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Humans are important agents of wildlife mortality, and understanding such mortality is paramount for effective population management and conservation. However, the spatial mechanisms behind wildlife mortality are often assumed rather than tested, which can result in unsubstantiated caveats in ecological research (e.g. fear ecology assumptions) and wildlife conservation and/or management (e.g. ignoring ecological traps). We investigated spatial patterns in human-caused mortality based on 30 years of brown bear *Ursus arctos* mortality data from a Swedish population. We contrasted mortality data with random locations and global positioning system relocations of live bears, as well as between sex, age and management classes ('problem' versus 'no problem' bear, before and after changing hunting regulations), and we used resource selection functions to identify potential ecological sinks (i.e. avoided habitat with high mortality risk) and traps (i.e. selected habitat with high mortality risk). We found that human-caused mortality and mortality risk were positively associated with human presence and access. Bears removed as a management measure were killed in closer proximity to humans than hunter-killed bears, and supplementary feeding of bears did not alter the spatial structure of human-caused bear mortality. We identified areas close to human presence as potential sink habitat and agricultural fields (oat fields in particular) as potential ecological traps in our study area. We emphasize that human-caused mortality in bears and maybe in wildlife generally can show a very local spatial structure, which may have far-reaching population effects. We encourage researchers and managers to systematically collect and geo-reference wildlife mortality data, in order to verify general ecological assumptions and to inform wildlife managers about critical habitat types. The latter is especially important for vulnerable or threatened populations.

Understanding mortality is paramount for effective management and conservation of wildlife populations (Primack 2002). Humans are an important agent of mortality for many wildlife species. For example, humans exploit wildlife as a food resource (e.g. commercial fishing) or for recreation (e.g. sport hunting), wildlife are often killed in traffic, and undesired species are sometimes extirpated (Woodroffe et al. 2005). Human-caused mortality can have direct effects on a population, such as reduced numbers and distribution or altered sex ratios (Noyes et al. 1996), as well as indirect effects, such as altered reproductive strategies and/or behavioral or trait-mediated effects induced by the 'human predator' (Darimont et al. 2009). Direct and indirect effects of mortality can each act as selective pressures on a population and, consequently, influence trophic cascades throughout an ecosystem (Creel and Christianson 2008).

As with all ecological processes, mortality is embedded in a spatial setting. Because space use by both humans and wildlife depends on a suite of factors, both external (e.g. climate, land-cover type, terrain ruggedness, accessibility, etc.) and internal (e.g. personality, social organization, reproductive and physical state, etc.) (Ciuti et al. 2012), it is unlikely that spatial patterns in human-caused wildlife mortality are homogenously distributed across the landscape. Knowledge about spatial patterns of wildlife mortality is important for management and conservation, for example to identify secure habitat, sink habitats (i.e. avoided habitat, in which mortality

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rates exceed birth rates), and ecological traps (i.e. habitat low in quality for survival and reproduction that is nevertheless selected for) (Pulliam 1988, Donovan and Thompson 2001), or age- and sex-related spatial bias and selectivity in human-caused mortality (Elfström et al. 2014b). Such knowledge is important within a broader ecological context. For example, many studies presume a human-induced 'landscape of fear', in which animals are expected to avoid landscape structures that are related to the 'human predator'. However, this presumption has rarely been verified in large mammals (Berger 2007, Ordiz et al. 2011).

Here, we investigate patterns in human-caused mortality in a large mammal, the brown bear *Ursus arctos*, in a hunted population in Sweden. Human-caused mortality explains at least 80% of all bear mortality in Sweden, and approximately 75% of that is caused by hunting (Bischof et al. 2008). Hunting rates recently have increased dramatically, and the population size has shown a downwards trend since 2008 (Kindberg and Swenson 2014).

We evaluated the general presumption (H1) that bears should avoid humans to reduce mortality risk (Martin et al. 2010, Ordiz et al. 2012). Therefore, we predict that (H1a) bear mortality distribution (i.e. mortality versus random locations) and (H1b) risk (i.e. mortality versus bear habitat use) is higher in areas relatively close and/or accessible to humans (i.e. settlements, buildings, roads and trails) (Nielsen et al. 2004). We predict that (H1c) mortality risk and mortality distribution are strongly correlated. In addition, we predict (H1d) that areas close to human presence act as potential sink habitat (i.e. avoided habitat with high mortality risk).

Brown bears have a despotic social organization, in which the presence of larger males is the main driving force behind the spatial structure of a population, because they pose a risk to subadult bears and females with dependent offspring (Elfström et al. 2014b). Consequently, subadult bears and females with offspring often select for areas close to human habitation, e.g. in the form of vehicular traffic (forest roads), recreation (cabins and water), and residence (village and buildings) (Steyaert et al. 2013, Elfström et al. 2014b). Therefore, we expected (H2) spatial differentiation in human-caused mortality among (H2a) males and lone females (with females having higher odds of being killed near human habitation than large males), (H2b) subadult (<5 years old) and adult bears (subadults having a higher probability of being killed near human habitation), and (H2c) subadult males and all other bears (subadult males having a higher probability of being killed near human habitation than all other bears).

Human-bear interactions are a crucial aspect of bear management. One common management measure is the lethal removal of 'problem' bears (i.e. bears that come close to human settlements) (Elfström et al. 2014b). Such problem behavior is often believed to be stimulated by supplementary feeding or baiting; i.e. animals may relate supplementary feeding with humans, lose their natural wariness of humans, and become a nuisance (Steyaert et al. 2014). For that very reason, baiting for bear hunting was banned in Sweden in 2001. Therefore, we hypothesized (H3) that (H3a) lethal management removals occurred closer to human habitation than bears removed by hunting, and that (H3b) bears were killed closer to human habitation before the ban on baiting than after.

As suggested in some Canadian brown bear populations (Nielsen et al. 2006, Northrup et al. 2012), we hypothesized that (H4) potential ecological traps (i.e. selected habitat with high mortality risk) in our study system occur as (H4a) agricultural fields, and especially as (H4b) oat *Avena sativa* fields. Nutritious crops such as oats and corn *Zea mays* may attract bears, and expose them to a greater risk of being hunted compared to more covered habitat types and with less predictable bear occurrence. We tested our hypotheses based on 30 years of geo-referenced human-caused bear mortalities ($n = 381$), and GPS relocation data of 71 individual live bears.

Methods

Study area

The study area was located in Dalarna and Gävleborg counties in south–central Sweden (~ 61°N, 15°E) and consists of approximately 8100 km^2 of intensively managed boreal forest. Elevations range between 200 and 700 m a.s.l. in a gently rolling landscape. Temperature ranges from an average daily minimum temperature of –7°C in January to maximum 15°C in July. Snow cover lasts from late October to early May. The area is sparsely populated and contains a few scattered small settlements ($<$ 200 inhabitants). Larger settlements and villages ($\geq$ 200 inhabitants) are mainly located in the north and south of the study area. Agricultural fields cover approximately 0.5% of the study area and are mostly located near villages. Recreational cabins are, however, dispersed throughout the study area. The landscape is intersected by a dense network of logging roads (0.7 km km^{-2}) and a few high-traffic roads (0.14 km km^{-2}). Human presence is highest during summer and fall, and is mainly related to hunting, as well as berry and mushroom picking (Martin et al. 2010).

Study population

The Swedish bear population was close to extinction during the early 1900s, due to human persecution. Protective measures were implemented in the late 1800s, and the population slowly started growing again in the 1930s, and increased especially in the 1970s in number and range (Swenson et al. 1995). The 2008 population estimate was 3298 (95% confidence interval: 2968–3667) individuals (Kindberg et al. 2011). Concurrent with the beginning of the population recovery, hunting was reintroduced in 1943. The hunting quota gradually increased to approximately 50 individuals per year in 2005, after which the quota increased dramatically (e.g. N_{quota} 2012: 319; 2013: 306) (Sahlén 2013). The Swedish bear population has shown a negative trend in population size from 2008 onwards (Kindberg and Swenson 2014). Bear hunting is allowed during autumn (depending on the area, between 21 August – 30 September or 15 October, or until the quotas are filled) by stalking, hunting with dogs, still hunting, and, until 2001, also at bait sites. A ban on supplementary feeding bears and baiting was issued in 2000, predominantly because of human safety concerns (Bischof et al. 2008).

Between 1984 and 2006, human-caused mortality accounted for at least 79% of the deaths of 208 marked individuals. Hunting accounted for 59.6% of all mortality, other human-caused mortality (i.e. traffic, management actions, self-defense, capture-related mortality, confirmed illegal hunting) accounted for 19.8%, 13.5% died a natural death (i.e. predominantly intraspecific mortality), and the cause of death was unknown for 7.2% (Bischof et al. 2009). No clear demographic bias is apparent in the Swedish bear harvest statistics (Bischof et al. 2009). However, members of family groups (mothers and their offspring) are protected from regular hunting.

Bear mortality data

Bear mortality data is routinely collected by the Swedish National Veterinary Institute (< www.sva.se >). Swedish regulations require that all bears killed by humans or found dead must be reported to the authorities. For all dead bears, date and location of death (global positioning system [GPS] location or referenced to the nearest 100 m on a topographical map), as well as sex, age (based on tooth cementum annuli), and cause of death are recorded. By regulation, successful hunters are required to provide this information to official inspectors, as well as the police (Bischof et al. 2009). We obtained mortality data for the period 1982–2012. We removed cubs-of-the-year from the dataset, because their space use is not independent from their mother. We excluded all records with 'natural' (e.g. intraspecific mortality, starvation) or unknown causes of death, because we were especially interested in human-caused mortality.

Spatial data

We linked the mortality locations with landscape data of known or expected importance in bear ecology based on previous research (Martin et al. 2010, Ordiz et al. 2011, Steyaert et al. 2013); i.e. distance (m) to the nearest village or settlement, single-standing buildings outside villages or settlements, roads (i.e. accessible for motorized vehicles), hiking trails, and water bodies (rivers and lakes); land-cover type (forest, bogs, and agricultural fields), and terrain ruggedness (local scale – based on the eight neighboring cells surrounding a given cell; landscape scale – based on terrain ruggedness within a 1000-m radius surrounding each cell). We calculated terrain ruggedness following Steyaert et al. (2012) based on a 50 × 50 m digital elevation model (DEM). We derived distances to infrastructure and land cover rasters (25 × 25 m cell size) from a digital topographical map. Both the DEM and the digital topographical maps were obtained from the National Land Survey Sweden (<www.lantmateriet.se>, license no. I 2012/901). We did not consider dynamic landscape characteristics (e.g. vegetation density, forest age classes) in our analyses because of the long-term nature of the mortality data. We used ArcGIS 10.0 for all geospatial processing.

Data analyses

We used four complementary types of analyses to evaluate spatial patterns in brown bear mortality, following the approach of Nielsen et al. (2004). First, we used a 'use versus availability' design to model the spatial distribution of bear mortality over the landscape. Second, we modeled mortality risk for brown bears, by relating GPS relocations of live bears with mortality locations; and third, we identified spatial patterns in mortality in relation to sex and age classes, cause of death, and changes in the hunting regulations (i.e. ban on baiting). In addition, we used resource selection functions (RSF) to pinpoint potential sink habitats and ecological traps.

Mortality distribution

We used the RSF approach of Manly et al. (2002) to identify spatial patterns in bear mortality locations compared to random locations using logistic regression (random location = 0, mortality location = 1) to maximize the 'use-availability' likelihood (McDonald 2013). We sampled random locations within the 100% minimum convex hull of all mortality locations, after masking water bodies (i.e. not bear habitat) from the study area. We systematically increased the number of random locations in the sample until the availability of the land cover types did not vary more than 1% (Serrouya et al. 2011). We included the land cover types as dummy variables in the models. We defined six candidate models a priori, based on a specific set of landscape variables; i.e. a full model, a terrain model, a land cover model, a human model, an expert model (i.e. based on our previous research), and the null model (Table 1). We selected the most parsimonious model based on the information theory and Akaike's information criteria (AIC) (ΔAIC_c – second order bias-corrected AIC difference values, AIC_{cw} – second order bias-corrected AIC weights). We used model averaging if ΔAIC_c values between candidate models were small (< 4) compared to the top ranked model (Burnham and Anderson 2002).We evaluated the relative importance of each model term in the most parsimonious model by systematically including or excluding a specific term in the model and recalculating the ΔAIC_c. We validated the most parsimonious model using a 10-fold cross-validation following Maindonald and Braun (2007). For all analyses, we used a Pearson product-moment correlation coefficient threshold level of 0.6 to identify collinearity among model variables, and considered a model term informative when the 95% confidence interval did not include 0.

Mortality risk

Brown bears do not use their habitat randomly. This implies that mortality risk is conditional upon space use; i.e. an individual can only be killed where it is present (Nielsen et al. 2004). Therefore, using the same approach as for the mortality distribution model, we contrasted a random set of brown bear GPS relocations with the mortality data. We sampled an equal number of GPS relocations as random points in the mortality distribution model from a quality-screened GPS relocation database (2003–2012, 158 bear-years covering all sex and age classes except cubs-of-the-year) of the Scandinavian Brown Bear Research Project (< www.bearproject.info >). We assumed that space use of bears during 2003–2012 represented space use for the entire study period, and that resource availability remained stable during the entire study period. Because human-caused bear mortality occurred predominantly between 05:00 and

Table 1. Model structure and model selection diagnostics of six a priori defined candidate models to identify spatial patterns in human-caused mortality and mortality risk in brown bears in southcentral Sweden between 1982 and 2012. ΔAICc and AICcw indicate the second-order bias-corrected Akaike's information criteria difference values, respectively; and no. indicates model rank. Check marks indicate inclusion in a certain model. 'Dist. to' = distance to the nearest, 'TRI' = terrain ruggedness index. The full mortality risk model did not converge because of singularities.

	Landscape variables										Mortality distribution			Mortality risk		
Hypotheses	Bog	Forest	Agriculture	Dist. to building	Dist. to village	Dist. to road	Dist. to trail	Dist. to water	TRI - local	TRI - landscape	no.	ΔAICc	AICcw	no.	ΔAICc	AICcw
Full	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	2	5.65	0.056	1	–	–
Expert		✓	✓		✓	✓		✓		✓	1	0	0.943	2	6.22	0.043
Human			✓	✓	✓	✓	✓			✓	3	12.82	0.002	1	0	0.957
Land cover	✓	✓	✓								4	27.91	0	3	96.39	0
Terrain	✓	✓	✓						✓	✓	5	30.63	0	4	98.90	0
Null											6	54.28	0	5	150.14	0

20:00 (96% of all records) and in late summer and autumn (August–October, 94% of all records), we only considered GPS relocations from that specific time window.

Mortality distribution versus mortality risk

We compared the spatial predictions of the mortality distribution and mortality risk models using a Pearson product–moment correlation test based on spatially independent points distributed over the study area. We identified spatial autocorrelation in the mortality distribution and mortality risk models using semivariograms with a Gaussian link function based on 9999 random locations in the study area. We considered the semivariogram range as the distance at which locations become spatially independent. We used this distance (555 m) as a minimum distance criterion to sample random locations (n = 993) for identifying the spatial relationship between the mortality distribution and mortality risk model (Hiemstra et al. 2009).

Spatial patterns in mortality among bears

We used logistic regression to identify spatial patterns in mortality in relation to sex (female = 0, male = 1), age class (model 1: subadults, ≤ 5 years old = 0, adults, > 5 years old = 1; model 2: subadult males = 1, other bears = 0), cause of death (legal hunt = 0, management removal = 1), and hunting regulations (before the ban on baiting = 0, after the ban on baiting = 1; included hunted bears only). We constructed six candidate models a priori, based on a specific combination of landscape and time (i.e. year, month) variables (Table 2). We used the same model selection and model validation approach as with the mortality distribution and risk models.

Identifying potential sinks and traps

Identifying true ecological traps and sink habitat requires relating habitat specific mortality as well as reproductive rates to population growth (Pulliam 1988, Donovan and Thompson 2001), and falls beyond the scope of this paper. Therefore, and in analogy with Nielsen et al. (2006) and Northrup et al. (2012), we used RSFs in combination with mortality risk models to identify potential sink habitat (avoided and high mortality risk habitat) and potential ecological traps (selected and high mortality risk habitat). We used the parameter estimates of habitat covariates in the mortality risk models as a surrogate for land-cover specific habitat quality (i.e. high mortality risk ~ low habitat quality). We only considered habitat covariates that were included in the most parsimonious mortality risk model. We generated a buffer of 17.84 km around land-cover types included in the most parsimonious risk model and constructed an RSF based on all GPS bear relocations that were included in the buffer zone and an equal number of random locations drawn from within the buffer area. We chose 17.84 km as a buffer distance, because it is a commonly used distance threshold for bear density estimates and it approximates the average radius of the home range of male bears in our study area (Zedrosser et al. 2006). We assumed that all bears inside a given buffer area also could use all habitat contained within the buffer. We used a mixed-effect logistic regression model to model the RSF with the same fixed effect structure of the mortality risk model, and included 'bear ID' and 'year' as random effects on the intercept (Zuur et al. 2009). We evaluated the relative importance of each land cover type as outlined above ('mortality distribution').

Table 2. Candidate models to evaluate spatial patterns in human-caused brown bear mortality in relation to sex, age, and cause of death in south–central Sweden (1982–2012). Check marks indicate inclusion in a certain model.

	Landscape variables											
Hypotheses	Bog	Forest	Agriculture	Dist. to building	Dist. to village	Dist. to road	Dist. to trail	Dist. to water	TRI - local	TRI - landscape	Year	Month
Full	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Expert					✓	✓				✓		
Human			✓	✓	✓	✓	✓			✓		
Land cover	✓	✓	✓									
Terrain	✓	✓	✓						✓	✓		
Null												

Table 3. Model output of the most parsimonious model (Expert model, AICcw = 0.94) of six a priori defined candidate models to identify spatial patterns in human-caused brown bear mortality in south–central Sweden (1982–2012). β's indicate parameter estimates, σ = standard error, LL = lower limit of the 95% confidence interval, UL = upper limit of the 95% confidence interval, ΔAICc = second-order bias-corrected AIC weights of specific model terms.

Model term	β	σ	LL	UL	ΔAICc
Distance to the nearest road	–0.00015	0.00015	–0.00044	0.00013	–0.89
Distance to the nearest water	0.00032	0.00011	0.00010	0.00054	5.78
Distance to the nearest village	–0.00010	0.00003	–0.00015	–0.00005	13.66
Forest versus Not forest	0.48870	0.23830	0.02163	0.95577	2.69
Agriculture versus Not agriculture	2.59500	0.54160	1.53346	3.65654	20.98
Terrain ruggedness - landscape scale	5.26600	4.48300	–3.52068	14.05268	–0.66

Results

Mortality data

We obtained data for 381 (168 males, 211 females, 2 unknown sex) human-caused bear mortalities in our study area between 1982 and 2012. The mean and median age of all dead bears of known age (n = 338, including cubs-of-the-year) was 5.8 and 4 years old, respectively, within a range of 0 to 30 years old. Most bears were killed during the legal hunt (n = 344, 90.3%), followed by management removals (n = 15, 3.9%) and bears killed in self-defense (n = 13, 3.4%). Six bears (1.6%) were killed in traffic, and three (0.8%) were killed illegally. We removed all (n = 9) records of cub-of-the-year mortalities from the data to avoid mother-cub data dependencies.

Mortality distribution

The availability of land cover classes did not vary > 1% after selecting seven random locations for each mortality location; we thus sampled 'use vs. availability' for modeling mortality distribution in a 1:7 ratio, yielding a total of 2303 random locations. The expert model was the most parsimonious model (AICcw = 0.94) of the six candidates to identify patterns in the spatial distribution of human-caused brown bear mortality (Table 1). We considered the other models as inconclusive (all ΔAICc values ≥ 5.65). In order of decreasing relevance, the expert model included the land cover type 'agriculture' (i.e. removing the term 'agriculture' penalized the AICc score of the most parsimonious model with 20.98, hereafter 'penalized AICc'), distance to the nearest village (penalized AICc = 13.66), distance to the nearest water body (penalized AICc = 5.78), and the land cover type 'forest' (penalized AICc = 2.69). Terrain ruggedness at the landscape scale and distance to the nearest road were uninformative model terms of the expert model (penalized AICc = –0.66 and –0.89, respectively) (Table 3). The expert model had good predictive accuracy (internal estimate of accuracy = 0.88).

Mortality risk

As for mortality distribution, we again randomly selected seven relocations for each bear mortality location out of the SBBRP relocation database, yielding a total of 2303 relocations from 71 bears (45 females, 26 males). The average number relocations per bear was 37, and ranged between 1 and 127. The human model was the most parsimonious model (AICcw = 0.96) of 6 candidates (Table 1). We considered all other models as inconclusive (all ΔAICc values ≥ 6.22; the full model did not converge because of singularities). The human model included, in order of decreasing relevance, distance to the nearest village (penalized AICc = 41.33), the land cover type 'agriculture' (penalized AICc = 19.29), distance to the nearest road (penalized AICc = 18.25), and distance to the nearest building (penalized AICc = 17.9). Distance to the nearest trail and terrain ruggedness at the landscape scale were uninformative terms in the human model (penalized AICc = –0.4 and –0.53, respectively) (Table 4). The human model had good predictive accuracy (internal estimate of accuracy = 0.89). Mortality risk was strongly and positively spatially correlated with mortality distribution (correlation coefficient: 0.769, 95% confidence interval: 0.743–0.794).

Spatial patterns in mortality among classes of bears, mortality type and change in bait hunting regulations

No apparent spatial differentiation was present in mortality between males and females, subadults versus adults, subadult males versus other sex and age classes, and the

Table 4. Model output of the most parsimonious model (Human model, AICcw = 0.96) of six a priori defined candidate models to identify spatial patterns in human-caused brown bear mortality risk in south–central Sweden (mortality data, 1982–2012; GPS relocation data, 2003–2012). β's indicate parameter estimates, σ = standard error, LL = lower limit of the 95% confidence interval, UL = upper limit of the 95% confidence interval, ΔAICc = second-order bias-corrected AIC weights of specific model terms.

Model term	β	σ	LL	UL	ΔAICc
Distance to the nearest road	–0.00077	0.00018	–0.00113	–0.00041	18.25
Distance to the nearest trail	–0.00018	0.00015	–0.00047	0.00011	–0.4
Distance to the nearest village	–0.00019	0.00003	–0.00025	–0.00013	41.33
Distance to the nearest building	–0.00035	0.00008	–0.00052	–0.00019	17.9
Agriculture versus Not agriculture	3.35900	1.05600	1.28924	5.42876	19.29
Terrain ruggedness - landscape	–6.89300	5.08800	–16.86548	3.07948	–0.53

ban on baiting. Both the expert and the land cover models obtained considerable model weight compared to the null model to differentiate spatial patterns in mortality between males and females (null: AICcw = 0.697, ΔAICc = 0; expert: AICcw = 0.146, ΔAICc = 3.13; land cover: AICcw = 0.113, ΔAICc = 3.65), subadult and adults (null: AICcw = 0.558, ΔAICc = 0; expert: AICcw = 0.126, ΔAICc = 2.98; land cover: AICcw = 0.204, ΔAICc = 2.02), subadult males versus other bears (null: AICcw = 0.554, ΔAICc = 0; expert: AICcw = 0.091, ΔAICc = 3.58; land cover: AICcw = 0.091, ΔAICc = 3.58 (Supplementary material Appendix 1 Table A1). Averaging the results of models with ΔAICc scores in a range of 0–4, however, did not identify any clear spatial differentiation among classes of bears (Supplementary material Appendix 1 Table A2–A4). Including the nine cubs-of-the-year in the age-class analysis did not affect the results (Supplementary material Appendix 1 Table A5). The ban on bait hunting did not spatially differentiate human-caused bear mortality (no other models had ΔAICc scores < 4 compared to the null model, AICcw = 0.78) (Supplementary material Appendix 1 Table A1). The expert model was the most parsimonious model to identify spatial patterns in bear mortality in relation to the cause of death (hunted or management removal). However, the human model was ranked closely (AICcw = 0.214, ΔAICc = 2.52). The model-averaged results indicated that legally hunted bears were generally killed farther from villages than bears killed as a management measure ($\beta = -0.00043$, $\sigma = 0.00021$, LL = –0.0008, UL = –0.000024, Supplementary material Appendix 1 Table A6).

Potential sinks and traps

We constructed an RSF based on 15 669 GPS relocations from 27 bears (14 males, 13 females, average 1119 positions/bear, range 6–3970) that were included in a 17.84 km buffer around agricultural fields in our study area. 'Agricultural field' was the only land cover type that was included in the most parsimonious risk model. A 1:1 use vs. availability ratio was sufficient to sample the land-cover types within this area. Bears selected for areas relatively far from roads (penalized AICc = 496.77), buildings (penalized AICc = 87.91), and villages (penalized AICc = 2644.85), and for areas close to trails (penalized AICc = 114.58) (Table 4). Bears tended to select for the least rugged terrain (penalized AICc = 174.55), and for agricultural fields (penalized AICc = 11.36). Updating our model by only including oat fields instead of all agricultural fields strongly improved the model (penalized AICc = 140.59), and oat fields were strongly selected for (penalized AICc = 151.95) (Table 5). Areas close to roads, villages, and buildings contained high mortality risk (Table 4, 5) but were avoided, and can thus be considered as potential sink habitats. Despite a high mortality risk, agricultural fields (oat fields in particular) were strongly selected for and can thus be considered as potential ecological traps (Table 4, 5).

Discussion

We found that both mortality distribution and mortality risk were not homogenously distributed throughout the landscape, but were biased towards human-related landscape variables (H1a,b), and that mortality risk and mortality distribution were strongly spatially correlated (H1c). We identified areas close to humans as potential sink habitat (H1d). A disproportionate number of bears were killed in agricultural fields, in forests, relatively far from water bodies, and in relative close proximity to villages. Mortality risk was consequently largest near villages, roads, and buildings, and on agricultural fields. We could not detect spatial differentiation in human-caused mortality among sex and age classes (H2), nor in relation to changing hunting regulations (H3b). We did, however, find spatial differentiation between hunted bears and management removals, i.e. management removals generally occurred in closer proximity to villages than hunter-killed bears (H3a). Our results suggest that agricultural fields (H4a), and oat fields in particular (H4b), may act as ecological traps for bears in our study area.

Mortality distribution and risk in a brown bear population in the Canadian Rocky Mountains was also positively associated with human access (Nielsen et al. 2004). In addition, Nielsen et al. (2004) found that mortality risk was positively associated with water and edge features, and was negatively influenced by vegetation density and terrain ruggedness. In contrast to Nielsen et al. (2004), terrain ruggedness was never included as an influential landscape variable in our models, and mortality risk was negatively associated with water. Nielsen et al. (2004) suggested that bears in the Canadian Rockies may select for the most rugged terrain, as it may act as a refuge against hunter access. We suggest that terrain ruggedness in our study area was not variable enough

Table 5. Resource selection function model results for brown bears within a 17.84-km buffer area around agricultural fields in our study area in southcentral Sweden. β's indicate parameter estimates, σ = standard error, LL = lower limit of the 95% confidence interval, UL = upper limit of the 95% confidence interval, ΔAICc = second-order bias-corrected AIC values of specific model terms. 'Response' indicates whether or not a certain habitat covariate was avoided or selected. Note that positive values for the 'distance to' covariates indicate avoidance. 'Risk' indicates how a landscape covariate contributed to mortality risk. '–' indicates a nonsignificant (95% confidence intervals include 0) effect of a certain covariate in the RSF or the risk models. Type indicates potential sink (S, avoided low-quality habitat) or potential ecological trap habitat (T, selected low-quality habitat). We use mortality risk as a surrogate for habitat quality.

Model term	β	σ	LL	UL	ΔAICc	Response	Risk	Type
Distance to the nearest road	0.0017	0.00008	0.001537	0.001847	492.47	avoid	high	S
Distance to the nearest trail	–0.0005	0.00004	–0.000535	–0.000366	113.22	select	–	–
Distance to the nearest village	0.0003	0.00001	0.000264	0.000287	2646.7	avoid	high	S
Distance to the nearest building	0.0002	0.00002	0.000138	0.000208	94.5	avoid	high	S
Oatfield versus Not oatfield	3.4950	0.45930	2.5764	4.4136	151.95	select	high	T
Terrain ruggedness - landscape	–16.5500	1.23800	–19.026	–14.074	166.3	avoid	–	–

to reduce human access and provide refuge for bears. In our study area, bears generally avoid water (Steyaert et al. 2012, 2013), presumably because of relatively high probabilities of meeting people (e.g. recreation, fishing), and we suggest that this avoidance was also reflected in the distribution of human-caused bear mortality.

Studies that relate landscape features to survival in wildlife are becoming widespread in the literature (Nielsen et al. 2004, Ciuti et al. 2012, Lone et al. 2014). Even if such studies use different approaches and methodologies, the conclusions are generally comparable; i.e. human presence and access of an area are important factors affecting the spatial structure of wildlife populations (Woodroffe et al. 2005), their behavior (Ordiz et al. 2014), and their survival (Lone et al. 2014).

Fear ecology theory predicts that animals respond to predation risk by adjusting their spatiotemporal behavior to avoid the risk source, and therefore trade resources (typically food) for safety (Brown et al. 1999). Animals are expected to respond rapidly to changes in predictable risk regimes (Lima and Bednekoff 1998). For our study system, this implies that bears should avoid areas of human presence and access most strongly during the hunting season, which coincides with hyperphagia. During this period, bears spend up to 80% of the time feeding on berries (bilberry *Vaccinium myrtillis*, lingonberry *V. vitis-idaea* and crowberry *Empetrum nigrum*) to acquire sufficient fat reserves for hibernation (Welch et al. 1997). Scandinavian bears derive approximately 81% of their annual digestible energy from berries (Dahle et al. 1998), and female autumn body condition is a strong determinant of subsequent reproductive success (Welch et al. 1997). Our results indicate that bears should indeed avoid areas close to human presence and access to reduce mortality risk, as suggested by Martin et al. (2010) and Ordiz et al. (2011). According to fear ecology theory, bears are expected to be less efficient in foraging on berries during hyperphagia as a consequence of hunting. However, whether or not bears face such a tradeoff between spatiotemporal avoidance of humans and foraging efficiency, as well as how such risk effects affect fitness and population growth, remain important, unanswered questions. It must be stressed, however, that animal responses to human presence and access of an area are not unambiguous and may differ among species, sex and age classes, and reproductive status. For example, roads and human presence may also act as a virtual shield against predation (Berger 2007) or infanticide (Steyaert et al. 2013), and human presence can also be attractive in terms of food supply (Elfström et al. 2014c).

Surprisingly, we did not detect any spatial sex and age differences in human-caused bear mortality, nor effects of a pronounced change in the hunting regulations. Elfström et al. (2014b) documented that younger bears were shot more often than older individuals in areas of higher human density in both a Swedish and a Slovenian population, and suggested that the despotic socio-spatial nature of a brown bear population forced younger individuals closer to human habitation. Consequently, these younger bears were also more often considered as problem individuals, and removed from the population by managers (Elfström et al. 2014b). As expected, we found that management removals generally occurred in closer proximity to villages; however, we could not detect such an age effect. In our analyses, we dichotomized age into two classes, which probably resulted in the loss of some information. In addition, the sample size used in Elfström et al. (2014b) was much larger than in this study ($>$1000 individuals in both Sweden and Slovenia), which probably facilitated the detection of such patterns in the data.

Supplementary feeding of wildlife (e.g. baiting) is controversial, especially when it involves species that can be dangerous for humans (Steyaert et al. 2014), such as bears. Supplementary feeding of bears is often assumed to stimulate nuisance behavior and consequently is discouraged or prohibited (e.g. in Sweden and North America), whereas in other countries or regions (e.g. Slovenia), supplementary feeding is advised or even compulsory as a tool to lure individuals away from undesired locations (Steyaert et al. 2014). Recent studies, however, showed that supplementary feeding neither stimulates nuisance behavior nor is effective in mitigating human-wildlife conflicts (Kavčič et al. 2013, Steyaert et al. 2014). Our findings concur with Kavčič et al. (2013) and Steyaert et al. (2014) because baiting did not result in more or fewer bears being killed close to human habitation.

Our results suggested that agricultural fields (especially oat fields) may act as an ecological trap for bears in our study area, because bears selected for these fields, despite their disproportionately large mortality risk (8.4% of the bears were killed in agricultural fields covering $<$ 0.5% of the study area, whereas only 1% of all bear GPS relocations were registered within that land cover type). It is not unlikely, however, that such fields increase the carrying capacity of our study area and facilitate a denser bear population than would have been the case without human derived foods. Such mechanism was reported, for example, in Slovenia, where supplementary feeding facilitates locally extremely high bear densities ($>$400 individuals/1000 km^2) (Kavčič et al. 2013); or in the Greater Yellowstone Ecosystem, where open-pit garbage dumps with virtually unlimited food resources stimulated population growth (Craighead et al. 1995). An ecological trap is defined as an area strongly selected for, of low quality habitat in terms of survival and reproduction, and which negatively affects population growth (Pulliam 1988, Delibes et al. 2001). How habitat availability and selection influences reproductive rates and, consequently, population growth in our study population is currently unknown and warrants further investigation.

Oats are a highly preferred food item of brown bears and DNA metabarcoding revealed that 48.1% of 120 scat samples collected from 21 bears in our study area contained oats (Elfström et al. 2014a). Cultivating oat fields as a bait site to hunt brown bears is common practice in Russia (Vaisefeld and Chestin 1993), and agricultural land can act as ecological traps for brown bears (Naves et al. 2003, Nielsen et al. 2006, Northrup et al. 2012) and a range of other mammals, birds, reptiles, amphibians and fishes (Schlaepfer et al. 2002). We identified areas nearby human presence and access as potential sink habitats, i.e. areas which were low in habitat quality (in terms of survival) and which were generally avoided by bears. This implies that human encroachment and habitat fragmentation by, for example, the construction of logging roads effectively reduces good-quality habitat, both in terms of habitat selection, as well as survival. Because sink habitats and ecological traps can have large demographic and evolutionary consequences (Delibes et al. 2001), we recommend that researchers should attempt to identify such traps and that managers should incorporate such knowledge into wildlife management.

Conclusions

Our results confirm that bear mortality and mortality risk are not homogenously distributed throughout the landscape, but are heavily influenced by human presence and accessibility. Thus, we verified that bears indeed should avoid human presence and access to reduce the risk of being killed. How such avoidance further affects life history, fitness, and population growth remains, however, unanswered. Our results indicate that spatial patterns in mortality can be extremely concentrated, and that such concentrations may act as ecological traps. Furthermore, we suggest that human encroachment and habitat fragmentation due to road construction reduces the total area of suitable habitat in terms of habitat selection and survival. We encourage wildlife researchers and managers to systematically collect and geo-reference (human-caused and other) wildlife mortality data, and to evaluate spatial patterns at local and regional scales in order to verify general ecological assumptions, but also to identify (potential) ecological traps and sink habitats. The latter is especially important for wildlife populations that struggle for survival, because local management interventions that focus on ecological traps and sinks can have wide-ranging population effects.

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Supplementary material (available online as Appendix wlb-00165 at <www.wildlifebiology.org/appendix/wlb-00165>). Appendix 1.