RESEARCH ARTICLE

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

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Abstract

1. There is a growing recognition of the importance of indirect effects from hunting on wildlife populations, e.g. social and behavioural 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 shown that survivors exhibit a spatial response to vacated home ranges caused by hunting casualties, even in nonterritorial 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.

1 | 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, Moss, Durant, Baker, & Sayialel, 2001). In response to this removal, surviving individuals may exhibit a spatial reorganization (Gese, 1998; Leclerc, Frank, Zedrosser, Swenson, & Pelletier, 2017), which in turn may affect social structure, reproduction and ultimately population dynamics (Cooley, Wielgus, Koehler, & Maletzke, 2009; Robinson, Wielgus, Cooley, & Cooley, 2008). 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 (Loveridge et al., 2016; Maletzke et al., 2014). 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 (Loveridge et al., 2016; Maletzke et al., 2014).

Sex is an important factor for determining life-history strategies, social systems and consequently population structure (Bonenfant, Gaillard, Klein, & Loison, 2002; Lott, 1991). 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, Viitala, Marienberg, & Ritvanen, 1998; Wright, Stredulinsky, Ellis, & Ford, 2016; Wronski & Apio, 2005). 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 (Clutton-Brock & Huchard, 2013b; McComb et al., 2001). In comparison, unrelated survivors may benefit from removals, which may result in stronger spatial responses towards 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, Balme, Dickerson, Slotow, & Hunter, 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, Richardson, Brouwer, Bristol, & Komdeur, 2008). Increasing population density can increase competition for food resources and breeding opportunities (e.g. McLoughlin, Boyce, Coulson, & Clutton-Brock, 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 (Comer, Kilgo, D'Angelo, Glenn, & Miller, 2005; Porter, Mathews, Underwood, Sage, & Behrend, 1991).

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, Endrestøl, Hackländer, Swenson, & Zedrosser, 2012). However, related females form aggregations (Støen, Bellemain, Sæbø, & Swenson, 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, McDonald, Thomas, McDonald, & Erickson, 2002) to investigate which factors affect the spatial responses of survivors during the 2 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.

2 | 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 and 2015, we captured 499 brown bears from a helicopter using a remote drug delivery system (Dan-Inject®; 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) programmed to relocate a bear with varying schedules (≤1 hr). In addition, we acquired data on location, sex and age (determined as above) for all known dead brown bears in Sweden between 1981 and 2014 ($n = 3,960$), of which 83% was caused by legal hunting.

2.1 | 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 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 neighbouring bears of the casualty's home range under the null hypothesis absent of competitive exclusion. We used 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).

2.2 | Location data

We only included adult bears (≥4-year olds; Støen, Zedrosser, Saebo, & Swenson, 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-hr minimum interval between successive positions (yielding a maximum of four 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 to 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).

2.3 | 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 faeces using six microsatellites (see Bellemain, Swenson, Tallmon, Brunberg, & Taberlet, 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 10 × 10 km cells and adopted the method of Jerina, Jonozovič, Krofel, and Skrbinšek (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 (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 3 × 3 cell moving window (30 × 30 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, Aars, Ehrich, & Wiig, 2009). Additionally, the mean values of the relatedness estimates closely matched the theoretical relatedness in our pedigree (Figure 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 Section 2.4).

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 centred on its HR centroid (Figure 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 neighbours.

2.4 | Model structure

2.4.1 | 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 four-way interaction including the casualty's sex (two levels), the survivor's sex (two levels), the period (factor with three levels: Y0, Y1 and Y2; see Figure 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
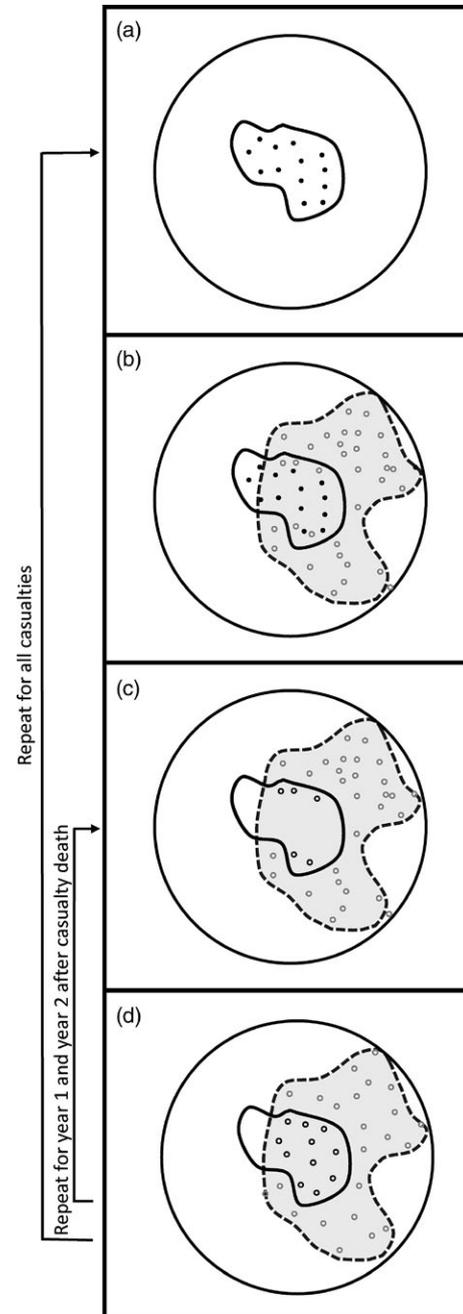

FIGURE 1 Schematic representation of data handling. For each brown bear casualty (a), we determined its 95% kernel HR and calculated a 40-km radius circular buffer centred on the HR centroid. We used (b) all GPS locations of the casualty (filled black points) and those belonging to surviving bears (open grey points) within the circular buffer to calculate a 95% kernel density isocline (shaded with dashed grey border), representing the sampling space, and (c) determined if the survivor relocations were inside (open black points) or outside (open grey points) the casualty's HR. We generated the same number of random (d) as real GPS relocations and determined if the random locations were inside (open black points) or outside (open grey points) the casualty's HR. We repeated the same process (c and d) for the next 2 years using the same sampling space. We repeated the same process (a–d) for all casualties

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

Model	Variable[a]	K	LL	ΔBIC	ω
1	None	4	−416,857	3,512	0
2	Inside × Period	9	−416,120	2,104	0
3	Casualty sex × Inside × Period	15	−415,877	1,698	0
4	Survivor sex × Inside × Period	15	−415,304	552	0
5	Model 3 + Model 4	21	−415,069	162	0
6	Casualty sex × Survivor sex × Inside × Period	27	−414,948	0	1

[a]Period (three-level factor: Y0, Y1, Y2 in reference to casualty death), Inside (two-level factor: inside or outside of casualty's home range), Casualty Sex (two-level factor: male or female), Survivor Sex (two-level factor: male or female).

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 3-year period, and 601,398 survivor relocations used for analyses.

2.4.2 | 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 and hunting intensity) were most important in modulating the patterns observed in Step I. These model datasets 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).

2.5 | 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, Gregersen, Brøseth, Ellegren, & Flagstad, 2016). We used ʀ 3.2.4 for all statistical analyses (R Core Team, 2016).

3 | RESULTS

3.1 | 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 Table 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 (Figure 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 (Figure 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 (Figure S2). As all other spatial responses were virtually the same across isoclines, we only present the 95% isocline results in Step II.

3.2 | 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 Table S4). The best female–female model kept relatedness (ΔBIC = 2,371), the casualty's age (ΔBIC = 290) and hunting intensity (ΔBIC = 106) (Table 2 and Table S5). The most important variable for the male–female combination was density (ΔBIC = 3,544), followed by the survivor's age (ΔBIC = 2,792) and hunting intensity (ΔBIC = 1,780) (Table 2 and Table 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 (Figure 3a,b). The positive change in a female survivor's use of a female casualty's HR was similar across periods for both low (25th percentile) and high relatedness (75th percentile) (Figure 3b).

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

Model	Variable	K	Male–Male			Female–Female			Male–Female		
			LL	ΔBIC	ω	LL	ΔBIC	ω	LL	ΔBIC	ω
1	None	4	−26,524	1,516	0	−178,430	5,538	0	−182,879	6,275	0
2	Inside × Period	9	−26,051	622	0	−177,124	2,988	0	−182,850	6,281	0
3	C_{age} × Inside × Period	15	−26,044	671	0	−176,795	2,404	0	−182,221	5,096	0
4	C_{age} × Inside × Period	15	−25,885	353	0	−177,097	3,009	0	−181,741	4,137	0
5	Hunting × Inside × Period	15	−25,978	540	0	−176,991	2,798	0	−182,596	5,847	0
6	Density × Inside × Period	15	−25,940	463	0	−176,999	2,814	0	−181,859	4,372	0
7	Relatedness× Inside × Period	15	−25,936	456	0	−175,723	262	0	−182,463	5,581	0
8[a]	$C_{age} + S_{age}$	21	−25,865	377	0	−176,749	2,388	0	−181,122	2,974	0
9[a]	C_{age} + Hunting	21	−25,961	570	0	−176,741	2,371	0	−182,102	4,935	0
10[a]	C_{age} + Density	21	−25,921	490	0	−176,750	2,390	0	−181,527	3,783	0
11[a]	C_{age} + Relatedness	21	−25,928	503	0	−175,608	106	0	−181,957	4,644	0
12[a]	S_{age} + Hunting	21	−25,858	363	0	−176,955	2,800	0	−181,407	3,544	0
13[a]	S_{age} + Density	21	−25,847	341	0	−176,968	2,826	0	−180,525	1,780	0
14[a]	S_{age} + Relatedness	21	−25,685	18	0	−175,712	315	0	−181,497	3,723	0
15[a]	Hunting + Density	21	−25,898	443	0	−176,915	2,720	0	−181,031	2,792	0
16[a]	Hunting + Relatedness	21	−25,828	302	0	−175,700	290	0	−182,226	5,182	0
17[a]	Density + Relatedness	21	−25,836	319	0	−175,690	270	0	−181,614	3,957	0
18[a]	$C_{age} + S_{age}$ + Hunting	27	−25,837	384	0	−176,691	2,347	0	−180,972	2,749	0
19[a]	$C_{age} + S_{age}$ + Density	27	−25,838	386	0	−176,702	2,368	0	−180,274	1,353	0
20[a]	$C_{age} + S_{age}$ + Relatedness	27	−25,658	27	0	−175,597	159	0	−181,002	2,809	0
21[a]	C_{age} + Hunting + Density	27	−25,857	425	0	−176,705	2,375	0	−180,966	2,737	0
22[a]	C_{age} + Hunting + Relatedness	27	−25,803	316	0	**−175,518**	**0**	**1**	−181,850	4,505	0
23[a]	C_{age} + Density + Relatedness	27	−25,821	353	0	−175,597	160	0	−181,358	3,521	0
24[a]	S_{age} + Hunting + Density	27	−25,803	316	0	−176,876	2,716	0	**−179,598**	**0**	**1**
25[a]	S_{age} + Hunting + Relatedness	27	**−25,645**	**0**	**0.98**	−175,688	341	0	−181,210	3,224	0
26[a]	S_{age} + Density + Relatedness	27	−25,675	61	0	−175,680	324	0	−180,447	1,698	0
27[a]	Hunting + Density + Relatedness	27	−25,782	274	0	−175,649	263	0	−180,901	2,607	0
28[a]	$C_{age} + S_{age}$ + Hunting + Density	33	−25,768	310	0	−176,654	2,348	0	−179,576	32	0
29[a]	$C_{age} + S_{age}$ + Hunting + Relatedness	33	−25,617	8	0.02	−175,507	54	0	−180,862	2,604	0
30[a]	$C_{age} + S_{age}$ + Density + Relatedness	33	−25,654	82	0	−175,586	212	0	−180,231	1,341	0
31[a]	C_{age} + Hunting + Density + Relatedness	33	−25,760	294	0	−175,496	31	0	−180,854	2,588	0
32[a]	S_{age} + Hunting + Density + Relatedness	33	−25,629	31	0	−175,638	316	0	−179,580	39	0
33[a]	$C_{age} + S_{age}$ + Hunting + Density + Relatedness	39	−25,597	31	0	−175,485	85	0	−179,561	76	0

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

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 (Figure 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 (Figures 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 (Figure 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 (Figure 4b). Older female
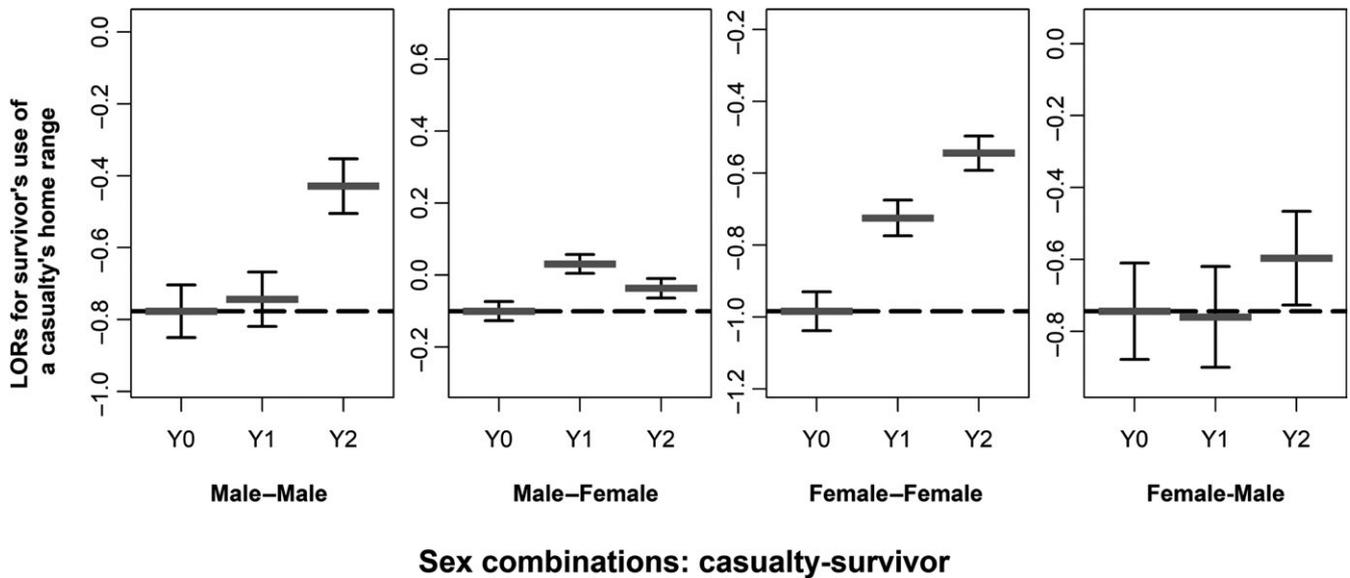
Sex combinations: casualty-survivor

FIGURE 2 Log odd 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

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 (Figure 4c,d,e). The most common retained variable was hunting intensity, which was generally associated with increased use of a casualty's HR (Figures 3c,d 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.

4 | 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 were 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 behaviours (e.g. Zabala et al., 2007), which are linked to sexual dimorphism (Beerman, Ashe, Preedy, & Williams, 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
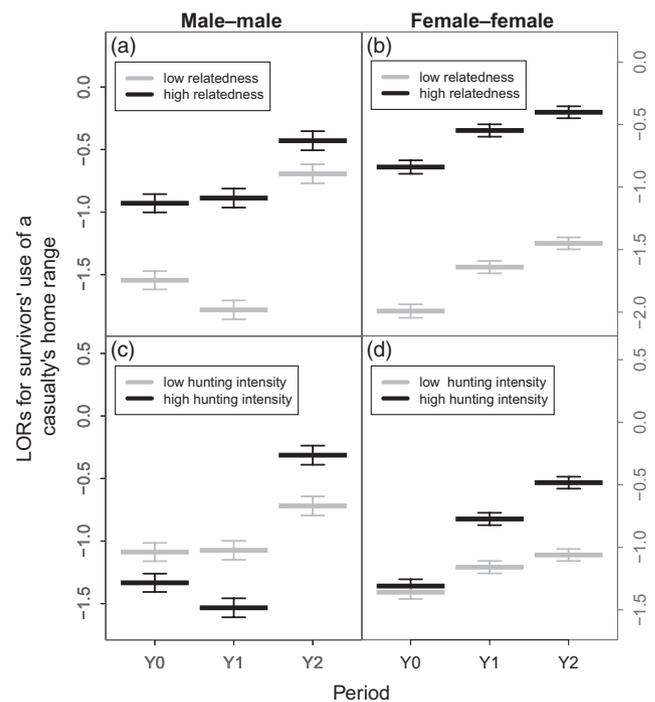

FIGURE 3 Log odd ratios of nearby surviving brown bears' (survivors') use of hunter-killed bears' (casualties') HRs during the year in which the casualty died (Y0), the first year after the casualty's death (Y1) and the second year after its death (Y2) in response to casualty–survivor relatedness (a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

HR overlap is common. Therefore, fewer studies on competition exist in these species (Pilfold et al., 2014), but observed segregation in habitat selection between the sexes within areas of HR
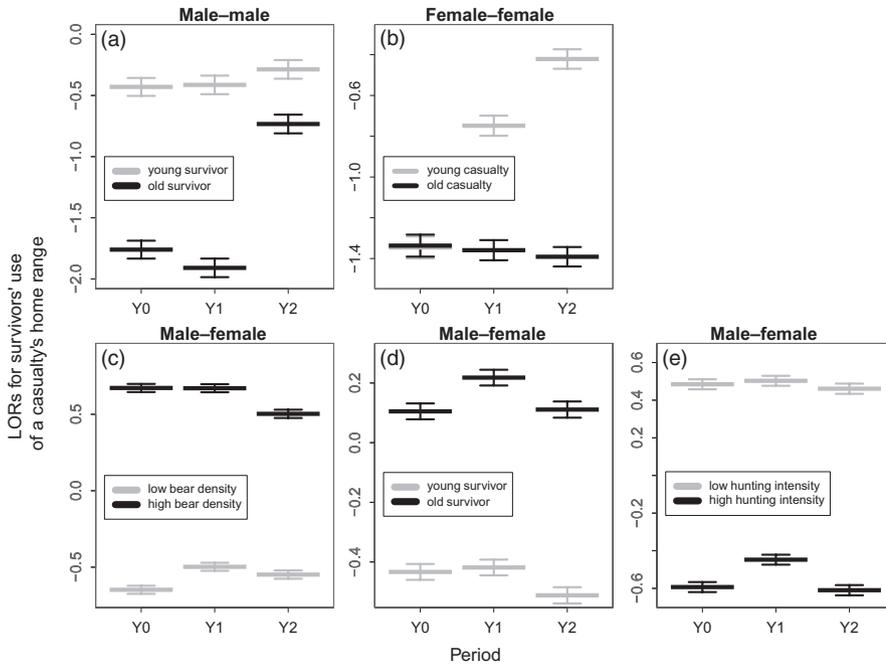
FIGURE 4 Log odd ratios of surviving brown bears' (survivors') use of nearby hunter-killed bears' (casualties') home ranges during the year in which the casualty died in the fall (Y0), the first year after the casualty's death (Y1) and the second year after its death (Y2), in response to casualty and 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 dataset. 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

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 behaviour and dominance may play a larger role in space use in both sexes in the study population than previously thought (Ordiz, Stoen, Swenson, Kojola, & Bischof, 2008; Støen et al., 2005; Zedrosser, Støen, Sæbø, & Swenson, 2007). 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; Odden, Ims, Stoen, Swenson, & Andreassen, 2014; Støen et al., 2005). 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, 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 (Figure 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, Lendrum, Quigley, & Caragiulo, 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 neighbours was constant across individual females' ages (Figure 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 pre-existing 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 philopatric 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 (Noyce & Garshelis, 2014; Perdue, Snyder, Zhihe, Marr, & Maple, 2011). 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 (*Ursus 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 towards 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 and 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 towards 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, appear to drive spatial responses of survivors and, therefore, likely alter 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 (e.g. Geisser & Reyer, 2004; Teichman, Cristescu, & Darimont, 2016). 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).

AUTHORS' CONTRIBUTIONS

S.C.F., M.L., R.B., J.E.S., F.R., F.P. and A.Z. participated in the study design. S.C.F., M.L. and R.B. carried out statistical analyses. A.Z., J.E.S. and F.P. secured funding. J.E.S., A.Z. and J.K. coordinated work in the Scandinavian Brown Bear Research Project. H.G.E. and S.B.H. 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).

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