MR. SHANE C. FRANK (Orcid ID : 0000-0001-8153-6656)

MR. MARTIN LECLERC (Orcid ID : 0000-0002-4429-697X)

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Sociodemographic factors modulate the spatial response of brown bears to vacancies created by hunting.

Shane C. Frank[1*], Martin Leclerc[2], Fanie Pelletier[2], Frank Rosell[1], Jon. E. Swenson[3,4], Richard Bischof[3], Jonas Kindberg[4,5], Hans Geir Eiken[6], Snorre B. Hagen[6], Andreas Zedrosser[1,7]

[1]Faculty of Technology, Natural Sciences, and Maritime Sciences, Department of Natural Sciences and Environmental Health, University College of Southeast Norway, NO-3800 Bø, Telemark, Norway

[2]Canada Research Chair in Evolutionary Demography and Conservation, Département de Biologie, Université de Sherbrooke, Sherbrooke, J1K2R1, Canada

[3]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, PO Box 5003, NO-1432 Ås, Norway

[4]Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

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[5]Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies, SE-90183 Umeå, Sweden

[6]Norwegian Institute of Bioeconomy Research, NO-XXXX Svanhovd, Norway

[7]Department of Integrative Biology, Institute of Wildlife Biology and Game Management, University of Natural Resources and Applied Life Sciences, Vienna, Gregor Mendel Str. 33, A - 1180 Vienna, Austria

*Correspondence to: shane.frank@usn.no

Summary

1. There is a growing recognition of the importance of indirect effects from hunting on wildlife populations, e.g., social and behavioral changes due to harvest, which occur after the initial offtake. Nonetheless, little is known about how the removal of members of a population influences the spatial configuration of the survivors.

2. We studied how surviving brown bears (*Ursus arctos*) used former home ranges that had belonged to casualties of the annual bear hunting season in southcentral Sweden (2007-2015). We used resource selection functions to explore the effects of the casualty's and survivor's sex, age, and their pairwise genetic relatedness, population density, and hunting intensity on survivors' spatial responses to vacated home ranges.

3. We tested the competitive release hypothesis, whereby survivors that increase their use of a killed bear's home range are presumed to have been released from intraspecific competition. We found strong support for this hypothesis, as survivors of the same sex as the casualty consistently increased their use of its vacant home range. Patterns were less pronounced or absent when the survivor and casualty were of opposite sex.

4. Genetic relatedness between the survivor and the casualty emerged as the most important factor explaining increased use of vacated male home ranges by males, with a stronger response from survivors of lower relatedness. Relatedness was also important for females, but it did not influence use following removal; female survivors used home ranges of higher related female casualties more, both before and after death. Spatial responses by survivors were further influenced by bear age, population density, and hunting intensity.

5. We have showed that survivors exhibit a spatial response to vacated home ranges caused by hunting casualties, even in non-territorial species such as the brown bear. This spatial reorganization can have unintended consequences for population dynamics and interfere with management goals. Altogether, our results underscore the need to better understand the short- and long-term indirect effects of hunting on animal social structure and their resulting distribution in space.

Keywords

Spatial response, kinship, competition, spatial reorganization, harvest, social structure, mortality, *Ursus arctos*

Introduction

Hunting has important direct and indirect effects on wildlife populations (Milner, Nilsen & Andreassen 2007). By removing individuals, hunting creates vacancies in a population's social and spatial configuration (McComb *et al.* 2001). In response to this removal, surviving individuals may exhibit a spatial reorganization (Gese 1998; Leclerc *et al.* 2017), which in turn may affect social structure, reproduction, and ultimately population dynamics (Robinson *et al.*

2008; Cooley *et al.* 2009). It is therefore important to better understand the effects of hunting on the space use of surviving individuals for sustainable hunting practices.

One consequence of the removal of conspecifics (hereafter *casualties*) is the release of surviving individuals (hereafter *survivors*) from competition or social constraints (Maletzke *et al.* 2014; Loveridge *et al.* 2016). Competitive release may manifest itself in the increased use of a casualty´s former home range (HR; hereafter *vacancy*) by survivors (Gese 1998; Goodrich *et al.* 2010), i.e. a spatial response, which in turn could be influenced by several sociodemographic factors (Maletzke *et al.* 2014; Loveridge *et al.* 2016).

Sex is an important factor for determining life history strategies, social systems, and consequently population structure (Lott 1991; Bonenfant *et al.* 2002). Same-sex individuals compete for breeding opportunities or for resources necessary for reproduction (Clutton-Brock & Huchard 2013a). Sex-differences in morphology and habitat selection likely decrease intersexual competition, enabling the sharing of space and mating opportunities (e.g. Zabala, Zuberogoitia & Martinez-Climent 2007). Therefore, the removal of same-sex individuals has the potential to induce stronger spatial responses by survivors than the removal of opposite-sex individuals, if intrasexual competition is a spatially limiting factor for a given sex (e.g. Nelson 1995).

Kin selection theory states that the degree of genetic relatedness can influence competition among individuals (Hamilton 1964). Higher genetic relatedness between individuals has been linked to higher HR overlap and increased spatial aggregations (Ratnayeke, Tuskan & Pelton 2002; Wronski & Apio 2005). Within these socio-spatial relationships, relatedness has been shown to increase reproductive output, foraging efficiency, and tolerance (Pusenius *et al.* 1998; Wronski & Apio 2005; Wright *et al.* 2016). The removal of kin from a population in social species can lower the competitive ability of the surviving kin to gain access to space and

associated resources, as well as breeding opportunities (McComb *et al.* 2001; Clutton-Brock & Huchard 2013b). In comparison, unrelated survivors may benefit from removals, which may result in stronger spatial responses toward vacancies belonging to nonkin. Kin-based aggregations in mammals are more common in females than males, due to female-biased philopatry (Waser & Jones 1983). Furthermore, there is increasing evidence that female space use among solitary carnivores is linked to mother-daughter home range overlap, a pattern not observed between mothers and sons (Fattebert *et al.* 2015; Fattebert *et al.* 2016). Therefore, the influence of relatedness on survivors' spatial responses may differ between the sexes and be stronger for females in philopatric species.

Additional factors commonly modulate the level of intra- and intersexual competition in space use. For example, age is often associated with dominance status (Clutton-Brock & Huchard 2013a), reproductive success (e.g. King, Festa-Bianchet & Hatfield 1991), and access to resources (McComb *et al.* 2001). The removal of older, dominant individuals from a population allows nearby survivors to exploit resources previously denied to them either directly through aggression or indirectly through increased use (Pilfold, Derocher & Richardson 2014) of the killed animal's HR. Furthermore, older nearby survivors may be able to better take advantage of vacancies (i.e., HRs of a removed individual), as seen in Seychelles warblers (*Acrocephalus sechellensis*) (Eikenaar *et al.* 2008). Increasing population density can increase competition for food resources and breeding opportunities (e.g. McLoughlin *et al.* 2006). The removal of an individual decreases direct competition experienced by a nearby survivor, but the magnitude of this effect may depend on population density. At higher densities, the spatial response of a nearby survivor can be limited, due to prevailing spatial competition among a higher number of other survivors (Leclerc *et al.* 2017). At the same time, populations with higher hunting

intensities or individual turnover are typically less stable in terms of social structure, which can increase spatial responses (Porter *et al.* 1991; Comer *et al.* 2005).

Examining the combined effects of sociodemographic factors on survivors' spatial responses to the removal of conspecifics requires detailed individual-based data. Most studies on the effects and mechanisms of removal on spatial reorganization have been conducted on territorial birds, many of which were not hunted populations (e.g. Eikenaar *et al.* 2008). The paucity of knowledge on spatial responses in mammals and those which are hunted is likely due to the scarcity of individual-based data needed to investigate their social structure (Clutton-Brock & Sheldon 2010).

Here we use detailed individual-based, social, spatial and genetic data on brown bears (*Ursus arctos*) to explore the effects of removing individuals in a hunted population on survivors' spatial responses. The brown bear is a large solitarily-living carnivore (Steyaert *et al.* 2012). However, related females form aggregations (Støen *et al.* 2005), and HRs of both sexes vary similarly according to food availability and population density (Dahle & Swenson 2003). Leclerc *et al.* (2017) found for male brown bears that survivors' increased use of casualties' HRs was modulated by bear age, population density, and hunting intensity. This study builds upon those findings to explore the responses in both sexes and evaluate whether kinship between casualties and survivors modulates the post-hunt spatial reorganization. By considering a casualty's former home range as an area containing resources, we used resource selection functions (RSFs) (Manly *et al.* 2002) to investigate which factors affect the spatial responses of survivors during the two years following the removal of a nearby individual. Based on the competitive release hypothesis, we predicted that: (P1a) survivors would increase their use of a casualty's HR and (P1b) this increase would be stronger when survivors and casualties are of the

same sex. (P2) Genetic relatedness should be negatively correlated with survivors' increase in use of casualties' HRs if both are females, but not if they are males or bears of the opposite sex. (P3) Ages of both survivors and casualties would be positively related to a survivor's increase in use of a casualty´s HR. (P4) Population density would be negatively related to a survivor's increase in use of a casualty´s HR, whereas (P5) hunting intensity will be positively related to increases in use.

Materials and Methods

The study area is located in southcentral Sweden (61°N, 15°E) and is composed of bogs, lakes, and intensively managed and mixed-aged forest stands. Between 1985-2015, we captured 499 brown bears from a helicopter using a remote drug delivery system (Dan-Inject®, Børkop, Denmark) (Fahlman *et al.* 2011). All captures and handling were approved by the Swedish Board of Agriculture, Uppsala Ethical Committee on Animal Experiments, and the Swedish Environmental Protection Agency. We determined the bears' sex at capture and extracted a premolar tooth for age determination (Matson 1993) from individuals not captured as a yearling (n = 181). Starting in 2003, we equipped bears with GPS collars (GPS Plus; Vectronic Aerospace GmbH, Berlin, Germany) programmed to relocate a bear with varying schedules (≤1 hour). In addition, we acquired data on location, sex, and age (determined as above) for all known dead brown bears in Sweden between 1981-2014 (n = 3,960), of which 83% was caused by legal hunting.

MODEL DEVELOPMENT

We assumed that a vacancy created through the removal of a conspecific was a spatially explicit 'resource' or a collection of resources available to remaining survivors. We used resource

selection functions (RSFs; Manly *et al.* 2002) to determine whether survivors showed a spatial response over time to vacancies. RSFs contrast relocations of use and those randomly available, while explaining the pattern of use with a set of covariates, e.g., whether a location falls inside or outside a specific area or a casualty's former HR in this case. We coded the dependent variable as either a real GPS (= 1) or a simulated, randomly created (= 0) relocation; the latter represented the extent of use by neighboring bears of the casualty's home range under the null hypothesis absent of competitive exclusion. We used generalized linear mixed models (GLMM) with a logit link to assess the influence of sex on spatial responses (Step I). Then, to simplify model complexity, we evaluated how spatial responses was modulated by age, pairwise relatedness, density index, and hunting intensity separately by casualty-survivor sex combination (Step II).

LOCATION DATA

We only included adult bears (≥ 4 year-olds; Støen *et al.* 2006) in the analysis to avoid potential confounding effects of dispersing bears on the spatial response to harvest. We removed GPS fixes with dilution of precision values >10 to increase spatial accuracy (D'Eon & Delparte 2005). To reduce autocorrelation caused by a lack of independence among successive GPS positions, we used a 6-hour minimum interval between successive positions (yielding a maximum of 4 relocations per bear/day). We excluded bears that had <75% of days with relocations during May 1 – August 21 (after den exit until the start of hunting) in a given year from 2007-2015 to have adequate coverage of the bear's nondenning period. We defined casualties' HRs with the 95th percentile isocline from a kernel density distribution, using the 'reference' bandwidth (*ad hoc* method) and a fixed kernel in the R package 'adehabitatHR' (Calenge 2006).

COVARIATE DESCRIPTION

We extracted an annual population density index for each casualty. This index was derived using spatially-referenced genetic data obtained from county-level scat collections in Sweden. Individual bears were identified from feces using six microsatellites (see Bellemain *et al.* 2005; Kindberg *et al.* 2011). Scat collections occurred in different years among counties and collection was not spatially homogenous. Therefore, we chose a grid size of 10x10 km cells and adopted the method of Jerina et al. (2013) to sum the weighted values of an individual bear's (multiple) scats across this spatial grid. An individual's scat count was weighted ($1/\sqrt{n}$) according to the number of samples collected, so that the sum of the weighted values was equal among all individuals (Jerina *et al.* 2013). The weighted scat values were then summed by cell at the county level, after which the county-level distribution was annually corrected using county-level trends of the Large Carnivore Observation Index (LCOI; provided by the Swedish Association for Hunting and Wildlife Management; Kindberg, Ericsson & Swenson 2009; Kindberg *et al.* 2011) during the study period. All county grids were then summed and joined to produce an annual density index for the study area for 2007-2015. The resulting grids were then smoothed using a 3x3 cell moving window (30x30 km) (see Appendix S1). Density index values were extracted at the casualties' HR centroids.

We used 16 autosomal microsatellites (Table S1; Støen *et al.* 2005) to construct a pedigree and to calculate relatedness estimates between individuals (Lynch & Ritland 1999). This pedigree (Table S2) included genetics from captured and recovered dead bears (N = 1,614). To estimate relatedness, we chose Lynch and Ritland's (1999) estimator, because it has shown the highest correlation with theoretical relatedness values from a simulated pedigree of known relationships compared to other estimators (Csillery *et al.* 2006). We used the relatedness

estimates calculated using the microsatellites rather than from the pedigree, because it avoided information loss caused by missing parental assignments in the pedigree (Zeyl *et al.* 2009). Additionally, the mean values of the relatedness estimates closely matched the theoretical relatedness in our pedigree (Fig. S1).

We calculated a proxy for hunting intensity based on the number of dead bears located within a 40-km buffer of a casualty's HR centroid 3 years prior to its death. We only used dead bears of the same sex as the casualty in this calculation, to keep the additive effect on changes in the spatial response by survivors consistent by sex (see Step I under *Model Structure*).

For each casualty, we 1) determined its annual 95% kernel HR for the year in which it was killed and 2) calculated a 40-km radius circular buffer centered on its HR centroid (Fig. 1). We chose the 40-km buffer radius, because it is the distance within which most HR centroids of successful mates occur (Bellemain *et al.* 2006) and it is beyond the range of a dead male's influence on sexually-selected infanticide (SSI) and cub survival (Gosselin *et al.* 2017). We used the GPS relocations of all survivors and that of the casualty within the circular buffer during the year of the casualty's death to 3) calculate a 95% kernel isocline (hereafter sampling space), and 4) we determined if relocations of each survivor were inside or outside the casualty's HR for a given year (see period below). For each survivor, we 5) generated the same number of random as real GPS relocations within the sampling space and 6) assigned them the same attributes (i.e. sex and age, population density, pairwise relatedness, and hunting intensity) as the observed relocations. We 7) determined if the random relocations were inside or outside the casualty's HR. We repeated steps 4-7 for a 3-year period (Y0 = before the casualty bear died, Y1 = first year after death, and Y2 = second year after death) while keeping the sampling space constant from that derived in Y0. The sampling space was kept constant, because we did not want to

create a sampling landscape that had never existed by varying according to the former home range of a shot bear with that of future positions from its neighbors.

MODEL STRUCTURE

Step I: effect of sex on survivors' spatial responses

We tested the sex effect on survivor responses (Step I: sex-effect model). We compared candidate models of increasing complexity (Table 1), with the complete model consisting of a 4-way interaction including the casualty's sex (2 levels), the survivor's sex (2 levels), the period (factor with 3 levels: Y0, Y1, and Y2; see Fig. 1), as well as a dummy variable representing whether the relocations were inside (= 1) or outside (= 0) the casualty's HR. To control for unequal sample sizes among individuals and possible temporal collinearity within pairs, we nested the survivor's ID into the casualty's ID as a random effect on the intercept. Additionally, we used the year of the survivor's response as a random intercept to account for possible interannual environmental effects on survivors' responses. The sex-effect dataset (Step I) consisted of 26 casualties (14 females, 12 males), 26 survivors (with a mean of six female and two male survivors per casualty), yielding 216 casualty and survivor dyads over a three-year period, and 601,398 survivor relocations used for analyses.

Step II: additional factors modulating survivors' spatial responses

Based on the results of Step I, we reduced model complexity and controlled for the sex effect in Step II by creating separate candidate models for all sex combinations of casualty-survivor bears. We evaluated which factors (age, pairwise relatedness, density index, hunting intensity) were most important in modulating the patterns observed in Step I. These model data sets consisted of 38,266 relocations for male-male (11 casualties; 7 survivors), 263,838 relocations for male-female (11 casualties; 15 survivors), and 257,420 relocations for female-

female (14 casualties; 19 survivors). We built candidate models of increasing complexity, with the complete model consisting of additive factors each interacting with the dummy variables "Inside" and "Period" (see Table 2). We used the same random effects structure as in Step I. For all models tested in Steps I and II, the variance inflation factor (VIF) values for all variables were < 3 (Zuur, Ieno & Elphick 2010).

MODEL SELECTION AND VALIDATION

We used the Bayesian Information Criterion (BIC) to select the "best model" for each Step I and Step II model results, i.e., the model that best fit the data while concurrently penalizing the number of parameters estimated in the model fitting process. We assessed the relative importance of variables within the best models by dropping each variable of the model and monitoring the ΔBIC. The larger the relative increase in BIC compared to the best model, the more important we considered the variable. We assessed the robustness of our results by varying the kernel isocline (i.e. 75%, 90%, and 95%) of the sampling space and compared model predictions across isoclines (*sensu* Bischof *et al.* 2016). We used R 3.2.4 for all statistical analyses (R Development Core Team 2016).

Results

EFFECT OF SEX ON SURVIVORS' SPATIAL RESPONSES TO VACANCIES

The complete model, keeping all fixed terms and interactions, had the best fit (Table 1 and S3). It suggested that survivors increased their use of a casualty's HR, especially if they were of the same sex. However, male survivors did not increase their use of a female casualty's HR (Fig. 2). A male survivor was 1.03 (95% CI: 0.89 – 1.20) and 1.42 (95% CI: 1.22 – 1.64) times more likely to use a male casualty's HR during the first (Y1) and second (Y2) year after the

casualty's death (Y0), respectively (Fig. 2). A female survivor was 1.30 (95% CI: 1.17 – 1.44) and 1.55 (95% CI: 1.40 – 1.72) times more likely to use a female casualty's HR during the first (Y1) and second (Y2) year after the casualty's death (Y0), respectively. We detected no clear temporal trends in casualties and survivors belonging to different sexes. For example, a female survivor was 1.14 (95% CI: 1.08 – 1.20) more likely to use a male casualty 's HR in the first year after his death (Y1), but this dropped to near baseline level (Y0), i.e., 1.07 (95% CI: 1.01 – 1.13) during the second year (Y2). Most patterns were robust against varying isoclines (75%, 90%, and 95%) on the sampling space, with the exception of male-male spatial responses at the 75% isocline, which were no longer detectable at this scale (Fig. S2). As all other spatial responses were virtually the same across isoclines, we only present the 95% isocline results in Step II.

ADDITIONAL FACTORS MODULATING SURVIVOR SPATIAL RESPONSES TO VACANCIES

We excluded the female-male dyads for Step II analyses, because male survivors did not change their use of female casualties' HRs. In decreasing order of importance, the best model for the male-male model retained relatedness (ΔBIC = 363), the survivor's age (ΔBIC = 302), and hunting intensity (ΔBIC = 18) (Table 2 and S4). The best female-female model kept relatedness (ΔBIC = 2371), the casualty's age (ΔBIC = 290), and hunting intensity (ΔBIC = 106) (Table 2 and S5). The most important variable for the male-female combination was density (ΔBIC = 3544), followed by the survivor's age (ΔBIC = 2792), and hunting intensity (ΔBIC = 1780) (Table 2 and S6).

In both male-male and female-female dyads, higher relatedness (ranging from -0.31 to -0.17 and from -0.41 to 0.44, respectively) explained the higher magnitude of a survivor's use of a

casualty's HR (Fig. 3a and b). The positive change in a female survivor's use of a female casualty's HR was similar across periods for both low (25^{th} percentile) and high relatedness (75^{th} percentile) (Fig. 3b). In contrast, male survivors with lower relatedness to a male casualty showed a stronger increase in use of its HR from Y1 to Y2 than male survivors of higher relatedness (Fig. 3a). Furthermore, the increase in use of a male casualty's HR from Y1 to Y2 was stronger when male survivors were older and in areas of high hunting intensity (Fig. 3c and 4a). Similarly, the increase in use of a female casualty's HR by female survivors was stronger in areas of higher hunting intensity (Fig. 3d). There was no increase in use of a female casualty's HR if the female casualty was older, whereas the increase was strong when the casualty was younger (Fig. 4b). Older female survivors in low density with high hunting intensity increased their use of a male casualty's HR in Y1, but this was reduced or reversed in Y2 (Fig. 4c, 4d, and 4e). The most common retained variable was hunting intensity, which was generally associated with increased use of a casualty's HR (Fig. 3c, 3d and 4e). For all models, the random intercepts on casualty ID and on survivor ID nested in casualty ID had a variance below 0.02. Furthermore, the random intercept on year was virtually zero (< 0.001) for all models.

Discussion

The removal of bears by hunters had a pronounced effect on the spatial configuration of survivors. We found that spatial responses to hunter-created vacancies and the role of modulating factors was highly dependent on sex of survivors and casualties. In support of our predictions, the pattern of increased use of a casualty's HR (P1a) by same-sex survivors (P1b) was best explained by intrasexual competition. Intrasexual HR exclusion often contrasts with intersexual HR overlap in territorial species (e.g. Persson, Wedholm & Segerström 2009), presumably due to

stronger competition within the sexes to maximize mating opportunities and access to other resources (Clutton-Brock & Huchard 2013b). Some territorial species reduce intersexual competition through a seasonally flexible social organization (e.g. Erlinge & Sandell 1986) or sexual differences in habitat selection and behaviors (e.g. Zabala, Zuberogoitia & Martinez-Climent 2007), which are linked to sexual dimorphism (Beerman *et al.* 2015).

It is noteworthy that we detected these pronounced spatial patterns in a nonterritorial species. Competition for resources in nonterritorial, solitary-living species, such as the brown bear, is harder to detect than in territorial species, because inter- and intrasexual HR overlap is common. Therefore fewer studies on competition exist in these species (Pilfold, Derocher & Richardson 2014), but observed segregation in habitat selection between the sexes within areas of HR overlap implies competition or at least conflicts of interests (e.g. SSI; Steyaert *et al.* 2016). Furthermore, resource availability can vary annually within HRs, which could modulate an individual bear's decision whether to increase its use of a vacancy. However, the random intercept on year accounted for very little variance across all models, giving little evidence that interannual variation of resources had an effect on the spatial response of survivors to vacancies in our study.

Although bears are generally considered nonterritorial, dominance hierarchies have been observed around clustered food sources, like salmon (*Oncorhynchus* spp.) spawning rivers and garbage dumps (e.g. SSI; Gende & Quinn 2004; Peirce & Van Daele 2006). Furthermore, territorial behavior and dominance may play a larger role in space use in both sexes in the study population than previously thought (Støen *et al.* 2005; Zedrosser *et al.* 2007; Ordiz *et al.* 2008). This is most pronounced in female kin aggregations, where females may exclude unrelated females through “social fences,” i.e., increasing density results in increasing aggression between

members of different female aggregations during dispersal (Hestbeck 1982; Støen *et al.* 2005; Odden *et al.* 2014). Our results did not provide evidence for social fences in modulating spatial responses, as bear density was not retained in the best model for the female-female dyad and relatedness did not explain changes in the magnitude of a female survivor's use of a female casualty's HR over time. It is likely that vacancies are filled by both nearby survivors as well as immigrant dispersers (e.g. Benson, Chamberlain & Leopold 2004). Our study included adults that had already dispersed and established HRs, so kin-based social fences could still influence dispersal between female aggregations. Contrary to our prediction (P2), low relatedness between females did not correspond to a stronger increase in use of a female casualty's HR across time. Higher relatedness did explain the higher magnitude of use of female vacancies by survivors of the same sex, which corresponds with kin-based aggregations of females due to philopatry (Støen *et al.* 2005; Støen *et al.* 2006). However, it remains unknown if the presence of nearby female kin results in fitness benefits (Støen *et al.* 2005).

Surprisingly, we found that relatedness best explained a male survivor's increase in use of a male casualty's HR, with lower relatedness explaining larger increases in use in the second year following death. This contrasts our prediction (P2), that kinship would only be important for females. We confirmed that male spatial structure did not exhibit kin-based aggregations, as seen in females (Fig. S3; Støen *et al.* 2005), implying that male kinship may be important at the local level, but not at a larger spatial scale. Even without kin-based aggregations among males, male-male interactions among solitary carnivores are likely more complex than previously thought (e.g. Elbroch *et al.* 2016). For example, males of the solitary-living fossa (*Cryptoprocta ferox*) can remain solitary or form stable associations, with kinship among other factors proposed as explanations (Lührs & Kappeler 2013). In our study, it is possible that male-male kinship created

contexts in which males exhibited higher tolerance for one another at the local scale, as evidenced by stronger apparent competitive release of survivors to casualties of lower relatedness. However, we treat this interpretation with caution, because the range of estimated relatedness values among male dyads in our study was lower (from -0.31 to 0.17) relative to female (from -0.41 to 0.44) and male-female (from -0.31 to 0.3) dyads, indicating that patterns in male dyads may not be biologically significant. The smaller range for male dyads is likely a result of male-biased dispersal (Zedrosser *et al.* 2007).

In contrast to our prediction (P3), female survivors increased their use of the HRs of younger female casualties, but not those of older female casualties. We suggest two alternative explanations: (1) that the location of younger and older female HRs occurred in areas of low and high HR overlap, respectively (sensu Maletzke *et al.* 2014), or (2) that surviving females consistently avoided older female HRs even after death. Neither explanation was supported, as a post-hoc analysis showed that HR overlap between individual females and their female neighbors was constant across individual females' ages (Fig. S4). Nevertheless, areas of higher female HR overlap may be more resilient to spatial responses following the removal of female conspecifics, as the costs of responding spatially may outweigh its benefits. One example is increased predation mortality due to site unfamiliarity (e.g. Forrester, Casady & Wittmer 2015). Spatial responses of male bears to harvest-induced vacancies is consistent with the risk of SSI (Leclerc *et al.* 2017), but it is unclear how female spatial responses, i.e., their exploration of previously denied resources, may enhance the risk of SSI. Although female bears modulate SSI risk through differential habitat selection, the relative risk of SSI has not been studied at the HR scale (Steyaert *et al.* 2016). A female exhibiting high HR overlap with a killed female may have both limited costs in a spatial response, due to preexisting familiarity with her surroundings, and

limited benefits, due to already optimally used resources. However, through gradual expansion, females can also increase their access to other resources, such as space for future philopatic offspring, as seen in striped mice, *Rhabdomys pumilio* (Schradin *et al.* 2010).

As predicted (P3), older males exhibited a stronger increase in their use of a male vacancy than younger males, perhaps due to differences in experience. Male bears have larger HRs than females and potentially also larger cognitive maps (Perdue *et al.* 2011; Noyce & Garshelis 2014). Greater experience and spatial knowledge may improve abilities to find and relocate resources, as seen in African elephants (*Loxodonta africana*) (McComb *et al.* 2001). In American black bears (*U. americanus*), Noyce and Garshelis (2014) found that migratory movement patterns appeared to be based on social cues, with males as leaders in paving the way toward important first-come, first-served food resources. Although age was not important in their study, age and experience play a role in social learning for other species (Galef & Laland 2005). Furthermore, dominant individuals might be more successful at taking over novel HR vacancies than subordinates, e.g. in side-blotched lizards (*Uta stansburiana*) (Fox, Rose & Myers 1981). The same first-come, first-served process may work with HRs as they become available, e.g. due to the death of conspecifics, with an older/dominant survivor taking advantage of newly available resources.

Our prediction (P4) that density would be negatively related to increases in use of vacancies by survivors was confirmed for female survivors and male casualties, but was absent for all other casualty-survivor sex combinations. Low density areas have lower concentrations of females and were near the periphery of our population (Swenson, Sandegren & Soderberg 1998). The strong increase in use of male vacancies by females in low-density areas might suggest that females can take advantage of resources previously dominated by males at the population

periphery. Conversely, females at high densities did not increase their use of male vacancies, so density may represent a larger response of nearby survivors competing for this recently vacated HR. The absent effect of density in explaining spatial responses by same-sex survivors suggests that other context-dependent social factors (sex, relatedness, age), such as hunting intensity, are more important for a survivor's decision to respond spatially rather than the number of conspecifics surrounding it.

Higher hunting intensity provides more vacancies toward which nearby survivors can respond spatially (Leclerc *et al.* 2017). Although the spatial distribution of these vacancies available to survivors may vary, hunting intensity had (P5) a consistently positive relationship with the increased use of a vacancy by survivors for all casualty-survivor sex combinations depicting spatial responses. Furthermore, hunting intensity was the only factor retained in the best model for all sex combinations. Therefore, we found evidence for a consistent, additive effect of hunting intensity on a surviving animal's spatial response towards a vacancy, which suggests a long-term effect of hunting on the dynamics of HRs.

Management decisions, such as the degree of hunting intensity, appears to drive spatial responses of survivors and, therefore, likely alters competition for resources among survivors. Furthermore, we suggest that solitary species may be more social, with a basis in kinship, and that male-male relationships may be more complex than previously considered. The spatial reorganization caused by hunting and potentially compounding effects of continued hunting on social structure could be an important consideration when developing plans for sustainable harvest of wildlife populations, or for achieving other management goals, such as decreasing human-wildlife conflicts. Altogether, our results underscore the need to better understand the short- and long-term indirect effects of hunting on animal social structure and their resulting

distribution in space, which, if not understood, could have unforeseen consequences on population parameters such as fitness and population growth (Frank *et al. in press*).

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Author Contribution Statement:

SCF, ML, RB, JES, FR, FP, and AZ participated in the study design. SCF, ML, and RB carried out statistical analyses. AZ, JES, and FP secured funding. JES, AZ, and JK coordinated work in the Scandinavian Brown Bear Research Project. HGE and SBH provided expertise and work on the genetics. All authors contributed to the writing of the manuscript.

Data Accessibility

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.m7m8n (Frank et al. 2017).

Table captions

Table 1. Results of the candidate models tested to determine the spatial responses of surviving brown bears to the death of nearby hunter-killed bears (casualties). The number of parameters (K), log-likelihoods (LL), the change in BIC (ΔBIC) from the best model, and the model weights (ω) are shown.

Table 2. Results of the candidate models tested to determine the effect of age, pairwise relatedness, density index, and hunting intensity in modulating the spatial responses of surviving brown bears (survivors; S) to the death of nearby hunter-killed bears (casualties; C). The number of parameters (K), log-likelihoods (LL), the change in BIC (ΔBIC) from the best model, and the model weights (ω) are shown for each casualty-survivor combination.

Table 1.

Model	Variable*	K	LL	ΔBIC	ω
1	None	4	-416857	3512	0
2	Inside × Period	9	-416120	2104	0
3	Casualty Sex × Inside × Period	15	-415877	1698	0
4	Survivor Sex × Inside × Period	15	-415304	552	0
5	Model 3 + Model 4	21	-415069	162	0
6	Casualty Sex × Survivor Sex × Inside × Period	27	-414948	0	1

*Period (3-level factor: Y0, Y1, Y2 in reference to casualty death), Inside (2-level factor: inside or outside of casualty's home range), Casualty Sex (2-level factor: male or female), Survivor Sex (2-level factor: male or female).

Table 2.

			Male–Male			Female–Female			Male–Female		
Model	Variable	K	LL	ΔBIC	ω	LL	ΔBIC	ω	LL	ΔBIC	ω
1	None	4	-26524	1516	0	-178430	5538	0	-182879	6275	0
2	Inside × Period	9	-26051	622	0	-177124	2988	0	-182850	6281	0
3	C_{age} × Inside × Period	15	-26044	671	0	-176795	2404	0	-182221	5096	0
4	C_{age} × Inside × Period	15	-25885	353	0	-177097	3009	0	-181741	4137	0
5	Hunting × Inside × Period	15	-25978	540	0	-176991	2798	0	-182596	5847	0
6	Density × Inside × Period	15	-25940	463	0	-176999	2814	0	-181859	4372	0
7	Relatedness× Inside × Period	15	-25936	456	0	-175723	262	0	-182463	5581	0
8*	C_{age} + S_{age}	21	-25865	377	0	-176749	2388	0	-181122	2974	0
9*	C_{age} + Hunting	21	-25961	570	0	-176741	2371	0	-182102	4935	0
10*	C_{age} + Density	21	-25921	490	0	-176750	2390	0	-181527	3783	0
11*	C_{age} + Relatedness	21	-25928	503	0	-175608	106	0	-181957	4644	0
12*	S_{age} + Hunting	21	-25858	363	0	-176955	2800	0	-181407	3544	0
13*	S_{age} + Density	21	-25847	341	0	-176968	2826	0	-180525	1780	0
14*	S_{age} + Relatedness	21	-25685	18	0	-175712	315	0	-181497	3723	0
15*	Hunting + Density	21	-25898	443	0	-176915	2720	0	-181031	2792	0
16*	Hunting + Relatedness	21	-25828	302	0	-175700	290	0	-182226	5182	0
17*	Density + Relatedness	21	-25836	319	0	-175690	270	0	-181614	3957	0
18*	C_{age} + S_{age} + Hunting	27	-25837	384	0	-176691	2347	0	-180972	2749	0
19*	C_{age} + S_{age} + Density	27	-25838	386	0	-176702	2368	0	-180274	1353	0
20*	C_{age} + S_{age} + Relatedness	27	-25658	27	0	-175597	159	0	-181002	2809	0
21*	C_{age} + Hunting + Density	27	-25857	425	0	-176705	2375	0	-180966	2737	0
22*	C_{age} + Hunting + Relatedness	27	-25803	316	0	**-175518**	**0**	**1**	-181850	4505	0
23*	C_{age} + Density + Relatedness	27	-25821	353	0	-175597	160	0	-181358	3521	0
24*	S_{age} + Hunting + Density	27	-25803	316	0	-176876	2716	0	**-179598**	**0**	**1**
25*	S_{age} + Hunting + Relatedness	27	**-25645**	**0**	**0.98**	-175688	341	0	-181210	3224	0
26*	S_{age} + Density + Relatedness	27	-25675	61	0	-175680	324	0	-180447	1698	0

27*	Hunting + Density + Relatedness	27	-25782	274	0	-175649	263	0	-180901	2607	0
28*	C_{age} + S_{age} + Hunting + Density	33	-25768	310	0	-176654	2348	0	-179576	32	0
29*	C_{age} + S_{age} + Hunting + Relatedness	33	-25617	8	0.02	-175507	54	0	-180862	2604	0
30*	C_{age} + S_{age} + Density + Relatedness	33	-25654	82	0	-175586	212	0	-180231	1341	0
31*	C_{age} + Hunting + Density + Relatedness	33	-25760	294	0	-175496	31	0	-180854	2588	0
32*	S_{age} + Hunting + Density + Relatedness	33	-25629	31	0	-175638	316	0	-179580	39	0
33*	C_{age} + S_{age} + Hunting + Density + Relatedness	39	-25597	31	0	-175485	85	0	-179561	76	0

*Model 8 to 33: Every variable is in a 3-way interaction with Inside × Period as shown in model 3. Bolded values are from the best models

Figure captions

Figure 1. Schematic representation of data handling. For each brown bear casualty (panel a), we determined its 95% kernel HR and calculated a 40-km radius circular buffer centered on the HR centroid. We used (panel b) all GPS locations of the casualty (filled black points) and those belonging to surviving bears (open gray points) within the circular buffer to calculate a 95% kernel density isocline (shaded with dashed gray border), representing the sampling space, and (panel c) determined if the survivor relocations were inside (open black points) or outside (open gray points) the casualty's HR. We generated the same number of random (panel d) as real GPS locations and determined if the random locations were inside (open black points) or outside (open gray points) the casualty's HR. We repeated the same process (panel c and d) for the next two years using the same sampling space. We repeated the same process (panel a-d) for all casualties.

Figure 2. Log-odds ratios of brown bear survivors' use of a casualty's HR during the year in which the casualty died (Y0), the first (Y1) and second (Y2) year after the casualty's death for different casualty-survivor sex combinations. The dashed line is the baseline year (Y0) indicating the survivor's use of the casualty's HR before the casualty's death.

Figure 3. Log-odds ratios of nearby surviving brown bears' (survivors') use of hunter-killed bears' (casualties') HRs during the year in which the casualty died (Y0), the first year after the casualty's death (Y1), and the second year after its death (Y2) in response to casualty-survivor relatedness (panel a, b) and previous hunting intensity (panel c, d). Low and high values of relatedness and hunting intensities represent the 25^{th} and 75^{th} percentiles found in the male-male (panel a, c) and female-female (panel b, d) datasets. Note: the values on the y-axis are different among plots.

Figure 4. Log-odds ratios of surviving brown bears' (survivors') use of nearby hunter-killed bears' (casualties') home ranges during the year in which the casualty died in the fall (Y0), the first year after the casualty's death (Y1), and the second year after its death (Y2), in response to casualty and survivor age, density index, and hunting intensity. Low and high values represent the 25th and 75th percentiles of the variable for the respective casualty-survivor data set. Note: in panel b, young casualty and old casualty almost completely overlap one another at Y0; the scales and intervals are different among the plots.

Figure 1.

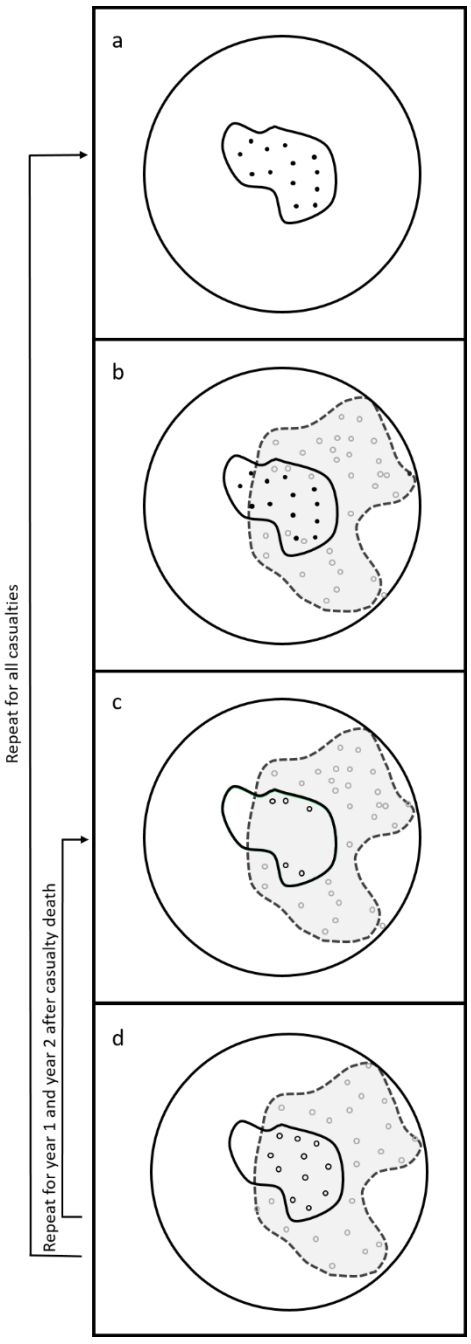


Figure 2.

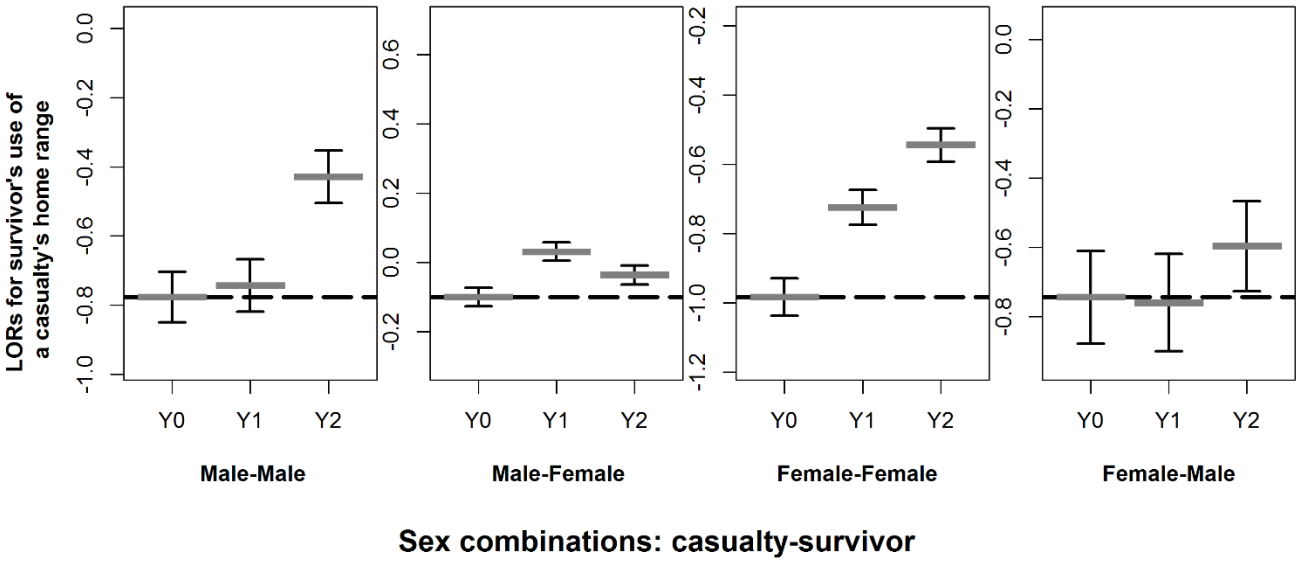


Figure 3.

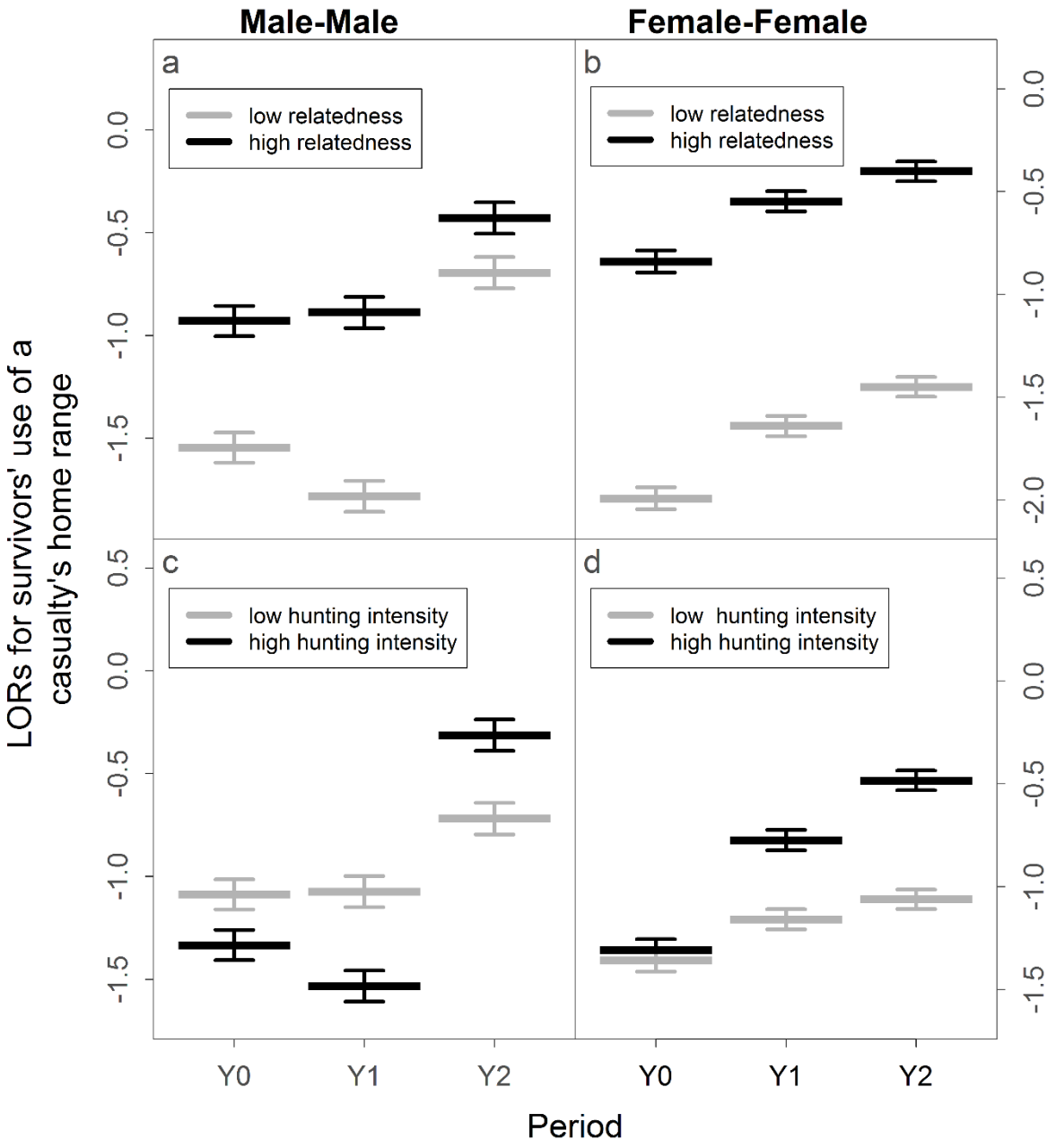
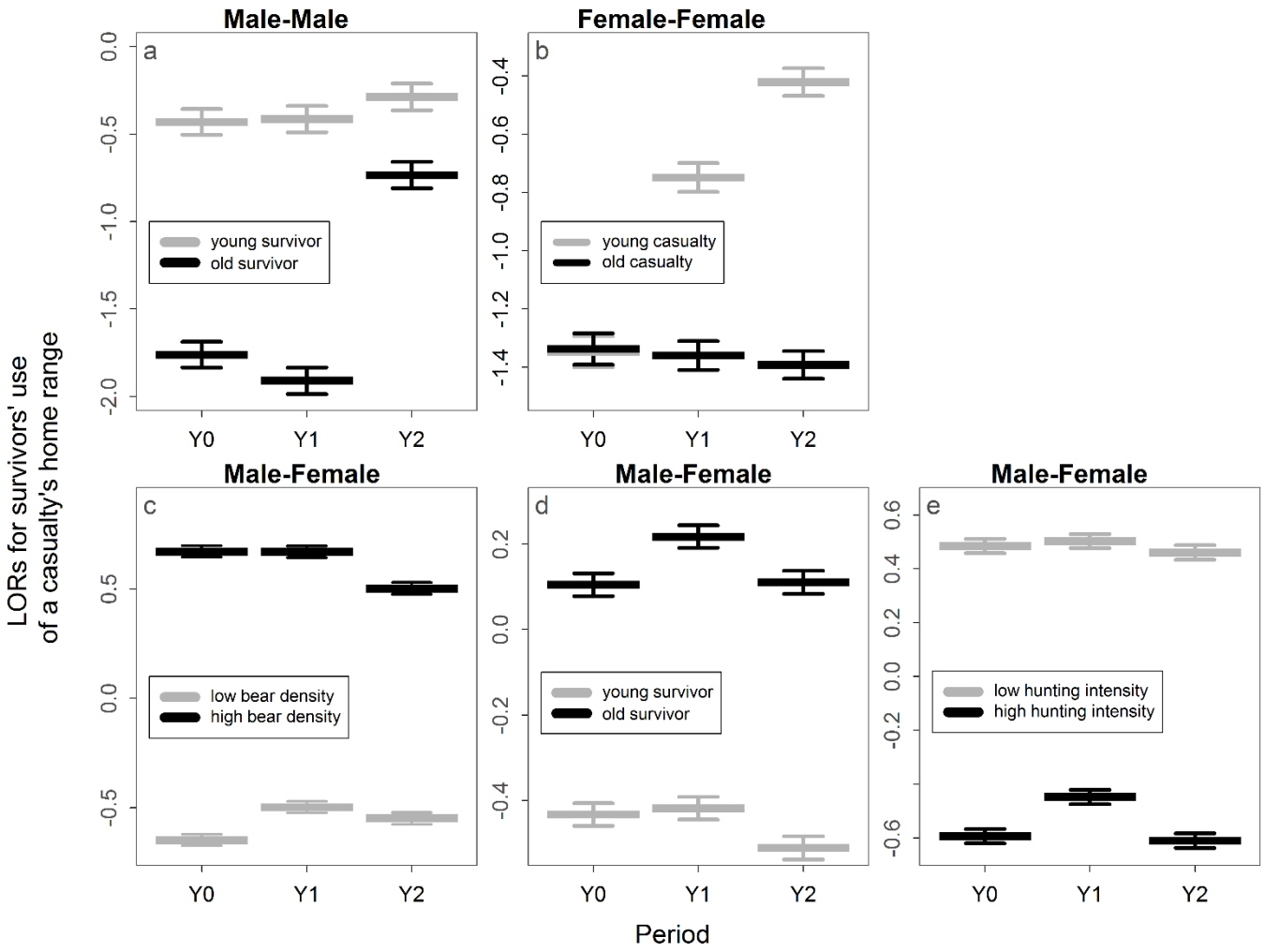


Figure 4.



References

Beerman, A., Ashe, E., Preedy, K. & Williams, R. (2015) Sexual segregation when foraging in an extremely social killer whale population. *Behavioral Ecology and Sociobiology,* **70,** 189-198.

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. *Conservation biology,* **19,** 150-161.

Bellemain, E., Zedrosser, A., Manel, S., Waits, L.P., Taberlet, P. & Swenson, J.E. (2006) The dilemma of female mate selection in the brown bear, a species with sexually selected infanticide. *Proceedings of the Royal Society B,* **273,** 283-291.

Benson, J.F., Chamberlain, M.J. & Leopold, B.D. (2004) Land Tenure and Occupation of Vacant Home Ranges by Bobcats (Lynx Rufus). *Journal of Mammalogy,* **85,** 983-988.

Bischof, R., Gregersen, E.R., Brøseth, H., Ellegren, H. & Flagstad, Ø. (2016) Noninvasive genetic sampling reveals intrasex territoriality in wolverines. *Ecology and Evolution,* **6,** 1527-1536.

Bonenfant, C., Gaillard, J.-M., Klein, F. & Loison, A. (2002) Sex- and age-dependent effects of population density on life history traits of red deer Cervus elaphus in a temperate forest. *Ecography,* **25,** 446-458.

Calenge, C. (2006) The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling,* **197,** 516-519.

Clutton-Brock, T. & Huchard, E. (2013a) Social competition and its consequences in female mammals. *Journal of Zoology,* **289,** 151-171.

Clutton-Brock, T. & Sheldon, B.C. (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology and Evolution,* **25,** 562-573.

Clutton-Brock, T.H. & Huchard, E. (2013b) Social competition and selection in males and females. *Philosophical Transactions of the Royal Society B,* **368,** 20130074.

Comer, C.E., Kilgo, J.C., D'Angelo, G.J., Glenn, T.C., Miller, K.V. & DeWoody (2005) Fine-Scale Genetic Structure and Social Organization in Female White-Tailed Deer. *Journal of Wildlife Management,* **69,** 332-344.

Cooley, H.S., Wielgus, R.B., Koehler, G. & Maletzke, B. (2009) Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. *Animal Conservation,* **12,** 321-328.

Csillery, K., Johnson, T., Beraldi, D., Clutton-Brock, T., Coltman, D., Hansson, B., Spong, G. & Pemberton, J.M. (2006) Performance of marker-based relatedness estimators in natural populations of outbred vertebrates. *Genetics,* **173,** 2091-2101.

D'Eon, R.G. & Delparte, D. (2005) Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. *Journal of Applied Ecology,* **42,** 383-388.

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. *Journal of Zoology,* **260,** 329-335.

Eikenaar, C., Richardson, D.S., Brouwer, L., Bristol, R. & Komdeur, J. (2008) Experimental evaluation of sex differences in territory acquisition in a cooperatively breeding bird. *Behavioral Ecology,* **20,** 207-214.

Elbroch, L.M., Lendrum, P.E., Quigley, H. & Caragiulo, A. (2016) Spatial overlap in a solitary carnivore: support for the land tenure, kinship or resource dispersion hypotheses? *Journal of Animal Ecology,* **85,** 487-496.

Erlinge, S. & Sandell, M. (1986) Seasonal Changes in the Social Organization of Male Stoats, Mustela erminea: An Effect of Shifts between Two Decisive Resources. *Oikos,* **47,** 57.

Fahlman, Å., Arnemo, J.M., Swenson, J.E., Pringle, J., Brunberg, S. & Nyman, G. (2011) Physiologic Evaluation of Capture and Anesthesia with Medetomidine–Zolazepam–Tiletamine in Brown Bears (Ursus arctos). *Journal of Zoo and Wildlife Medicine,* **42,** 1-11.

Fattebert, J., Balme, G., Dickerson, T., Slotow, R. & Hunter, L. (2015) Density-dependent natal dispersal patterns in a leopard population recovering from over-harvest. *PloS one,* **10,** e0122355.

Fattebert, J., Balme, G.A., Robinson, H.S., Dickerson, T., Slotow, R. & Hunter, L.T.B. (2016) Population recovery highlights spatial organization dynamics in adult leopards. *Journal of Zoology,* **299,** 153-162.

Forrester, T.D., Casady, D.S. & Wittmer, H.U. (2015) Home sweet home: fitness consequences of site familiarity in female black-tailed deer. *Behavioral Ecology and Sociobiology,* **69,** 603-612.

Fox, S.F., Rose, E. & Myers, R. (1981) Dominance and the Acquisition of Superior Home Ranges in the Lizard Uta Stansburiana. *Ecology,* **62,** 888-893.

Frank, S.C., Ordiz, A., Gosselin, J., Hertel, A., Kindberg, J., Leclerc, M., Pelletier, F., Steyaert, S.M.J.G., Støen, O.-G., Van de Walle, J., Zedrosser, A. & Swenson, J.E. Indirect effects of bear hunting: a review from Scandinavia. *Ursus*.

Frank, S.C., Leclerc, M., Pelletier, F., Rosell, F., Swenson, J.E., Bischof, R., Kindberg, J., Eiken, H.G., Hagen, S.B. and Zedrosser, A. (2017)Data from: Sociodemographic factors modulate the spatial response of brown bears to vacancies created by hunting. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.m7m8n

Galef, B.G. & Laland, K.N. (2005) Social learning in animals: Empirical studies and theoretical models. *BioScience,* **55,** 489-499.

Geisser, H., Reyer, H.-U. & Krausman (2004) Efficacy of Hunting, Feeding, and Fencing to Reduce Crop Damage by Wild Boars. *Journal of Wildlife Management,* **68,** 939-946.

Gende, S.M. & Quinn, T.P. (2004) The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. *Canadian Journal of Zoology,* **82,** 75-85.

Gese, E.M. (1998) Response of neighboring coyotes (Canis latrans) to social disruption in an adjacent pack. *Canadian Journal of Zoology,* **76,** 1960-1963.

Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Kerley, L.L., Quigley, H.B. & Hornocker, M.G. (2010) Spatial structure of Amur (Siberian) tigers (Panthera tigris altaica) on Sikhote-Alin Biosphere Zapovednik, Russia. *Journal of Mammalogy,* **91,** 737-748.

Gosselin, J., Leclerc, M., Zedrosser, A., Steyaert, S.M., Swenson, J.E. & Pelletier, F. (2017) Hunting promotes sexual conflict in brown bears. *Journal of Animal Ecology,* **86,** 35-42.

Hamilton, W.D. (1964) The genetical evolution of social behaviour. I, II. *J Theor Biol,* **7,** 1–52

Hestbeck, J.B. (1982) Population Regulation of Cyclic Mammals - the Social Fence Hypothesis. *Oikos,* **39,** 157-163.

Jerina, K., Jonozovič, M., Krofel, M. & Skrbinšek, T. (2013) Range and local population densities of brown bear Ursus arctos in Slovenia. *European Journal of Wildlife Research,* **59,** 459-467.

Kindberg, J., Ericsson, G. & Swenson, J.E. (2009) Monitoring rare or elusive large mammals using effort-corrected voluntary observers. *Biological Conservation,* **142,** 159-165.

Kindberg, J., Swenson, J.E., Ericsson, G., Bellemain, E., Miquel, C. & Taberlet, P. (2011) Estimating population size and trends of the Swedish brown bear Ursus arctos population. *Wildlife Biology,* **17,** 114-123.

King, W.J., Festa-Bianchet, M. & Hatfield, S.E. (1991) Determinants of reproductive success in female Columbian ground squirrels. *Oecologia,* **86,** 528-534.

Leclerc, M., Frank, S.C., Zedrosser, A., Swenson, J.E. & Pelletier, F. (2017) Hunting promotes spatial reorganization and sexually selected infanticide. *Sci Rep,* **7,** 45222.

Lott, D.F. (1991) *Intraspecific variation in the social systems of wild vertebrates*. Cambridge University Press, New York, USA.

Loveridge, A.J., Valeix, M., Chapron, G., Davidson, Z., Mtare, G. & Macdonald, D.W. (2016) Conservation of large predator populations: Demographic and spatial responses of African lions to the intensity of trophy hunting. *Biological Conservation*.

Lührs, M.L. & Kappeler, P.M. (2013) Simultaneous GPS tracking reveals male associations in a solitary carnivore. *Behavioral Ecology and Sociobiology,* **67,** 1731-1743.

Lynch, M. & Ritland, K. (1999) Estimation of Pairwise Relatedness With Molecular Markers. *Genetics,* **152,** 1753-1766.

Maletzke, B.T., Wielgus, R., Koehler, G.M., Swanson, M., Cooley, H. & Alldredge, J.R. (2014) Effects of hunting on cougar spatial organization. *Ecology and Evolution,* **4,** 2178-2185.

Manjerovic, M.B., Green, M.L., Mateus-Pinilla, N. & Novakofski, J. (2014) The importance of localized culling in stabilizing chronic wasting disease prevalence in white-tailed deer populations. *Preventative Veterinary Medicine,* **113,** 139-145.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Springer Netherlands.

Matson, G.M. (1993) *A laboratory manual for cementum age determination of Alaska brown bear first premolar teeth*. Alaska Dept. of Fish and Game, Division of Wildlife Conservation.

McComb, K., Moss, C., Durant, S.M., Baker, L. & Sayialel, S. (2001) Matriarchs as repositories of social knowledge in African elephants. *Science,* **292,** 491-494.

McLoughlin, P.D., Boyce, M.S., Coulson, T. & Clutton-Brock, T. (2006) Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B: Biological Sciences,* **273,** 1449-1454.

Milner, J.M., Nilsen, E.B. & Andreassen, H.P. (2007) Demographic side effects of selective hunting in ungulates and carnivores. *Conserv Biol,* **21,** 36-47.

Nelson, J. (1995) Intrasexual Competition and Spacing Behaviour in Male Field voles, Microtus agrestis, under Constant Female Density and Spatial Distribution. *Oikos,* **73,** 9.

Noyce, K.V. & Garshelis, D.L. (2014) Follow the leader: social cues help guide landscape-level movements of American black bears (Ursus americanus). *Canadian Journal of Zoology,* **92,** 1005-1017.

Odden, M., Ims, R.A., Stoen, O.G., Swenson, J.E. & Andreassen, H.P. (2014) Bears are simply voles writ large: social structure determines the mechanisms of intrinsic population regulation in mammals. *Oecologia,* **175,** 1-10.

Ordiz, A., Stoen, O.G., Swenson, J.E., Kojola, I. & Bischof, R. (2008) Distance-dependent effect of the nearest neighbor: spatiotemporal patterns in brown bear reproduction. *Ecology,* **89,** 3327-3335.

Peirce, K.N. & Van Daele, L.J. (2006) Use of a garbage dump by brown bears in Dillingham, Alaska. *Ursus,* **17,** 165-177.

Perdue, B.M., Snyder, R.J., Zhihe, Z., Marr, M.J. & Maple, T.L. (2011) Sex differences in spatial ability: a test of the range size hypothesis in the order Carnivora. *Biology Letters,* **7,** 380-383.

Persson, J., Wedholm, P. & Segerström, P. (2009) Space use and territoriality of wolverines (Gulo gulo) in northern Scandinavia. *European Journal of Wildlife Research,* **56,** 49-57.

Pilfold, N.W., Derocher, A.E. & Richardson, E. (2014) Influence of intraspecific competition on the distribution of a wide-ranging, non-territorial carnivore. *Global Ecology and Biogeography,* **23,** 425-435.

Porter, W.F., Mathews, N.E., Underwood, H.B., Sage, R.W. & Behrend, D.F. (1991) Social-Organization in Deer - Implications for Localized Management. *Environmental Management,* **15,** 809-814.

Pusenius, J., Viitala, J., Marienberg, T. & Ritvanen, S. (1998) Matrilineal kin clusters and their effect on reproductive success in the field vole Microtus agrestis. *Behavioral Ecology,* **9,** 85-92.

Ratnayeke, S., Tuskan, G.A. & Pelton, M.R. (2002) Genetic relatedness and female spatial organization in a solitary carnivore, the raccoon, Procyon lotor. *Molecular Ecology,* **11,** 1115-1124.

Robinson, H.S., Wielgus, R.B., Cooley, H.S. & Cooley, S.W. (2008) Sink Populations in Carnivore Management: Cougar Demography and Immigration in a Hunted Population. *Ecological Applications,* **18,** 1028-1037.

Schradin, C., Schmohl, G., Rödel, H.G., Schoepf, I., Treffler, S.M., Brenner, J., Bleeker, M., Schubert, M., König, B. & Pillay, N. (2010) Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study. *Animal Behaviour,* **79,** 195-203.

Steyaert, S.M., Leclerc, M., Pelletier, F., Kindberg, J., Brunberg, S., Swenson, J.E. & Zedrosser, A. (2016) Human shields mediate sexual conflict in a top predator. *Proceedings of the Royal Society B: Biological Sciences,* **283**.

Steyaert, S.M.J.G., EndrestØL, A., HacklÄNder, K., Swenson, J.E. & Zedrosser, A. (2012) The mating system of the brown bear Ursus arctos. *Mammal Review,* **42,** 12-34.

Støen, O.-G., Bellemain, E., Sæbø, S. & Swenson, J.E. (2005) Kin-related spatial structure in brown bears Ursus arctos. *Behavioral Ecology and Sociobiology,* **59,** 191-197.

Støen, O.G., Zedrosser, A., Saebo, S. & Swenson, J.E. (2006) Inversely density-dependent natal dispersal in brown bears Ursus arctos. *Oecologia,* **148,** 356-364.

Swenson, J.E., Sandegren, F. & Soderberg, A. (1998) Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *Journal of Animal Ecology,* **67,** 819-826.

Teichman, K.J., Cristescu, B. & Darimont, C.T. (2016) Hunting as a management tool? Cougar-human conflict is positively related to trophy hunting. *BMC Ecol,* **16,** 44.

Waser, P.M. & Jones, W.T. (1983) Natal Philopatry Among Solitary Mammals. *The Quarterly review of biology,* **58,** 355-390.

Wright, B.M., Stredulinsky, E.H., Ellis, G.M. & Ford, J.K.B. (2016) Kin-directed food sharing promotes lifetime natal philopatry of both sexes in a population of fish-eating killer whales, Orcinus orca. *Animal Behaviour,* **115,** 81-95.

Wronski, T. & Apio, A. (2005) Home-range overlap, social vicinity and agonistic interactions denoting matrilineal organisation in bushbuck, Tragelaphus scriptus. *Behavioral Ecology and Sociobiology,* **59,** 819-828.

Zabala, J., Zuberogoitia, I. & Martinez-Climent, J.A. (2007) Spacing pattern, intersexual competition and niche segregation in American mink. *Annales Zoologici Fennici,* **44,** 249-258.

Zedrosser, A., Støen, O.-G., Sæbø, S. & Swenson, J.E. (2007) Should I stay or should I go? Natal dispersal in the brown bear. *Animal Behaviour,* **74,** 369-376.

Zeyl, E., Aars, J., Ehrich, D. & Wiig, O. (2009) Families in space: relatedness in the Barents Sea population of polar bears (Ursus maritimus). *Molecular Ecology,* **18,** 735-749.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution,* **1,** 3-14.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Annual bear density Index.

Table S1. Summary statistics for microsatellites used for pedigree reconstruction.

Table S2. Summary of parentage assignment from pedigree construction.

Table S3. Parameter estimates of the best 'sex' model (Step I).

Table S4. Parameter estimates of the best 'additional factors' model (Step II) for male-male casualty-survivor combination.

Table S5. Parameter estimates of the best 'additional factors' model (Step II) for female-female casualty-survivor combination.

Table S6. Parameter estimates of the best 'additional factors' model (Step II) for male-female casualty-survivor combination.

Figure S1. The distribution of relatedness estimates from Lynch-Ritland's (1999) estimator.

Figure S2. Comparison of three isoclines (a: 95%; b: 90%; c: 75%) for the sampling spaces and respective model results are shown for the sex-effect model, yielding similar results across isoclines.

Figure S3. Pairwise relatedness plotted against distances between home range centroids of brown bears.

Figure S4. Proportion home range overlap between individual females and their female neighbors against individual female age.