

Shane Carl Frank

**The effects of harvest on the sociospatial and
genetic structure of a solitary-living large carnivore,
the brown bear *Ursus arctos***





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Partners and collaborating institutions:



A PhD dissertation in
Ecology

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Faculty of Technology, Natural Sciences and Maritime Sciences
University College of Southeast Norway
Kongsberg, 2017

Doctoral dissertations at the University College of Southeast Norway no. 28

ISSN: 2464-2770 (print)

ISSN: 2464-2483 (electronic)

ISBN: 978-82-7206-450-0 (print)

ISBN: 978-82-7206-451-7 (electronic)



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Print: University College of Southeast Norway
Cover Photo: Ilpo Kojola

This thesis was conducted under joint supervision between the University College of Southeast Norway (formerly Telemark University College) and the Norwegian University of Life Sciences.

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Acknowledgements

I would first like to thank my wife, Marie, who is currently working on something a lot more important than a PhD—our soon-to-be first born. She has somehow managed to bring up the troughs and at the same time maintain the peaks of the PhD for me, all the while moving to a new place with a new language, leaving behind familiarity, entering into a new adventure, starting a new practice, bringing a new life into the world, and helping to grow our marriage and family into a moveable feast. Thank you for being a great partner in life. Plus, I thank Oskar for training patience into me, which has proved useful in the process of the PhD.

When I first arrived to the field station of the bear project (SBBRP) in Tackåsen in 2010, I walked along 'the' road to Storhamrasjön, a picturesque lake, and back. I smelled the fresh cut timber, saw aggregated frog eggs in roadside drainages, and heard birds I hadn't heard before. The very first picture I took near Tackåsen was along this road on 08 May 2010 at 13:07:38, and it was befitting of the unknown journey ahead:



Thanks to Ilse Storch for putting me in contact with Jon Swenson, thereby getting me involved with large carnivore research. Jon—you have been an important person in grounding and ground-truthing my experiences as a foreign national in Sweden and Norway—and you have good taste in whisk(e)y—let it go to your head. Furthermore, I fear your kindness is under-recognized, due to your mild manners and modesty—that's

okay for the rest of us who get to thank you for it. A special thanks to Tackåsen, where I enjoyed bipolar experiences between complete solitude and sometimes the strangest mixes of internationals. Thanks to Sven Brunberg for valuing my work there, as well as being an important mentor, possibly unbeknownst to him—to be remedied. I'd especially like to thank a core group of friends from the project since my involvement: Sam Steyaert, Richard Bischof, Marcus Elfström, and Andreas Zedrosser. Your consistency in active friendship, notwithstanding a hiatus in both time (several years) and space (the Atlantic Ocean)—knew I'd get Led Zeppelin in here somewhere—has helped me appreciate friendship in a different light. Your respective families have warmly welcomed mine and supported us—for that, we are heartily grateful. Furthermore, I cannot boast enough about your skills as researchers. To that end, other colleagues and friends I have gained along the way who have also been integral in helping me develop as a researcher and in some cases personally: Martin Leclerc, Joanie Van de Walle, Jack Beardsley, Anne Hertel, Andrés Ordiz, Gro K. Moen, Therese Sivertsen, Fanie Pelletier, Ole-Gunnar Støen, Jonas Kindberg, Veronica Sahlén, Ellinor Sahlén, Frank Rosell, Joris Cromsigt, and Göran Spong. A special thanks goes to my PhD office comrades: Martin Mayer for constantly drawing me out to play tennis, talking about parasitology/herpetology, and patiently listening to my thought experiments/ramblings (yes, patiently—I noticed); Priyank Nimje for taking care of what we care about—our dogs, talking genetics, trying to feed me peanuts, and for being a good friend to us; Jean-Marc Costanzi for being the devil's advocate, sometimes even contradicting his own point in the middle of a sentence, but particularly toward Martin—that was grand entertainment, almost as grand as your generosity; Patricia Graf for being laid back, bringing people together, and having a consistently positive outlook; Roisin Campbell (absent yet still part of the office) for lessons on how to speak funny-sounding English and providing practical outlooks on important conservation issues; Hannah Cross for smiling, chatting about whatever, and reminiscing about CO; and Odko Tuemdemberel for perspective, delicious dumplings (!), and helping bring a balance to the office. To all of you for various conversations and dialogues on all things that interested us, whether stemming from home or work. Thanks to Øyvind S. for going

birding and general banter; and Live S., Anette F., Veronica T., John S., Jan H., Rune P., Rune R., Andrew J., Mona S., Christian R., Asle Ø., Steffi R. and Nicolas D.P., and Frode B. for further support at USN. Thanks to IRSAE for giving me so many coursework opportunities to improve my knowledge. Of course, thanks to my supervisors in Bø, Andreas and Frank, for being open and available to talk. In particular, I thank Andreas for rooting for me the whole way through and pulling me out of the office every now and again to go to the range. It is not lost on me how much you have supported me/my family in this process.

There are too many people from SBBRP to mention since joining it in 2010, but I'd like to thank the people that make it possible to collect data in the field: obviously Sven; David Alqvist for your aim, positivity, and random bursts into (ridiculous) song; Andrea Friebe for getting order on things; Jon M. Arnemo, Alina Evans, Johanna Painer, Nikolaus Huber, Monica Bando, Nuria Esteruelas, Åsa Fahlman, Susanne Küker, and the many other vets who take great care and responsibility for the bears in the field; Walter—a person who is a unique island of specialized knowledge and surprising depth; and to the many volunteers and masters students I have not mentioned here. I'd also like to thank invisible hands of people in genetics labs, such as LECA and in Svanhovd, which work hard to provide good data. Thanks to Eva Bellemain, Siv Grethe Aarnes, Snorre Hagen, Alex Kopatz, and Audrey Bourret for helping me wrap my head around these tiny packages of coded information.

Thanks to my family in Europe: John, Karianne & Olav, Karen, Ann, Lars, Jessica, Sebastian, Anders, Karoline & Thomas, Josh & Jennifer, Lucy, Toby, Rune, Stine, Ella, and Maria. And family in Colorado: Mom, Kevin, Dave & Amy, Peter, and Kristian, and the Atwoods, but also the East Coasters. We are spread out and it seems to be an increasing trend, due to increasing opportunities—thanks for the steady support and your presence despite these distances. Thanks to Ethan, Aaron, Rob, and Justin who helped me get through the years, the last one in particular, with minimal scar tissue.

This last year or so studying the mortality of bears did not pass without irony. My (Norwegian) grandma, father, and our dog of nearly 15 years all passed away. I dedicate this thesis to those our family has lost and rather than wax poetic on their contribution to my life and this work here, I have showed them all as much in person. However proud I am of the work in this thesis, I am significantly more proud of capitalizing on the moments I had with them—it was only from great advice from a good friend. It is written here only to act as a reminder for me to keep doing it and for others to do the same—to constantly remind others what they mean to us. We can be such forgetful creatures. Keep your eye on the ball...

Abstract

Understanding the effects of harvest is integral for sustainable wildlife management and conservation. And yet, the focus of managers has predominantly been on the direct mortality of harvest, often ignoring the indirect effects of harvest, such as those resulting from changes to sex, age, and social structure, the behavior of individuals, and the potential for human-induced selection. Such effects can influence population growth rate beyond that expected from direct mortality. This thesis reviewed the indirect effects of harvest on the Swedish brown bear population, explored the spatial reorganization of bears following harvest, examined whether the spatial reorganization of males can contribute to sexually-selected infanticide (SSI), and evaluated whether hunting has played a role in affecting fine-scale genetic structure of matriline. The best documented indirect effect of bear harvest in Sweden is SSI. The disruption to social structures due to harvest causes a spatial reorganization in brown bears, seemingly as a result of competitive release from conspecifics. This is most pronounced among surviving individuals living in proximity of hunter-killed bears of the same-sex. These survivors consistently increased their use of the now vacant home ranges. Furthermore, the strength of spatial responses of surviving individuals during reorganization was modulated by the sex, pairwise relatedness, and age of surviving and killed bears, in addition to hunting intensity and population density. For males, their spatial reorganization is consistent with the time lag (~two years following harvest) of SSI found in other studies. We also found that harvest could contribute to the decrease in fine-scale genetic structure of brown bear matriline. Fine-scale genetic structure is commonly used to identify important management units of wildlife populations. Female brown bears are socially and spatially organized in matriline. It is unknown how alterations to FGS could affect the persistence of populations. In the case of the Scandinavian brown bear population, changes to FGS could be an indication of selective harvest, the redistribution of male reproductive success, altered dispersal patterns, and increased individual turnover associated with high hunting pressure. However, we provide empirical evidence that indirect effects of harvest exist, particularly through a

Frank: The effects of hunter harvest on the sociospatial and genetic structure of a solitary-living large carnivore, the brown bear *Ursus arctos*.

spatial reorganization following harvest that can influence the risk of SSI. We suggest that managers of bear and other large carnivore populations apply the precautionary approach and assume that indirect effects do exist, which could have a potential impact on population structure and growth.

Keywords: hunting, social structure, spatial reorganization, brown bear, *Ursus arctos*, genetic structure, matriline

List of papers

Paper I

Frank, SC, Ordiz A, Gosselin J, Hertel A, Kindberg J, Leclerc M, Pelletier F, Steyaert SMJG, Støen OG, Van de Walle J, Zedrosser A, and Swenson JE. "Indirect effects of bear hunting: a review from Scandinavia." In press in *Ursus*.

Paper II

Frank, SC, Leclerc M, Pelletier F, Rosell F, Swenson JE, Bischof R, Kindberg J, Eiken HG, Hagen SB, Zedrosser A. "Sociodemographic factors modulate the spatial response of brown bears to vacancies created by hunting." In press (as of 2017-09-23) in *Journal of Animal Ecology*.

Paper III

Leclerc M, **Frank SC**, Zedrosser, A, Swenson JE, Pelletier F (2017). "Hunting promotes spatial reorganization and sexually selected infanticide." *Scientific Reports* 7: 45222. DOI: 10.1038/srep45222

Paper IV

Frank, SC, Pelletier F, Bourret A, Garant D, Rosell F, Swenson JE, Eiken HG, Hagen SB, Zedrosser A. "A smoking gun: hunting disrupts fine-scale genetic structure among matrilineal lines of a large carnivore." Manuscript.

Frank: The effects of hunter harvest on the sociospatial and genetic structure of a solitary-living large carnivore, the brown bear *Ursus arctos*.

Abbreviations

BIC	Bayesian information criterion
FGS	Fine-scale genetic structure
HR	Home range
GLMM	Generalized linear mixed model
SBBRP	Scandinavian Brown Bear Research Project
SSI	Sexually selected infanticide)

Frank: The effects of hunter harvest on the sociospatial and genetic structure of a solitary-living large carnivore, the brown bear *Ursus arctos*.

Table of Contents

1 Introduction	1
2 Objectives	5
3 Materials and Methods	7
3.1 Study Area	7
3.2 The study population and animals.....	8
3.3 Animal captures and dead bears	9
3.4 GPS location Data.....	10
3.5 Genotyping and pedigree construction	11
3.6 Statistical Analysis	12
3.6.1 Paper II and III: Model development and selection.....	12
3.6.2 Paper IV: Fine-scale genetic structure and male mating success	15
3.6.3 Paper IV: Survival analysis.....	16
3.7 Ethical statement	17
4 Results and Discussion	19
4.1 Paper I: Documented and potential indirect effects of bear harvest.....	19
4.2 Paper II: Spatial responses to harvest-induced vacancies and their modulating factors	22
4.3 Paper III: Harvest-induced vacancies and sexually selected infanticide.....	26
4.4 Paper IV: Effects of hunting mortality on fine-scale genetic structure	29
5 Conclusions and perspectives	35
6 References	39

Frank: The effects of hunter harvest on the sociospatial and genetic structure of a solitary-living large carnivore, the brown bear *Ursus arctos*.

1 Introduction

"For the main reason why so many mammals are said to be solitary seem[s] to be that they can only be shot one at a time... [and] the only mammal one could conceivably speak of as being socially indifferent is a dead one."

~ Paul Leyhausen (Leyhausen 1964)

Humans dominate the world's ecosystems (Vitousek 1997) and have considerable influence over its biodiversity and wildlife populations (McRae et al. 2017). For example, humans are today considered one of the "world's greatest evolutionary force[s]" (Palumbi 2001), and exploitation by humans can change morphological, behavioral, and life history traits of wildlife (Palumbi 2001, Hendry et al. 2008, Darimont et al. 2009, Darimont et al. 2015, Leclerc et al. 2017). This is of particular concern for the management and conservation of wild populations, because humans can select for 'undesirable traits' (Coltman et al. 2003a, Mysterud and Bischof 2010) or those contrary to the direction of natural selection (Conover 2007, Olsen and Moland 2010, Kvalnes et al. 2016), and negatively affect the viability and persistence of populations (Allendorf and Hard 2009). Although the role of harvest in wildlife management is supported by a solid scientific foundation (Williams et al. 2002, Fryxell et al. 2014), much remains unknown about its effects, particularly for large carnivores (Treves 2009).

Common goals in wildlife management are to 1) make a population increase, 2) make it decrease, 3) hunt it for a continuing yield, or 4) do nothing except monitor the population (Caughley 1977, Fryxell et al. 2014). Managers usually focus on the effects of direct hunting mortality on a population's growth rate to reach these population objectives (e.g., Knight and Eberhardt 1985, Miller 1990). Nevertheless, there is a growing number of studies showing that indirect or "side" effects of harvest, which managers often do not consider, also may affect population growth and even population persistence (e.g., Whitman et al. 2004, Milner et al. 2007a, Pauli and Buskirk 2007,

Treves 2009). I generalize indirect effects here as the hunting-induced changes in a population that result in a change in population growth rate beyond that caused by the initial offtake from direct mortality, i.e., "super-additive effects" (Creel et al. 2016). These effects can result from changes to a population's age, sex, and social structure, and to the behavior of remaining individuals (Milner et al. 2007b). Linking such changes to population growth are challenging, particularly changes in social structure (i.e., interactions and relationships among animals), as it requires intensive monitoring and detailed individual-based data including sex, age, and relatedness (Clutton-Brock and Sheldon 2010). Studies on the effects of harvest on sex and age structure are relatively numerous with a longer standing in the literature (e.g. Pahoheimo and Fraser 1981, Ginsberg and Milner-Gulland 1994, Coltman 2008, Mysterud 2011, Rughetti 2016), compared to those on social structure (e.g. Ausband et al. 2015, 2017).

Changes to social structure from harvest and natural mortality (including predation) are a certainty in wild populations, as the removal of individuals from a population inevitably results in the loss of interactions and relationships for surviving animals (Snijders et al. 2017). However, relative to natural predation, humans are exceptional predators that can quickly disrupt wild animal populations (Darimont et al. 2009, Zeckhauser 2017). Harvest rates by humans can exceed that of natural mortality or be additive (Stenseth and Dunlop 2009, Sandercock et al. 2011). Another unique aspect of hunting by humans is their ability to harvest adult individuals that otherwise experience little predation (Darimont et al. 2015). The harvest of adult individuals that are important for reproduction can disproportionately affect population growth (Lindberg et al. 2013, Caudill et al. 2017), perhaps also owing to their ability to maintain stable social structures (Snijders et al. 2017). For example, the removal of matriarchal and bull African elephants (*Loxodonta africana*) can affect the composition of groups, decrease access to resources, change male mating success, and lower overall reproductive output (McComb et al. 2001, Ishengoma et al. 2007, Evans and Harris 2008, Gobush et al. 2008, Gobush et al. 2009). For social species, the loss of even a single breeder to harvest can greatly affect group composition, genetic composition, and population growth (Ausband

et al. 2017). Conversely, the protection of populations following harvest can facilitate recovery toward more natural social and genetic structures (Rutledge et al. 2010), with stable social structures having higher reproductive output (Berger 1983).

Understanding the potential mechanisms linking hunting-induced social structure changes to population growth is important for managers to develop plans that mitigate potential harmful effects or avoid unintentional consequences (Loveridge et al. 2016). Tracking the mechanisms behind the effects of harvest-induced social structures on population growth may require detailed information on animal locations (Gosselin et al. 2017). For example, by removing individuals, hunting creates vacancies in a population's spatial configuration (McComb et al. 2001, Loveridge et al. 2007). In response to vacancies, surviving individuals may exhibit a spatial reorganization (Lovallo and Anderson 1995, Gese 1998), which in turn can affect social structure, reproduction, and ultimately population dynamics (Robinson et al. 2008, Cooley et al. 2009, Rutledge et al. 2010). Spatial reorganization is most likely driven by competition for resources, such as access to mates or resources necessary for reproduction (Clutton-Brock and Huchard 2013a, Maletzke et al. 2014).

This is well supported by studies on species in which sexually selected infanticide (SSI) occurs (Balme and Hunter 2013, Gosselin et al. 2015). SSI is a male reproductive strategy whereby males gain mating opportunities by killing dependent young (Hrdy 1979). The SSI hypothesis states that males should only kill offspring that they have not sired, infanticide should trigger estrus in a victimized mother, i.e., quickening her receptivity, and the perpetrator should be the father of the victimized mothers' subsequent offspring (Trivers 1972, Hrdy 1979). For example, high male turnover of males in African lions (*Panthera leo*) due to trophy hunting can alter their sociospatial structure by increasing interterritorial movements and immigrant males, thereby increasing infanticide as males enter new prides (Loveridge et al. 2007). As a result, hunting pressure can indirectly cause a negative effect on population growth and increase extinction risk, but these effects can be controlled and managed if understood (Whitman et al. 2004, Creel et al. 2016).

The persistence and extinction risk of populations have been linked to their genetic composition (Dunham et al. 1999, Allendorf et al. 2008) and genetic structure is important for identifying management units of populations (Allendorf and Luikart 2007). Harvest and subsequent protection can potentially alter fine-scale genetic structure (FGS), i.e., structure across subdivisions within populations (Ruzzante et al. 2001, Nussey et al. 2005, Frantz et al. 2007). A stable social structure and the recruitment of reproductive adults are integral to developing and maintaining genetic structures in wild populations (Storz 1999, Parreira and Chikhi 2015). Despite this, the effects of hunting on social structure and its consequent effects on genetic structure are not well understood (Harris et al. 2002, Allendorf et al. 2008, Ehrich et al. 2011).

In this thesis, I used the brown bear (*Ursus arctos*) as model species to assess the effects of harvest on the population's sociospatial and genetic structure. Brown bears are considered solitary-living and nonterritorial (e.g. Craighead et al. 1995, Dahle and Swenson 2003), meaning they come together for the purpose of breeding, but otherwise generally avoid one another (Sandell 1989). The mating system of the brown bear is best described as polygamous, with members of each sex acquiring numerous mates (Steyaert et al. 2012). Dispersal in brown bears is male-biased, with females typically exhibiting philopatry (McLellan and Hovey 2001, Støen et al. 2006). As a result of philopatry, females are often spatially clustered into matriline (Støen et al. 2005). Home ranges (HRs) overlap significantly within and between the sexes (e.g., McLoughlin et al. 2000), but is highest between female kin (Støen et al. 2005). HR size varies widely among populations for both sexes (males: 115–8171 km²; females: 24–2434 km²) (McLoughlin et al. 2000) and covaries with density and food availability (Dahle and Swenson 2003, Dahle et al. 2006).

2 Objectives

The overarching aim of this thesis was to evaluate the effects of harvest on the sociospatial and genetic structure of a solitary-living large carnivore. The brown bear was used as a model organism. The following questions were examined in more detail:

1. Review the documented and potential indirect effects of harvest, focusing on a well-studied brown bear population in southcentral Sweden (paper I).

We describe how harvest-induced changes to age, sex, and social structure, to individual behavior, and human-induced selection could result in an additive change to population growth beyond that expected from direct mortality.

2. Document the spatial responses of surviving animals to harvest-induced vacancies. (paper II and III).

We tested the competitive release hypothesis, i.e., whether the removal of conspecifics ('casualties') and resulting vacancies induced an increase in use of such vacancies by neighbors ('survivors'). We also explored whether casualty and survivor sex, age, and relatedness, population density, and hunting intensity were important in modulating these spatial responses.

3. Examine whether spatial responses of males to harvest-induced vacancies could mechanistically contribute to SSI (paper III).

We explored whether the spatial responses between male casualties and survivors were consistent with the timing of SSI found in other studies and how this could affect population management.

4. Evaluate whether hunting has a role in affecting fine-scale genetic structure (FGS) in this study population (paper IV).

We assessed the FGS of female brown bears and their matriline between periods of low (1990-2005) and high (2006-2011) hunting pressure using four different metrics. We further quantified changes in survival probability of females, mother-daughter pairs, and males, in bear dispersal, and in male gene flow across periods, to evaluate other effects of hunting which may contribute to changes in FGS.

3 Materials and Methods

3.1 Study Area

The Scandinavian Brown Bear Research Project (SBBRP) has two study areas; one in northern Sweden (67°N, 18°E) from 1984-2013, where 254 individual brown bears have been radiomarked and followed, mostly with VHF telemetry (8,000 km²; termed “north”), and one in central Sweden-southeastern Norway (61°N, 15°E) from 1985 to the present (13,000 km²; termed “south”). There, 499 individuals were radiomarked and followed with VHF telemetry and, from 2003, increasingly with GPS technology.

The south is composed of bogs, lakes, and intensively managed and mixed-aged forest stands. The dominant tree species are Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and birch (*Betula* spp.). Elevations range between 150 and 725 m asl. Gravel roads (0.7 km/km²) are more abundant than paved roads (0.14 km/km²). The north consists of alpine mountain and coniferous forest habitats and includes parts of some national parks. The topography is characterized by valleys, glaciers, and plateaus ranging up to 2,000 m, with tree line occurring at about 600 m (Zedrosser et al. 2006). The valleys are dominated by mountain birch (*Betula pubescens*), Scotch pine, and Norway spruce. In the south and north, mean annual precipitation is similar at about 600-1000 mm and 500-1000, respectively. Snow cover is shorter-lasting in the south, typically arriving late October (early October in the north) and disappearing early May (late May in the north). The bulk of this thesis utilized data collected from the south, though paper I also drew upon research findings from the north. See Martin et al. (2010) and Zedrosser et al. (2006) for further information about the study areas.

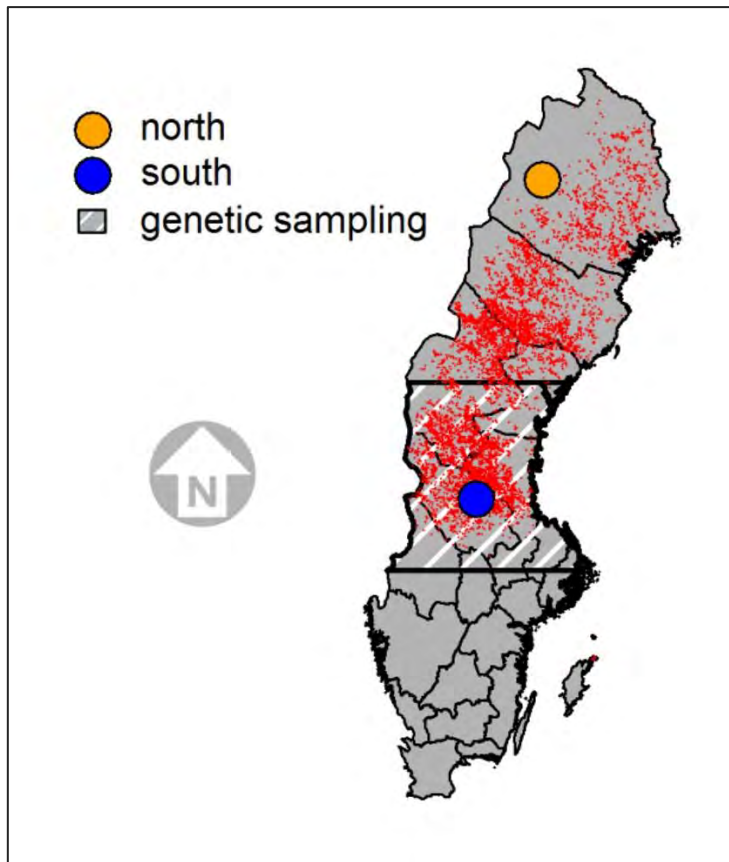


Figure 1. Map of the study areas in the south (solid blue circle) and the north (solid orange circle) of Sweden. Small red dots represent brown bear presence via scat sampling. The white-hatched polygon is where genetic samples were collected for brown bear pedigree construction in the south.

3.2 The study population and animals

Hunting brown bears outside national parks has been legal in Sweden since 1943. The hunting season is presently from 21 August until the area-specific, annually established quota has been filled (Swenson et al. 2017). Quotas have been set at variable spatial scales in Sweden, but today are set typically at county or subcounty levels (Swenson et al. 1994, 1998, 2017). The Scandinavian bear population has increased from around 300 individuals in the 1940s to around 3,000 bears today, with approximately 95% of those found in Sweden (Swenson et al. 1994, Kindberg et al. 2011, Swenson et al. 2017). Only recently (2008-2013) has bear population size decreased in Scandinavia, most likely due to an increase in harvest rate in Sweden (Swenson et al. 2017). Population density varies

and is approximately ~ 30 bears/1,000 km² and 15 bear/1,000 km² in the south and north, respectively (Solberg et al. 2006, Zedrosser et al. 2006).

All hunters passing a shooting proficiency test and with access can hunt bears. There is no bag limit on bears, and any bear can be killed, except females and their cubs, which are all protected regardless of the cubs' age. Bears are hunted using stalking, sitting at posts, with dogs, or at bait sites; dog hunting is gaining in importance (Bischof et al. 2008, Swenson et al. 2017). It is legally required for all harvested bears and dead bears found to be reported to local authorities and samples (e.g., tissue, hair, a premolar tooth for aging) and measurements (e.g., weight) are taken, and sex determined (see Animal Captures and Dead Bears).

Hunting is the most important cause of bear mortality in Sweden, as 60% of all marked bears ≥ 1 year of age that are recovered dead have been killed legally by hunters, with 13% dying naturally, and the rest dying of other causes (e.g. management control, self-defense, traffic, etc.) (Bischof et al. 2009). In Sweden, data from 1984-2006 suggest that hunters exhibit low selectivity for age, size, and sex, except for a slight bias towards males in the north (Bischof et al. 2009). However, more recent analyses, based on an expanded data set collected during a time of increased harvest pressure, shows greater selectivity towards older bears (SBBRP, unpublished data), larger yearlings, and larger adult females over time (Leclerc et al. 2016). The mean age of a harvested bear was ~ 5 years and males made up a slightly greater share of the harvest than females (55:45) in 1981-2015 (paper I).

3.3 Animal captures and dead bears

We captured brown bears from a helicopter using a remote drug delivery system (Dan-Inject[®], Børkop, Denmark) and various combinations of medetomidine and tiletamine-zolazepam based on animal mass (Arnemo et al. 2011). We determined sex at capture and extracted a vestigial first premolar tooth from individuals not captured as a yearling for age determination (Matson 1993). We equipped bears with GPS collars (GPS Plus;

Vectronic Aerospace GmbH, Berlin, Germany) programmed to relocate a bear with varying schedules (≤ 1 hour intervals). In addition, we acquired data on location, sex, and age (determined as above) for all known dead brown bears in Sweden from the Swedish State Veterinary Institute between 1981-2015 ($N = 4,445$), of which $\sim 80\%$ were caused by legal hunting. Note that this number is higher than the 69% reported by Bischof et al. (2009), who only used captured bears. DNA from tissue and hair were collected from both captured and dead bears between 1985 and 2014. Tissue was temporarily stored in 95% alcohol prior to DNA extraction. Hair was stored in paper envelopes for drying. Multiple tissue and hair samples were taken from individuals that were captured multiple times and/or were also recovered dead, which were used to assess genotyping error rate (below).

3.4 GPS location Data

In paper II and III, 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 and 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. 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 hunter-killed bear HRs with the 95th percentile isocline from a kernel density distribution (Calenge 2006).

In paper IV, location data of bears came from both VHF and GPS collars with variable relocation schedules, e.g., once a week to ≤ 1 hour, respectively, from 1985-2015. All GPS positions with a dilution of precision > 5 and location errors detected, using the method of Bjørneraas et al. (2010) adjusted to bear movement rates, were removed from the relocation data set. Location data were used to calculate centroids of bear HRs. As many VHF-collared individuals had few observations, we estimated HR centroids

using several methods, i.e., a median centroid or a-LoCoH centroid based on relocation coordinates. We calculated distances from natal HR centroids of offspring while with her mother to all subsequent HR centroids belonging to the offspring following separation. We took the mean of all such distances for bears ≥ 4 years. Bears were assigned to "early" or "late" depending on which year dispersal took place, which was assumed to be at age 4 (Støen et al. 2006, Zedrosser et al. 2007b).

3.5 Genotyping and pedigree construction

The amplification and analysis of short tandem repeat loci (hereafter 'microsatellites') of 16 autosomal microsatellites (Table 1) was performed in two labs, the Laboratory of Alpine Ecology (LECA) and Bioforsk Svanhovd. LECA performed amplification following the protocol from Waits et al. (2000). Genotyping efforts were calibrated between the two labs, in order to ensure consistency (Aarnes et al. 2009). Using 120 individuals that were genotyped twice, we calculated an error rate from the sum of mismatches between paired loci divided by the total number of loci genotyped (Table 1).

We used Cervus 3.0 (Marshall et al. 1998, Kalinowski et al. 2007) and COLONY (Jones and Wang 2010) to assign parentage to offspring and construct a pedigree. We chose a critical LOD delta score with a confidence level of 95% as a cut-off for parentage assignment when comparing our empirical data to that simulated in Cervus using observed allelic frequencies. We then used COLONY (Jones and Wang 2010) for sibship reconstruction, which simultaneously reconstructs unknown father genotypes, enabling us to recover potential fathers and sibship missed in parentage assignment from Cervus.

Table 1. Summary statistics for microsatellites used for pedigree reconstruction and Lynch and Ritland's (1999) relatedness index for brown bears (N = 1614) in southcentral Sweden. N_A: Number of alleles, H_o: observed heterozygosity, H_e: expected heterozygosity, P_{ex}: probability of exclusion for a single unknown parent, P_{id}: probability of identity for unrelated individuals, G_e (%): genotyping error rate by locus. Averages were calculated for N_A, H_o, H_e, and G_e whereas overall probabilities across all loci were calculated for P_{ex} and P_{id}.

Locus	N _A	H _o	H _e	P _{ex}	P _{id}	G _e
G1A ^a	6	0.625	0.630	0.380	0.810	0.0
G1D ^a	7	0.592	0.620	0.340	0.786	0.4
G10B ^a	8	0.699	0.703	0.442	0.855	0.0
G10C ^b	5	0.697	0.698	0.460	0.864	0.5
G10J ^c	6	0.574	0.570	0.325	0.762	0.4
G10H ^c	9	0.525	0.545	0.308	0.740	0.6
G10L ^a	8	0.757	0.760	0.544	0.905	0.0
G10O ^a	3	0.392	0.397	0.166	0.564	0.9
G10P ^b	6	0.736	0.757	0.535	0.902	0.0
Mu05 ^d	8	0.640	0.636	0.365	0.797	0.5
Mu10 ^d	8	0.806	0.806	0.610	0.933	0.0
Mu15 ^d	4	0.658	0.643	0.364	0.805	0.0
Mu23 ^d	8	0.709	0.699	0.485	0.876	4.7
Mu50 ^d	10	0.735	0.756	0.538	0.903	1.1
Mu51 ^d	9	0.824	0.796	0.592	0.926	2.0
Mu61 ^d	4	0.529	0.542	0.272	0.714	0.0
Average/Overall	7	0.656	0.660	>0.99	>0.99	0.1

^aPaetkau and Strobeck (1994); ^bPaetkau et al. (1995); ^cPaetkau et al. (1998); ^dTaberlet et al. (1997).

3.6 Statistical Analysis

3.6.1 Paper II and III: Model development and selection

We assessed the spatial responses of surviving bears (hereafter 'survivors') to hunter-induced vacancies left by removed bears (hereafter 'casualties'). For each casualty we 1) determined its annual 95% kernel HR for the active period (May to the day before it was killed or 30 September, whichever came first) of the year in which it was killed and 2) calculated a 40-km radius circular buffer centered on its HR centroid (Figure 2, panel

a). In a given year, we used GPS relocations of the casualty and all the GPS locations of survivors within the buffer to 3) calculate a 95% kernel isocline (hereafter called "sampling space"; Figure 2, panel b). For each survivor, we 4) generated as many random as GPS relocations within the sampling space (Figure 2, panel c to d) and 5) determined whether GPS and random relocations were inside or outside the casualty's HR (Figure 2, panels c and d). We repeated steps 3–5 for 3 consecutive years, i.e. the year a casualty had been killed and the two following years. We updated the sampling space annually by keeping the casualty' relocations the year it was killed constant for the three years, and used the appropriate relocations of survivors for each year. We only used survivors that were alive and monitored during the three-year period. We repeated these steps for each casualty.

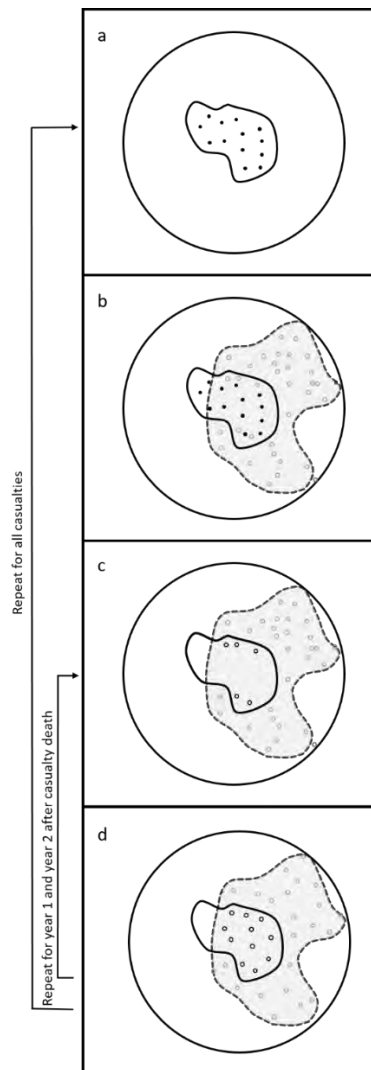


Figure 2. Schematic representation of extracting observed and randomly available location data for survivors in vacancies, i.e., former home ranges (HRs) of casualties. For each brown bear casualty (panel a), we determined its 95% kernel HR and calculated a 40-km radius circular buffer centered on the 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.

We assigned a population density index value extracted from the casualties' HR centroids, a proxy for hunting intensity based on the number of bears shot in the 40-km buffer for three years before casualty death, casualty and survivor sex and age, and casualty-survivor pairwise relatedness to each relocation, whether observed or randomly generated.

We used generalized linear mixed models (GLMM) with a logit link to assess the influence of sex on spatial responses in paper II (just males in paper III). 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 in paper II and paper III, although paper III did not include relatedness as a modulating factor in the analysis. 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. We used the Bayesian Information Criterion (BIC) to select the "best model" (Aho et al. 2014).

3.6.2 Paper IV: Fine-scale genetic structure and male mating success

We calculated Weir and Cockerham's F_{ST} (Weir and Cockerham 1984) and Hedrick's G'_{ST} (Hedrick 2005) with functions from the R packages 'hierfstat' (Goudet 2005) and 'mmod', respectively, and by using two different population subdividing units. We used "period" as the population subdividing unit for all females of the population ('population data set') and a subset of females that were successfully assigned to matriline ('matriline data set'), to detect whether there was genetic differentiation among females between the early (1990-2005) and the late (2006-2011) periods. The early and the late period corresponded to low and high hunting pressure, respectively (Gosselin et al. 2015). We also used permutation tests ($\alpha = 0.05$) to evaluate whether these results were significantly different from zero. To detect whether genetic structure among matriline had changed between early and late periods, matriline ID was used as the population

subdivision for the matriline data set, and FST and G'ST were independently calculated for each early and late period.

We also calculated an index of structure among matriline using pairwise relatedness (rxy). For the matriline data set, we calculated the difference between among- and within mean rxy of matriline by period: mean rxy of individuals belonging to different matriline minus the mean rxy of individuals belonging to the same matriline. This was calculated independently for early and late periods. All rxy calculations were carried out using each the pedigree and LR relatedness estimates. To attain measures of precision, we bootstrapped all FST, G'ST, and rxy structure calculations.

Because bears are long-lived, several bears (N = 42 of 110 or 38%) lived in both early and late periods (hereafter straddlers). We assigned straddlers to either period according to the period the bear had lived the majority of its life. For bears that evenly straddled the two periods (N = 3 or 3%), we used 10 iterations, randomly putting the bear in either the early or late period and recalculated all fine-scale genetic structure metrics along with associated bootstraps.

3.6.3 Paper IV: Survival analysis

To test whether the probability of a female living to a given age was influenced by period, we used survival analysis, i.e., a cox proportional hazards model (Cox 1972). We used all marked female bears and their annually reconstructed ages from 1990-2011 as the 'survival time'. Female bears' observed ages were partitioned into a covariate 'period' as either 'early' or 'late' depending on the year in which the age occurred (early: 1990-2005, late: 2006-2011). Survival analysis allows information to be used despite the censoring of data, i.e., when complete life histories are not available or the event does not occur for an individual within a sampling interval. In the case of female survival, the 'event' modeled was whether her death occurred. In quantifying the probability of joint mother-daughter survival, the 'event' occurred when at least one of the two individuals in a mother-daughter pair died, but otherwise had the same model structure as the probability of female survival using the package 'survival':

coxph(Surv(entry.age, exit.age, event) ~ period)

For each model we tested the proportionality of hazards assumption using the `cox.zph` function in R (Therneau and Lumley 2009).

3.7 Ethical statement

All captured bears were part of the SBBRP and all experiments, captures, and handling were performed in accordance with relevant guidelines and regulations and were approved by the appropriate authorities and ethical committees: the Swedish Board of Agriculture (ref: 31-11102/12) , Uppsala Ethical Committee on Animal Experiments (Uppsala; ref: C 18/15), the Swedish Environmental Protection Agency (ref: NV-01758-14), and the Norwegian Food Safety Authority (ref: 2017/3442).

Frank: The effects of hunter harvest on the sociospatial and genetic structure of a solitary-living large carnivore, the brown bear *Ursus arctos*.

4 Results and Discussion

4.1 Paper I: Documented and potential indirect effects of bear harvest

In paper I, we reviewed documented and potential indirect effects from hunting due to four major sources; 1) changes to a population's age and sex structure, 2) changes to a population's social structure, 3) changes in individual behavior, and 4) human-induced selection (Figure 3). We found two quantitative estimates of indirect effects of hunting on lambda in bear populations; an increased mortality of cubs of the year (hereafter 'cubs') due to SSI in brown bears in Scandinavia (Swenson et al. 1997, Gosselin et al. 2017), and a reduced reproductive rate of female grizzly bears in Alberta (Canada), due to females selecting less productive habitats as a counter strategy to SSI (Wielgus and Bunnell 1994, Wielgus and Bunnell 2000, Wielgus et al. 2001) (Figure 3). Although not reviewed in paper I, hunting bears and other large carnivores also could affect their role in an ecosystem (Ordiz et al. 2013) and indirectly affect other species in the trophic network. Such information on interspecific interactions is also useful for management, because adjusting hunting quotas of ungulates that are both hunted and predated upon by carnivores might be necessary to meet multiple goals, such as yield and conservation of carnivores (Jonzén et al. 2013). Although we documented several indirect effects (Figure 3), e.g. increased risk of SSI due to male turnover, other potential indirect evolutionary effects are generally more difficult to document and quantify, particularly compared to direct effects of harvest. For example, in wild bighorn sheep (*Ovis canadensis*), paternal effects on maternal investment appears to be adaptive, meaning that males of higher reproductive success can induce higher maternal investment in their sons, whereas the opposite is true for sons of relatively less successful sires (Douhard et al. 2016). Therefore, a change in male age structure from harvest can alter the distribution of male reproductive success (Hard et al. 2006, Costello et al. 2009), thereby altering the evolutionary trajectory and adaptive potential of a population. However, this is difficult to document as it requires long-term, individual-based data on

sex, age, and relatedness among individuals within a population, which are rare (Clutton-Brock and Sheldon 2010).

The main point of our review was to stress that indirect effects of harvest deserve more attention by managers, because they can influence population growth rates. In societies where wildlife management is an important public issue, e.g., where wildlife populations are managed under the public trust doctrine (Batcheller et al. 2010, Treves et al. 2017), the public may increasingly require that managers not only document the direct, numerical effects of management decisions, but also their indirect and potential human-induced selection effects. Although research on indirect effects of hunting on fitness can be challenging, it is an important responsibility for managers to fund and carry out research on this topic. Long-term monitoring of harvest effects on bears and other species also provides opportunities for managers to make informed decisions while considering uncertainty (Bischof et al. 2012, Regehr et al. 2017). As we await the outcome of such research, managers of bear populations should apply the precautionary principle and assume that indirect effects do exist and have a potential impact on bear population structure and growth that may differ from that predicted by harvest models based on direct effects alone.

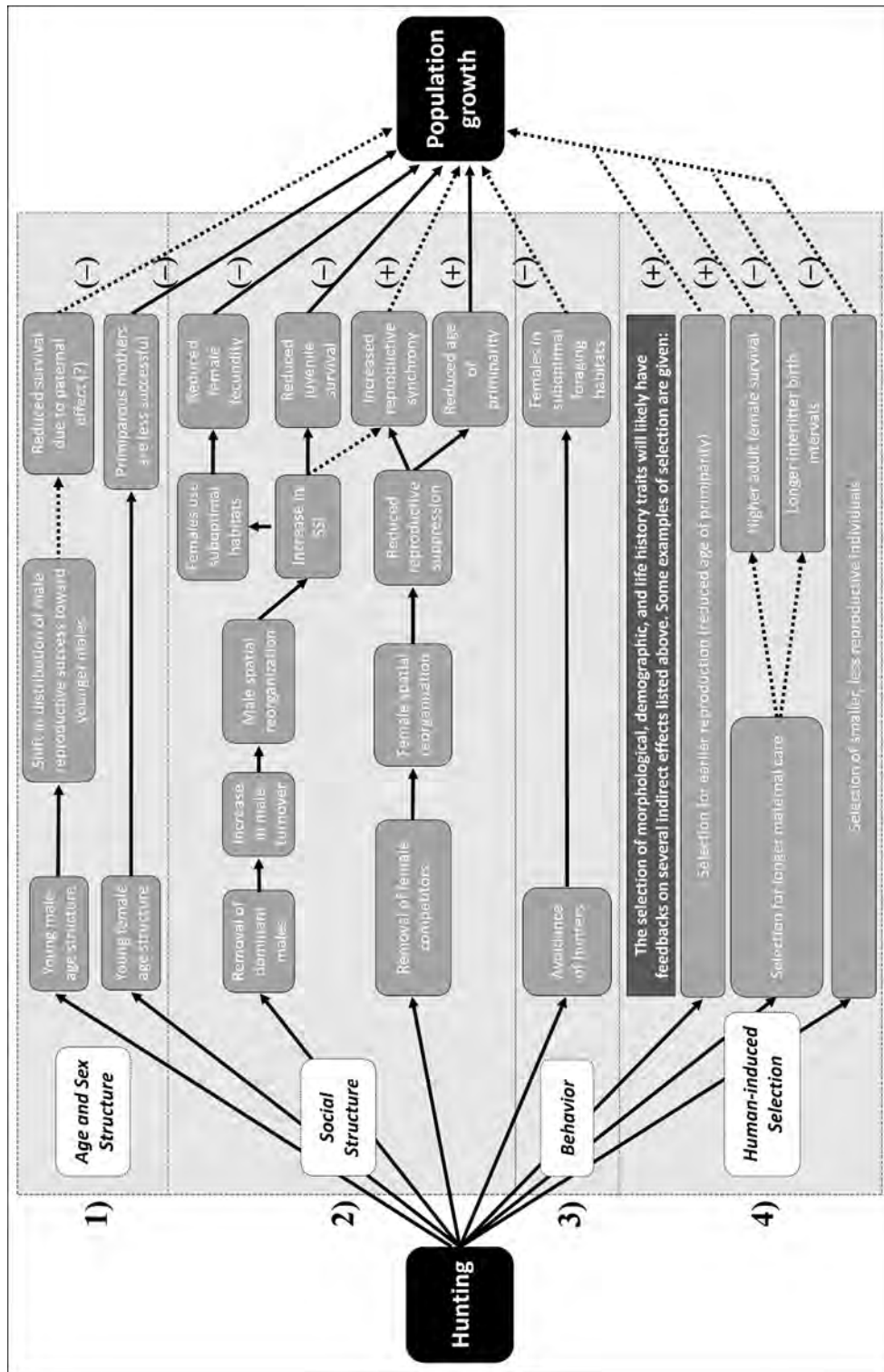


Figure 3. A summary of the indirect effects on population growth of bear hunting discussed in Paper 1. The solid arrows show relationships that have been documented statistically and the dotted arrows show potential

4.2 Paper II: Spatial responses to harvest-induced vacancies and their modulating factors

In papers II and III, we investigated whether surviving bears increased their use of vacancies from the removal of bears due to harvest. In paper II, the strength of spatial responses varied according to sex. In female-female dyads (casualty-survivor), survivors consistently increased their spatial use of a vacancy in the first and second years following the casualty's death (Figure 4). Male-male survivors increased their use of a vacancy in the second year (Figure 4). Survivors in male-female dyads increased their use of a vacancy in the first year after a casualty's death, but it dropped to near baseline level in the second year, and was relatively weaker compared to spatial responses of male-male and female-female dyads (Figure 4). There did not appear to be a spatial response by males to a vacancy left by a killed female (Figure 4). There was support for the competitive release hypothesis, in which the removal of a conspecific is expected to cause an increase in use of this vacancy (Loveridge et al. 2007, Maletzke et al. 2014), but primarily for same-sex dyads. This suggests that a harvest-induced vacancy could be an opportunity for bears to gain access to resources, e.g. habitat or mates, which are deprived directly or indirectly by same-sex conspecifics.

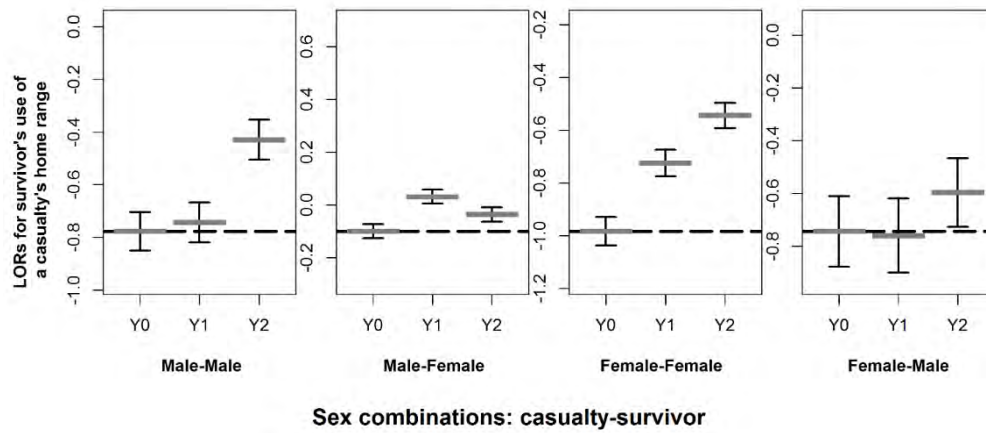


Figure 4. Log-odds ratios of brown bear survivors' use of a casualty's HR during the year in which the casualty died (Y0), the first (Y1) and second (Y2) year after the casualty's death for different casualty-survivor sex combinations. The dashed line is the baseline year (Y0) indicating the survivor's use of the casualty's HR before the casualty's death.

The most important factors modulating these responses also varied depending on sex. Pairwise relatedness was the most important predictor in modulating spatial responses for both female-female and male-male dyads, but it was not important for male-female spatial responses (it was not included in the final model). For female-female dyads, this corresponds to higher overlap between related individuals (Støen et al. 2005), as higher relatedness reflected a higher magnitude of relative use, but the increase in use of a vacancy was virtually equal between females of low and high relatedness (Figure 5, panels b). These results suggest that there is little difference in competitive relationships between related and unrelated bears, which is in contrast to previous suggestions related to female-female space-use and kinship (Støen et al. 2005). Younger females had stronger spatial responses to a female vacancy (not shown), possibly indicating that areas of older females are more resilient to spatial perturbations from harvest. Alternatively, younger females could be more responsive to possible benefits and less wary of the costs associated with shifting HRs (Forrester et al. 2015).

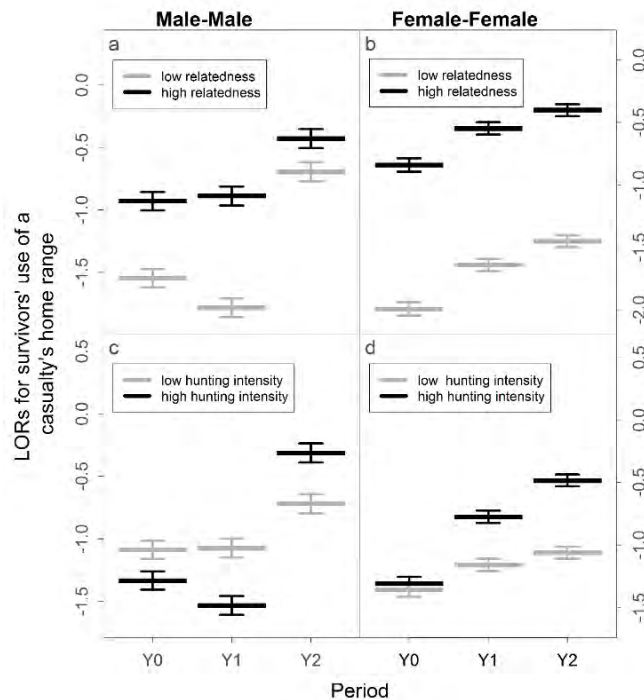


Figure 5. Log-odds ratios of nearby surviving brown bears' (survivors') use of hunter-killed bears' (casualties') HRs during the year in which the casualty died (Y0), the first year after the casualty's death (Y1), and the second year after its death (Y2) in response to casualty-survivor relatedness (panel a, b) and previous hunting intensity (panel c, d). Low and high values of relatedness and hunting intensities represent the 25th and 75th 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.

Contrary to our prediction in paper II, relatedness also was important for male-male dyads, with lower relatedness corresponding to a stronger increase in use of a vacancy (Figure 5, panel a). Previous research did not find a kin-related spatial structure for males in this study population (Støen et al. 2005), but our results suggest that solitary males in localized social contexts could be influenced by relatedness. In group-living species, higher relatedness between males has been associated with increased tolerance during social interactions (Clutton-Brock and Huchard 2013b) and this association appears to be rarer in solitary species, but this could be a result of fewer studies assessing such associations (Gehrt et al. 2008, Lode 2008, Maher 2009, Elbroch et al. 2016). Male-male interactions among solitary carnivores are likely more complex than previously thought, as they may associate more than previously expected and have different environmental drivers between such interactions (e.g. Lührs and Dammhahn 2009, Lührs and Kappeler

2013, Elbroch et al. 2016). Nevertheless, we consider the effect of kinship on male-male interactions with caution in our study, because the range of relatedness values among male dyads was low (from -0.31 to 0.17). Older males exhibited a stronger spatial response than younger males (not shown), perhaps owing to a greater ability in detecting HR changes with larger cognitive maps (Galef and Laland 2005, Noyce and Garshelis 2014) and older/dominant male bears may be better at capitalizing novel resources (Fox et al. 1981, Gende and Quinn 2004).

Furthermore, hunting intensity was the most common variable modulating spatial responses across all sex combination dyads. Hunting intensity consistently had a positive effect on increases in use of a vacancy (Figure 5, panels c and d; male-female not shown), indicating possible long-term effects of harvest on animal spatial responses. 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. For example, to mitigate the intensifying effect of harvest on the instability of social structures, attempts to redistribute harvest, such as creating harvest refugia for several years to allow the recovery of a more natural social structure (*sensu* leaving an agricultural field fallow for the recovery of soil), could be an experimental option. The results of such an experiment could give better insight into the role of social structure on individual fitness and population dynamics. 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.

4.3 Paper III: Harvest-induced vacancies and sexually selected infanticide

In paper III, we investigated whether a hunting-induced spatial reorganization of males could contribute to SSI. The analysis in paper III did not use relatedness as a covariate, whereas the analysis in paper II did. This resulted in slightly different results between papers II and III. In both papers, male bears increased their use of vacancies two years after the harvest of a nearby male conspecific. In paper III, the spatial reorganization of males was influenced by ages of casualties and survivors (i.e. the bear surviving for two years after a harvest event), hunting intensity, and bear density. The age of casualties was an important modulating factor of spatial responses for male-male dyads in paper III, but not in paper II. The importance of casualty age may have become emphasized, because relatedness was not a part of the fixed effects structure in paper III. In paper III, older casualties resulted in a stronger spatial response from survivors, perhaps owing to the removal of a stronger dominant and competitive presence (Figure 7, panel D). Survivors had a higher initial overlap with the hunter-killed male and showed a weaker spatial response at higher densities (Figure 7, panel C). A weaker response at higher densities could be explained by stronger competition and limited space between remaining survivors. The effects of survivor age as well as hunting intensity on spatial responses were similar in paper II and III (results on survivor age from paper II not shown here), except that there was virtually no spatial response of young survivors in paper II, whereas it was quite strong in paper III (Figure 7, panel A). Similar to the differences in the importance of casualty age between papers II and III, the absence of relatedness from the analysis in paper III may have also emphasized the importance of survivor's age in explaining male-male spatial responses.

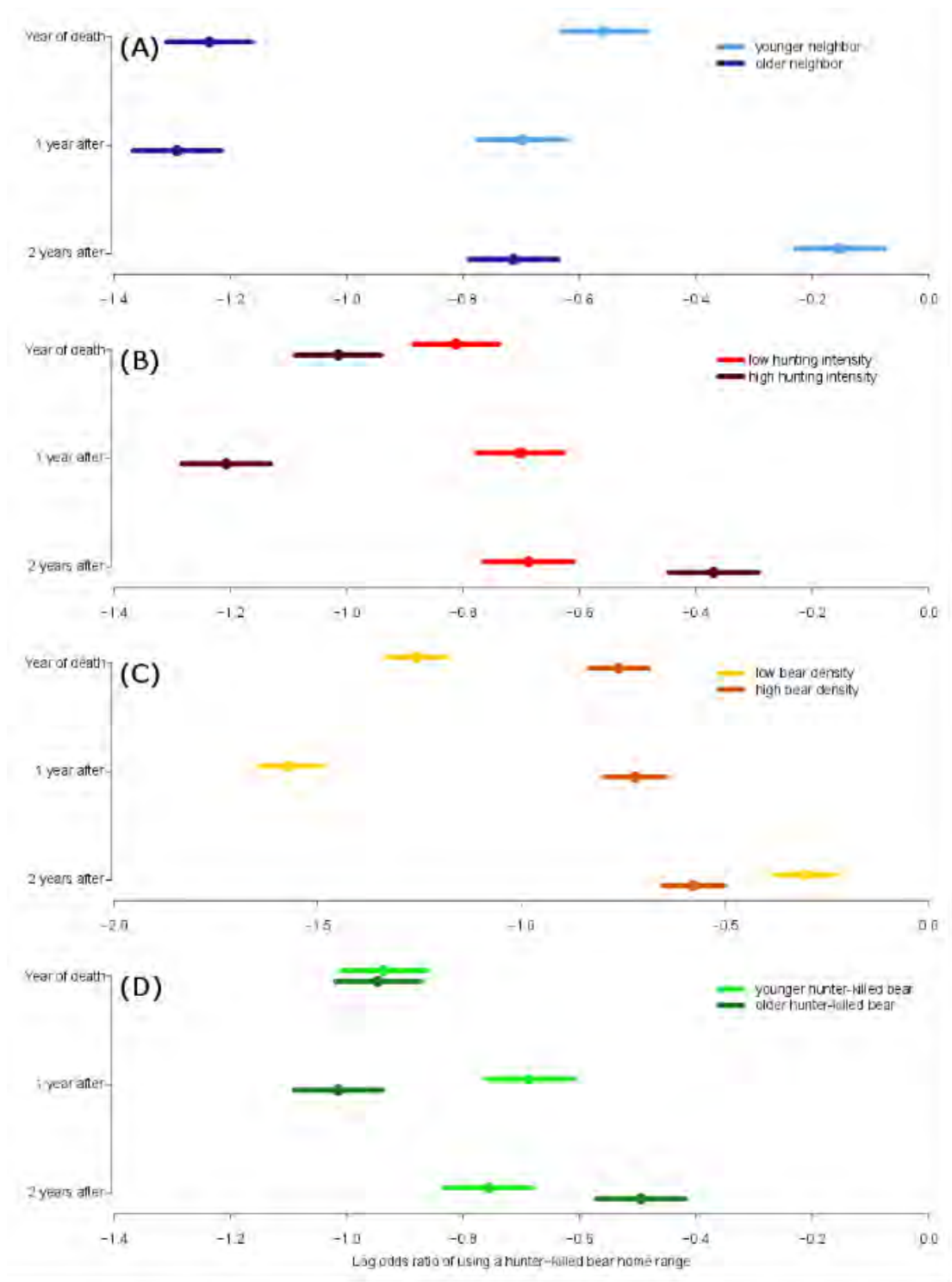


Figure 7. Influence of intrinsic and extrinsic factors on the speed and strength at which a surviving male used hunter-killed neighboring males' HRs. Shown are the coefficients and 95% confidence intervals for three consecutive years, i.e. the year the hunter-killed male was shot (baseline) and the following two years, depending on the surviving male's age (A), hunting intensity (B), population density (C), and hunter-killed male's age (D). The low and high values in each panel represent the 25th and 75th percentiles, respectively, observed in the database.

However, we found consistent indirect evidence that hunting destabilized the spatial organization of the population for at least two years after a male had been killed. This is consistent with earlier studies on the same population that showed lower cub survival following a two-year time lag after a male had been killed (Swenson et al. 1997, Gosselin et al. 2017). The two-year period before male bears exhibited a spatial response to vacancies could be due to their biology, i.e., their need to hibernate. For example, a male entering hibernation soon after harvest may not detect the absence of a male neighbor until later in the following year, then increasing its use of a vacancy during the subsequent spring. This timing coincides with the 1.5-year delayed effect on juvenile survival reported in Swenson et al. (1997). Although potentially influenced by denning in bears, long-term effects from harvest resulting in SSI are also observed in other carnivores. In African lions, male turnover due to harvest induces HR shifts and territory takeovers, and increases the risk of SSI both in the short- and long-term (Loveridge et al. 2007, Elliot et al. 2014). In addition to infanticide from incoming males, male turnover causes juvenile males to disperse prematurely, incurring a relatively higher risk of mortality, which has been labeled as "delayed infanticide" (Elliot et al. 2014).

Harvest and harvest intensity can contribute to long-term effects on SSI and population growth. Male bears appear to assess their paternity through their mating history (Soltis et al. 2000). Harvest causes HR shifts and these spatial responses are amplified by harvest intensity. This would increase the probability that a male could encounter a female with whom he had not previously mated and increase the probability of SSI (Gosselin et al. 2017). Although male turnover occurs in natural populations, a social disruption such as this is likely to be stronger in harvested populations, where the number of removals can exceed that of natural mortality or be additive. Moreover, the spatial distribution of the hunting mortality of bears in our study area is heterogeneous (Steyaert et al. 2016), potentially causing spatial variation in the effects of social disruptions. Such disruptions through the removal of animals can degrade social network cohesion (Williams and Lusseau 2006) and influence reproduction (Gobush et al. 2008). In our study population, neighboring females can influence each other's

probability to have cubs (Ordiz et al. 2008). Harvest can therefore increase heterogeneity of survival and reproduction on the landscape through direct mortality, the indirect effect of increasing cub mortality due to SSI, and the potential reproductive impacts on female social networks. These effects combined could increase demographic variability and ultimately affect effective population size (Lande et al. 2003, Vindenes et al. 2008). Understanding the indirect consequence of hunting over long time scales is critical for developing sustainable management practices and for the viability of harvested populations.

4.4 Paper IV: Effects of hunting mortality on fine-scale genetic structure

In paper IV, we assessed the effect of hunting pressure on female fine-scale genetic structure (FGS) (i.e. structure across subdivisions of a population; Coltman et al. 2003b) by dividing the female bear population into matriline and by temporally dividing them into low and high hunting pressure periods, i.e., "early" (years 1990-2005) and "late" (years 2006-2011), respectively. These periods reflect a change in management regimes. We found that FGS decreased from the early to the late period for each FGS metric used (Figure 8, panels A-D). Conversely, both hunting pressure and population size increased significantly from early to late periods (median values: from 0.13 to 0.29 and from 1639 to 2975, respectively). Population size did not appear to reduce FGS (Nussey et al. 2005), as there were nearly equal numbers of breeding females between early and late periods. Moreover, the temporal subdivision alone on the female population, i.e., excluding matriline, did not differ in structure between early and late periods for either the population or matriline data sets (Figure 8, panels A and B).

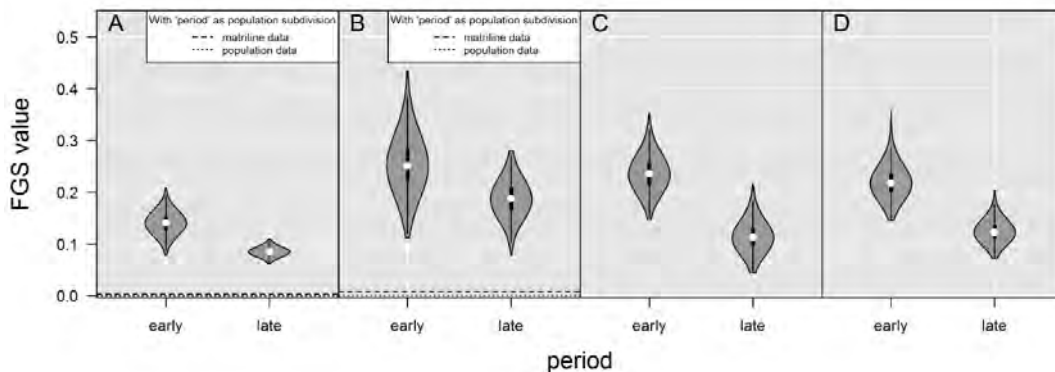


Figure 8. Indices of fine-scale genetic structure (FGS) using matriline as the population subdivision in brown bears in Sweden between periods of low and high hunting pressure, i.e., "early" (years 1990-2005) and "late" (years 2006-2011), respectively. Indices used were F_{ST} (panel A), G'_{ST} (panel B), r_{xy} structure from Lynch-Ritland (1999) (panel C), and r_{xy} structure from a constructed pedigree (panel D). Each index was bootstrapped ($N = 1000$); for F_{ST} and G'_{ST} , indices were bootstrapped across loci, whereas r_{xy} indices were bootstrapped across individuals. For F_{ST} and G'_{ST} , 'period' was also used as a population subdivision to assess whether females showed different structure between early and late periods. Two data sets, i.e. a matriline data set and a population data set, were each used to assess this, both of which showed little evidence of structure among females between periods (broken lines). However, fine-scaled genetic structure was evident among matriline, which has decreased from early to late periods for every index used.

Higher hunting pressure, i.e., the late period, significantly lowered the survival of females and mother-daughter pairs (Figure 9, panels A and B). Cox proportional hazards model results indicated that adult females (≥ 4 years) and mother-daughter pairs had lower probabilities of survival in the late period (Fig. 9, panel A). Therefore, it was less probable that a matriline would form or be maintained in the late compared to the early period (Figure 9, panel B).

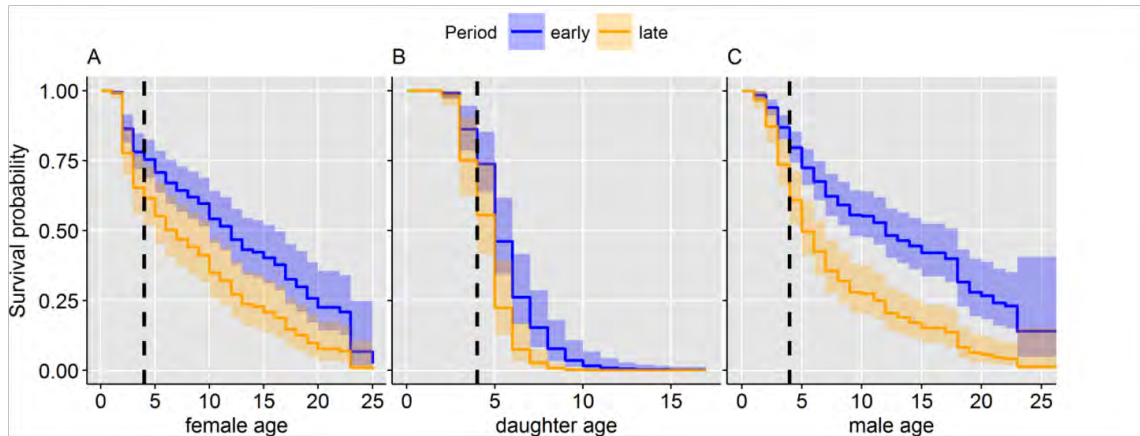


Figure 9. The probability of survival using cox proportional hazards model for marked female brown bears (panel A), mother-daughter pairs (panel B) and males (panel C) in Sweden. In all panels, the broken lines indicate age 4, i.e., at which a female or male was considered reproductive, and when a female was a part of a matriline in our study. Model predictions suggested that matriline formation and maintenance was less probable in the period of high hunting pressure (late, 2006-2011) compared to low hunting pressure (early, 1990-2005). Both reproductive females and males had lower survivorship in the late compared to the early period, particularly after reaching adulthood.

Despite nearly equal numbers of females between periods, the proportion of males siring offspring increased in the late period (mean early: 0.26; mean late: 0.38). Previous research has suggested that heterogeneity in male reproductive success is indicative of male dominance structure during the mating season in this population (Zedrosser et al. 2007a), as seen in other bear populations (Kovach and Powell 2003, Costello et al. 2009). Hunting can disrupt social structures and cause spatial reorganizations of both sexes in this population (papers II and III) and enhance SSI (Swenson et al. 1997, Gosselin et al. 2017). SSI is a strategy used by males to gain access to novel females. As more males, including dispersers, become successful breeders across matriline during the mating season with higher hunting mortality, the relative male gene flow among matriline would increase.

Differential dispersal distances between the sexes between periods may have also affected male gene flow. For instance, female dispersal distances decreased between early and late periods (median values: 11.4 and 6.7 km; N = 36 and N = 39, respectively), whereas there was no evidence of a change in dispersal distances in males (median values: 89.2 and 81 km; N = 27 and N = 26, respectively). As a result, the longer male dispersal distances relative to that of females in the late period likely increased male

gene flow among matriline. At high densities, stronger competition can increase costs of breeding and cause heterogeneity in reproductive success, favoring more dominant individuals (Festa-Bianchet et al. 1998), but we observed a wider distribution of reproductive success despite high densities. This suggests that male dominance structures in this population (Zedrosser et al. 2007a) were rather disrupted by harvest. Hunting pressure has been linked to differences in sex-specific dispersal patterns in other large carnivore populations (Robinson et al. 2008, Cooley et al. 2009, Elliot et al. 2014). Furthermore, hunting has affected social structure, mating patterns, and genetic structure in other species (Rutledge et al. 2010, Ausband et al. 2017).

By using several FGS metrics, coupled with individual-based survival probabilities and proxies for dispersal distances and male gene flow, our study highlights that hunting can contribute to a decrease in FGS. Genetic structure is important for the conservation and management of wildlife, because it affects and reflects fundamental processes, such as dispersal, mating, and ultimately individual fitness and persistence of populations (Fryxell et al. 2014). Specifically, we propose that hunting has (1) removed adult females from matriline and adult males from the population and (2) redistributed breeding success among males, all of which has contributed to the decrease in FGS among matriline. It remains unclear how such alterations of FGS can affect the long-term viability, persistence, and/or conservation of populations. It has been suggested that asymmetric gene flow among matriline, which can increase FGS, may be important for the adaptive potential of species or populations (Baltazar-Soares and Eizaguirre 2016). Despite many unknowns, changes in genetic structure due to harvest certainly warrant further attention, so that harvest management plans can be developed to safeguard populations against potential harmful effects (Allendorf et al. 2008). For example, changes in FGS due to hunting could be a smoking gun, with reference to otherwise undetected changes at the population or interpopulation level, and could be an indication of how hunting is selective at different scales within a population. This emphasizes the need to both collect genetic samples over time (Allendorf et al. 2008) and analyze populations including 'social' scales, e.g., along matriline (Parreira and

Chikhi 2015). We stress the importance of using multiple scales when assessing changes in genetic structure, particularly in hunted populations of long-lived species in which changes to genetic structure might take longer to recover from (Allendorf and Hard 2009).

Frank: The effects of hunter harvest on the sociospatial and genetic structure of a solitary-living large carnivore, the brown bear *Ursus arctos*.

5 Conclusions and perspectives

This thesis provides a background of documented and potential indirect effects of brown bear harvest, which can influence population growth rate beyond that expected from direct mortality. Although the findings here can be specific to the brown bear or the Swedish brown bear population, it is probable that indirect effects of harvest are more prominent than currently considered, given that many wild populations incur changes to age, sex, and to social structure from harvest. Furthermore, we show that changes to social structure due to harvest resulted in a spatial reorganization of surviving animals, which can provide a mechanism for unintended consequences for population growth, such as enhancing SSI. We also provide evidence that harvest could decrease the FGS of brown bear matriline. However, PhDs invariably result in more questions, challenges, and opportunities.

For example, we did not make an explicit link between harvest-induced changes in social structure to individual fitness and population growth. A potential way forward with this is social network analysis that could be used to link network 'position' and patterns of relationships or interactions to fitness (Wey et al. 2008, Snijders et al. 2017). The effect of harvest on social structure can be quantified with such tools, for example, through the number of 'interactions' among individuals (e.g. via spatiotemporal proximity of GPS positions) while taking into consideration explanatory effects from covariates, such as pairwise relatedness between individuals.

Furthermore, with this method, bears can be evaluated in relation to the solitary species hypothesis by explicitly tested for the presumed lack of continued associations between individuals during the nonbreeding season. For instance, we have observed three generations of bears interacting via GPS locations (grandmother, mother, and daughter), and siblings can stay in contact following separation from their mother (SBBRP unpublished data). Whether these interactions or associations are consistent phenomena across populations or how they can affect life history has not been

examined yet. An individual's network position (i.e. relationships), even in solitary species, could influence heterogeneity in survival and reproduction. Harvest can reduce such possibilities and other relationships between adults from developing. As a result, harvest affects the stability of social structures and, hence, populations (Williams and Lusseau 2006, Gobush et al. 2008). The challenge of knowing the effects of harvest in this regard are two-fold: there are no control populations (though a proxy can be generated through a randomized social network representing a 'null' hypothesis) and it is difficult to conduct actual experiments on wild populations due to many potential, influential variables. Though we do not yet know how the degree of interactions and consequent relationships can influence individual fitness in solitary-living species, these species could be more 'social' than previously thought (Elbroch and Quigley 2016). In defining a species' social organization (i.e., group size and composition; Kappeler and van Schaik 2002, Schradin 2013), as either "solitary" or "group-living", there is a risk of oversimplifying its sociality, i.e., the degree to which individuals interact, recognize one another, and form relationships (Kappeler et al. 2015). Such oversimplification could be detrimental to managing threatened populations containing few individuals, in which the relative importance of these relationships are increased (e.g. the Allee effect; Berec et al. 2007).

Quite intriguing is the idea that animal relationships and the products of interactions (e.g. aggression or dominance structures) are themselves phenotypes, i.e., an expression of "interacting phenotypes" between individuals (Moore et al. 1997, Wolf et al. 1999, Moore et al. 2002, McGlothlin et al. 2010). Through this lens, it is quite possible that human harvest can be selective of sociality in populations by altering the frequency of individual phenotypes and thereby interacting phenotypes found within populations. For example, if "bold" animal personalities are selectively harvested from a population (Ciuti et al. 2012, Leclerc et al. 2017), it is possible that this could be correlated with the removal of other social traits and, thus, interacting phenotypes in populations. In fact, the social organization of species can vary due to several sources, including genetics, phenotypic plasticity, social flexibility, and mortality (Schradin 2013). Moreover,

intraspecific variation in animal social systems (which includes its social organization) is commonplace, with harvest management suggested as an influencing factor (Lott 1991), but this has not been well studied (Deblinger and Alldredge 1989).

Such knowledge could be useful for managers to create sustainably managed populations by adjusting the selectivity of harvest. This is speculative, but it runs parallel to the management of morphological and other life history traits in populations through harvest (Harris et al. 2002, Allendorf et al. 2008). For this to be a viable tool, interpopulation comparisons are needed. This is true in general to enhance our understanding of species. For example, we highlight that SSI has been a rather contentious issue in paper I, particularly because there were different findings between North America and Scandinavia. A meta-analysis of SSI (e.g. presence/absence or frequency) including multiple brown bear populations would elucidate potential drivers and how managers can influence this indirect effect of harvest.

Also highlighted in this thesis is how humans can affect wildlife. The "Anthropocene" coincides with a massive defaunation, now commonly referred to as the sixth mass extinction (Dirzo et al. 2014, Ceballos et al. 2017). Indeed, most of the world's terrestrial megafauna populations are declining, including both large carnivores (≥ 15 kg) and the largest herbivores (≥ 100 kg) (Ripple et al. 2016). In light of these labels and population trends, the prospects of conserving wildlife, particularly those which are most threatened such as large carnivores (Ripple et al. 2014), can seem dismal. Indeed, the effect of humans on the world has been called an ecological and a biodiversity crisis (White 1967, Wilson 1985). John F. Kennedy once stated "in a crisis, be aware of the danger--but recognize the opportunity." In the field of ecology, it is easy to find the 'danger' in terms of habitat destruction, overexploitation, the introduction of invasive species, all of which contribute to endangering species (IUCN 2017). And, these facts should be taken seriously. Learning how populations are unable to cope with such exploitation and other anthropogenic effects, however, might prevent the destruction of other populations. For example, despite the danger posed by invasive species, novel approaches toward their eradication can provide understanding of overexploitation and

its effects on animal social structure. Particularly noteworthy is how small population size and harvest may have interacting effects on a species' social system, which holds particular value for the conservation of endangered species for which experimentation for their recovery is not possible. Similar to using surrogate species to test reintroduction techniques for their use on more threatened species (Powell and Cuthbert 1993), eradication programs can be used to understand the overexploitation of threatened species. Such studies could bridge the gap from correlational studies on harvest to experimental, causal ones. As an example, extensive monitoring of individual animals during the eradication or "overexploitation" of the invasive American mink (*Neovison vison*) in parts of Europe could provide an understanding of the concurrent social effects, i.e., on its social organization, social structure, and mating system. This could provide useful information for the conservation of the endangered Eurasian mink (*Mustela lutreola*) in areas where exploitation is a cause of decline or where reintroduction of few individuals is planned. Such findings would certainly spur on further questions and hopefully give managers more tools for a range of issues, such as managing human-wildlife conflicts, population size of game species, and conserving endangered populations on which knowledge or the ability to conduct studies is limited.

6 References

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Paper I:

Frank, SC, Ordiz A, Gosselin J, Hertel A, Kindberg J, Leclerc M, Pelletier F, Steyaert SMJG, Støen OG, Van de Walle J, Zedrosser A, and Swenson JE. "Indirect effects of bear hunting: a review from Scandinavia." In press in *Ursus*.

Indirect effects of bear hunting: a review from Scandinavia

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Abstract: Harvest by means of hunting is a commonly used tool in large carnivore management. To evaluate the effects of harvest on populations, managers usually focus on numerical or immediate direct demographic effects of harvest mortality on a population's size and growth. However, we suggest that managers should also give consideration to indirect and potential evolutionary effects of hunting, e.g., the consequences of a change in the age, sex, and social structure, and their effects on population growth rate. We define "indirect effects" as hunting-induced changes in a population, including human-induced selection, that result in an additive change to the population growth rate " λ " beyond that due to the initial offtake from direct mortality. We considered four major sources of possible indirect effects from hunting of bears; 1) changes to a population's age and sex structure, 2) changes to a population's social structure, 3) changes in individual behavior, and 4) human-induced selection. We identified empirically supported, as well as expected, indirect effects of hunting, based primarily on > 30 years of research on the Scandinavian brown bear population. We stress that some indirect effects have been documented, e.g., habitat use and daily activity patterns of bears change when hunting seasons start and changes in male social structure induces sexually-selected infanticide and reduces population growth. Other effects may be more difficult to document and quantify in wild bear populations, e.g., how a younger age structure in males may lead to decreased offspring survival. We suggest that managers of bear and other large carnivore populations apply the cautionary principle and assume that indirect effects do exist, have a potential impact on population structure, and, ultimately, may have an effect on population growth that differs from that predicted by harvest models based on direct effects alone.

The manipulation of populations is the core around which wildlife management activities are organized (Fryxell et al. 2014). Caughley's (1977) original list of four general objectives in wildlife management are still relevant (Fryxell et al. 2014): 1) make a population increase, 2) make it decrease, 3) hunt it for a continuing yield, or 4) do nothing except monitor the population. Harvest is a common management practice to reach population goals (i.e., objectives 2 and 3) in mammal populations, including carnivores (Lindsey et al. 2007, Linnell et al. 2008, Packer et al. 2009, Swenson et al. 2017). However, it is essential to understand the population dynamics of exploited species in order to determine the appropriate harvest rates to reach a population objective (Sinclair 1991).

Although the harvest of populations is supported by solid scientific underpinnings, there are still knowledge gaps about the consequences of hunting in wild populations, particularly for the harvest of large carnivores (Treves 2009). For example, managers usually focus on the effects of direct hunting mortality on a population's growth rate (e.g., Knight and Eberhardt 1985, Miller 1990, Linnell et al. 2010). Nevertheless, there is an increasing number of studies showing that indirect effects, which managers often do not consider, also may affect population growth (e.g., Milner et al. 2007, Pauli and Buskirk 2007, Treves 2009). For the purpose of this review, we define "indirect effects" as hunting-induced changes in a population, including human-induced selection, that result in an additive change to the population growth rate " λ " beyond that due to the initial offtake from direct mortality. Understanding the causal relationships between harvest and indirect effects on population growth is thus crucial for the management and conservation of wild mammal populations.

Here, we focus on hunting-induced changes to population age, sex and social structures, in the behavior of remaining individuals, and we address hunting-induced selection in bear populations (termed demographic side effects in Milner et al. (2007)). We primarily review the literature from the Scandinavian Brown Bear Research Project (SBBRP), because it is illustrative to discuss the subject in one system where brown bears (*Ursus arctos*) have been managed as a game species for >70 years. We distinguish between pathways that have been documented statistically and those that are expected to occur (see Fig. 1). In addition, we also include literature about indirect effects of harvest on growth rates in other bear populations.

Study areas and hunting regime in Sweden

The SBBRP has had two study areas; one in northern Sweden from 1984-2013, where 254 individual brown bears have been radiomarked and followed, mostly with VHF telemetry

(8,000 km²; termed “north”), and one in central Sweden-southeastern Norway from 1985 to the present (13,000 km²; termed “south”). There, 449 individuals were radiomarked and followed with VHF telemetry and, from 2003, with GPS technology. The north consists of alpine mountain and coniferous forest habitats and included parts of some national parks. The south was exclusively managed coniferous forests. See Zedrosser et al. (2006) for more detailed descriptions of the study areas, and see Arnemo et al. (2011) for capture methods. Our behavioral studies were conducted in the south.

Hunting brown bears has been legal in Sweden since 1943, outside the national parks, and generally lasts from 21 August until the area-specific, annually established quota has been filled (Swenson et al. 2017). Quotas have been set at variable spatial scales in Sweden, but today are set typically at county or subcounty levels (Swenson et al. 1994, Swenson et al. 1998b, Swenson et al. 2017). Furthermore, recent population objectives have varied by county and most objectives have not been met, with local numbers of bears either remaining stable or declining (Swenson et al. 2017). The Scandinavian bear population has increased from around 300 individuals in the 1940s to around 3,000 bears today, with approximately 95% of those found in Sweden (Swenson et al. 1994, Kindberg et al. 2011, Swenson et al. 2017). Not until recently (2008-2013) have bears exhibited a decrease in population size across Scandinavia, which is most likely due to an increase in harvest rate in Sweden (Swenson et al. 2017). Population density varies and is approximately ~11 bears/1,000 km² in the north and ~30 bears/1,000 km² in the south (Solberg et al. 2006, Zedrosser et al. 2006).

All bear hunters are required to possess an annual hunting license, pass an annual shooting test, and it is common to take a hunting test specific for bears, but is not required by law. There is no bag limit on bears, and any bear can be killed, except females and their cubs, which are all protected regardless of the cubs' age. Bears are hunted using stalking, sitting at posts, with dogs, or at bait sites; dog hunting is gaining in importance (Bischof et al. 2008, Swenson et al. 2017). It is legally required for all harvested bears and dead bears found to be reported to local authorities, at which point samples (e.g., tissue, hair, a premolar tooth for aging) and measurements (e.g., weight, sex) are taken.

Hunting is the most important cause of bear mortality in Sweden, as 60% of all marked bears ≥ 1 year of age that are recovered dead have been killed legally by hunters, with an additional 13% dying naturally (Bischof et al. 2009). In Sweden, data from 1984-2006 suggest that hunters exhibit low selectivity for age, size, and sex, except for a slight bias towards males in the north (Bischof et al. 2009). This is probably because of limited encounter rates, traditions, and difficulties to distinguish males from females in the wild

(Bischof et al. 2008). Also, because there are no individual bag limits and harvest quotas, Swedish hunters may have a low incentive to pass up an opportunity to kill a bear that they encounter (Bischof 2009). However, more recent analyses, based on an expanded data set collected during a time of increased harvest pressure, shows greater selectivity towards older bears (SBBRP, unpublished data), larger yearlings, and larger adult females over time (Leclerc et al. 2016a). The mean age of a harvested bear was ~5 years and males made up a slightly greater share of the harvest than females (55:45) in 1981-2015 (Fig. 2).

We used annual harvest rates of the Swedish population in conjunction with periodic population estimates (Swenson et al. 2017) to define a threshold for "high harvest" in relation to the indirect effects of hunting. A temporal threshold between low and high hunting pressure was set by Gosselin et al. (2015), who found that up to 14% of the variation in population growth rate could be explained by an indirect effect of harvest during high hunting pressure (i.e., after 2005; hereafter "high harvest"). Therefore, we use here the same temporal threshold, i.e., 2005-2006 as the boundary between low and high harvest rates. We conservatively defined the minimum harvest rate observed in the high harvest period as high harvest, which was 7% of the population estimate in Sweden. Although we do this for convenience in having a quantifiable measure to discuss indirect effects, we recognize that indirect effects can come from lower harvest rates than those set here, there can be compensatory effects, and this will vary across populations and hunting regimes.

Changes in a population's age and sex structure

Harvest can affect a population's age and sex structure, influenced by the degree of hunters' selectivity, hunting method, habitat, food availability, and other factors, as shown for different bear species (e.g., McLellan and Shackleton 1988, Derocher et al. 1997, Noyce and Garshelis 1997, Bischof et al. 2008). Although harvesting can change a population's sex structure, this will not necessarily affect reproductive rates in species with polygamous mating systems (e.g., Ginsberg and Milner-Gulland 1994, Milner et al. 2007), such as bears (Steyaert et al. 2012). The harvest of the most productive segment of the population, adult females, has the greatest effect on a bear population growth rate (Knight and Eberhardt 1985, Miller 1990, Zedrosser et al. 2013, Gosselin et al. 2015). Harvest can result in a lower proportion of older animals in the population, even if harvest is not selective to age (Bischof et al. 2008). A reduction in the population-wide age of females should reduce population growth, because primiparous females have a lower litter size and higher cub mortality than multiparous females (Zedrosser et al. 2009, Gosselin et al. 2017) (Fig 1.).

Human-induced mortality can also change the male age structure and influence their age-specific reproductive rates (Bellemain et al. 2006b, Zedrosser et al. 2007). Suggested as a result from greater illegal or unrecorded harvest of bears in the north, only one reproductively dominant adult male brown bear was present in this area for several years, leading to a more skewed operational sex ratio (OSR), with more reproductive females per adult male, compared with the south, which had a less human-influenced age structure, resulting in a less skewed OSR (Zedrosser et al. 2007). This resulted in a significantly higher mean male reproductive success in the north than in the south. Although older and larger males had a higher reproductive success in both areas, age was relatively more important in the north, because the one old male dominated the reproduction (~33% of known offspring in 1990-1997; A. Zedrosser, unpublished data). This uneven age distribution enabled a relatively higher proportion of young males to gain reproductive success in the north than in the south (Zedrosser et al. 2007). In the south, age was more similar among males, potentially favoring larger individuals during intrasexual competition (Zedrosser et al. 2007). As female brown bears exhibit mate choice (Bellemain et al. 2006a, Bellemain et al. 2006b), the removal of older and larger males could result in less desired, younger, and smaller males siring offspring, which could result in lower-quality cubs, i.e. with fitness-decreasing traits or those reducing survival, and therefore potentially lower recruitment. This has not been shown in large carnivores, to our knowledge, but it has been shown in large ungulates (Milner et al. 2007, Martin et al. 2014, Douhard et al. 2016, Kvalnes et al. 2016).

Changes in a population's social structure

There is growing evidence that the harvest of large carnivores can cause changes to their social structure, the space use of survivors, and population growth rate (Rutledge et al. 2010, Newby et al. 2013, Maletzke et al. 2014, Ausband et al. 2015, Fattebert et al. 2016). For bears, the removal of conspecifics through hunting creates vacancies on the landscape and induces surviving animals to shift their home ranges toward these vacancies (Frank et al, in review; Leclerc et al. 2017a). Home range shifts are strongest when the surviving animal is the same sex as the killed animal, which can increase sexually selected infanticide (SSI) by males and enhance female-female competition (Frank et al, in review; Leclerc et al. 2017a). Although little is known about how this spatial reorganization affects individual fitness, links have been made between hunting, male home range shifts, SSI, and variation in population growth (Swenson et al. 1997, Swenson et al. 2001, Swenson 2003, Gosselin et al. 2015, Gosselin et al. 2017, Leclerc et al. 2017a).

SSI is a male reproductive strategy where males gain mating opportunities by killing dependent young (Hrdy 1979). Males should only kill offspring that they have not fathered (SSI requirement #1), litter loss should trigger estrus in a victimized mother and shorten her interlitter interval (requirement #2), and the perpetrator should sire the victimized mothers' subsequent offspring (requirement #3) (Trivers 1972, Hrdy 1979). SSI can be increased through male turnover in both solitary and social species (Soltis et al. 2000, Loveridge et al. 2007) and is the most plausible explanation for infanticide among Scandinavian brown bears (Swenson 2003, Steyaert et al. 2012). Brown bears have extended maternal care (typically 1.5 – 2.5 years in Scandinavia; Dahle and Swenson 2003), and mothers generally do not mate during this period (but see Swenson and Haroldson 2008). After losing a litter during the mating season, however, females are able to enter estrus within a few days (Steyaert et al. 2014). The majority (>90%) of females that lose their litter during a mating season mate successfully and give birth during the subsequent winter (requirement #2 of the SSI hypothesis) (Steyaert et al. 2014). Males can thus generate an almost immediate mating opportunity by killing a litter of cubs-of-the-year instead of waiting until the female becomes receptive again after weaning her young 1.5 to 2.5 years later. In Scandinavia, ~80% of all cub mortality, which is about 42% annually, occurs during the mating season (Gosselin et al. 2015, Gosselin et al. 2017) and is due to infanticide by males (Bellemain et al. 2006a, Bellemain et al. 2006b, Steyaert et al. 2014). No male has been recorded killing his own offspring, likely because of female recognition through his mating history (Wolff and Macdonald 2004) and perpetrators typically sire the offspring of victimized mothers (requirements #1 and #3 of the SSI hypothesis; Bellemain et al. 2006a, Bellemain et al. 2006b, Steyaert et al. 2014). Residents are defined as males whose home ranges overlap with a victimized mother's home range during the mating season before and during the year of infanticide (Bellemain et al. 2006a), and both resident and immigrant males can commit SSI (McLellan 2005, Bellemain et al. 2006a).

In the Scandinavian brown bear, hunting promotes SSI and can indirectly contribute to negative population growth through increased juvenile mortality (Swenson et al. 1997, Swenson et al. 2001, Swenson 2003, Gosselin et al. 2015, Gosselin et al. 2017). Between 1984 and 1995, Swenson et al. (1997, 2001) contrasted cub survival between the north and south. In the north, with few old males and no legal hunting, cub survival was very high (98%) and relatively stable over time. In the south, even under a low harvest rate, cub survival was negatively correlated with the removal of males from the population (24% and 42% lower 0.5 and 1.5 years after harvest, respectively) (Swenson et al. 1997). Furthermore,

Swenson et al. (1997, 2001) calculated that removing one male from the population was equivalent to a recruitment loss of 0.5 to 1.0 adult female and decreased population growth rate by 3.4%. Gosselin et al. (2015) found similar patterns; cub survival was lower under high harvest (2006-2011) compared to low hunting pressure (1990-2005) and, assuming that all cub mortality during the mating season is due to SSI, it could explain ~14% of the variation in population growth rate. Furthermore, Gosselin et al. (2017) showed that male removal decreased cub survival only during the mating season, consistent with the SSI hypothesis, that cub survival increased with distance to the nearest male killed during the previous 1.5 years, and that the spatiotemporal distribution of male harvest is more important than the absolute number of males killed. After the death of a resident male, its male neighbors shift their home ranges towards the 'vacant' area (Leclerc et al. 2017a). This shift is most apparent during the second year after the residents' death, and provides a mechanistic explanation for the 1.5-year time lag in decreased cub survival after male removal (Leclerc et al. 2017a).

Because hunting can promote SSI in Scandinavia, it may also stimulate infanticide counterstrategies and associated costs for females (Agrell et al. 1998, Ebensperger 1998, Palombit 2015). Female brown bears apply several strategies to reduce SSI risk, including aggression to deter infanticidal males (Swenson 2003), multimale mating, and multiple paternity litters to confuse paternity (Bellemain et al. 2006a, Bellemain et al. 2006b). Mothers also adjust their movements and modify their habitat selection to avoid infanticidal males (Steyaert et al. 2013a, Steyaert et al. 2014, Steyaert et al. 2016b). Furthermore, avoiding infanticidal males restricts foraging behavior and carries a nutritive cost (Steyaert et al. 2013b). The reproductive costs imposed by constraints on habitat and diet selection to counter SSI risk have not been estimated in the Scandinavian brown bear, but it has been estimated to decrease female reproductive success by 6% in a hunted brown bear population in Alberta (Wielgus and Bunnell 1994, Wielgus and Bunnell 2000, Wielgus et al. 2001a).

SSI might also have a compensatory effect on population growth by synchronizing reproduction. Ordiz et al. (2008) discussed that SSI may be a mechanism involved in the observed reproductive synchrony among female bears whose home ranges centroids were 10-20 km apart. This implies that an increase in reproductive synchrony, due indirectly to harvest, conceivably could have a positive effect on population growth (Fig. 1), thus somewhat compensating for the negative effect of harvesting. However, this implication is theoretical and there is no empirical support for it.

Whereas hunting promotes SSI in Scandinavia, hunting can have the opposite effect in other populations and enhance cub survival (McLellan 2005). Male-biased hunting can reduce the OSR and may relax male-male competition and eventually reduce SSI risk (Miller et al. 2003, McLellan 2005). Such a mechanism has been suggested in several populations of North American brown bears (Miller et al. 2003, McLellan 2005, 2015) and black bears (*Ursus americanus*) (Czertwytynski et al. 2007, Obbard and Howe 2008). The role of OSRs in explaining variation in SSI and the potential effects on population growth rate may thus vary among bear populations according to local ecological and evolutionary constraints. It should be noted, however, that the occurrence of SSI in North America is a controversial subject. Little evidence of SSI has been found in several North American black and brown bear populations (Miller et al. 2003, McLellan 2005, Czertwytynski et al. 2007, Obbard and Howe 2008), although it has been reported in one study of American black bears (LeCount 1987).

The disruption of female social structure in bear populations has been studied less than for males. However, female social structure likely influences how females compete for the resources necessary for reproduction (Clutton-Brock and Huchard 2013). Indeed, female spatial distribution is one of the most important drivers of mating systems (Andersson 1994, Shuster and Wade 2003) and, for most mammals, including brown bears, the female is the more philopatric sex (Greenwood 1980). Harvest has altered dispersal rates in other large carnivores (Sweanor et al. 2000, Newby et al. 2013), which could have large impacts on female distribution and, consequently, population growth (Robinson et al. 2008, Cooley et al. 2009). Harvest effects on animal movement can also be more localized, for example, inducing home range shifts (e.g., Lovallo and Anderson 1995). Female-female competition for reproduction has been reported in our study area (Støen et al. 2006, Ordiz et al. 2008, Zedrosser et al. 2009) and female Scandinavian brown bears appear to exhibit a competitive release following the removal of nearby females through harvest (Frank et al. in review). Reduced female-female competition through harvest may improve female condition and reproductive performance, with a positive effect on population growth rate; although this remains to be documented.

Reproduction is suppressed in young philopatric female brown bears, with age of primiparity being higher for philopatric females compared to dispersers (Støen et al. 2006, Ordiz et al. 2008). Harvesting females could relax reproductive suppression and competition for food, favoring earlier reproduction and early cub survival (Zedrosser et al. 2009), which is expected to have a positive effect on population growth rate (Fig. 1). Competition among

females for reproduction also occurs after primiparity; the probability of a female brown bear having cubs in a given year varies in relation with distance to the closest neighboring female and whether or not the latter has cubs (Ordiz et al. 2008). Thus, dominant pregnant adult female brown bears appear to inhibit reproduction in their female neighbors, imposing reproductive asynchrony (Ordiz et al. 2008). This reproductive asynchrony may be a factor limiting population growth, suggesting the existence of a population-regulatory nature that is typically found in social species, rather than solitary animals (Ordiz et al. 2008).

Dispersal in large carnivores has been shown to change due to harvest (e.g., Cooley et al. 2009), which could affect the distribution of females across the landscape (e.g., Robinson et al. 2008); there is some evidence of this in brown bears near the Swedish-Norwegian border (Bischof and Swenson 2012, Gilroy et al. 2015). The number of bears in Sweden has decreased in the past few years, due to a higher hunting quota (Swenson et al. 2017) and simultaneously the number of bears detected in Norway has decreased from 2009 to 2015 (Aarnes et al. 2016). The increased harvest in Sweden has probably reduced the dispersal of bears from the high-density areas and provided more vacancies in the nearby peripheral areas in Sweden, such as along the Norwegian border (Swenson et al. 1998a), which could result in reduced movement of bears into Norway. However, the effect of altered dispersal and female distribution on lambda is still unknown.

Behavioral indirect effects from hunting

Wildlife are generally sensitive to human-induced disturbances (e.g., see George and Crooks 2006 and references therein). Bears are no exception and generally avoid people and their activities [e.g., Peyton et al. (1998) for Andean bears *Tremarctos ornatus*; Goodrich and Berger (1994) and Stillfried et al. (2015) for American black bears; Fortin et al. (2016) for North American brown bears; Nellemann et al. (2007) and Ordiz et al. (2013b) for Scandinavian brown bears]. Here we review the effects caused by the disturbance of hunting on bears' behavior and their potential effects on population growth.

After encountering a human (e.g., a hunter), a Scandinavian brown bear's daily activity patterns are altered immediately and for several days (Moen et al. 2012, Ordiz et al. 2013b, Sahlén et al. 2015). At the onset of the hunting season, bears immediately alter their habitat use and movement pattern (Ordiz et al. 2011, Ordiz et al. 2012). Solitary bears increase their movement during the dark hours, losing their normal nocturnal rest, presumably to compensate for reduced diurnal activity (Ordiz et al. 2012, Hertel et al. 2016b). However, the change in movement patterns of females with cubs, which are legally

protected from hunting, was much lower in magnitude (17%) than that observed for solitary bears at the onset of the hunting season, perhaps because they still have to meet the elevated energy requirements of maternal care (Ordiz et al. 2012).

An important question is whether the consequences of hunter-caused disturbances are great enough to influence population growth. To maximize food intake, foraging bears select locations providing the highest energetic gain (Hertel et al. 2016a) or forage at times when prey detection is easiest (MacHutchon et al. 1998) and prey are most vulnerable (Klinka and Reimchen 2002, 2009). For instance, brown bears are very efficient in preying on Pacific salmon (*Oncorhynchus* spp.) and reindeer calves (*Rangifer tarandus*) at night (Klinka and Reimchen 2002, Ordiz et al. 2017), whereas bears forage in the best berry habitat patches during the crepuscular and light hours (McLellan and McLellan 2015, Hertel et al. 2016b). Because bears have a limited period to acquire resources prior to hibernation, any alteration to their foraging behavior may have negative effects on their body condition and fitness (Hertel et al. 2016b).

Hunting can be perceived by bears as a predation risk (Ordiz et al. 2011, Sahlén et al. 2015, Steyaert et al. 2016b), forcing them to increase vigilance at the expense of foraging activity during the hunting season and therefore suggesting that a human-induced landscape of fear exists in our hunted population of brown bears (Sahlén et al. 2015, Støen et al. 2015, Steyaert et al. 2016a). Similar findings have been reported in ungulates (Lone et al. 2014) and other large carnivores (Oriol-Cotterill et al. 2015), including black bears (Laske et al. 2011, Stillfried et al. 2015). Hunting can thus induce behavioral changes that may carry nutritional costs due to decreased energy intake and/or increased energy expenditure (Lima and Dill 1990). During the hunting season in Sweden, bears reduce their foraging activity and, even while foraging, pay a nutritional cost by using less productive berry patches when mortality risk is highest (Hertel et al. 2016b). Foraging activity and efficiency remain unaffected during less risky times, so bears appear to be unable to compensate for lost foraging opportunities (Hertel et al. 2016b). Efficient foraging is particularly important in critical phases of energy expenditure or weight gain, e.g., during lactation or preparation for hibernation (Farley and Robbins 1995, López-Alfaro et al. 2013). In years of food shortage, bears may not be able to trade off forage intake with antipredation behaviors (Johnson et al. 2015), which might make them more vulnerable to hunting.

No study, however, has yet documented quantitatively that these recreational-caused effects on behavior depress food intake to the point that it decreases bear reproduction or survival (Fortin et al. 2016) (Fig. 1). This may be because bears seem to be flexible in

exhibiting compensatory foraging in disturbance-free periods (Ayres et al. 1986, Beckmann and Berger 2003) or switching to alternative food resources away from risky areas (Rode et al. 2007). Nevertheless, the topic warrants further research.

Human-induced selection and potential evolutionary effects

Harvest by hunting is usually selective, whether intentionally, through conscious selection by hunters and regulations, or unintentionally, through the interplay between individual variation in spatial and temporal vulnerability (Festa-Bianchet 2003, Fenberg and Roy 2008, Bunnefeld et al. 2009). When there is opportunity for a choice, hunters usually show preferences for particular traits (Myserud 2011). There are several examples of negative selective and demographic effects of size-selective harvesting and trophy hunting in fishes and ungulates (Coltman et al. 2003, Garel et al. 2007, Jørgensen et al. 2007, Allendorf and Hard 2009). However, there is little evidence from large carnivores (but see Loveridge et al. 2007 for a demographic effect in African lions *Panthera leo*). In North America, hunters may show preferences towards larger and older bears, mostly males (McLellan and Shackleton 1988, Kohlmann et al. 1999). The disproportionate removal of older and male bears could disrupt population age and sex structure (see above), but it could also artificially select for smaller and less reproductively successful phenotypes.

Hunter selectivity does not depend only on animal morphology, but also on the hunting methods used, harvest intensity, and management regulations (Myserud 2011). For example, harvest could select for behavioral traits (Leclerc et al. 2017b) and restrictions limiting hunting to daylight hours could select for more nocturnal bears. In addition, it has been suggested that the long persecution period of brown bears in Europe might explain why bears are generally more nocturnal in Europe than in North America (Swenson 1999, Ordiz et al. 2011).

Legal protection of family groups is a common practice in bear management strategies in North America and Europe, including Sweden, and has often been stressed as a factor explaining bias in hunting data and differential vulnerability of age and sex classes to hunting (McLellan and Shackleton 1988, Kohlmann et al. 1999, Krofel et al. 2012, Leclerc et al. 2016a). The main consequence of legally protecting family groups is the protection of adult females with offspring and the increased selective harvest of males and solitary females (Solberg et al. 2000, Zedrosser et al. 2013, Rughetti and Festa-Bianchet 2014). Because

females may gain a fitness benefit through increased survival when associating longer with dependent offspring (Zedrosser et al. 2013, Leclerc et al. 2016a), legal protection of family groups can select for longer periods of maternal care (Van de Walle et al. unpublished data). The strength of this selective pressure depends on harvest intensity, but also on the duration of maternal care and the timing of the hunting period (before or after weaning time; McLellan and Shackleton 1988), which varies among bear populations. Nevertheless, in Scandinavia we have witnessed a general increase in the average duration of maternal care in recent years (Leclerc et al. 2016a), which may have adverse consequences on recruitment and population growth rate. On the other hand, protecting adult females, i.e., the demographic parameter depicting the greatest elasticity on population growth, should also result in a higher population growth (Van de Walle et al. unpublished data; Knight and Eberhardt 1985, Gosselin et al. 2015), potentially compensating for reduced reproductive output.

Even in the absence of apparent selectivity by hunters or hunting regulation, there is usually heterogeneity in individual vulnerability to hunting. Bolder and more active individuals are more frequently caught in traps or killed by hunters in several species (Biro and Post 2008, Ciuti et al. 2012, Leclerc et al. 2017b). In Sweden, hunters do not kill bears randomly within the landscape, but generally kill them closer to human infrastructure (Steyaert et al. 2016a). In addition, the individual differences in habitat selection patterns found in Scandinavia (Leclerc et al. 2016b) could lead to different levels of vulnerability to hunting. Because behaviors are often heritable, we could expect evolutionary changes in response to harvest-induced selection (Postma 2014, Dochtermann et al. 2015). For example, it was suggested that the wariness of brown bears in Scandinavia may be an adaptation resulting from the long-term human persecution that almost eradicated the species by 1930 (Swenson et al. 1995).

Even in the absence of age, sexual, morphological, and behavioral selectivity, high mortality rates can exert selective pressure on life history traits (Festa-Bianchet 2003, Olsen et al. 2004). Because higher mortality rates select for reproduction at smaller size and younger age (Stearns 1992), hunting can select for larger investment in reproduction (Festa-Bianchet 2003, Law 2007, Darimont et al. 2009) and accelerate life histories (Servanty et al. 2011). Centuries of brown bear persecution in Europe may have selected for faster life histories, potentially explaining why females there reproduce earlier and produce more cubs relative to their body mass compared to their North American counterparts (Zedrosser et al. 2011). This “ghost of persecution past” may explain why the historically heavily persecuted

Swedish population has one of the fastest life histories documented (reviewed in Nawaz et al. 2008) and can now sustain relatively high levels of harvest.

Although evolution was once thought to be a process occurring over a very long time including many generations, recent studies show that evolution can occur over just a few generations (Olsen et al. 2004, Kvalnes et al. 2016, Pigeon et al. 2016) and influence ecological processes (Pelletier et al. 2009). Human-induced selection has the potential to cause rapid phenotypic changes (Darimont et al. 2009) and hard-to-reverse evolutionary changes in exploited populations (Palumbi 2001, Olsen et al. 2004, Pigeon et al. 2016). Therefore, it represents one of the most pervasive effects of hunting, warranting caution when making management decisions (Festa-Bianchet 2003, Jørgensen et al. 2007).

Concluding remarks

Usually managers focus on the effects of direct harvest mortality on vital rates and population growth rate (e.g., Miller 1990) and rarely consider indirect effects of hunting (Milner et al. 2007, Pauli and Buskirk 2007, Ordiz et al. 2013a). In this review, we show both statistically supported evidence and reason to suspect that indirect effects of hunting can have measurable effects on a population's growth rate (Fig. 1). We have concentrated on the Scandinavian population of brown bears, because it is a particularly well studied system since the 1980's, but we suggest that indirect effects of hunting on population dynamics is likely a general phenomenon. In addition, hunting can cause human-induced selection, which may further affect vital rates and population growth in the long-term. Our focus on brown bears alone has excluded the indirect and potential evolutionary effect of bear harvest on community and ecosystems processes. Hunting bears and other large carnivores also could affect their ecological role in an ecosystem (Ordiz et al. 2013a) and indirectly affect other species in the trophic network. For example, Scandinavian bears can have a strong, lasting effect on the behavior of their prey species, such as moose (*Alces alces*) (Sahlén et al. 2016) and may affect the expansion patterns and predation rates of other large carnivores, such as the gray wolf (*Canis lupus*) (Ordiz et al. 2015, Tallian et al. 2017). Such information on interspecific interactions is also useful for management, for instance, to adjust hunting quotas of ungulates that are both hunted and predated upon by bears and sympatric wolves (Jonzén et al. 2013).

The main point of our review is to stress that indirect effects of harvest deserve more attention by managers, because they can influence population growth rates. Some of the effects have been documented and most certainly exist (Fig. 1), but indirect and evolutionary effects are generally more difficult to document and quantify than direct effects of harvest. We found two quantitative estimates of indirect effects of hunting on bears on λ ; an increased mortality of cubs of the year due to SSI in brown bears in Scandinavia (Swenson et al. 1997, Swenson et al. 2001, Gosselin et al. 2015, Gosselin et al. 2017), and a reduced reproductive rate of female grizzly bears in Alberta, due to females selecting less productive sites as a counter strategy to SSI (Wielgus et al. 2001b).

In societies where wildlife management is an important public issue, e.g., where wildlife populations are managed under the public trust doctrine (Batcheller et al. 2010, Treves et al. 2017), the public may increasingly require that managers not only document the direct, numerical effects of management decisions, but also their indirect and potential human-induced selection effects. Although research on indirect effects of hunting on fitness is difficult and requires long-term monitoring of individuals in a population that has experienced different harvest rates, it is an important responsibility for managers to carry out or fund research on this topic. Long-term monitoring of harvest effects on bears also provides opportunities for managers to make informed decisions while considering uncertainty (Regehr et al. 2017). As we await the outcome of such research, managers of bear populations should apply the cautionary principle and assume that indirect effects do exist and have a potential impact on bear population structure and growth that may differ from that predicted by harvest models based on direct effects alone.

ACKNOWLEDGEMENTS

This is scientific publication No. XXX from the SBBRP, which was funded by the Swedish Environmental Protection Agency, the Norwegian Environmental Agency, the Austrian Science Fund, the Research Council of Norway, and the Swedish Association for Hunting and Wildlife

Management. We acknowledge the support of the Center for Advanced Study in Oslo, Norway, which funded and hosted our research project “Climate effects on harvested large mammal populations” during the academic year of 2015-2016 and funding from the Polish-Norwegian Research Program operated by the National Center for Research and Development under the Norwegian Financial Mechanism 2009-2014 in the frame of Project

Contract No POL354 NOR/198352/85/2013. We thank Gro Kvelprud Moen and Richard Bischof for comments on previous versions of the manuscript.

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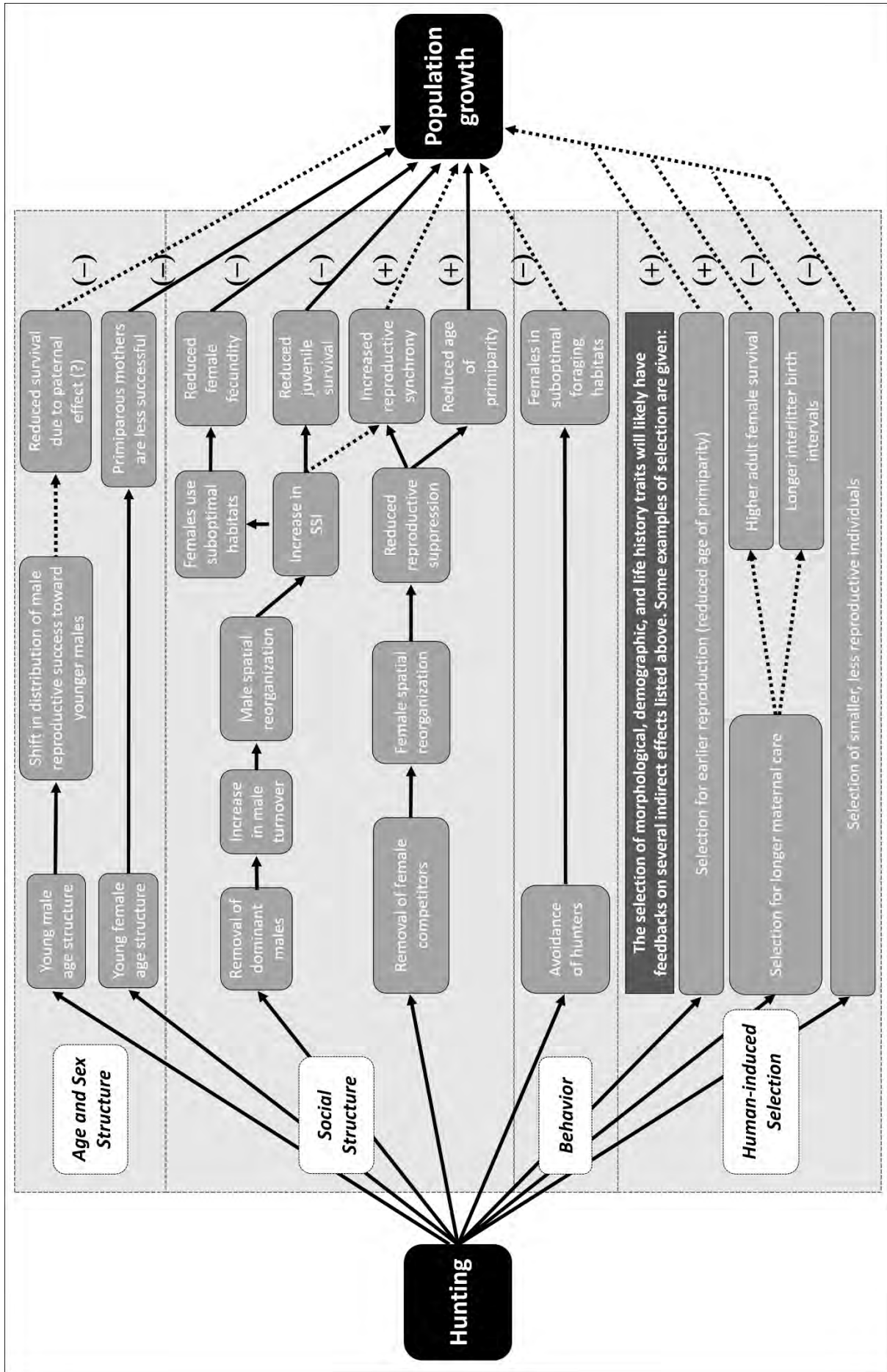
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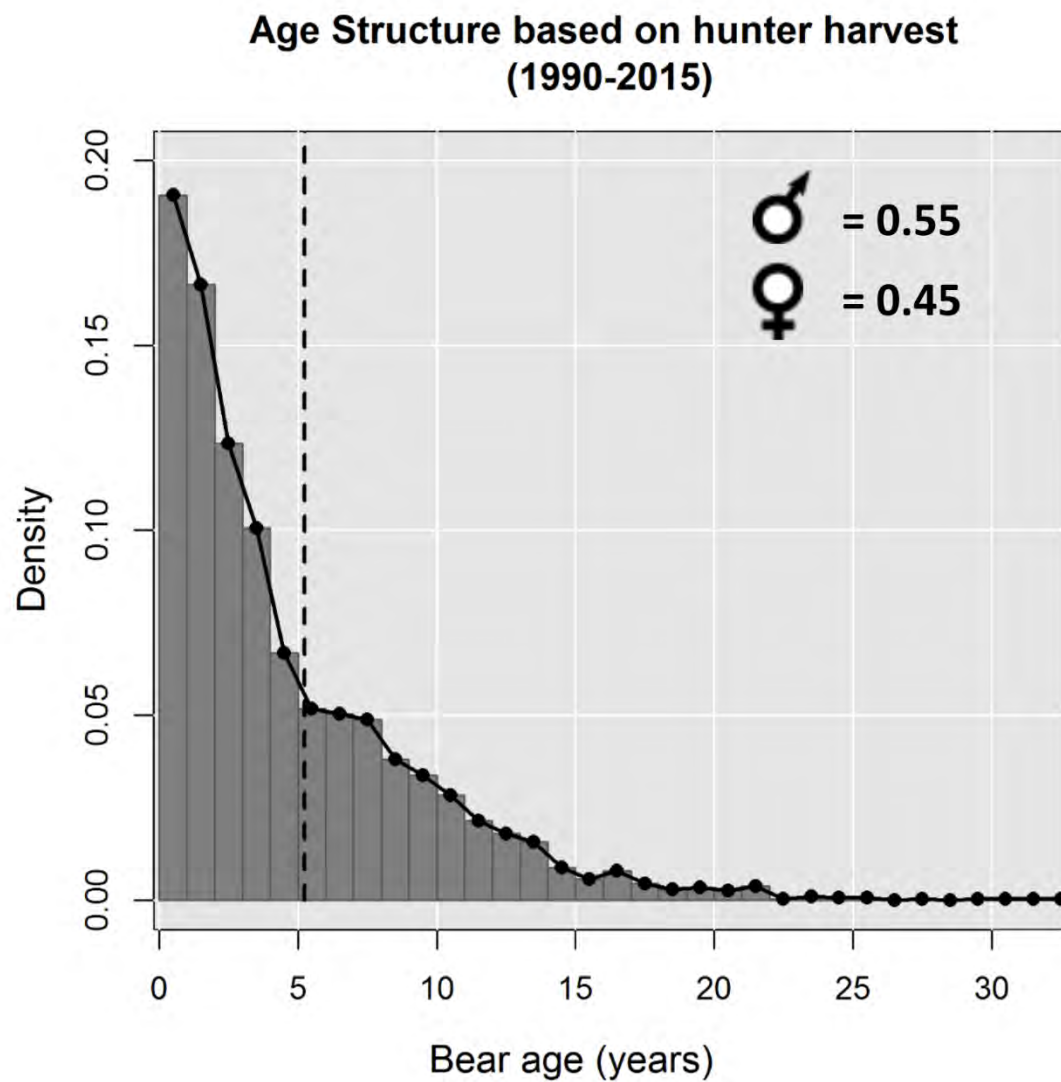
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Fig. 1. A summary of the indirect effects on population growth of bear hunting discussed in this paper. The solid arrows show relationships that have been documented statistically and the dotted arrows show potential relationships. Effects on population growth are noted in parentheses along the lines directly connecting with the "Population growth" box. This figure was inspired from Milner et al. (2007).



2 Fig. 2. The age structure of hunter-killed brown bears in Sweden during 1990-2015. The vertical
3 dotted line shows the mean age of bears (~5 years) killed. The frequencies of males and females
4 harvested are shown.



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Paper II:

Frank, SC, Leclerc M, Pelletier F, Rosell F, Swenson JE, Bischof R, Kindberg J, Eiken HG, Hagen SB, Zedrosser A.

"Sociodemographic factors modulate the spatial response of brown bears to vacancies created by hunting." In press (as of 2017-09-23) in *Journal of Animal Ecology*.

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

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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; 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 Δ BIC. 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 ($\Delta\text{BIC} = 363$), the survivor's age ($\Delta\text{BIC} = 302$), and hunting intensity ($\Delta\text{BIC} = 18$) (Table 2 and S4). The best female-female model kept relatedness ($\Delta\text{BIC} = 2371$), the casualty's age ($\Delta\text{BIC} = 290$), and hunting intensity ($\Delta\text{BIC} = 106$) (Table 2 and S5). The most important variable for the male-female combination was density ($\Delta\text{BIC} = 3544$), followed by the survivor's age ($\Delta\text{BIC} = 2792$), and hunting intensity ($\Delta\text{BIC} = 1780$) (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 (25th percentile) and high relatedness (75th 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. This was manifested as an increase in survivors' use of hunter-caused vacancies (P1a),

when casualties were of the same sex (P1b). We found that spatial responses to hunter-created vacancies and the role of modulating factors was highly dependent on sex of survivors and casualties. As expected, there was little support for competitive release when casualties and survivors were of opposite sex (P1b). Contrary to our prediction (P2), relatedness between male casualties and survivors was a key factor influencing the speed and strength of survivors' spatial responses. For females, relatedness was important in explaining the magnitude of a female survivor's use of a female casualty's HR, but not changes over time. Survivor age amplified the spatial response of male survivors following a neighbor's death (P3). Female survivors' spatial responses were larger toward vacancies left by younger female casualties. In contrast to (P4), higher densities did not inhibit the increased use of a casualty' HR by survivors, but there was evidence of this for female survivors using male casualties' HRs. (P5) was supported, as hunting intensity was positively correlated with survivors' increase in use of casualties' HRs across all casualty-survivor sex combinations.

The pattern of increased use of a casualty's HR by same-sex survivors 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 home range 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 F-F 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 low (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 home range 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 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 differences in experience. Male bears have larger home ranges 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), in addition to 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 distribution of these vacancies can attract a nearby survivor, 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.

Spatiotemporal effects of hunting on animal behavior can be viewed as an effective management tool, such as reducing human-wildlife conflicts (e.g. Geisser, Reyer & Krausman 2004) or disease transmission (e.g. Manjerovic *et al.* 2014), but, if not properly understood, they may interfere with or even counteract management goals (e.g. Teichman, Cristescu & Darimont 2016). However, the effects of hunting on social structure, competition, and spatial reorganization, particularly for solitary species, have not been well studied. We have shown that the removal of individuals through hunting could influence spatial responses by neighboring, surviving individuals, particularly those of the same sex. We also showed that these spatial responses are dependent on social contexts (e.g. kinship), most likely reflecting previous competition between casualties and nearby survivors. Management decisions, such as the degree of hunting intensity, appears to drive spatial responses of survivors. Furthermore, we suggest that solitary species may be more social and 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*).

Acknowledgments

This is scientific publication No. XXX from the SBBRP, whose long-term funding comes primarily from the Swedish Environmental Protection Agency, the Norwegian Environment Agency, the Swedish Association for Hunting and Wildlife Management, and the Austrian Science Fund. We thank three anonymous reviewers for their constructive comments on earlier manuscript drafts. We thank S. Brunberg, D. Ahlqvist, J. Arnemo, A. Evans, and J. Painer for making the data collection possible in the field. We acknowledge the support of the Center for Advanced Study in Oslo, Norway, that funded and hosted our research project “Climate effects on harvested large mammal populations” during the academic year of 2015-2016 and funding from the Polish-Norwegian Research Program operated by the National Center for Research and Development under the Norwegian Financial Mechanism 2009-2014 in the frame of Project Contract No POL-NOR/198352/85/2013. ML was supported financially by NSERC, and FP was funded by NSERC discovery grant and by the Canada Research Chair in Evolutionary Demography and Conservation.

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: doi: XXXXXXX (Frank et al. 2017).

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 (Δ BIC) from the best model, and the model weights (ω) are shown.

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

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

Model	Variable	K	Male–Male			Female–Female			Male–Female		
			LL	Δ BIC	ω	LL	Δ BIC	ω	LL	Δ BIC	ω
1	None	4	-26524	1516	0	-178430	5538	0	-182879	6275	0
2	Inside \times Period	9	-26051	622	0	-177124	2988	0	-182850	6281	0
3	C _{age} \times Inside \times Period	15	-26044	671	0	-176795	2404	0	-182221	5096	0
4	C _{age} \times Inside \times Period	15	-25885	353	0	-177097	3009	0	-181741	4137	0
5	Hunting \times Inside \times Period	15	-25978	540	0	-176991	2798	0	-182596	5847	0
6	Density \times Inside \times Period	15	-25940	463	0	-176999	2814	0	-181859	4372	0
7	Relatedness \times Inside \times 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

6

7 *Model 8 to 33: Every variable is in a 3-way interaction with Inside \times Period as shown in model 3.

8 Bolded values are from the best models

9

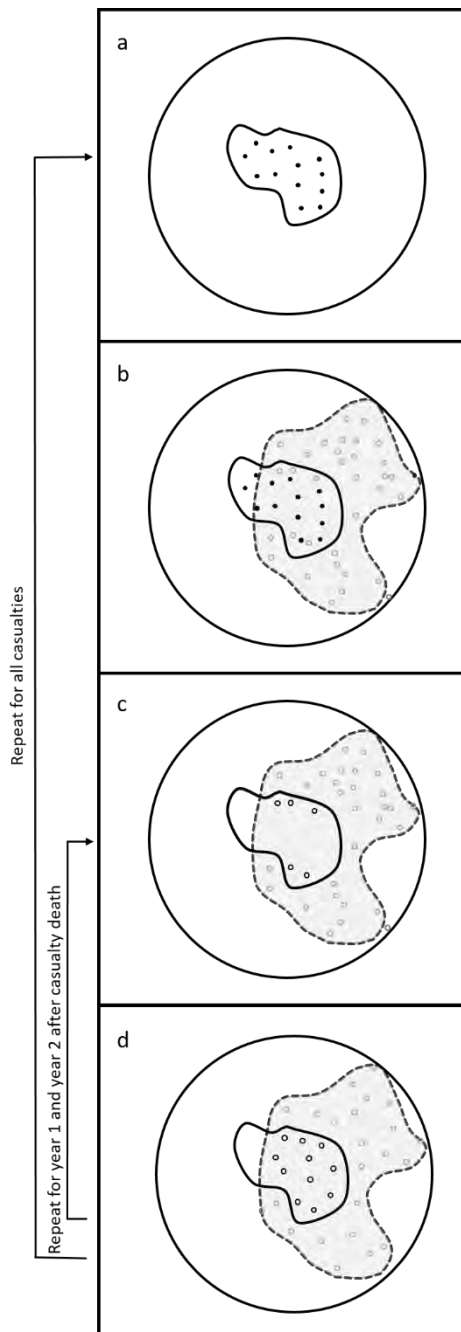
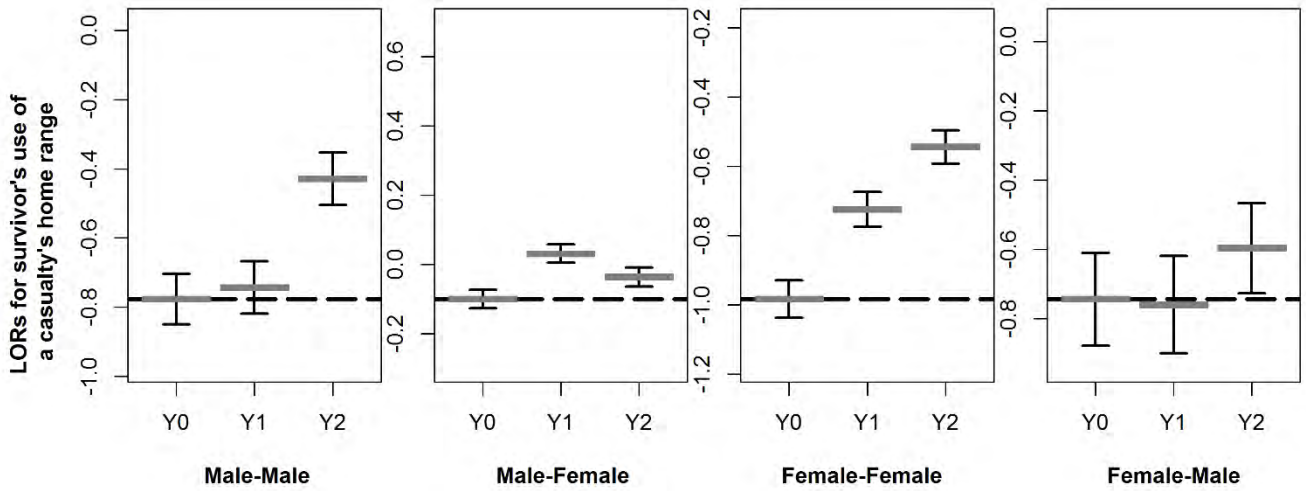


Figure 1. Schematic representation of data handling. For each brown bear casualty (panel a), we determined its 95% kernel HR and calculated a 40-km radius circular buffer centered on the HR centroid. We used (panel b) all GPS locations of the casualty (filled black points) and those belonging to surviving 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.



Sex combinations: casualty-survivor

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.

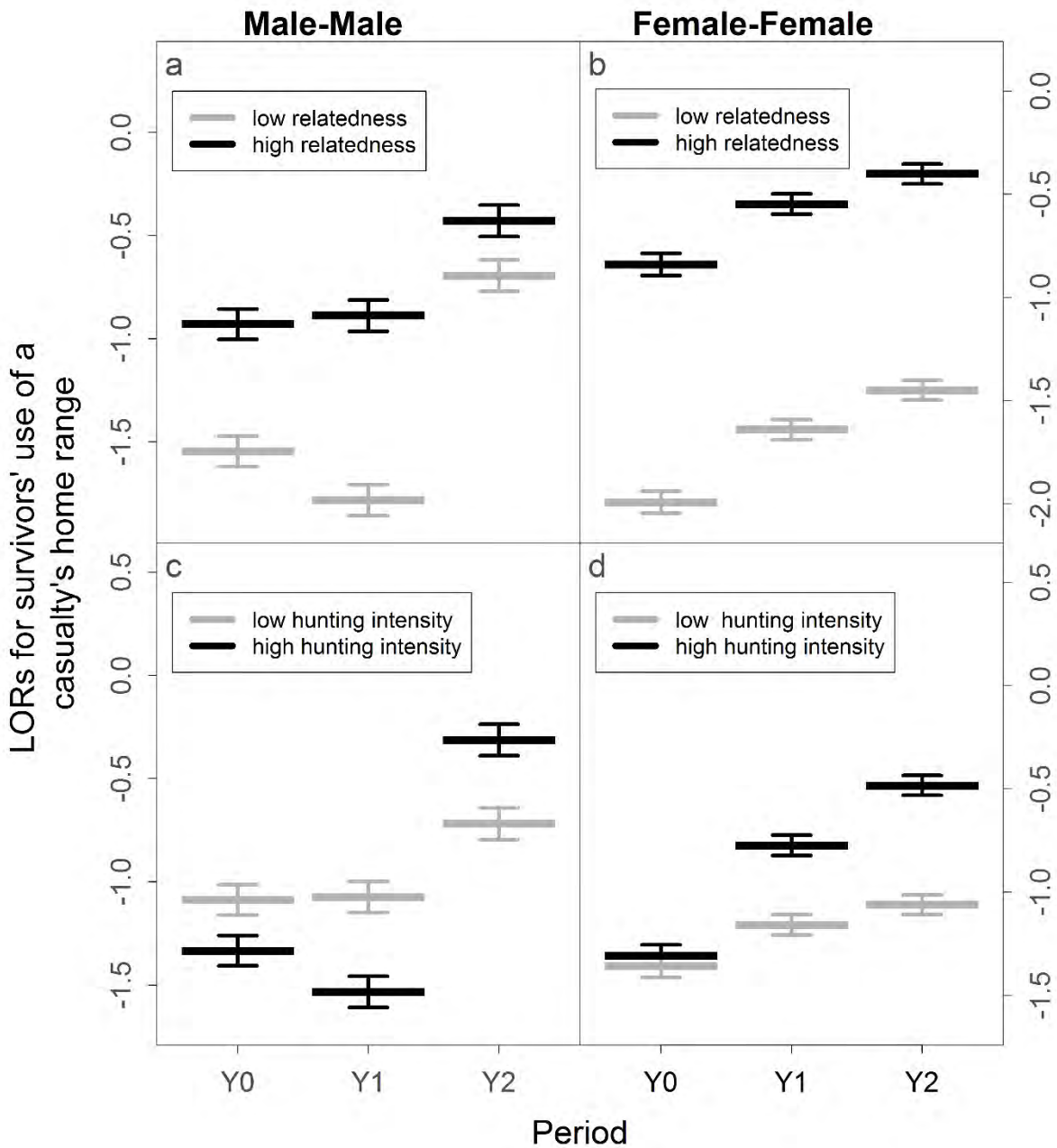


Figure 3. Log-odds ratios of nearby surviving brown bears' (survivors') use of hunter-killed bears' (casualties') HRs during the year in which the casualty died (Y0), the first year after the casualty's death (Y1), and the second year after its death (Y2) in response to casualty-survivor relatedness (panel a, b) and previous hunting intensity (panel c, d). Low and high values of relatedness and hunting intensities represent the 25th and 75th 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.

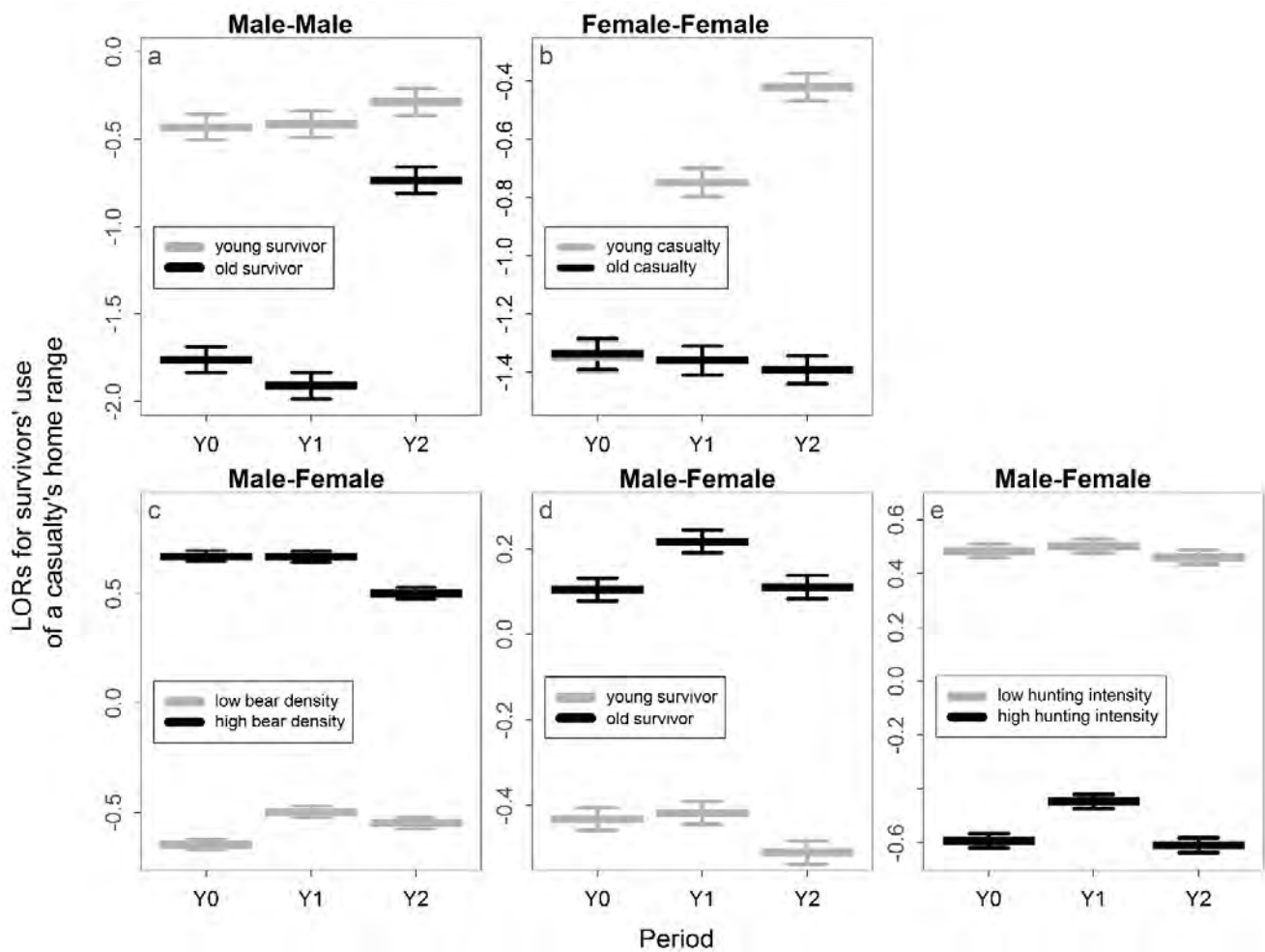


Figure 4. Log-odds ratios of surviving brown bears' (survivors') use of nearby hunter-killed bears' (casualties') home ranges during the year in which the casualty died in the fall (Y0), the first year after the casualty's death (Y1), and the second year after its death (Y2), in response to casualty 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.

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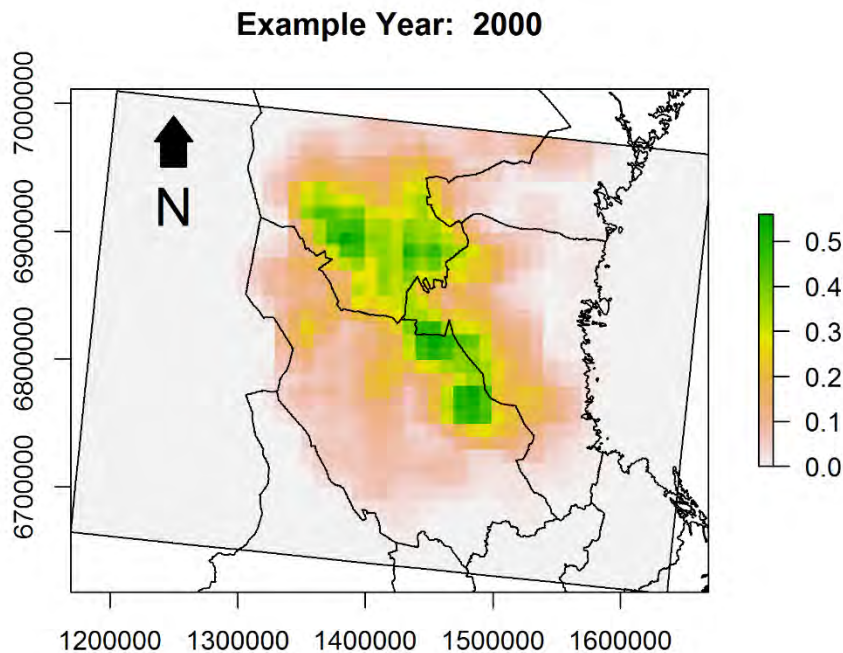
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Supporting Information

Appendix S1. Annual bear density Index.

The annual bear density index was estimated using two sources of information: (1) individually identified bears, based on DNA in scats collected during organized efforts (available at <http://rovbase.no>; Bellemain *et al.* 2005) and (2) the Swedish Large Carnivore Observation Index (LCOI), both of which were collected during the fall hunting season (Kindberg, Ericsson & Swenson 2009). The latter information came from Swedish hunters, whose efforts covered virtually the entire areas of four counties of Gävleborg, Dalarna, Jämtland, and Västernorrland (for more details on collection efforts, see Kindberg, Ericsson & Swenson 2009). Scat collection data were used to create spatially explicit density index distributions, according to the county and the year in which an individual's scat collection took place.



We adopted the method of Jerina *et al.* (2013), by summing the weighted values of individual bear scat locations on a grid of 10 X 10 km cells, to account for the different number of samples among individuals. Grid cells were then smoothed with a 3x3 cell filter (i.e. a 30x30 km moving window) to derive county-specific density index distributions. Years of scat collection varied among counties. Thus, these maps were not directly comparable without an annual correction, for which we used the LCOI. The Swedish LCOI was initiated in 1998 by the Swedish Association for Hunting and Wildlife Management (Kindberg *et al.* 2011). Moose hunters report the number of bears they observe during the first week of moose hunting; the index is effort-corrected using hunter

hours (Ericsson & Wallin 1999; Sylvén 2000). We approximated temporal trends in the LCOI for the period 1998-2015 for each county by fitting quadratic models using LCOI as the response and "year" plus year-squared as predictors. The latter term was used to smooth the relationship between year and the interannual LCOI values, which could vary substantially among years. Predicted LCOI values from these models were then used to calculate a multiplicative annual correction factor (C) (**Eq. 1**), which was multiplied with each county's density distribution (d_j) (**Eq. 2**).

$$C_{ij} = \frac{LCOI_{ij}}{LCOI_{scat\ year,j}} \quad \text{Eq. 1}$$

Years in which scat was actually collected in a given county ($i = scat\ year$) were given a correction factor of "1". Therefore, the annual density index (D) for a given county was derived using the following equation (**Eq. 2**) for the i th year, j th county, and the scat (collection) year.

$$D_{ij} = C_{ij} * d_j \quad \text{Eq. 2}$$

County grids were then summed together by year to obtain the annual density index (D_i) grid (a plot of D_{2000} is shown in the figure above using the UTM coordinate system: 'RT90 2.5 gon V'). The bear density index was extracted for each surviving bear's relocation in a given study period year (i.e., Y0, Y1, and Y2).

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Table S1. Summary statistics for microsatellites used for pedigree reconstruction and Lynch and Ritland's (1999) relatedness index for brown bears (N = 1,614) in southcentral Sweden. N_A: Number of alleles, H_o: observed heterozygosity, H_e: expected heterozygosity, P_{ex}: probability of exclusion for a single unknown parent, P_{id}: probability of identity for unrelated individuals.

Locus	N _A	H _o	H _e	P _{ex}	P _{id}
G1A ^a	6	0.625	0.630	0.380	0.810
G1D ^a	7	0.592	0.620	0.340	0.786
G10B ^a	8	0.699	0.703	0.442	0.855
G10C ^b	5	0.697	0.698	0.460	0.864
G10J ^c	6	0.574	0.570	0.325	0.762
G10H ^c	9	0.525	0.545	0.308	0.740
G10L ^a	8	0.757	0.760	0.544	0.905
G10O ^a	3	0.392	0.397	0.166	0.564
G10P ^b	6	0.736	0.757	0.535	0.902
Mu05 ^d	8	0.640	0.636	0.365	0.797
Mu10 ^d	8	0.806	0.806	0.610	0.933
Mu15 ^d	4	0.658	0.643	0.364	0.805
Mu23 ^d	8	0.709	0.699	0.485	0.876
Mu50 ^d	10	0.735	0.756	0.538	0.903
Mu51 ^d	9	0.824	0.796	0.592	0.926
Mu61 ^d	4	0.529	0.542	0.272	0.714
average	7	0.656	0.660	0.420	0.821

^aPaetkau and Strobeck (1994); ^bPaetkau *et al.* (1995); ^cPaetkau, Shields and Strobeck (1998);

^dTaberlet *et al.* (1997).

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Table S2. Summary of parentage assignment from pedigree construction using Cervus 2.0 (initial assessment; Marshall *et al.* 1998; Kalinowski, Taper & Marshall 2007)) and Colony 3.0 (sibship reconstruction and recovery of further father assignments; Jones & Wang 2010). Only some mothers were known (not fathers) during assignment, with the rest based on genetics.

Parentage Assignment	Count	Proportion of Offspring
Offspring sample size	1463	NA
<i>Maternity of offspring</i>		
Known mothers	321	0.22
Assigned mothers with genetics alone	455	0.31
Total Assigned mothers	776	0.53
<i>Paternity of offspring</i>		
Assigned fathers (known genotypes)	666	0.46
Assigned fathers (reconstructed genotypes*)	68	0.05
Total assigned fathers	734	0.50

*Colony 3.0 reconstructed sibship across known and reconstructed father genotypes. The latter is shown on a separate line.

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Table S3. Parameter estimates of the best sex-effect model (Step I; Model 6 in Table 1).

Variable	β	95 % Confidence intervals	
		Lower	Upper
Intercept	0.075	0.054	0.095
Survivor Sex = M	-0.012	-0.050	0.026
Casualty Sex = M	-0.034	-0.065	-0.002
Inside = True	-0.984	-1.034	-0.933
Period = Y1	-0.012	-0.032	0.008
Period = Y2	-0.025	-0.045	-0.006
Survivor Sex = M \times Casualty Sex = M	0.215	0.158	0.272
Inside = True \times Period = Y1	0.259	0.192	0.327
Inside = True \times Period = Y2	0.440	0.377	0.503
Survivor Sex = M \times Inside = True	0.240	0.118	0.361
Survivor Sex = M \times Period = Y1	0.010	-0.041	0.061
Survivor Sex = M \times Period = Y2	0.017	-0.033	0.066
Casualty Sex = M \times Inside = True	0.883	0.826	0.940
Casualty Sex = M \times Period = Y1	-0.043	-0.075	-0.012
Casualty Sex = M \times Period = Y2	-0.001	-0.032	0.030
Survivor Sex = M \times Inside = True \times Period = Y1	-0.275	-0.435	-0.116
Survivor Sex = M \times Inside = True \times Period = Y2	-0.293	-0.443	-0.142
Casualty Sex = M \times Inside = True \times Period = Y1	-0.128	-0.205	-0.051
Casualty Sex = M \times Inside = True \times Period = Y2	-0.376	-0.448	-0.304
Survivor Sex = M \times Casualty Sex = M \times Inside = True	-0.916	-1.055	-0.776
Survivor Sex = M \times Casualty Sex = M \times Period = Y1	0.038	-0.041	0.117
Survivor Sex = M \times Casualty Sex = M \times Period = Y2	-0.080	-0.157	-0.003
Survivor Sex = M \times Casualty Sex = M \times Inside = True \times Period = Y1	0.177	-0.003	0.357
Survivor Sex = M \times Casualty Sex = M \times Inside = True \times Period = Y2	0.577	0.404	0.750

Table S4. Parameter estimates of the best 'additional factors' model (Step II) for male-male casualty-survivor combination (Model 25 for male-male data set from Table 2).

Variable	β	95 % Confidence intervals	
		Lower	Upper
Intercept	0.256	0.167	0.346
Survivor Age	0.033	-0.048	0.114
Hunting	-0.081	-0.172	0.010
Relatedness	-0.063	-0.131	0.004
Inside = TRUE	-1.194	-1.292	-1.097
Period = Y1	-0.017	-0.077	0.043
Period = Y2	-0.091	-0.153	-0.029
Inside = TRUE \times Period = Y1	-0.079	-0.221	0.064
Inside = TRUE \times Period = Y2	0.651	0.527	0.775
Survivor Age \times Inside = TRUE	-1.279	-1.497	-1.060
Survivor Age \times Period = Y1	0.010	-0.065	0.084
Survivor Age \times Period = Y2	0.020	-0.054	0.094
Hunting \times Inside = TRUE	-0.172	-0.282	-0.062
Hunting \times Period = Y1	0.045	-0.025	0.114
Hunting \times Period = Y2	-0.094	-0.170	-0.017
Relatedness \times Inside = TRUE	0.598	0.497	0.699
Relatedness \times Period = Y1	-0.065	-0.125	-0.004
Relatedness \times Period = Y2	0.021	-0.040	0.082
Survivor Age \times Inside = TRUE \times Period = Y1	-0.159	-0.459	0.141
Survivor Age \times Inside = TRUE \times Period = Y2	0.850	0.606	1.093
Hunting \times Inside = TRUE \times Period = Y1	-0.150	-0.302	0.003
Hunting \times Inside = TRUE \times Period = Y2	0.456	0.311	0.601
Relatedness \times Inside = TRUE \times Period = Y1	0.271	0.134	0.407
Relatedness \times Inside = TRUE \times Period = Y2	-0.341	-0.470	-0.211

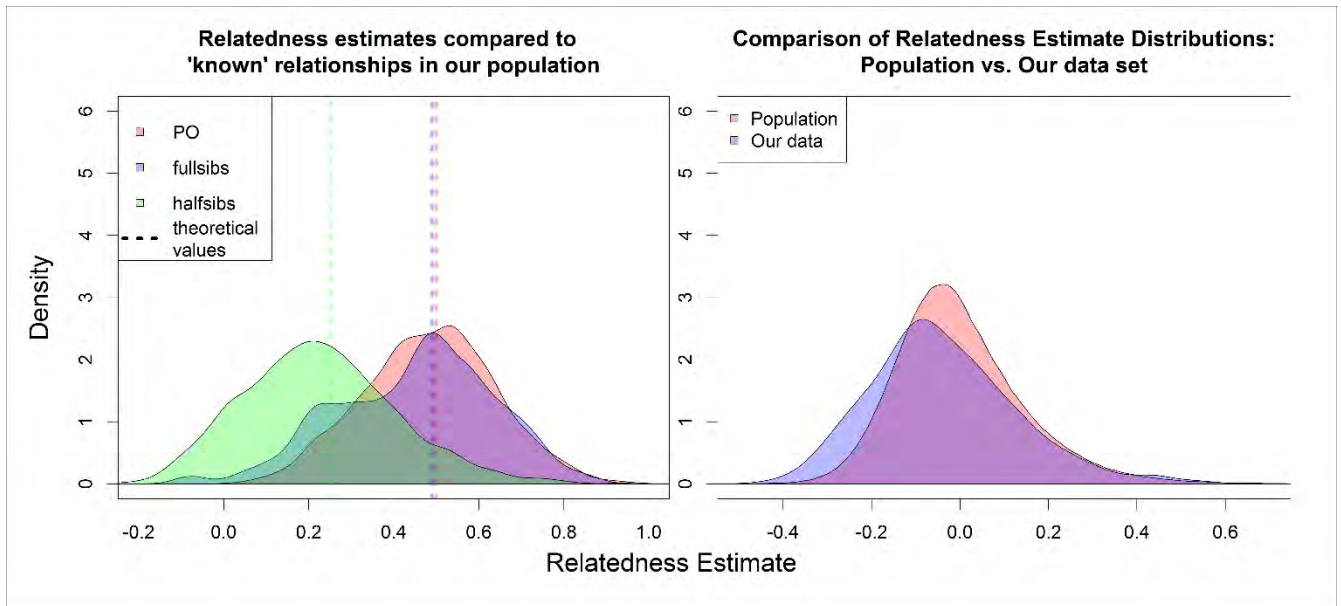
Table S5. Parameter estimates of the best 'additional factors' model (Step II) for female-female casualty-survivor combination (Model 22 for female-female data set from Table 2).

Variable	β	95 % Confidence intervals	
		Lower	Upper
Intercept	0.070	0.048	0.091
Casualty Age	0.006	-0.016	0.027
Hunting	-0.001	-0.023	0.021
Relatedness	-0.046	-0.064	-0.027
Inside = TRUE	-1.342	-1.405	-1.278
Period = Y1	-0.015	-0.035	0.004
Period = Y2	-0.029	-0.048	-0.009
Inside = TRUE \times Period = Y1	0.318	0.234	0.402
Inside = TRUE \times Period = Y2	0.483	0.400	0.567
Casualty Age \times Inside = TRUE	0.004	-0.052	0.061
Casualty Age \times Period = Y1	0.019	-0.001	0.039
Casualty Age \times Period = Y2	0.029	0.009	0.049
Hunting \times Inside = TRUE	0.028	-0.030	0.087
Hunting \times Period = Y1	0.002	-0.018	0.023
Hunting \times Period = Y2	0.004	-0.016	0.025
Relatedness \times Inside = TRUE	0.823	0.767	0.879
Relatedness \times Period = Y1	-0.013	-0.034	0.007
Relatedness \times Period = Y2	-0.017	-0.037	0.004
Casualty Age \times Inside = TRUE \times Period = Y1	-0.305	-0.383	-0.227
Casualty Age \times Inside = TRUE \times Period = Y2	-0.482	-0.561	-0.403
Hunting \times Inside = TRUE \times Period = Y1	0.194	0.112	0.275
Hunting \times Inside = TRUE \times Period = Y2	0.305	0.224	0.385
Relatedness \times Inside = TRUE \times Period = Y1	-0.042	-0.118	0.034
Relatedness \times Inside = TRUE \times Period = Y2	-0.074	-0.149	0.001

Table S6. Parameter estimates of the best 'additional factors' model (Step II) for male-female casualty-survivor combination (Model 24 for female-female data set from Table 2).

Variable	β	95 % Confidence intervals	
		Lower	Upper
Intercept	-0.011	-0.058	0.036
Hunting	0.237	0.187	0.286
Survivor Age	-0.213	-0.256	-0.170
Density	-0.320	-0.370	-0.271
Inside = TRUE	-0.061	-0.090	-0.032
Period = Y1	-0.032	-0.057	-0.006
Period = Y2	0.017	-0.010	0.043
Inside = TRUE \times Period = Y1	0.083	0.045	0.121
Inside = TRUE \times Period = Y2	-0.020	-0.059	0.019
Hunting \times Inside = TRUE	-0.442	-0.473	-0.412
Hunting \times Period = Y1	-0.030	-0.059	-0.002
Hunting \times Period = Y2	-0.009	-0.038	0.020
Survivor Age \times Inside = TRUE	0.443	0.414	0.471
Survivor Age \times Period = Y1	-0.058	-0.085	-0.031
Survivor Age \times Period = Y2	-0.043	-0.070	-0.016
Density \times Inside = TRUE	0.651	0.620	0.681
Density \times Period = Y1	0.028	0.000	0.055
Density \times Period = Y2	0.053	0.025	0.081
Hunting \times Inside = TRUE \times Period = Y1	0.052	0.012	0.092
Hunting \times Inside = TRUE \times Period = Y2	0.003	-0.038	0.044
Survivor Age \times Inside = TRUE \times Period = Y1	0.081	0.043	0.119
Survivor Age \times Inside = TRUE \times Period = Y2	0.069	0.031	0.108
Density \times Inside = TRUE \times Period = Y1	-0.075	-0.116	-0.034
Density \times Inside = TRUE \times Period = Y2	-0.132	-0.174	-0.091

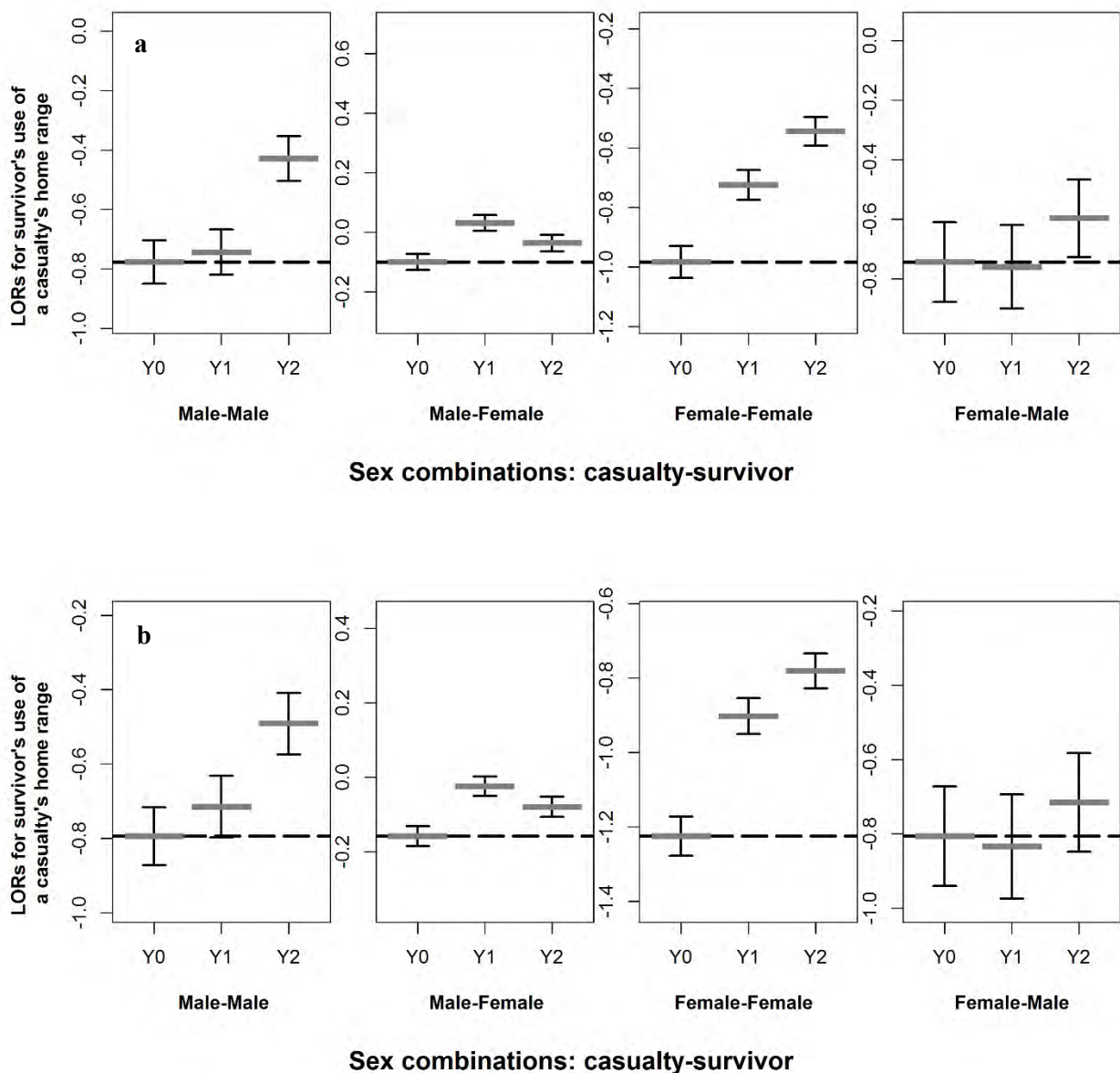
Figure S1. *Left panel:* The distribution of relatedness estimates from Lynch-Ritland's (1999) estimator compared to theoretical values from known relationships (PO = parent-offspring, full sibs, and half sibs) *Right panel:* The comparison between the estimated Lynch-Ritland's (1999) values of all brown bears we have genetic data on in the Scandinavian Brown Bear Research Project (SBBRP) and those used in our study sample. Mean values of Lynch-Ritland estimates are similar to theoretical values, and our sample is comparable to the population of Lynch-Ritland values for all bears in the SBBRP.



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Figure S2. Log-odds ratio (LOR; y-axis) 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), according to the sex combination of casualty-survivors. Comparison of the three isoclines (a: 95%; b: 90%; c: 75%) of the sampling spaces are shown, yielding similar results. The spatial response of male-male disappears as the sampling space is reduced to 75% isocline, which is the sex that depicts more extensive ranging behavior.



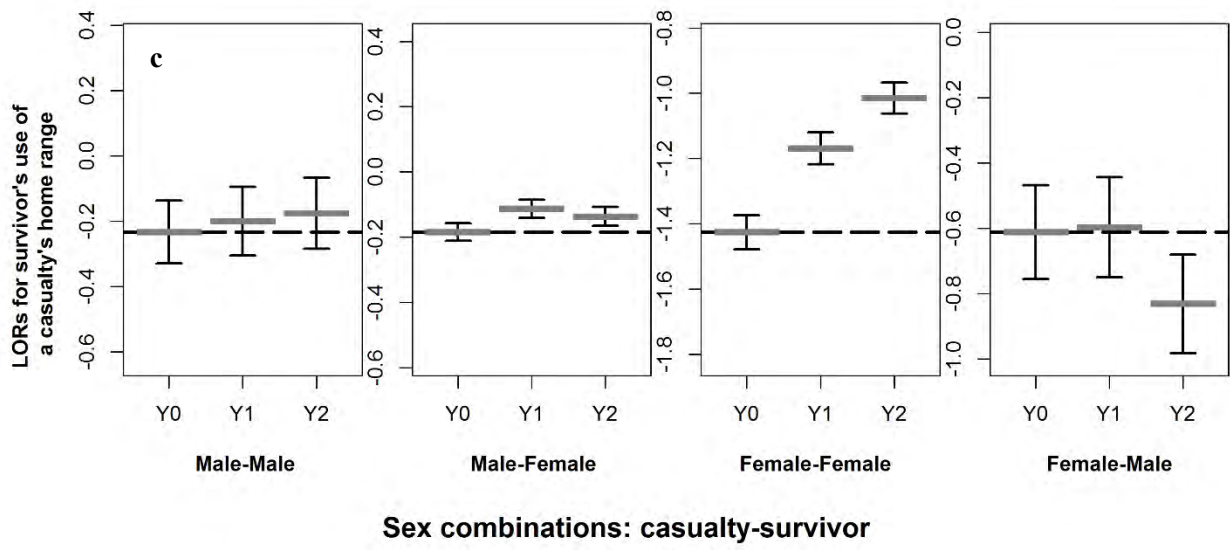


Figure S3. Pairwise relatedness (Lynch & Ritland 1999) plotted against distances between home range centroids of brown bears. Separate plots are shown for pairings between males (n = 948), females (n = 5086), and bears of the opposite sex (n = 4428). Gray dots are the raw data and red lines are plotted using LOWESS curves, providing nearly identical to the findings of Støen *et al.* (2005). Female pairings of higher relatedness are correlated with smaller distances between home range centroids, but there is no evidence of such a pattern for male pairings or those of the opposite sex.

Distance between home range centroids

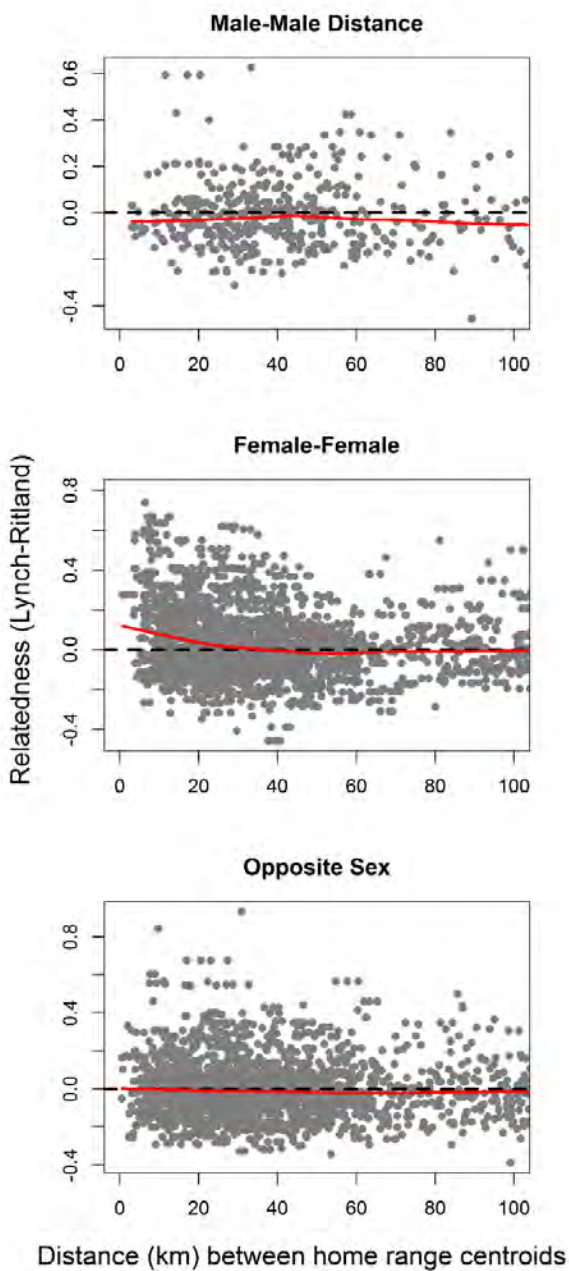
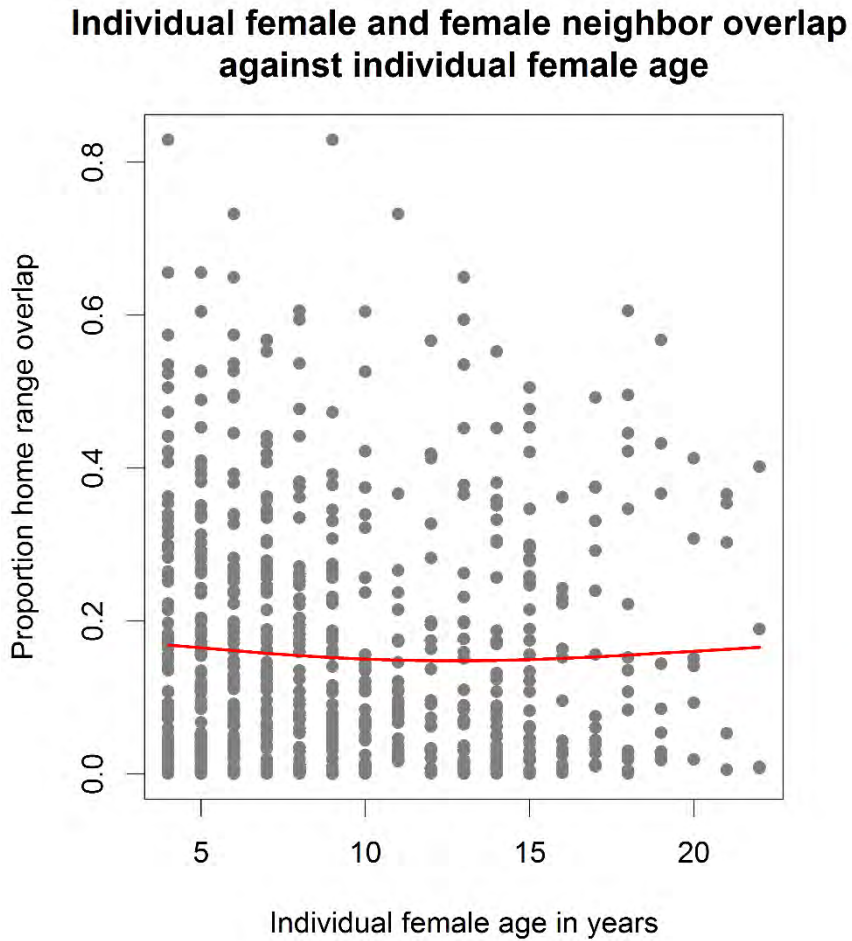



Figure S4. Proportion of home range overlap between individual females and their female neighbors against individual female age. Fitted values from a generalized additive model (red line) shows no significant relationship (smoother function: $p = 0.343$) between female-female home range overlap with a basis in female age ($n = 752$).



Paper III:

Leclerc M, Frank SC, Zedrosser, A, Swenson JE, Pelletier F (2017). "Hunting promotes spatial reorganization and sexually selected infanticide." *Scientific Reports* 7: 45222. DOI: [10.1038/srep45222](https://doi.org/10.1038/srep45222)

SCIENTIFIC REPORTS



OPEN

Hunting promotes spatial reorganization and sexually selected infanticide

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Received: 01 December 2016

Accepted: 21 February 2017

Published: 23 March 2017

Harvest can affect the ecology and evolution of wild species. The removal of key individuals, such as matriarchs or dominant males, can disrupt social structure and exacerbate the impact of hunting on population growth. We do not know, however, how and when the spatiotemporal reorganization takes place after removal and if such changes can be the mechanism that explain a decrease in population growth. Detailed behavioral information from individually monitored brown bears, in a population where hunting increases sexually selected infanticide, revealed that adult males increased their use of home ranges of hunter-killed neighbors in the second year after their death. Use of a hunter-killed male's home range was influenced by the survivor's as well as the hunter-killed male's age, population density, and hunting intensity. Our results emphasize that hunting can have long-term indirect effects which can affect population viability.

Human activities are a major evolutionary force affecting wild populations¹. There is increasing evidence that human exploitation leads to changes in morphological and life history traits worldwide^{1–4}. For example, recent studies have shown that size-selective harvest by commercial fisheries and trophy hunting can induce evolution of heritable traits^{5–9}. Harvest-induced evolution might not be desirable as the selection induced by human exploitation can be in the opposite direction of natural selection^{10–12}.

Hunting can also have indirect effects on wildlife, although such effects are often ignored by managers, even though the removal of key individuals by hunting could change a population's social structure¹³. For example, simulations suggest that the social networks of killer whales (*Orcinus orca*) may be vulnerable to targeted removal of individuals¹⁴. In African elephants (*Loxodonta africana*) the enhanced discriminatory abilities of the oldest individuals influences the social knowledge and reproductive success of entire groups¹⁵, suggesting that the loss of older individuals could decrease the fitness of all females within the group. In social species, the removal of any individual could affect social dynamics by changing the social structure. However, empirical evidence linking hunting and spatiotemporal reorganization of the social structure is lacking and the data needed to investigate this question are rarely available. Given the large number of species targeted by harvest, understanding the potential effects of removal on subsequent space use, social structure, and the fitness consequences for surviving individuals is critical to achieve sustainable hunting practices.

Here, we used detailed individual behavioral information from a Scandinavian brown bear (*Ursus arctos*) population (monitored from 2008–2015) to evaluate whether surviving adult males (hereafter referred to as survivors) shift their home range use after a neighboring adult male has been killed by hunting (Table S1). We further investigated the intrinsic and extrinsic factors driving the spatiotemporal reorganization of male spatial structure. In this population, the removal of adult males through hunting increases the risk of sexually selected infanticide (SSI)^{16,17}, which is a major determinant of population growth¹⁸. Although important for sustainable wildlife management¹⁹, the mechanism behind the harvest-induced increase of SSI remains unknown [but see Loveridge *et al.*²⁰].

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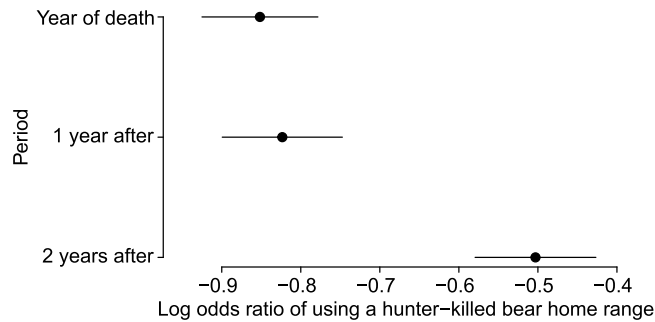


Figure 1. Changes in surviving male brown bears use of hunter-killed neighboring males' home ranges over time. Shown are the coefficients and 95% confidence intervals for three consecutive years, i.e. the year the hunter-killed male was shot (baseline) and the following two years.

Spatial reorganization due to hunting of males may be the responsible mechanism, by increasing the probability that a female will encounter a new male that is unlikely to be the father of her cubs^{13,16}.

Results

We found that survivors increased their use of the home ranges of hunter-killed males in the second year after their death (Fig. 1, Table S2). This time lag in the response likely is related to the bear's ecology. Bears den from October to April^{21,22}, shortly after the hunting season in late August–September. The size of the annual home range in our study population is mainly defined by space use during the mating season (May to mid-July), when males exhibit a roam-to-mate behavior²³. Therefore, we hypothesize that survivors do not readjust their home range until after the first mating season without the hunter-killed neighbor. This could explain the two-year time lag in spatial reorganization. Our results support the contention that the spatiotemporal reorganization of male home ranges is an important mechanism linking hunter harvest to an increase in SSI, described above. It is also consistent with earlier studies in the same population showing lower cub survival following a two-year time lag after a male had been killed^{16,17}.

We further investigated which intrinsic (ages of hunter-killed and surviving males) and extrinsic factors (population density and hunting intensity) modulated the speed and strength of the survivors' response to hunting removals (Fig. 2, Tables S3 and S4). The use of a hunter-killed male's home range by its surviving neighbors was influenced by (in order of decreasing relative importance) survivor's age ($\Delta\text{BIC} = 115$), hunting intensity ($\Delta\text{BIC} = 76$), population density ($\Delta\text{BIC} = 74$), and hunter-killed male's age ($\Delta\text{BIC} = 6$). Older survivors used a hunter-killed male's home range less strongly following the hunter-killed male's death than younger survivors (Fig. 2A). This suggests that older males may already have held home ranges with better resources, including food and females. Age-dependent home range quality could also explain why survivors increased their use of an old hunter-killed male's home range more than that of a younger hunter-killed male (Fig. 2D).

Survivors more strongly increased their use of a hunter-killed male's home range in the second year after its death when hunting intensity was greater (Fig. 2B). As increasing hunting intensity will increase the number of openings for surviving males, this should lead to a higher degree of spatial reorganization. We previously reported that the killing of an adult male within 25 km of a female strongly reduced the survival of her cubs, with a two-year time lag, although an increase in the number of killed males within 25 km had no significant additive effect¹⁷. Even though the degree of spatial reorganization increased with increased hunting intensity, this might not always translate into a correspondingly lower cub survival, because even though more surviving males may respond to increased hunting removal, only one infanticidal male is sufficient to kill most of females' cubs. The other extrinsic factor affecting shifts in a survivor's home range use was population density (Fig. 2C). Survivors at higher densities had higher initial overlap with the hunter-killed male and showed a weaker reorganization response than survivors at lower densities (Fig. 2C). Stronger competition for space between neighbors might explain why we observed higher initial overlap, with a weaker response at higher densities.

Discussion

We identified a key behavioral mechanism linking hunting to an increase in SSI and show how post-hunt spatiotemporal reorganization of males was modulated by both intrinsic and extrinsic factors. By removing males from the population, hunters destabilized the spatial organization of the population for at least two years after a male had been killed. This period of two years might be specific to brown bears, due to their denning period and could be different in other harvested species with SSI, such as lions (*Panthera leo*)²⁰ or cougars (*Puma concolor*)²⁴. Nevertheless, hunting increases shifts in home range use by surviving males and increases the probability of SSI^{16,17}. Male bears seem to assess their paternity through their mating history²⁵, and increasing the magnitude of shifts in home range use would increase the probability that a male could encounter a female with whom he had not previously mated. Such a pattern is expected regardless of the cause of death (e.g., vehicle collision, management kill, natural mortality). However, hunting is often additive to natural mortality, as in our study system²⁶, which increases the occurrence of SSI compared to unharvested systems.

The spatial distribution of the hunting mortality of bears was not homogenous in our study area²⁷. Spatial and social relationships of bears are likely to change more rapidly in areas with higher hunting mortality, thereby potentially decreasing the cohesion of their social network^{28,29} but see ref. 30. Such effects could also influence

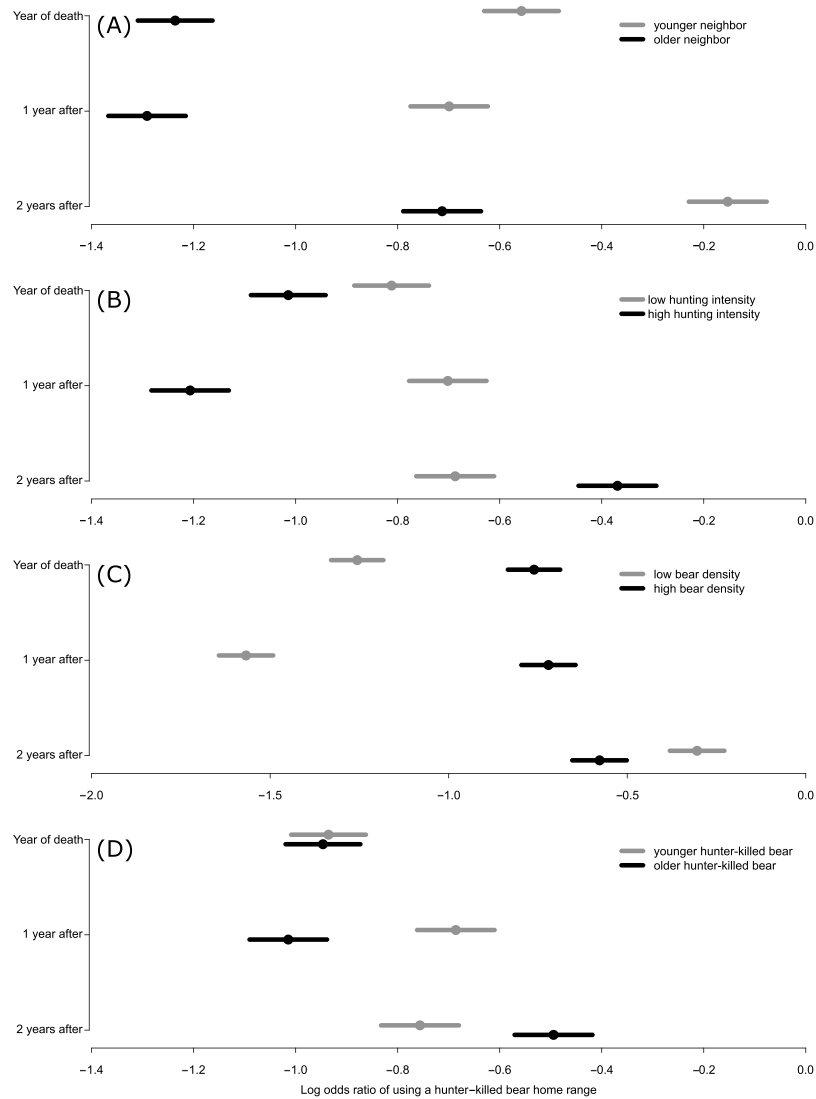


Figure 2. Influence of intrinsic and extrinsic factors on the speed and strength at which a surviving male will use hunter-killed neighboring males' home ranges. Shown are the coefficients and 95% confidence intervals for three consecutive years, i.e. the year the hunter-killed male was shot (baseline) and the following two years, depending on the surviving male's age (A), hunting intensity (B), population density (C), and hunter-killed male's age (D). The low and high values in each panel represent the 25th and 75th percentiles, respectively, observed in the database.

the female reproductive rate because female brown bears exhibit kin-related spatial structures³¹, where neighbors negatively affect each other's probability of having cubs^{32,33}. The direct effect of removals due to hunting, in addition to the indirect effects of increasing cub mortality due to SSI and the potential impacts of decreasing social network cohesion, all increases heterogeneity in survival and reproductive rates. These effects combined could increase demographic variability and ultimately affect effective population size^{34,35}. Therefore, we expect spatially structured demographic variability that could potentially result in source-sink dynamics^{35,36}.

Our study sheds light on the importance of animal behavior to explain time lags in the responses to hunting in the wild. Understanding the indirect consequence of hunting over long time scales is critical for developing sustainable management practices and for the viability of harvested populations.

Methods

The study area was in south-central Sweden (61°N, 15°E) and was composed of bogs, lakes, and intensively managed coniferous forest stands. The dominant tree species were Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), lodgepole pine (*Pinus contorta*), and birch (*Betula spp.*). Elevations ranged between 150 and 725 m asl. Gravel roads (0.7 km/km²) were more abundant than paved roads (0.14 km/km²). See Martin *et al.*³⁷ for further information about the study area.

We captured brown bears from a helicopter using a remote drug delivery system (Dan-Inject[®], Børkop, Denmark). We determined sex at capture and extracted a tooth from unknown individuals for age

determination³⁸. We equipped bears with GPS collars (GPS Plus; Vectronic Aerospace GmbH, Berlin, Germany) programed to relocate a bear with varying schedules (≤ 1 hour intervals). See Fahlman *et al.*³⁹ for details on capture and handling. All captured bears were part of the Scandinavian Brown Bear Research Project and all experiments, captures and handling were performed in accordance with relevant guidelines and regulations and were approved by the appropriate authority and ethical committee (Naturvårdsverket and Djuretiska nämnden i Uppsala, Sweden).

Spatial analysis. We used adult male bears ≥ 4 years in the analysis to exclude natal dispersers⁴⁰. We did not include natal dispersers because all male dispersers moved outside the study area where too few or no other males were GPS-collared. In addition, females actively defend their cubs during infanticide attempts. Therefore, younger dispersing males that have not yet attain full body size are less likely to successfully commit SSI than older, larger and better established males⁴¹. We screened the relocation data of adult males and removed GPS fixes with dilution of precision values > 10 to increase spatial accuracy. To reduce autocorrelation, we used a 6-hour minimum interval between successive positions for a given bear. We excluded bears in years for which an individual had $< 75\%$ of days with GPS locations from 1 May to 30 September.

We used an approach adapted from resource selection functions [RSFs;⁴²] developed by Bischof *et al.*⁴³. For each GPS-collared hunter-killed male we (1) determined its annual 95% kernel home range for the active period (1 May to 30 September or the day before he was killed) of the year in which he was killed and (2) calculated a 40-km radius circular buffer centered on its home range centroid. This radius was used because it represents the distance within which 95% of home range centroids of successful mates occurred⁴⁴ and the distance at which the effect of male removal on cub survival seems to disappear¹⁷. In a given year, we used GPS relocations of the hunter-killed male and all the GPS locations of surviving adult males within the buffer (hereafter called survivors) to (3) calculate a 95% kernel isocline (hereafter called sampling space). For each survivor, we (4) generated as many random than GPS relocations within the sampling space and (5) determined if GPS and random relocations were inside or outside the hunter-killed bear's home range. We repeated steps 3–5 for 3 consecutive years, i.e. the year a hunter-killed male had been killed and the two following years. We updated the sampling space annually by keeping the hunter-killed males' relocations the year he was killed constant for the three years, and used the appropriate relocations of survivors for each year. We only used survivors that were alive and monitored during the three-year period. We repeated these steps for each hunter-killed male. This enabled us to test whether survivors increased their use of a hunter-killed male's home range the years following its death.

For each hunter-killed male we also extracted a population density index derived from county-level scat collections in Sweden. We used the method of Jerina *et al.*⁴⁵ and summed the weighted values of an individual bear's multiple scats across a grid of 10×10 km. This was carried out for each county separately, after which the distribution was corrected temporally, using county-level trends of the Large Carnivore Observation Index^{46,47}, provided by the Swedish Association for Hunting and Wildlife Management. Lastly, we calculated a proxy of hunting intensity based on the number of dead adult males located within the 40-km radius circular buffer centered on a given hunter-killed male's home range centroid over a 3-year period prior to its death [see Gosselein *et al.*¹⁷ for further details].

Statistical analysis. As a first step, we determined if surviving males shifted their home range use in response to the removal of a hunter-killed male. To do so, we used a generalized linear mixed model (GLMM) with binomial distributed errors. We coded the dependent variable either as GPS (coded 1) or random (coded 0) relocation. As independent variables we used a dummy variable representing whether the relocations were inside (coded 1) or outside (coded 0) the hunter-killed males home range, as well as a variable representing the period of the relocations (3-level factor; the year of the hunter-killed male's death, as well as 1 and 2 years after the hunter-killed male's death). We evaluated 4 candidate models (Table S1) and selected the most parsimonious based on the Bayesian information criterion (BIC)⁴⁸. To control for the effect of year and unequal sample sizes across individuals, we included Year and the survivor ID nested within the hunter-killed males' ID as random intercepts in all candidate models.

In a second step, we examined how intrinsic (i.e., age of survivor and hunter-killed males) and extrinsic (i.e., population density and hunting intensity) factors influenced the speed and strength at which a survivor would adjust its home range use in response to the removal of a hunter-killed male. We used a GLMM with binomial distributed errors and coded the dependent variable either as GPS (coded 1) or random (coded 0) relocation. We evaluated the effect of six independent variables; inside vs outside the hunter-killed male home range, period, age of the survivor, age of the hunter-killed male, population density, and hunting intensity to build 17 candidate models (Table S3). We selected the most parsimonious model based on BIC. To control for the effect of year and unequal sample sizes across individuals, we included Year and the survivor ID nested within the hunter-killed males' ID as random intercepts in all candidate models. To facilitate model convergence, we scaled (mean = 0, variance = 1) all numerical covariates. We assessed the relative importance of variables within the most parsimonious model by dropping each variable and monitoring the Δ BIC. The larger the relative difference in BIC compared to the most parsimonious model, the more important we considered a variable. For all candidate models tested, the variance inflation factor (VIF) value was < 2 ⁴⁹. We used R version 3.2.3 for all statistical analyses⁵⁰.

We captured and GPS-monitored a total of 15 adult males between 2008 and 2015. The database contained 19,133 GPS and 19,133 random relocations of 11 hunter-killed males and 7 survivors, for a total of 23 survivor – hunter-killed male pairs.

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Acknowledgements

We would like to thank M. Festa-Bianchet, D. Garant, J. Van de Walle, one anonymous reviewer and the editor for useful comments on earlier version of the manuscript. ML was supported financially by NSERC and FRQNT. FP was funded by NSERC discovery grant and by the Canada research Chair in Evolutionary Demography and Conservation. This is scientific publication No. 232 from the SBBRP, which was funded by the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, the Research Council of Norway, the Austrian Science Fund, and the Swedish Association for Hunting and Wildlife Management. We acknowledge the support of the Center for Advanced Study in Oslo, Norway, that funded and hosted our research project “Climate effects on harvested large mammal populations” during the academic year of 2015–2016 and funding from the Polish-Norwegian Research Program operated by the National Center for Research and Development under the Norwegian Financial Mechanism 2009–2014 in the frame of Project Contract No POL-NOR/198352/85/2013.

Author Contributions

All authors participated in the study design. M.L. and S.C.F. carried out statistical analyses, F.P., J.E.S. and A.Z. secured funding, J.E.S. and A.Z. coordinated the Scandinavian Brown Bear Research Project. All authors participated in writing the manuscript.

Additional Information

Supplementary information accompanies this paper at <http://www.nature.com/srep>

Competing Interests: The authors declare no competing financial interests.

How to cite this article: Leclerc, M. *et al.* Hunting promotes spatial reorganization and sexually selected infanticide. *Sci. Rep.* **7**, 45222; doi: 10.1038/srep45222 (2017).

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Paper IV:

Frank, SC, Pelletier F, Bourret A, Garant D, Rosell F, Swenson JE, Eiken HG, Hagen SB, Zedrosser A. "A smoking gun: hunting disrupts fine-scale genetic structure among matrilineal groups of a large carnivore." Manuscript.

Title: A smoking gun: hunting disrupts fine-scale genetic structure among matriline of a large carnivore

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Abstract:

Harvest by humans can disrupt wild populations by removing adult animals that otherwise experience little predation pressure or have high survival. Furthermore, this disruption can alter breeding and dispersal patterns, in addition to changing fine-scale genetic structure of the population. We found that an increase in harvest can decrease the differential in dispersal distances between the sexes, redistribute male reproductive success, decrease fine-scale genetic structure of brown bear matriline, and lower the probability of forming and maintaining matriline. These findings have management implications for the selectivity of harvest, defining important conservation units, and the evolutionary trajectory of wild populations.

One Sentence Summary: Hunting pressure decreases the fine-scale genetic structure derived from several metrics among brown bear matriline.

Main Text:

The effect of humans on Earth's ecosystems is widespread (1) and relative to natural predation, humans are exceptional predators that can quickly disrupt wild animal populations through selectivity or harvest exceeding natural predation pressure (2-5). A unique aspect of hunting by humans is their ability to harvest adult individuals that otherwise experience little predation (6). Moreover, the hunting of adults has been shown to disrupt social structures across several mammalian species (7-9). A natural social structure and the recruitment of (reproductive) adults are integral to the development of fine-scale genetic structures in wild populations (10, 11), which have been used to designate important management and conservation units (12). For example, hunting on the periphery of wolf territories in Algonquin Park, Canada reduced kin-based composition of packs and can possibly affect evolutionary important social patterns (13).

Despite its potential importance, the effects of hunting on social structure and its consequent effects on genetic structure are not well known (14-16) and may become manifest especially in fine-scale genetic structure (FGS), i.e. among demes or subgroups of a population (17). Conversely, changes in fine-scale genetic structure of harvested populations can be used as indicators of harvested-induced changes to social structure, for example, from selective harvest (18). Social structure has long been recognized as important in influencing genetic structure in social mammals (10). Many social mammals form matrilineal-based stable groups, i.e., individuals descending from common female ancestors (19, 20). Similarly, females in solitary-living species are often spatially clustered into matrilineal groups, due to female philopatry, which can influence FGS in populations (21-25). Indeed, female philopatry is a common feature among most mammalian species (26, 27). In addition, individual heterogeneity in reproductive success among matrilineal groups can affect genetic structure (28). On the part of males, male-mediated gene flow among matrilineal groups also can affect FGS (29, 30). For example, dominant male African elephants, *Loxodonta africana*, mediate gene flow among matrilineal groups, and the poaching of adults from both sexes is suspected to decrease FGS among these groups (31).

Social structure, female and male longevity, and reproductive success can be heavily influenced by humans in hunted populations (32-37). Hunting can theoretically disrupt the underlying social and genetic structure of mammal populations (1) by removing important adult females in matrilineal groups and adult males that disproportionately contribute to future

progeny (31, 38, 39) and (2) by altering sex-specific natal dispersal and male mating patterns among matriline (15, 40-42).

Here we use the brown bear, *Ursus arctos*, as our model species to evaluate whether hunting contributes to changes in FGS among matriline. We use 30 years of individual-based genetic and demographic data from the Swedish brown bear population. A mean of approximately 7% (range: 4 – 10%) of this population has been harvested annually since 1942 (43). Although brown bears are considered solitary (44, 45), females exhibit spatial clusters into matriline in Scandinavia (46, 47). To assess changes in FGS, we subdivided females by matriline membership and in two periods, i.e., "early" (1990-2005) and "late" (2006-2011), which corresponded to periods of "low" and "high" hunting pressure, respectively (48). We used four indices to evaluate genetic structure between the two periods: Weir and Cockerham's F_{ST} (49), Hedrick's G'_{ST} (50), and pairwise relatedness (r_{xy}) from a constructed pedigree and from Lynch-Ritland's estimator (51). For the r_{xy} structure metrics, we assessed the difference between mean r_{xy} values among and within matriline. We also tested whether females exhibited structure between periods by excluding matriline as a subdivision and calculating F_{ST} and G'_{ST} . All genetic-structure metrics were derived from 16 autosomal, highly polymorphic microsatellites (Table S1). F_{ST} and G'_{ST} were assessed for females in matriline between early and late periods, and also for the total population of females between early and late periods. To test more specifically that FGS indices were indeed influenced by hunting, we also assessed female and male dispersal distance, female and male survival, the survival of mother-daughter pairs, and the proportion of unique males siring offspring for each early and late periods.

Population size and density-dependent processes can also affect dispersal, survival, and therefore genetic structure (17). Due to inverse density-dependent dispersal in this population (47), the documented increase in population size and density between early and late periods (43) would suggest a decrease in dispersal distance for both females and males. We used dispersal distance as a proxy to document how sex-specific distributions and therefore mating patterns may have changed between periods. Decreasing dispersal distances for the sexes could theoretically generate stronger FGS, if matriline clusters have "social fences" among them (52). Social fences, i.e., social barriers rendering social groups impermeable to non-members through agonistic behavior, have been suggested to occur among matriline clusters in this population (53).

We compared the survival of females and males between early and late periods to identify which ages were most impacted from hunting and to confirm that, at the level of individual, the population was indeed more heavily harvested during the late period. We also assessed the survival of mother-daughter pairs to infer the relative offtake of females from matriline between periods, i.e., a product of female survival. We considered the proportion of unique males siring offspring as a proxy for changes in male gene flow due to changes in male social structure, male dispersal, and access to females.

We predicted that the increased hunting pressure decreased FGS among matriline between early and late periods. We predicted that survival for both females and males would be lower for all ages in the late period, but particularly for adults (≥ 4 years of age). We also predicted lower survival of mother-daughter pairs during the late period. For males, we predicted an increase in the proportion of unique males siring offspring from the early period to late.

Fine-scale genetic structure and hunting pressure

We found that FGS decreased from early to late periods for each FGS metric used (Fig. 1, panels A-D; t-test, $P < 0.001$ for each pairwise-period comparisons of bootstrapped values). Conversely, hunting pressure and population size increased from early to late periods (Fig 2, panels A and B; Mann-Whitney U, $P < 0.003$ and $P < 0.001$, respectively). Although a larger population size might reduce FGS due to more adults occurring within the population (17), the number of breeding females was virtually equal between early and late periods in our study (matriline data set: $N_{early} = 56$, $N_{late} = 57$). Furthermore, although female FGS decreased from early to late periods, individual females did not exhibit a change in genetic structure between periods, regardless whether all females were used in the sample population (population data set: $N_{early} = 183$, $N_{late} = 154$; $FGS = 2.8 \times 10^{-4}$, $P = 0.31$) or only those assigned to matriline (matriline data set: $FGS = 2.7 \times 10^{-3}$, $P = 0.33$). Both results suggest that hunting pressure is more likely the cause for a decrease in FGS than population size. Thus, changes to genetic structure over time, due to an exogenous force such as hunting, might occur at the scale of FGS, rather than the population or inter-population level (11).

Changes in survival of females and mother-daughter pairs due to hunting pressure

Higher hunting pressure, i.e., during the later period, significantly lowered the survival of females and mother-daughter pairs (Fig. 3, panels A and B, $P = 0.003$ and $P < 0.001$,

respectively). Adult females in particular had lower probabilities of survival in the late period, and this effect was further enhanced during advanced ages (10-16 years) (Fig. 3, panel A). Furthermore, model predictions indicated lower survival probability for mother-daughter pairs, which suggests it was less probable to form and maintain a matriline in the late compared to the early period (Fig 3, panel B). In fact, most matriline experienced either a leveling-off or decrease in the number of females during the late period (Fig. S1). The most important factor limiting lifetime reproductive success in our study population is lifespan (32), with the single greatest cause being human-induced mortality (54). Heterogeneity in reproductive success among matriline due to differences in lifespan could ultimately affect the genetic structure of matriline (28). As a result, the removal of females from the population and from matriline has most likely altered the allocation of genetic variation among matriline from early to late periods. Although the hunting selectivity is generally considered to be low in this population in terms of sex and age (54), high hunting pressure appears to cause the selection of slower life histories and smaller size in adult females (55, 56). Therefore, the removal of females through hunting and the potential for hunter selectivity of phenotypes could have also contributed to a decrease in FGS among matriline (18, 57).

Altered male gene flow due to hunting pressure and sex-specific dispersal patterns

Female dispersal distances have decreased significantly between early and late period (Fig. 5, panel A; Mann-Whitney U test, $P < 0.01$), whereas there was no evidence of a change in dispersal distances in males (Fig. 5, panel B; Mann-Whitney U test, $P = 0.52$). As a result, male gene flow among matriline most likely increased. Dispersal is density-dependent in many mammal populations (58), so increasing population size and/or density cannot be ruled out as an influencing factor on FGS. Furthermore, a higher density may have contributed to the decrease in fine-scale genetic structure, due to the increase in spatial overlap among females (59, 60), but this would indicate that social fences either broken down or did not exist in this population. Although there is evidence of spatial structure among matriline (46), FGS in were derived genetically, not spatially *per se*. Thus, the potential for increased home range overlap among females should not have influenced our structure metrics directly, but it may have contributed to the decrease of FGS relative to increased male gene flow among matriline.

Post-dispersal breeding success was distributed across significantly more males in the late period (Fig. 4, t-test, $P < 0.001$). Previous research on reproductive skew in male

reproductive success, due to body size and age, could be indicative of male dominance structures during the mating season (61). Furthermore, hunting can disrupt social structures and cause spatial reorganizations of both sexes in this population (9, 62). Disruptions of social structure can affect mating patterns such as enhancing sexually selected infanticide through the increased contact between unfamiliar males and females during the breeding season (9, 63, 64). Although older and larger males often have higher breeding success across several mammalian species (61, 65, 66), disruptions to male social structure does not require harvest to be age- or size-selective (67-70). In some populations, harvest can shift breeding success to males of similar ages or size as the killed animals (71), whereas in others, it can redistribute breeding success across different male ages and sizes, or to more males in general (61, 72, 73). The effect of harvest on male breeding success is probably not linear and depends on operational sex ratios (74). However, given a near equal sex ratio or harvest during our study period, hunting pressure might be more crucial (75). We contend that the high hunting pressure during the late period (reaching ~10%), caused the male dominance structure during the mating season to be destabilized (63) due to high male turnover (33, 76), which would lead to increased male gene flow and decreased FGS among matriline. As more males become successful breeders across matriline and their relative dispersal distances increase, the relative male gene flow among matriline would increase.

Changes in fine-scale genetic structure—a smoking gun from hunting

In addition to density, hunting pressure has been linked to differences in sex-specific dispersal patterns in other large carnivore populations (77-79). Hunting pressure or quotas are commonly based on the population growth rate and size (80). Therefore the effects of hunting pressure and population size on social, genetic, and demographic structure of wild populations could be correlated or confounding (14). Nevertheless, by using several FGS metrics, coupled with individual-based survival probabilities and proxies for dispersal distances and male gene flow, our study highlights that hunting can contribute to a decrease in FGS.

Genetic structure is important for the conservation and management of wildlife, because it affects and reflects fundamental processes such as dispersal, mating, and ultimately individual fitness and persistence of populations (81). Human harvest of wildlife can modify ecological and evolutionary processes (3, 82). We provide empirical evidence that hunting has disrupted the social structure of male and female brown bears, as evidenced by changes in fine-scale genetic structure, but not necessarily in population-level genetic structure.

Specifically, we propose that hunting has (1) removed adult females and adult males from the population and (2) redistributed breeding success among males, all of which has contributed to the decrease in FGS among matriline. Asymmetric gene flow among matriline, which can increase FGS, may be important for the adaptive potential of species or populations, e.g., against harmful effects of climate change (83, 84). Despite many unknowns, changes in genetic structure due to harvest certainly warrant further attention, so that harvest management plans can be developed to safeguard populations against such potential harmful effects (14). For example, changes in FGS due to hunting could be a smoking gun, with reference to otherwise undetected changes at the population or inter-population level, and could be an indication of how hunting is selective at different scales within a population. This emphasizes the need to both collect genetic samples over time (14) and analyze populations at different 'social' scales, e.g., the population over time, along matriline, social groups, or demes (11). We stress the importance of using multiple scales when assessing changes in genetic structure, particularly in hunted populations of long-lived species in which changes to genetic structure might take longer to recover from (82).

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Acknowledgements: This is scientific publication No. XXX from the SBBRP, whose long-term funding comes primarily from the Swedish Environmental Protection Agency, the Norwegian Environment Agency, the Swedish Association for Hunting and Wildlife Management, and the Austrian Science Fund. We thank E. Bellemain and S.G. Aarnes for their vital help with the genetics data between the two labs. We thank R. Bischof for his useful input on survival analysis, I.M. Rivrud for aid in assessing bear centroids, S. Steyaert for help with screening location data, and G. Pigeon for lending out helpful R scripts. We also thank S. Brunberg, D. Ahlqvist, A. Friebe, J.M. Arnemo, A. Evans, and J. Painer for making the data collection possible in the field. We acknowledge the support of the Center for Advanced Study in Oslo, Norway, that funded and hosted our research project “Climate effects on harvested large mammal populations” during the academic year of 2015-2016 and funding from the Polish-Norwegian Research Program operated by the National Center for Research and Development under the Norwegian Financial Mechanism 2009-2014 in the frame of Project Contract No POL-NOR/198352/85/2013. FP was funded by NSERC discovery grant and by the Canada Research Chair in Evolutionary Demography and Conservation.

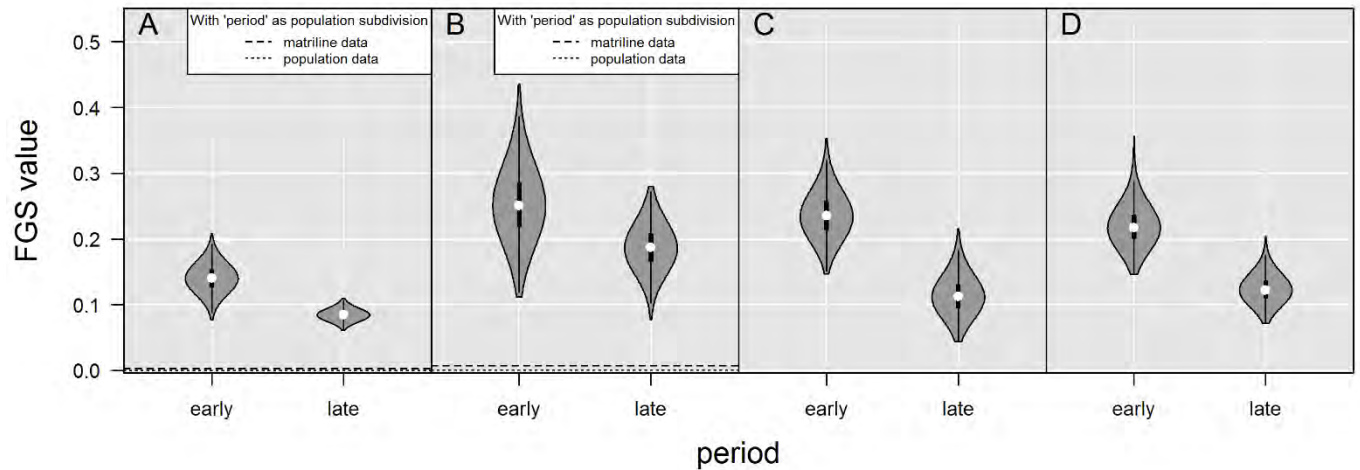


Fig 1. Indices of female fine-scale genetic structure (FGS) in brown bears in Sweden between periods of low and high hunting pressure, i.e., "early" (1990-2005) and "late" (2006-2011), respectively, using F_{ST} (panel A), G'_{ST} (panel B), r_{xy} structure from Lynch-Ritland (1999) (panel C), and r_{xy} structure from a constructed pedigree (panel D). Each index was bootstrapped ($N = 1000$); for F_{ST} and G'_{ST} , indices were bootstrapped across loci, whereas r_{xy} indices were bootstrapped across individuals. For F_{ST} and G'_{ST} , 'period' was also used as a population subdivision to assess whether females showed different structure between early and late periods. Two data sets, i.e. a matriline data set and a population data set, were each used to assess this, both of which showed little evidence of structure among females between periods. However, fine-scaled genetic structure was evident among matriline, which has decreased from early to late periods for every index used.

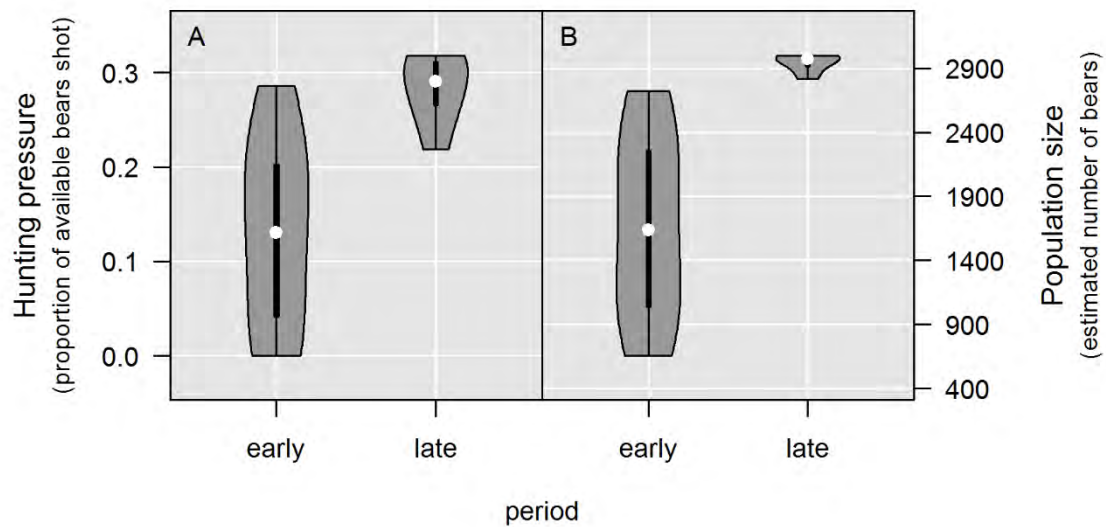


Fig. 2. Hunting pressure (Panel A), i.e., the proportion of available brown bears available in the study area in Sweden that were shot each year and its distribution in periods of low (early, 1990-2005) and high (late, 2006-2011) hunting pressure. Similarly, annual population size (Panel B) was estimated from the trend in population size across years (43) using a generalized additive model, with the model predictions of population size and its distribution shown in early and late periods. The central measures of both hunting pressure and population size increased from early to late periods ($P < 0.003$ and $P < 0.001$, respectively).

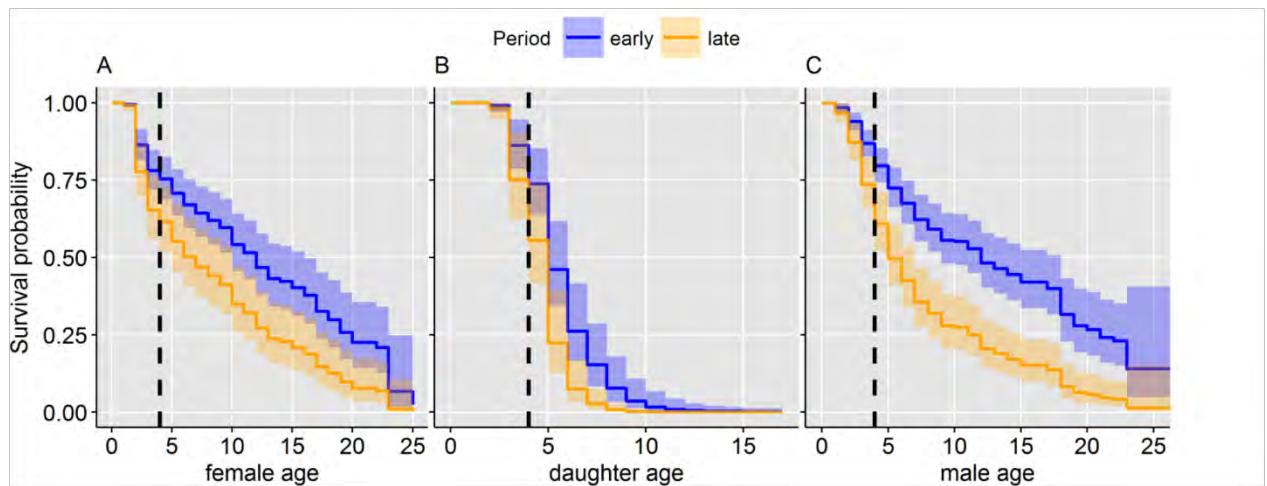


Fig. 3. The probability of survival using cox proportional hazards model for marked female brown bears (panel A), mother-daughter pairs (panel B) and males (panel C) in Sweden. In all panels, the broken lines indicate age 4, i.e., at which a female or male was considered reproductive, and when a female was a part of a matriline in our study. Model predictions suggested that matriline formation and maintenance was less probable in the period of high hunting pressure (late, 2006-2011) compared to low hunting pressure (early, 1990-2005). Both reproductive females and males had lower survivorship in the late compared to the early period, particularly after reaching adulthood.

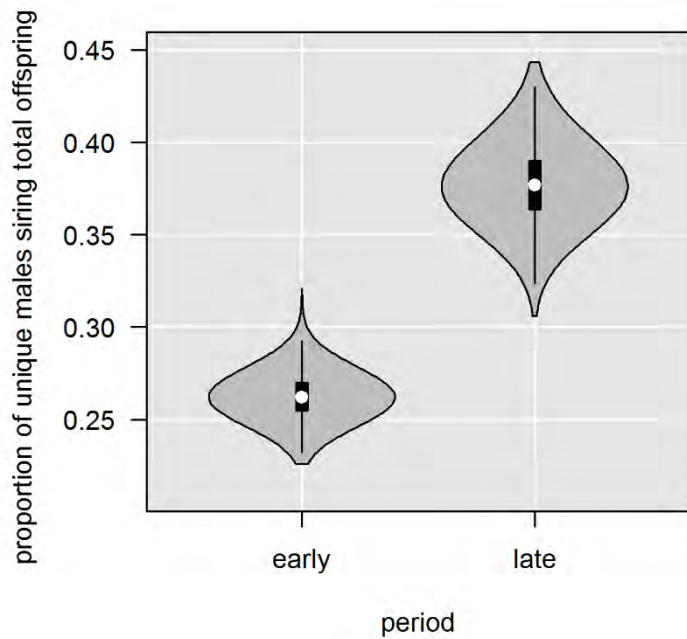


Fig. 4. The proportion of unique male brown bears siring total offspring by periods of low (early, 1990-2005) and high (late, 2006-2011) hunting pressure in Sweden ($N_{\text{offspring in early}} = 405$, $N_{\text{offspring in late}} = 233$). Data sets were bootstrapped ($N = 1000$) and proportions were calculated each time to attain distributions around observed values. The late period had a significantly higher proportion of unique males siring offspring compared to early (t-test, $P < 0.001$).

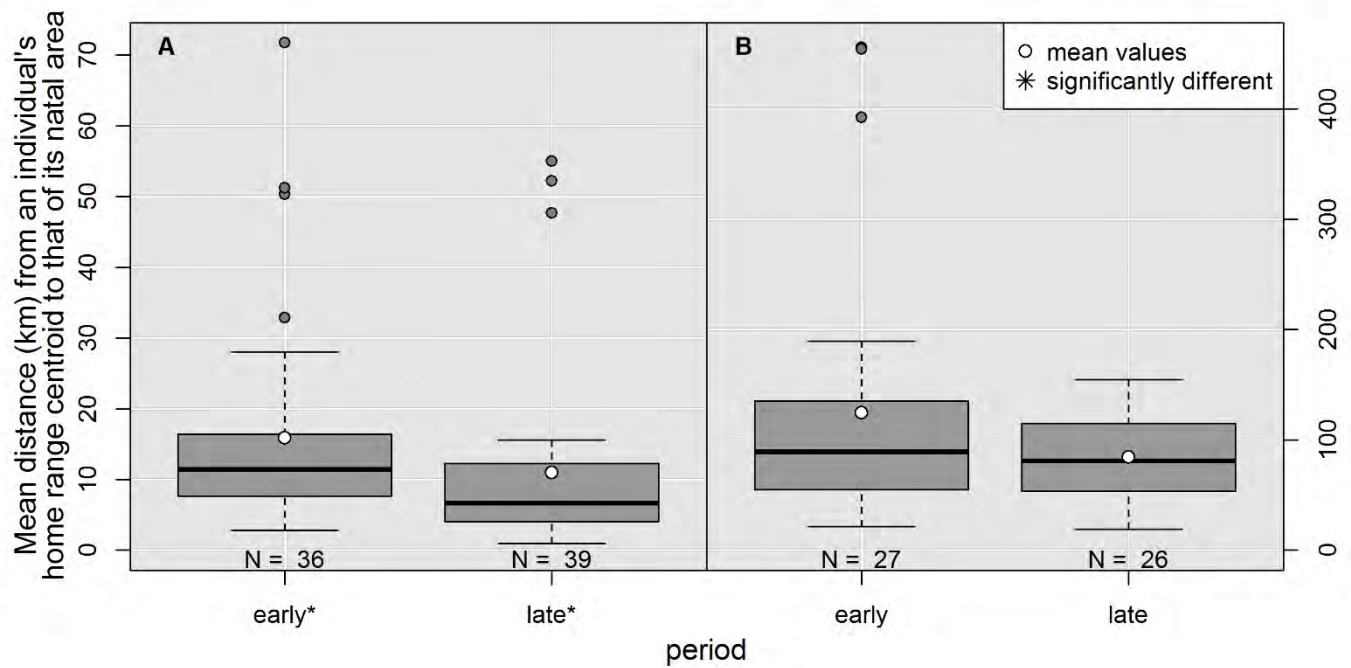


Fig. 5. The dispersal distances of female (panel A) and male (panel B) brown bears, respectively, between periods of low (early, 1990-2005) and high (late, 2006-2011) hunting pressure in Sweden. Female and males were assigned to early or late, depending on the period when they were at age 4. There was a significant difference between early and late periods for female distances ($P < 0.01$), but not for males ($P = 0.52$).

Supplemental Materials:

Materials and Methods

Figures S1-S2

Tables S1-S3

References (43, 48-51, 54, 85-110)

Supplemental Materials:

Materials and Methods:

Study area and study population

The study area consists of approximately 160,000 km² covering four counties (Dalarna, Gävleborg, Västernorrland, and Jämtland) in southcentral Sweden (61°N, 15°E). It is composed of bogs, lakes, and intensively managed, mixed-aged forest stands typically of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and birch (*Betula* spp.). Elevation ranges between 150 - 725 m. Gravel roads have a higher density (0.7 km/km²) than paved roads (0.14 km/km²). See Martin, Basille, Van Moorter, Kindberg, Allainé and Swenson (85) for further information about the study area.

The Scandinavian bear population has increased from near extirpation in 1930 to around 3,000 bears today, with approximately 95% of those occurring in Sweden (43, 86, 87). Our study population represents the southern subpopulation of the Scandinavian brown bear population (88). To the north lie other subpopulations, which are geographically and genetically distinct from the south, though male-mediated gene flow from northern immigrant males may occasionally enter the south (89).

Hunting regime and hunting pressure

In Sweden, brown bear hunting generally starts 21 August and lasts until the annually established quota has been filled in an area (43). Population density of bears varies and is approximately ~30 bears/1,000 km² in the south (90, 91). Previous research has shown that hunting pressure in this study population can be divided into two periods, depicting low (1990-2005) and high (2006-2011)(48). The high hunting pressure period coincides with the first observed decrease in population size across Scandinavia since the population's recovery

from near extirpation (43). Hunter sex and age selectivity is considered to be low and with the sex ratio (M:F) of harvest nearly 1:1 within these periods (54).

Captures

We captured brown bears (N =456) from a helicopter using a remote drug delivery system between 1985-2014 (Dan-Inject, Børkop, Denmark). We determined the bears' sex at capture and the ages of individuals not captured as a yearling (n = 181) by extracting a vestigial first premolar (92). Bears were fitted with VHF (1985-2014) and GPS collars (starting in 2003; GPS Plus; Vectronic Aerospace GmbH Berlin, Germany), the latter of which were programmed to be relocated with varying schedules (≤ 1 hour). See Fahlman, Arnemo, Swenson, Pringle, Brunberg and Nyman (93) for details on capture and handling. All bears captured and handled followed a protocol approved by the Swedish Board of Agriculture, Uppsala Ethical Committee on Animal Experiments, the Swedish Environmental Protection Agency, and the Norwegian Food Safety Authority.

DNA sampling, extraction, microsatellite genotyping, and error rate

Sources of DNA were tissue and hair between 1985 and 2014 from both captured and dead bears, the latter of which were mostly hunter-killed (79%). Every bear found dead is legally required to be examined by the Swedish State Veterinary Institute and tissue samples are taken for genetic analyses. Tissue was temporarily stored in 95% alcohol prior to DNA extraction. Hair was stored in paper envelopes for drying. Multiple tissue and hair samples were taken from individuals that were captured multiple times and/or were also recovered dead, which were used to assess genotyping error rate (below).

The amplification and analysis of short tandem repeat loci (hereafter microsatellites) of 16 autosomal microsatellites (Table S1) was performed in two labs, the Laboratory of Alpine Ecology (LECA) and Bioforsk Svanhovd. LECA performed amplification following the protocol from Waits, Taberlet, Swenson, Sandegren and Franzén (94). Genotyping efforts were calibrated between the two labs, in order to ensure consistency (95), resulting in 1,463 individual genotypes. Using 120 individuals that were genotyped twice, we calculated an error rate from the sum of mismatches between paired loci divided by the total number of loci genotyped (G_e , Table S1).

Pedigree construction

We used Cervus 3.0 (96, 97) and COLONY (98) to assign parentage to offspring and construct a pedigree. Assignments of a father (when the mother was known from field observations, N = 321) or both parents (N = 1142) were based on LOD delta scores. Critical LOD delta scores with a confidence level of 95% were assessed by simulations and candidate parents were determined based on minimum ages of first reproduction (males = 3 years, females = 4 years). We then used COLONY (98) for sibship reconstruction, which simultaneously reconstructs unknown father genotypes, enabling us to recover potential fathers and sibship missed in Cervus's parentage assignment. Sibship reconstruction was assessed for individuals with known mothers from field observation but without fathers genetically assigned (N = 68). The settings used for parentage assignment in Cervus and sibship reconstruction in COLONY are listed in Table S2.

Reconstruction of bear lives, the study period, and 'population data set'

Using ages of marked female bears (i.e., alive and recovered dead; N = 201) and unmarked female bears (i.e., recovered dead; N = 458) for which genetic information was available (Total = 659), we constructed the years in which females were alive between 1985-2014. Our study period began following five years of genetic sampling (1985-1989), in order to allow an adequate, representative genetic sampling of the population. Due to potential bias from the reconstruction of lives from recovered dead bears, we also truncated our available data on the right side of the sampling period by the mean age of female bears killed in 2014 (~3 years). These two strategies yielded a study period from 1990-2011 which we further divided into 'early' (1990-2005) and 'late' (2006-2011), based on low and high hunting pressure. Furthermore, as we wanted to examine the fine-scale genetic structure among matriline, we only included females ≥ 4 years old (N = 337), to avoid females still dependent on their mothers. We refer to this data set as the 'population data set' for females, as not all females were successfully assigned mothers and constituted a larger sample size of the population than those assigned to matriline.

The definition of a matriline and the 'matriline data set'

A matrilineal "founder" ID or the one belonging to the most ancestral female (ancestress) of a given matriline was extracted from the pedigree, which was used as the matriline ID for all her female descendants. The pedigree was incomplete, i.e., some female bears were not assigned mothers, which could result in erroneously assigned matriline IDs or those largely abbreviated, due to missing maternal links. To increase confidence in matrilineal assignments,

we used the reconstructed lives of females and their presence over time (Fig. S1). We chose a minimum threshold for the maximum number of living females observed in a matriline across years. To choose this threshold, we plotted the number of matriline resulting from the incremental increase in the threshold—where the curve levels out and changes became less pronounced is the threshold at which we considered "true matriline" (hereafter matriline) to occur (Fig. S2). This threshold was four individual females of ≥ 4 years of age that must have lived at the same time during at least one year of a matriline's tenure (Fig. S2—the intersection of the dashed lines is the chosen threshold; Fig S1—matriline shown in color, all others shown in gray with the dotted line depicting our chosen threshold). We subset the population data set to include only females that belonged to a matriline (hereafter 'matriline data set'). Fine-scale genetic structure metrics were calculated on both population and matriline data sets either using the variable "period" or "matriline ID" as the population subdividing unit (below).

Pairwise relatedness values: pedigree-derived and Lynch-Ritland estimates

The pedigree and microsatellite data were used to calculate pairwise relatedness values, with the latter implementing Lynch and Ritland's method (hereafter LR; 51). Although each comes with advantages and drawbacks, both pedigree-derived and LR estimates used in tandem can validate one another and therefore increase confidence in results making use of such relatedness metrics (99). We used Spearman's correlation coefficient between these two relatedness estimates for matriline data set, considering values ≥ 0.25 as within normal, expected ranges (100).

Fine-scale genetic structure metrics

We calculated Weir and Cockram's F_{ST} (49) and Hedrick's G'_{ST} (50) with functions from the R packages 'hierfstat' (101) and 'mmod', respectively, and by using two different population subdividing units. Though widely-used, F_{ST} has been criticized for having strong dependencies on within-population genetic diversity values (102). Therefore, we also calculated Hedrick's G'_{ST} , which standardizes F_{ST} according to its maximum value possible, given the observed genetic diversity of a population (50, 102). We used "period" ("early" or "late") as the population subdividing unit for both population and matriline data sets to detect whether there was genetic differentiation among females between early and late periods. We also used permutation tests ($\alpha = 0.05$) to evaluate whether these results were significantly different from zero. To detect whether genetic structure among matriline had changed

between early and late periods, matriline ID was used to subdivide the population into the matriline data set, for which F_{ST} and G'_{ST} were independently calculated for each early and late period.

We also calculated an index of structure among matriline using pairwise relatedness (r_{xy}). For the matriline data set, we calculated the difference between among- and within mean r_{xy} of matriline by period: mean r_{xy} of individuals belonging to different matriline minus the mean r_{xy} of individuals belonging to the same matriline. This was calculated independently for early and late periods. All r_{xy} calculations were carried out using each the pedigree and LR relatedness estimates. To attain measures of precision, we bootstrapped all F_{ST} , G'_{ST} , and r_{xy} structure calculations.

Because bears are long-lived, several bears ($N = 42$ of 110 or 38%) lived in both early and late periods (hereafter straddlers). We assigned straddlers to either period according to the period the bear had lived the majority of its life. For bears that evenly straddled the two periods ($N = 3$ or 3%), we used 10 iterations, randomly putting the bear in either the early or late period and recalculated all fine-scale genetic structure metrics along with associated bootstraps.

Hunting pressure and population size

Hunting pressure was calculated based as the proportion of marked bears shot of those available to be hunted in a given year and calculated from 1990-2011. Distributions of population size between early and late periods approximated published population size estimates in Sweden (43). We fit a generalized additive model to population estimates (43) with a smoother on 'year' from 1942-2013. Model predictions by year were then used to get distributions of population size estimates by period.

Relocation data and dispersal distances

Relocation data of bears came from both VHF and GPS collars with variable relocation schedules, e.g., once a week to ≤ 1 hour, respectively, from 1985-2015. All GPS positions with a dilution of precision > 5 and location errors detected using the method of Bjørneraas et al. (103) adjusted to bear movement rates were removed from the relocation data set. As many VHF-collared individuals had too few observations to obtain a confident home range estimate, we estimated HR centroids using several methods, i.e., a median centroid or a -LoCoH centroid based on relocation coordinates. For a -LoCoH, a minimum of 15 relocations was

required and the α -value was chosen according to Getz et al. (104) so that it was larger than the two longest distances between relocations, yielding a 100% density isopleth. We estimated centroids of natal home range areas for females and males, i.e., the HR centroid while with their mothers, as well as all available subsequent HR centroids belonging to bears following separation from their mothers. As multiple distances were observed between centroids of a bear's annual HRs and that of its natal home range area, we took the mean of all such distances for each bear. To be consistent with our definition of matriline, we only considered home ranges of female and males ≥ 4 years for comparison with their respective natal ranges. Bears were assigned to "early" (years 1990-2005) or "late" (years 2006-2011) depending on which year they were 4 years old. We considered these distances to be reflective of dispersal distances between a bear's HR and that of its natal area, which we compared between early and late periods using a Mann-Whitney U test.

Survival Analysis: probability of female survival and joint mother-daughter survival

To test whether the probability of a female living to a given age was influenced by period, we used survival analysis, i.e., a cox proportional hazards model (105). We used all marked female bears and their annually reconstructed ages from 1990-2011 as the 'survival time'. Female bears' observed ages were partitioned into a covariate 'period' as either 'early' or 'late' depending on the year in which the age occurred (early: 1990-2005, late: 2006-2011). Survival analysis allows information to be used despite the censoring of data, i.e., when complete life histories are not available or the event does not occur for an individual within a sampling interval. In the case of female survival, the 'event' modeled was whether her death occurred. In quantifying the probability of joint mother-daughter survival, the 'event' occurred when at least one of the two individuals in a mother-daughter pair died, but otherwise had the same model structure as the probability of female survival using the package 'survival':

coxph(Surv(entry.age, exit.age, event) ~ period)

For each model we tested the proportionality of hazards assumption using the `cox.zph` function in R (106).

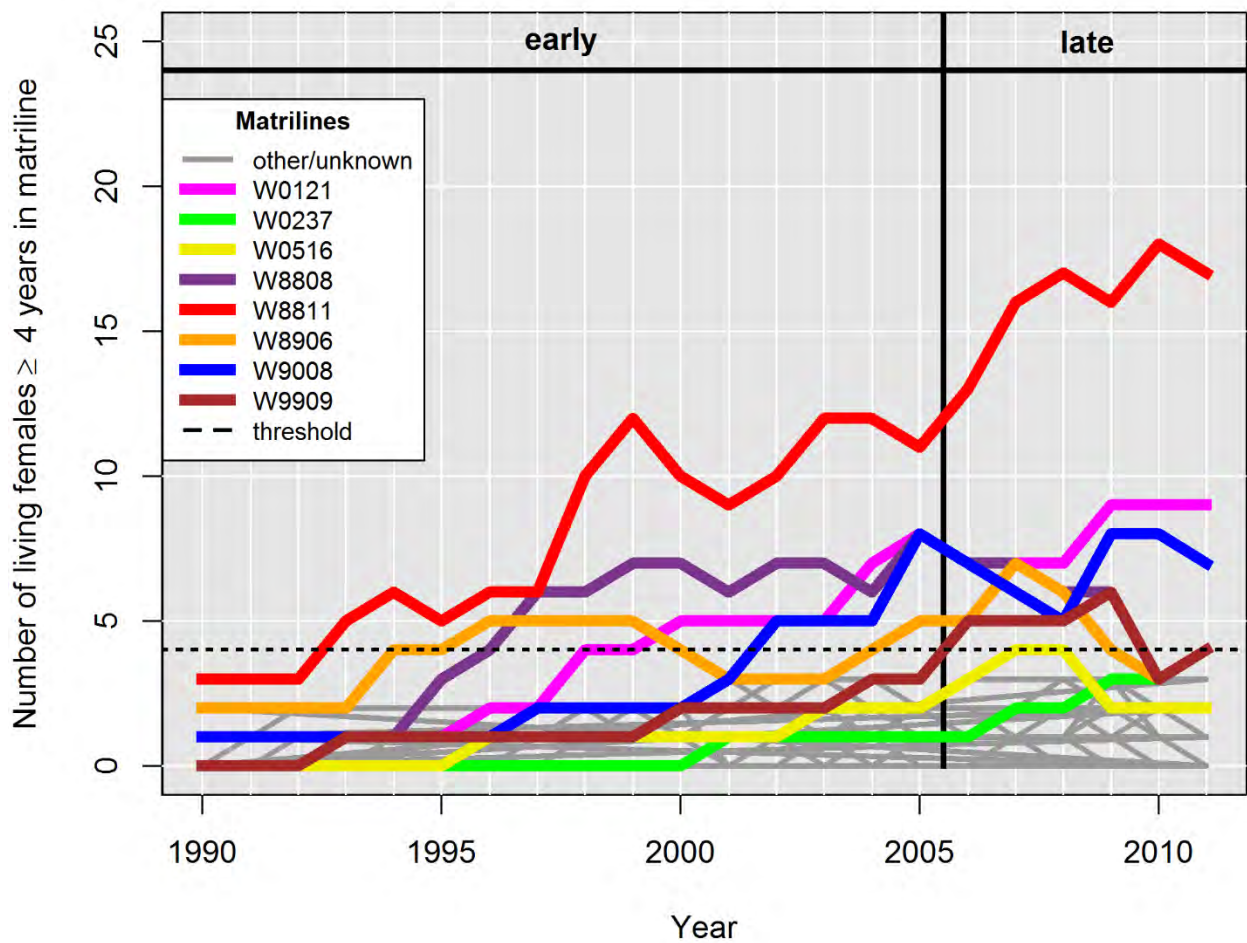


Fig. S1. The number of females belonging to matriline, i.e. labeled by founding females, across years from 1990-2011, grouped into periods of low and high hunting pressure, i.e., "early" (1990-2005) and "late" (2006-2011). The horizontal broken line signifies the number of female descendants (aged ≥ 4 years) that a founding female must have to be conservatively considered a matriline in this study. The category "other/unknown" is a result of that classification, i.e., not considered a part of a matriline (see text and Fig. S2).



Fig. S2.). The number of brown bear matriline groups (y-axis) produced from variable thresholds on the minimum number of living females ≥ 4 years of age observed (x-axis) belonging to a founding female, as depicted by yellow dots. The red steps illustrate where the decrease in number of matriline groups produced by various threshold values levels out. Leveling out occurred at four living females ≥ 4 years of age, which is shown by the intersecting broken black lines. We considered 8 matriline groups as 'true matriline groups', i.e., those belonging to a founding female that contained four or more living females of ≥ 4 years of age during at least one year of its tenure.

Table S1. Table was adapted from Frank et al. (in revision J.A.E.), which provides summary statistics for microsatellites used for pedigree reconstruction and Lynch and Ritland's (1999) relatedness index for brown bears (N = 1614) in southcentral Sweden. N_A: Number of alleles, H_o: observed heterozygosity, H_e: expected heterozygosity, P_{ex}: probability of exclusion for a single unknown parent, P_{id}: probability of identity for unrelated individuals, G_e (%): genotyping error rate by locus. Averages were calculated for N_A, H_o, H_e, and G_e whereas overall probabilities across all loci were calculated for P_{ex} and P_{id}.

Locus	N _A	H _o	H _e	P _{ex}	P _{id}	G _e
G1A ^a	6	0.625	0.630	0.380	0.810	0.0
G1D ^a	7	0.592	0.620	0.340	0.786	0.4
G10B ^a	8	0.699	0.703	0.442	0.855	0.0
G10C ^b	5	0.697	0.698	0.460	0.864	0.5
G10J ^c	6	0.574	0.570	0.325	0.762	0.4
G10H ^c	9	0.525	0.545	0.308	0.740	0.6
G10L ^a	8	0.757	0.760	0.544	0.905	0.0
G10O ^a	3	0.392	0.397	0.166	0.564	0.9
G10P ^b	6	0.736	0.757	0.535	0.902	0.0
Mu05 ^d	8	0.640	0.636	0.365	0.797	0.5
Mu10 ^d	8	0.806	0.806	0.610	0.933	0.0
Mu15 ^d	4	0.658	0.643	0.364	0.805	0.0
Mu23 ^d	8	0.709	0.699	0.485	0.876	4.7
Mu50 ^d	10	0.735	0.756	0.538	0.903	1.1
Mu51 ^d	9	0.824	0.796	0.592	0.926	2.0
Mu61 ^d	4	0.529	0.542	0.272	0.714	0.0
Average/Overall	7	0.656	0.660	>0.99	>0.99	0.1

^aPaetkau and Strobeck (107); ^bPaetkau, Calvert, Stirling and Strobeck (108); ^cPaetkau, Shields and Strobeck (109); ^dTaberlet, Camarra, Griffin, Uhrès, Hanotte, Waits, Dubois-Paganon, Burke and Bouvet (110).

Table S2. Settings for both Cervus 3.0 (parentage assignment) and COLONY (sibship reconstruction), the latter of which recovered fathers of unknown identity but held in common among offspring. Cervus analyses were performed for father only (when mothers were known) and for both parents. The output was used to construct a pedigree for brown bears in Sweden.

	Father only analysis	Both parents analysis
Cervus		
Simulations		
N offspring simulated	10,000	10,000
N candidate fathers	128	125
N candidate mothers	-	96
% sampled fathers	75	75
% sampled mothers	-	90
% loci typed	97	97
% loci mistyped	1	1
Minimum loci typed	8	8
Assignments		
N offspring	321	1463
N father assigned	253	407
N mother assigned	-	554
COLONY		
N offspring	68	-
N candidate mothers	36	-
Model type	Inbreeding	-
Mating system	Polygamy	-
Prob. a mother is included in the candidates	0.95	-

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ISBN: 978-82-7206-450-0 (print)
ISBN: 978-82-7206-451-7 (electronic)

usn.no

