDF are shown in relation to areas and bear categories in Fig. 1.

Table 1

Dietary composition of brown bear feces in relation to settlements by bear sex, age, and reproductive categories for all dietary items with $\geq 25\%$ frequency of occurrence among 106 fecal remains in south-central Sweden in 2010, identified by DNA metabarcoding and ranked in decreasing frequency. Dietary composition was based on separate generalized linear mixed-effect models (GLMM) with a binomial distribution for each food item, using area and bear category as fixed factors and bear identity as a random effect. AIC_c values ($w_i = AIC_c$ weights) are given for the intercept-only GLMM, when ranked against one alternative candidate GLMM (with area + bear category). Remote areas are reference level for prior to settlement visits (PSV) and settlement visits (SV). Adult males are reference level for females with cubs of the year (FC), females with yearlings (FY), lone parous females (FL) and subadults (SUB).

OTU ^a Name	Taxon ID	ΔAIC_c	w_i	PSV	SV	FC	FY	FL	SUB	Frequency (%)
gh_00001	<i>Vaccinium vitis-idaea</i>	0.00	0.71							85.8
mav_00001	<i>Formica</i> sp.	0.00	0.95							82.1
ast_00001	<i>Tussilago farfara</i>	0.00	0.98							81.1
ast_00003	<i>Taraxacum</i>	0.00	0.99							79.2
v05_00002	<i>Alces alces</i>	3.90	0.12							78.3
ast_00002	<i>Cirsium palustre</i>	0.00	0.92							74.5
poa_00003	<i>Avenella flexuosa</i>	0.00	0.98							64.2
ros_00001	<i>Rubus idaeus</i>	0.00	0.93							62.3
poa_00004	<i>Deschampsia</i> sp.	0.00	1.00							55.7
summed6	<i>Cicerbita alpina</i>	0.00	0.99							55.7
gh_00003	<i>Vaccinium myrtillus</i>	0.00	0.98							50.9
mav_00002	<i>Oliarces clara</i>	0.00	0.97							50.0
v05_00010	<i>Bos</i> sp.	0.00	0.98							50.0
ast_00012	<i>Hieracium</i> sp.	0.00	0.90							49.1
poa_00001	<i>Avena</i> sp.	0.00	0.95							48.1
v05_00003	<i>Sus scrofa</i>	12.87	0.00	+						47.2
poa_00002	Poeae	1.12	0.36							40.6
cyp_00002	<i>Carex</i> sp. 1	0.00	0.88							39.6
poa_00008	Poeae	0.00	0.99							38.7
summed7	<i>Crepis paludosa</i>	0.00	0.75							37.7
mav_00004	<i>Camponotus herculeanus</i>	0.00	0.99							36.8
ast_00010	<i>Cirsium</i> sp.	0.00	0.62							34.9
gh_00002	Asterales	0.00	0.55							34.9
gh_00007	Poeae	8.68	0.01			+++		+		31.1
gh_00005	<i>Empetrum</i> sp.	0.00	0.91							24.5

Relationships between the occurrence of a diet item and a factor are indicated based on the following significance $P_{z(>z)}$ values +++ = 0.001 and + = 0.05, and empty cells = 1 (+ indicates a positive relationship).

Plant species are indicated on light-gray, insects on dark-gray, and vertebrates on white background.

^a OTU-Operational taxonomic unit.

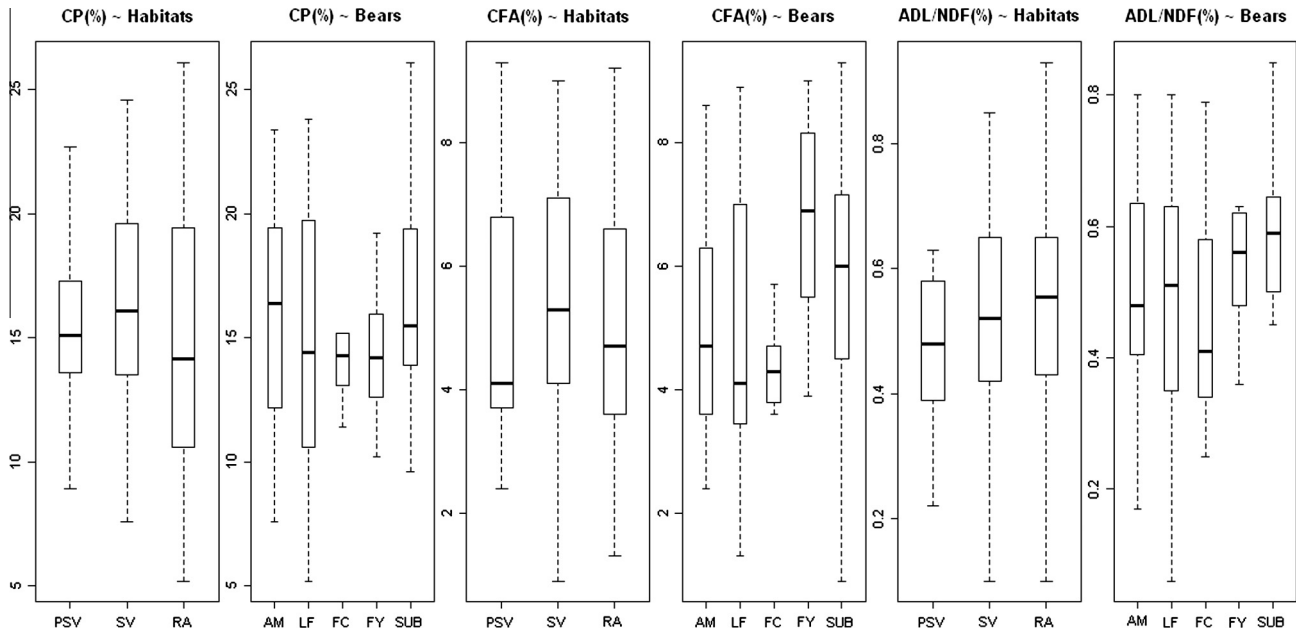


Fig. 1. Boxplots (i.e. median, 1st and 3rd quartiles and range) of fecal nutritive content for sex, age and reproductive categories of brown bears (AM-adult males, LF-lone parous females, FC-females with cubs of the year, FY-females with yearlings, SUB-subadult males and females) and in relation to prior to settlement visits (PSV), settlement visits (SV), and in remote areas (RA), during May–September 2010. Nutritive parameters are measured relative to the dry matter content (in %), based on near-infrared spectroscopy (CP-crude protein, CFA-crude fat, ADL-acid detergent lignin, NDF-neutral detergent fiber).

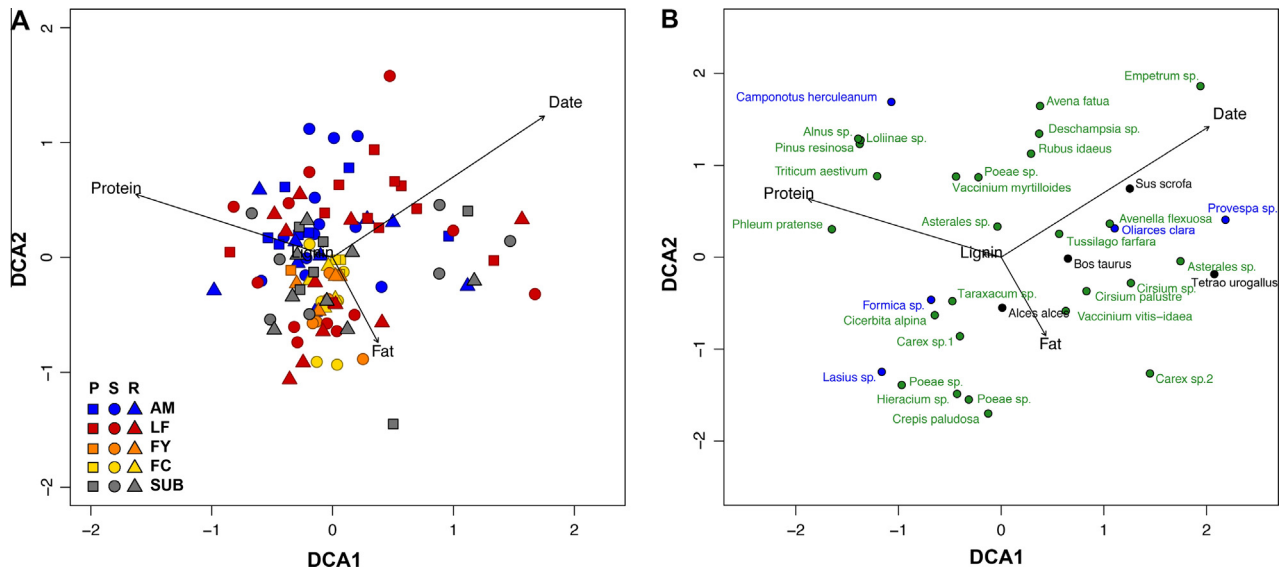


Fig. 2. Detrended correspondence analysis of diet composition and quality based on 106 fecal samples from brown bears of different sex, age and reproductive categories before or when they occurred near settlements, or used remote areas in south-central Sweden 2010. Dietary composition (A) shown in relation to settlements and sex, age and reproductive bear categories, and (B) shown in relation to common food items. Nutritive quality is based on near infrared spectroscopy and species identification of diet is based on the DNA metabarcoding approach. Categories are defined as follows: P-prior to settlement visits, S-settlement visits, R-remote areas, AM-adult males, LF-lone parous females, FY-females with yearlings, FC-females with cubs of the year, SUB-subadult females and males.

4.3. Diet composition and quality combined

Diet composition was significantly structured by time of year (Julian date), fecal CFA and CP, bear category, and bear identity (Fig. 2, Table A.7). The samples distributed along DCA axis 1 largely according to date and fecal CP, where low DCA axis 1 scores represented early season collections with high protein content. Samples were distributed along DCA axis 2 somewhat according to fecal CFA, with low DCA axis 2 scores representing higher fecal CFA. The species optima of common dietary items (occurring in >25% of fecal remains) were assorted along DCA axis 1 with common

insect items (*Formica* sp., *Camponotus herculeanus*, *Lasius* sp.) associated with low DCA axis 1 scores, and berries (*Vaccinium* sp., *Rubus idaeus*, *Empetrum* sp.) associated with the later part of the DCA axis 1 gradient. We found no significant differences between dietary composition and visitation of settlements based on DCA ordinations (correlation vector (r^2) = 0.02, P = 0.349). When the effects of date, bear category, and bear identity were removed (accounting for 26.6% of total variation in diet composition) in a CCA ordination, only 1.9% of the remaining total variability in diet composition was explained by area effects. Nevertheless, a statistical relationship was apparent (P = 0.001, r^2 = 0.40). The fecal nutritive measures

were, however, still not different among areas (CP: $r^2 < 0.00$, $P = 0.799$, CFA: $r^2 = 0.03$, $P = 0.226$, ADL/NDF: $r^2 = 0.01$, $P = 0.713$).

5. Discussion

Food search is the most common explanation for the occurrence of bears near settlements (Herrero, 1985; Elfström et al., 2014a). It is important to test this paradigm, to ensure that management efforts have a sound scientific basis. The composition of the individual bears' diet did not differ between settlement visits and when they were in remote areas. In addition, dietary quality, based on fecal CFA, CP and ADL/NDF, was similar among areas (i.e. in relation to settlements). When we combined composition and quality, the bears' diet was structured primarily by time of year, bear category, and individual dietary preferences, and was not strongly influenced by area. Variation in fecal CFA and CP were significantly correlated with dietary composition and similarly reflected the effects of time of year and bear category, but not area. Ordination structure primarily reflected a shift from a protein-rich, early-season diet that included a high frequency of ant species, to a less protein-rich diet late in the season, with a high frequency of berries. This was confirmed by a significant inverse relationship between fecal CP and Julian date. A CCA ordination, which partitioned out the effects of date, bear category, and individual, identified a significant effect of settlement visits on diet composition, but this accounted for only 1.9% of the remaining variation in diet composition. Because this structure did not correlate with CFA, CP, or ADL/NDF, and accounted for such a small proportion of the dietary variation, we considered the effects of settlement visits to be negligible in the overall determination of diet composition and quality. Thus, we found no support for a substantially different diet with higher nutritive quality near settlements, as predicted by the food-search hypothesis.

Our results contrast with reports from North America, where bears often seem to utilize human-related foods near settlements (Gunther et al., 2004; Hopkins et al., 2012). Others have reported a negative correlation between the abundance of naturally occurring bear foods and occurrence of "problem" bears and their use of human-related foods (Mattson et al., 1992; Schwartz et al., 2006), but, based on body condition indices, no such relation has been found in Scandinavia (Elfström et al., 2014b). Our results suggest that food availability or nutritive quality do not explain why bears visit settlements in Scandinavia. In general, brown bear populations in North America experience lower food productivity than those in Europe (Bojarska and Selva, 2012). In addition, it may be that North American brown bear populations experience a more pronounced difference in food quality in relation to distance to settlements. In North America, brown bear populations are confined to areas with low human population density compared to Europe where brown bears have to coexist in a multiuse landscape with relatively high human population density (Woodroffe, 2000; Linnell et al., 2001). This may explain why searching for food seems to be a more common factor behind brown bear occurrence near settlements in North America than Europe. Although food shortage also seems not to be a common factor behind brown bear occurrence near settlements in southern Europe (Elfström et al., 2014b), bears may utilize human-derived foods (e.g. fruit/nut orchards) near settlements more commonly in southern than northern Europe (Jerina et al., 2012).

Bears generally avoid settlements (Mace and Waller, 1996; Nellemann et al., 2007), suggesting that human activity is associated with costs to bears, such as disturbance (Martin et al., 2010; Ordiz et al., 2011). Nevertheless, it is plausible that especially dispersing subadult bears approach settlements because they lack experience of such costs (i.e. naivety) (Elfström et al., 2014a). Thus, no dietary advantages would be required to explain the occurrence

of naïve (young) bears near settlements. In contrast, bears could also approach settlements without having any dietary advantages, because they are habituated to humans (McCullough, 1982).

Bears more often ingested *S. scrofa* < 48 h prior to a settlement visit and while >150 m from a settlement than when at a settlement or in remote areas. The *S. scrofa* observed in our data originated from illegal dumps of domestic pig slaughter remains, because wild boars are not common in the study area (Kindberg et al., 2008), and because bears have not been documented to kill pigs in Sweden (Karlsson et al., 2013).

We detected no fecal nutritive differences between subadults or females with cubs-of-the-year and adult males, suggesting no dietary effects from interference competition. However, females with yearlings had lower fecal CP than adult males, which does suggest some form of a despotic distribution among bears, where predation-vulnerable individuals less frequently exploit important foods (e.g. protein-rich items), because they avoid dominant conspecifics (Steyaert et al., 2013b; Elfström et al., 2014a). However, females with cubs-of-the-year, a predation-vulnerable category, showed no significant differences in dietary composition or quality compared to adult males, except for a higher use of one unknown species of Poaeae. Also lone adult females ingested this same species more often than adult males. The sample sizes within bear categories were generally small, which elevated the risk of committing a type II error and, thus, we may have underestimated dietary differences among bear categories. When combining all females accompanied by offspring (cubs-of-the-year and yearlings), we found fecal remains of pigs less often among females with offspring (i.e. predation-vulnerable) compared to other bears. Predation avoidance may result in predation-vulnerable individuals utilizing habitats with lower diet quality (Nevin and Gilbert, 2005; Rode et al., 2006; Steyaert et al., 2013b). Our results indicated only weak support for a despotic distribution among bears in terms of diet, however, spatiotemporal differences in habitat use among sex, age and reproductive categories of bears could still be present (Steyaert et al., 2013a).

We identified berries (*V. vitis-idea*, *V. myrtillus*, *Empetrum* spp.), ants (*C. herculeanus*, *Formica* spp.), and moose (*A. alces*) among the most common food items of Scandinavian bears, which is consistent with earlier studies of diet from central Sweden and our study area using other methods (Dahle et al., 1998; Swenson et al., 1999; Rauset et al., 2012). Diet items with presumed association with settlements included oats (*Avena* sp.), which were relatively commonly identified in the bear feces. However, oat fields also occurred in remote areas.

Fecal NIRS has been reported to have very high ($r^2 \geq 0.9$) validation for fecal nitrogen and NDF in brown bears (Steyaert et al., 2012), however there are disadvantages of using NIRS of fecal remains. Fecal CFA content may be overestimated after feeding on seeds, because of undigested oil-rich seeds and waxes in feces. Fecal CP content may also be overestimated, because nonprotein nitrogen, e.g. nucleic acids, is falsely recovered as protein. However, by combining nutritive data based on fecal NIRS with dietary items based on DNA metabarcoding, we accounted for any differences in dietary constituents when comparing bear diets in relation to settlements and age, sex and reproductive categories.

6. Conclusions

Dietary composition and quality, based on feces, was similar when bears were near settlements and when the same individuals were in remote areas. Thus, we found no support for the food-search hypothesis. However, females with yearlings had lower fecal CP than adult males, and females with young of all ages utilized slaughter remains less often than other bear categories, suggesting that predation-vulnerable bears were affected to some degree by

the despotic behavior of dominant bears. Predation-vulnerable individuals also used deposited slaughter remains, which also occur more often near settlements, less frequently than other bears (Steyaert et al., 2013a; reviewed in Elfström et al., 2014a). This suggests that managers should not necessarily consider a bear close to settlements to be a food-conditioned animal, but also should take the social organization of bears into consideration. This is especially important when communicating with affected people when bears are observed near settlements. Removal of food or other attractants remains important to prevent food conditioning of bears. However, the public should be informed that bears will still occur near settlements, even though garbage or other attractants have been removed, and that this is not necessarily an 'unnatural' behavior. Predation-vulnerable or socially sub-dominant individuals may try to avoid conspecifics by seeking predation refuges near settlements during the mating season; the same bears may avoid settlements as they become older and are less vulnerable to intraspecific predation (Elfström et al., 2014a), according to the human-shield theory (Berger, 2007; Barber et al., 2009). Exploiting food attractants was not a prerequisite for the occurrence of bears near settlements. Especially adult male bears may have visited settlements with denser understory vegetation, which would provide cover to reduce exposure to disturbance and risk of detection by people, considering that adult males in general dominate in high-quality (e.g. remote) areas (Elfström et al., 2014a). Therefore, the maintenance of open areas without understory vegetation around settlements may be additionally important in order to prevent bears from approaching these areas (Ordiz et al., 2011), and may also prevent predation-prone individuals within other large carnivore species from seeking refuge near humans (Odden and Wegge, 2005; Schwartz et al., 2010).

Acknowledgements

We thank S. Frank, O. Gonzales, D. Haberkorn, B. Houben, F. Hütter, L. Novak, C. Reusch, V. Sahlén, S. Steyaert, J. Tisak, and I. Warrington for assistance with collecting data in the field. We thank the Swedish Environmental Protection Agency and the County Administrative Board of Dalarna for financial support. This is scientific publication number 172 from the Scandinavian Brown Bear Research Project.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.08.003>.

References

- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: *Proceeding of the Second International Symposium on Information Theory*. Budapest, Hungary, pp. 267–281.
- Arnemo, J.M., Evans, A., Fahlman, A., Ahlqvist, P., Andrén, H., Brunberg, S., Liberg, O., Linnell, J.D.C., Odden, J., Persson, P., Sand, H., Segerström, P., Sköld, K., Strömseth, T.H., Støen, O.-G., Swenson, J.E., Wabakken, P., 2011. Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx, Hedmark University College, Evenstad, Norway, pp. 14.
- Barber, J.R., Crooks, K.R., Fristrup, K.M., 2009. The costs of chronic noise exposure for terrestrial organisms. *Trends Ecol. Evol.* 25, 180–189.
- Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J.D.C., Odden, J., Andersen, R., Arild Høgda, K., Gaillard, J.-M., 2009. What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? *Ecography* 32, 683–691.
- Bates, D.M., Maechler, M., 2010. lme4: linear mixed-effects models using S4 classes R package version 0.999375-37. <<http://CRAN.R-project.org/package=lme4>>.
- Bellemain, E., Swenson, J.E., Tallmon, O., Brunberg, S., Taberlet, P., 2005. Estimating population size of elusive animals with DNA from hunter-collected feces: four methods for brown bears. *Conserv. Biol.* 19, 150–161.
- Ben-David, M., Titus, K., Beier, L.R., 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia* 138, 465–474.
- Berger, J., 2007. Fear, human shields and redistribution of prey and predators in protected areas. *Biol. Lett.* 3, 620–623.
- Bino, G., Dolev, A., Yosha, D., Guter, A., King, R., Saltz, D., Kark, S., 2010. Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. *J. Appl. Ecol.* 47, 1262–1271.
- 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.
- Bojarska, K., Selva, N., 2012. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. *Mammal Rev.* 42, 120–143.
- Burnham, K.P., Anderson, D.R., 2002. *Model selection and multimodel inference: a practical information-theoretic approach*, second ed. Springer-Verlag, New York.
- Cen, H.Y., He, Y., 2007. Theory and application of near infrared reflectance spectroscopy in determination of food quality. *Trends Food Sci. Technol.* 18, 72–83.
- Dahle, B., Swenson, J.E., 2003. 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.
- Dahle, B., Sørensen, O.J., Wedul, E.H., Swenson, J.E., Sandegren, F., 1998. The diet of brown bears *Ursus arctos* in central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*. *Wildlife Biol.* 4, 147–158.
- De Barba, M., Miquel, C., Boyer, F., Mercier, C., Rioux, D., Coissac, E., Taberlet, P., 2014. DNA metabarcoding multiplexing and validation of data accuracy for diet assessment: application to omnivorous diet. *Mol. Ecol. Res.* 14, 306–323.
- Elfström, M., Støen, O.-G., Zedrosser, A., Warrington, I., Swenson, J.E., 2013. Gut retention time in captive brown bears *Ursus arctos*. *Wildlife Biol.* 19, 1–8.
- Elfström, M., Zedrosser, A., Støen, O.-G., Swenson, J.E., 2014a. Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. *Mammal Rev.* 44, 5–18.
- Elfström, M., Zedrosser, A., Jerina, K., Støen, O.-G., Kindberg, J., Budic, L., Jonzovič, M., Swenson, J.E., 2014b. Does despotic behavior or food search explain the occurrence of problem brown bears in Europe? *J. Wildlife Manage.* 78, 881–893.
- Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* 6, 16.
- Gibeau, M.L., Clevenger, A.P., Herrero, S., Wierzchowski, J., 2002. Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. *Biol. Conserv.* 103, 227–236.
- Goszczyński, J., Jedrzejewska, B., Jedrzejewski, W., 2000. Diet composition of badgers (*Meles meles*) in a pristine forest and rural habitats of Poland compared to other European populations. *J. Zool.* 250, 495–505.
- Gunther, K.A., Haroldson, M.A., Frey, K., Cain, S.L., Copeland, J., Schwartz, C.C., 2004. Grizzly bear-human conflicts in the greater Yellowstone ecosystem, 1992–2000. *Ursus* 15, 10–22.
- Herrero, S., 1985. *Bear attacks: their causes and avoidance*, second ed. Lyons and Burford, New York, USA.
- Hill, M.O., 1979. DECORANA – a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University, New York, USA.
- Hill, M.O., Gauch Jr., H.G., 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42, 47–58.
- Hobson, K.A., McLellan, B.N., Woods, J.G., 2000. Using stable carbon (delta C-13) and nitrogen (delta N-15) isotopes to infer trophic relationships among black and grizzly bears in the upper Columbia River basin, British Columbia. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 78, 1332–1339.
- Hopkins, J.B., Koch, P.L., Schwartz, C.C., Ferguson, J.M., Greenleaf, S.S., Kalinowski, S.T., 2012. Stable isotopes to detect food-conditioned bears and to evaluate human-bear management. *J. Wildlife Management.* 76, 703–713.
- Hristienko, H., McDonald, J.E., 2007. Going into the 21st century: a perspective on trends and controversies in the management of the American black bear. *Ursus* 18, 72–88.
- Jerina, K., Krofel, M., Stergar, M., Videmšek, U., 2012. Factors affecting brown bear habituation to humans: a GPS telemetry study. Final report—summary for users. University of Ljubljana, Biotechnical Faculty, Ljubljana.
- Johansson, M., Sjöström, M., Karlsson, J., Brännlund, R., 2012. Is human fear affecting public willingness to pay for the management and conservation of large carnivores? *Soc. Natl. Res.* 25, 610–620.
- Kaczensky, P., Huber, D., Knauer, F., Roth, H., Wagner, A., Kusak, J., 2006. Activity patterns of brown bears (*Ursus arctos*) in Slovenia and Croatia. *J. Zool.* 269, 474–485.
- Karlsson, J., Danell, J., Månsson, J., Svensson, L., Hellberg, R., 2013. Viltskadestatistik 2012 – Skador av fredat vilt på tamdjur, hundar och gröda. [In Swedish], In Rapport från Viltskadecenter [Report from Grimsö Wildlife Damage Center] Report No. 2013-1, pp. 23.
- Kindberg, J., Holmqvist, N., Bergqvist, G., 2008. Årsrapport Viltövervakningen 2006/2007 [In Swedish], In Viltforum. Svenska Jägareförbundet [Swedish Association for Hunting and Wildlife Management], pp. 26.
- Kruskal, J.B., 1964a. Multidimensional scaling optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29, 1–27.
- Kruskal, J.B., 1964b. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29, 115–129.
- Linnell, J.D.C., Swenson, J.E., Andersen, R., 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Anim. Conserv.* 4, 345–349.

- Mace, R.D., Waller, J.S., 1996. Grizzly bear distribution and human conflicts in Jewel Basin Hiking Area, Swan Mountains, Montana. *Wildl. Soc. Bull.* 24, 461–467.
- MacHutchon, G., Himmer, S., Davis, H., Gallagher, M., 1998. Temporal and spatial activity patterns among coastal bear populations. *Ursus* 10, 539–546.
- Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allaine, D., Swenson, J.E., 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). *Can. J. Zool.* 88, 875–883.
- Mattson, D.J., Knight, R.R., Blanchard, B.M., 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *Ursus* 7, 259–273.
- Mattson, D.J., Blanchard, B.M., Knight, R.R., 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *J. Wildlife Manage.* 56, 432–442.
- McCullough, D.R., 1982. Behavior, bears, and humans. *Wildl. Soc. Bull.* 10, 27–33.
- Minchin, P.R., 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69, 89–107.
- Moe, T.F., Kindberg, J., Jansson, I., Swenson, J.E., 2007. Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). *Can. J. Zool.* 85, 518–525.
- Nellemann, C., Støen, O., Kindberg, J., Swenson, J.E., Vistnes, I., Ericsson, G., Katajisto, J., Kaltenborn, B., Martin, J., Ordiz, A., 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biol. Conserv.* 138, 157–165.
- Nevin, O.T., Gilbert, B.K., 2005. Measuring the cost of risk avoidance in brown bears: further evidence of positive impacts of ecotourism. *Biol. Conserv.* 123, 453–460.
- Odden, M., Wegge, P., 2005. Spacing and activity patterns of leopards *Panthera pardus* in the Royal Bardia National Park, Nepal. *Wildlife Biol.* 11, 145–152.
- Økland, R.H., 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? *J. Veg. Sci.* 7, 289–292.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2011. *Vegan: Community Ecology Package*. R Package Version 2.0-0. <<http://CRAN.R-project.org/package=vegan>>.
- 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.
- Pritchard, G.T., Robbins, C.T., 1990. Digestive and metabolic efficiencies of grizzly and black bears. *Canadian Journal of Zoology—Revue Canadienne De Zoologie* 68, 1645–1651.
- R Development Core Team, 2011. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, <<http://www.R-project.org/>>.
- Rauset, G.R., Kindberg, J., Swenson, J.E., 2012. Modeling female brown bear kill rates on moose calves using global positioning satellite data. *J. Wildlife Manage.* 76, 1597–1606.
- 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.
- Rode, K.D., Robbins, C.T., Shipley, L.A., 2001. Constraints on herbivory by grizzly bears. *Oecologia* 128, 62–71.
- Rode, K.D., Farley, S.D., Robbins, C.T., 2006. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology* 87, 2636–2646.
- Rogala, J.K., Hebblewhite, M., Whittington, J., White, C.A., Coleshill, J., Musiani, M., 2011. Human activity differentially redistributes large mammals in the Canadian Rockies national parks. *Ecol. Soc.* 16, 16–39.
- Schwartz, C.C., Haroldson, M.A., White, G.C., Harris, R.B., Cherry, S., Keating, K.A., Moody, D., Servheen, C., 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monogr.* 161, 1–68.
- Schwartz, C.C., Cain, S.L., Podrutzny, S., Cherry, S., Frattaroli, L., 2010. Contrasting activity patterns of sympatric and allopatric black and grizzly bears. *J. Wildlife Manage.* 74, 1628–1638.
- Steyaert, S.M.J.G., Hütter, F.J., Elfström, M., Zedrosser, A., Hackländer, K., Lê, M.H., Windisch, W., Swenson, J.E., Isaksson, T., 2012. Fecal spectroscopy: a practical tool to assess diet quality in an opportunistic omnivore. *Wildlife Biol.* 18, 431–438.
- Steyaert, S.M.J.G., Kindberg, J., Swenson, J.E., Zedrosser, A., 2013a. Male reproductive strategy explains spatiotemporal segregation in brown bears. *J. Anim. Ecol.* 82, 836–845.
- Steyaert, S.M.J.G., Reusch, C., Brunberg, S., Swenson, J.E., Hackländer, K., Zedrosser, A., 2013b. Infanticide as a male reproductive strategy has a nutritive risk effect in brown bears. *Biol. Lett.* 9, 1–4.
- Swenson, J.E., Jansson, A., Riig, R., Sandegren, F., 1999. Bears and ants: myrmecophagy by brown bears in central Scandinavia. *Canadian Journal of Zoology—Revue Canadienne De Zoologie* 77, 551–561.
- Taberlet, P., Coissac, E., Pompanon, F., Brochmann, C., Willerslev, E., 2012. Towards next-generation biodiversity assessment using DNA metabarcoding. *Mol. Ecol.* 21, 2045–2050.
- ter Braak, C.F.J., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67, 1167–1179.
- Tremblay, A., 2011. A suite of functions to back-fit fixed effects and forward-fit random effects, as well as other miscellaneous functions, <<http://cran.r-project.org/web/packages/LMERConvenienceFunctions/index.html>>.
- Valentini, A., Miquel, C., Nawaz, M.A., Bellemain, E.V.A., Coissac, E., Pompanon, F., Gielly, L., Cruaud, C., Nascetti, G., Wincker, P., Swenson, J.E., Taberlet, P., 2009. New perspectives in diet analysis based on DNA barcoding and parallel pyrosequencing: the *trnL* approach. *Mol. Ecol. Res.* 9, 51–60.
- Welch, C.A., Keay, J., Kendall, K.C., Robbins, C.T., 1997. Constraints on frugivory by bears. *Ecology* 78, 1105–1119.
- Wielgus, R.B., Bunnell, F.L., 1994. Sexual segregation and female grizzly bear avoidance of males. *J. Wildlife Manage.* 58, 405–413.
- Woodroffe, R., 2000. Predators and people: using human densities to interpret declines of large carnivores. *Anim. Conserv.* 3, 165–173.
- Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280, 2126–2128.
- Zedrosser, A., Støen, O., Sæbø, S., Swenson, J.E., 2007. Should I stay or should I go? Natal dispersal in the brown bear. *Anim. Behav.* 74, 369–376.
- 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*, first ed. Springer, New York, pp. 532–536.