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PhD-thesis

Spatial ecology of wolves in Scandinavia

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From spatio-temporal dynamics of wolf pairs to wolf population dynamics

PhD in Applied Ecology

2016

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Preface

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This thesis was written in LaTeX.

Contents

Sammendrag

For å kunne utvikle gode planer for bevaring og forvaltning av en art, er det nødvendig å forstå hvordan variasjoner i tid og rom kan forme populasjoner. I denne doktorgraden har jeg benyttet data fra langtidsstudier av ulv (*Canis lupus*), som er samlet inn i Skandinavia etter dens rekolonisering på begynnelsen av 1990-tallet. Mine hovedmål var å finne ut hvordan habitat kunne påvirke demografien til denne sosiale flokk-levende rovdyrarten. Flokkene er stort sett sammensatt av et revirhevdende ynglende par og deres avkom. Siden det revirhevdende paret spiller en viktig rolle i flokken, er de ofte sett på som den funksjonelle enheten av ulvebestanden. Jeg har derfor valgt å fokusere analysene mine på de revirhevdende parene. Ulveparene unngikk i hovedsak habitater som var påvirket av mennesker når de etablerte et revir. Tiden ei tispe og en hann klarte å holde sammen som et revirhevdende par viste seg å være kort (gjennomsnittlig 3 påfølgende vintre), og oppløsningen av paret var som oftest forårsaket av mennesker. Videre fant jeg ut at effekten av uttak (lisensjakt, skadefelling eller ekstraordinært uttak) på populasjonsveksten var sammensatt, da det også er andre årsaker (f.eks. innavl, illegal jakt, sykdom) som påvirker populasjonsvekst, noe som gjorde det vanskelig å finne effekten av selve uttaket. Jeg fant derimot ut at evnen parene hadde til å holde sammen over tid var en bedre faktor for å forutse populasjonsveksten enn dødelighet forårsaket av uttak. I tillegg fant jeg ut at konkurranse med brunbjørn (*Ursus arctos*) kan ha påvirket det romlige mønsteret for rekoloniseringen av ulv. At ulven unngår bjørn i både tid og rom kan forekomme på flere skalaer, helt fra avgjørelsen om hvor de skal etablere et revir, til habitatvalg innenfor det etablerte reviret. Mine resultater viser hvordan data fra langtidsstudier av ulv kan bli brukt for å gi viktig informasjon som setter demografi i sammenheng med habitat hos et sosialt rovdyr. I denne syntesen får jeg også frem viktigheten av en funksjonell enhet (det revirhevende paret hos ulver) for populasjonsdynamikken til en sosial art. Jeg anbefaler derfor overvåknings- og forvaltningsprogram til i fremtiden å ha fokus på par-nivå.

Abstract

Understanding how spatial and temporal variations shape populations is necessary to develop trustworthy conservation and management planning. In this thesis, I used individual-based long-term monitoring data of the grey wolf (*Canis lupus*) collected in Scandinavia during its recolonization phase since the early 1990's. My main goal was to identify how habitat could affect the demography of this social carnivore species living in packs. Packs are generally composed of a territorial breeding pair and their offspring. Because the pair plays an important role in the pack, they are generally considered as the functional unit of wolf populations. I therefore focused my analyses on the territorial pair. My results suggest that wolf pairs generally avoided habitat characterized by humans when establishing a territory. Wolf pair bond duration was short (on average 3 consecutive winters), and dissolutions were mostly caused by humans. Furthermore, I showed that the effect of wolf culling (*i.e.* legal harvest) on population growth was complex. Culling interacted with the intrinsic characteristics of the species and other causes of mortality making any predictions of the effect of culling rather challenging. However, I found that temporal pair bond stability was a better predictor of growth rate than individual culling mortality. Additionally, I found that interspecific competition with brown bears (*Ursus arctos*) could have contributed to shape spatial patterns of wolf recolonization. The spatio-temporal avoidance of bears by wolves could occur at several scales, from decisions on territory establishment to the habitat selected by wolves within their home ranges. My results showed how data from long-term monitoring programs can be used to provide key information linking demography with habitat in a social large carnivore. In this thesis, I also highlighted the importance of a functional unit (i.e. the wolf pair for wolves) for the population dynamics of a socially-living species. I therefore recommend monitoring, management and conservation programs to further focus their actions at the level of the wolf pair.

Key words: *Canis lupus* — demography — habitat — human — interspecific competition — monitoring — population dynamics — social species — *Ursus arctos* — wolf pair

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List of papers

This thesis is based on the following original publications and submitted manuscript.

Paper I:
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Paper II:
Milleret, C., Wabakken, P., Liberg, O., Åkesson, M., Flagstad, Ø., Andreassen, H. P., and Sand, H. (2016). Let's stay together? Intrinsic and extrinsic factors involved in pair bond dissolution in a recolonizing wolf population. *Journal of Animal Ecology*

Paper III:
Milleret, C., Chapron, G., Andreassen, H. P., Åkesson, M., Liberg, O., Sand, H., and Wabakken, P. Using an integrated population model to infer the impact of culling mortality and pair dissolution on wolf population dynamics. *Manuscript.*

Paper IV:
Milleret, C., Ordiz, A., Chapron, G., Andreassen, H. P., Kindberg, J., Månsson, J., Tallian, A., Wabakken, P., Wikenros, C., Zimmermann, B., Swenson, J., and Sand, H. Not in my back yard; habitat selection and niche overlap between two sympatric apex predators, brown bears and gray wolves. *Under review in Ecography.*

1 Introduction

1.1 The spatial component in ecology

In a broad sense, spatial ecology is the study of how specific spatial patterns influence individuals, populations and, ultimately, ecosystem dynamics (Tilman and Kareiva, 1997). Due to the rapid changes induced by humans on earth, a major field of spatial ecology focuses on identifying threats caused by humans (*e.g.* habitat loss and fragmentation) on free-ranging populations. Human-related threats often restrict populations in terms of distribution range, habitat use, size, and population growth (Kerr and Currie, 1995; Pimm et al., 2006). In heterogeneous environments, changes in habitat quality for a given species could lead to local demographic differences (MacArthur, 1972; Gaillard et al., 2010). High quality sites could then become sources (births exceeding mortality rates), while low-quality sites could lead to sinks (births lagging behind mortality rates) (Pulliam, 1988; Delibes et al., 2001). Adaptive habitat selection should allow animals to identify, and ultimately avoid, these low quality habitats (Rosenzweig, 1981). According to the ideal free distribution concept (Fretwell and Lucas, 1969), animals should be distributed spatially such as their fitness is maximized (Morris, 1987). However, low quality sites can be difficult to perceive for animals because high mortality, or breeding failure, can occur due to population extrinsic factors that may be different from those of their evolutionary history (*e.g.* human hunting or pollution).

The selection of low quality sites by animals can result in ecological traps (Schlaepfer et al., 2002; Battin, 2004) which occur in many different systems across the world (Dwernychuk and Boag, 1972; Falcucci et al., 2009; Mosser et al., 2009; Minnie et al., 2016). Beyond ecological science, it is also important to identify such areas in order to inform conservation-oriented management about populations in human-dominated landscapes. For example, protected areas have the role to maintain well-functioning ecological processes and function as source areas. However, many protected areas do not fulfill these roles (McKinney, 2002; Rauset et al., 2016), which brings real challenges for conservation and management (Battin, 2004). Therefore, there is a need to link ecological studies on animal space use with the performance of animals (*e.g.* survival or reproductive success) to understand how spatial heterogeneity may shape animal population dynamics (Gaillard et al., 2010).

1.1.1 Linking demography and habitat

Ecologists have made advances in understanding the importance of spatial heterogeneity on animal performance (Gaillard et al., 2010). A 'functional' description of habitat consists of conditions that determine the presence, survival and reproduction of an individual, such as resources, abiotic conditions (*e.g.* climatic variables), and interspecific interactions (Gaillard et al., 2010). This suggests that the set of conditions that are selected by an individual (*i.e.* resource selection) will lead to a given performance. Additionally, habitat can be defined as 'structural'. This describes the landscape by its characteristics (*e.g.* vegetation type), independently of its use or selection by an individual (Gaillard et al., 2010). The 'functional' and 'structural' classifications of the habitat can generally be seen as extrinsic forces acting on populations, and have been shown to be important in explaining variation in individual performance *e.g.* survival (Van Moorter et al., 2009; Basille et al., 2013; DeCesare et al., 2014) and reproduction (McLoughlin et al., 2007; Fisher et al., 2014).

The scale dependence of the habitat-performance relationship is a challenging issue (Johnson, 1980; Rettie and Messier, 2000; Basille et al., 2013). Indeed, the habitat may constrain the activities of animals such as feeding, moving, reproducing, or selecting home ranges, at different spatio-temporal scales (Gaillard et al., 2010). While immediate decisions on where to feed may occur within a few seconds, decisions concerning home range selection occur between months or years (reviewed in Gaillard et al., 2010). Therefore, the benefits of fine-scale decisions, such as where to feed, should be measured on a short-term temporal scale, *i.e.* immediate individual energy gain. However, benefits of large-scale spatial decisions, such as home range selection, should be measured at a greater temporal scale, *e.g.* lifetime reproductive success (Clutton-Brock, 1988). As a result of the multiscale aspect of the habitat, individuals may need to adjust their behavior against limiting factors in a hierarchical manner to maximize their fitness (Rettie and Messier, 2000; Dussault et al., 2005; Basille et al., 2013). For example, Rettie and Messier (2000) suggested that the avoidance of the most limiting factor should occur at the coarser scale. Hence, further advances of habitat-performance relationships not only require a better understanding of these hierarchical processes, but also require long-term data of recognizable individuals in order to link a measure of fitness with habitat (Gaillard et al., 2010).

1.1.2 Spatial ecology of large mammals

Large mammal species often have specific ecological characteristics that include large home ranges, low population density (Damuth, 1981), and a relatively low intrinsic rate of increase (Fenchel, 1974). They are, therefore, especially exposed to the indirect effects of human activities, *e.g.* habitat fragmentation and habitat loss (Andrén, 1994). Indeed, large body size in mammals is usually one of the traits associated with high extinction risk (Cardillo et al., 2005). By analyzing the threat category determined by the International Union for Conservation of Nature, Ripple et al. (2016) found that 59% of the world's largest carnivores, and 60% of the world's largest herbivores, were classified as threatened with extinction. In most of the cases, environmental conditions affecting extinction risks are determined by human impacts (*e.g.* mortality and habitat loss) (Cardillo et al., 2005). It has been argued that successfully conserving large mammals requires social, political, and financial commitments from nations around the world (Ripple et al., 2016). However, understanding how spatial-specific characteristics of the environment may influence individual fitness is essential to tackle conservation and management issues at local scales.

1.1.3 Socially living mammals – a special case

Extinction risk is also determined by the interaction between local environmental conditions and intrinsic traits of the species (Cardillo et al., 2005). While changes in individual fitness may strongly affect the population dynamics of solitary species (Gaillard et al., 2000; Caswell, 2001), similar changes might lead to more complex consequences for species living in social groups (Vucetich et al., 1997; Grimm et al., 2003; Chapron et al., 2016). In social species, the number of reproductive events is often restricted to the number of groups (Creel and Creel, 1991; Vucetich et al., 1997). Therefore, the group is usually considered the functional unit of the population. Maintenance of the group (*e.g.* temporal stability) usually determines species persistence (Grimm et al., 2003; Chapron et al., 2016). In addition, the group is important because species exhibiting a kin-based social structure can have fitness benefits associated with the adaptive evolution of sociality (Silk, 2007; Sánchez-Macouzet et al., 2014). Despite its importance for population dynamics, the sources of variation affecting the life history characteristics of the group have been largely overlooked. Indeed, detecting the importance of sociality on population dynamics is especially difficult for large, long-lived, and elusive species that are often challenging to monitor (Odden et al., 2014).

In a review, Odden et al. (2014) showed that a small herbivore (root vole, *Microtus oeconomus*) and a large carnivore (brown bear, *Ursus arctos*) with contrasting life history strategies were subject to similar intrinsic mechanisms regulating their populations, which they argued was due to their similarity in social structure. However, the authors recognized that the susceptibility of voles and bears to extrinsic factors was very different.

While voles could be affected by strong predation pressure, and stochastic climatic events, brown bears were mostly affected by humans (Odden et al., 2014). Extrinsic factors that regulate the population of social species may sometimes interact with population intrinsic determinants and have further consequences on population dynamics (Odden et al., 2014). For example, human-caused mortality in species that have strong social bonding between group members, or experience sexually-selected infanticide, can result in the social disruption of the group and/or the loss of dependent offspring (Milner et al., 2007; Brainerd et al., 2008; Gosselin et al., 2015). Understanding how life history characteristics of the social group are affected by habitat is, therefore, crucial from an evolutionary, conservation and management perspective.

1.2 Spatial ecology of large carnivores

1.2.1 Large carnivores are recolonizing human-dominated landscapes

Large carnivores are located at the top of the food chain and can have special importance for ecosystem functioning as keystone species (Estes et al., 2011; Ripple et al., 2014). They are also some of world's most iconic species, yet, they are suffering from human persecution. However, large carnivores have recently shown partial recovery in part of their former range, expanding into and recolonizing human-dominated landscapes (Chapron et al., 2014; Ripple et al., 2014). Large carnivores are a special case of large mammals because their presence often results in conflicts with humans, by damaging livestock, competing with humans for game, and causing fear among people (Chapron and López-Bao, 2016). They are therefore often directly affected by legal or illegal human-caused mortality (Mech, 1995; Bischof et al., 2009; Persson et al., 2009; Liberg et al., 2011). In addition, they are especially affected by the indirect effects of human activities such as habitat loss (Delibes et al., 2001), prey depletion (Palomares et al., 2001), and geographical or management boundaries (Bischof et al., 2015). Their presence is often restricted to small and fragmented areas and, with small population size. This can lead to inbreeding depression, which, in turn, may have strong consequences for population viability (Keller and Waller, 2002; Liberg et al., 2005).

The concurrent recovery of large carnivore species that occupy the same trophic level brings new and interesting ecological questions regarding the mechanisms involved in their coexistence. Spatio-temporal segregation between competing species might be one of the mechanisms allowing coexistence (Rauset et al., 2012; López-Bao et al., 2016). This segregation can take place at several scales, from a large landscape scale where species avoid each other's home ranges (May et al., 2008), to a fine scale movement pattern where individuals have real-time spatial awareness of the competitors and adjust their behavior accordingly (López-Bao et al., 2016). Understanding how one species affects another, or the mechanisms facilitating coexistence among carnivore species, not only has important ecological relevance, but also has implications for management and conservation (Périquet et al., 2015; López-Bao et al., 2016). For example, the simultaneous recolonization of several large carnivore species brings new challenges since their presence may have complex consequences for the population dynamics of their prey (Gervasi et al., 2012). In such cases, it may require an adjustment of hunter harvest strategy in order to maintain a certain level of prey population density (Jonzén et al., 2013; Wikenros et al., 2015).

1.2.2 The grey wolf: a large, social carnivore

The grey wolf (*Canis lupus*) is a socially living carnivore, typically living in a family-based group (*i.e.* the pack, Mech and Boitani, 2003). A pack consists of a territorial breeding wolf pair together with their offspring. The wolf is currently the best-studied large carnivore species (Zimmermann, 2014). It inhabits a large range of habitat types distributed over the Northern Hemisphere (Mech and Boitani, 2003). While many factors influence wolf population dynamics, these can be summarized into three key categories: 'food, people, and source populations' (Fuller et al., 2003). Their relative influence is generally population-specific. For example, while density-dependent intraspecific aggression was found to be a major driver of adult survival of wolves in Yellowstone National Park (Cubaynes et al., 2014), human related-mortality was found to be the main driver slowing down the recolonization of the Scandinavian wolf population (Liberg et al., 2011). Therefore, spatial variation linked to the characteristics of the population (*e.g.* population size and density dependence), and/or of the landscape (*i.e.* anthropogenic activities) may drive the dynamics of different wolf populations. In the pack, the breeding individuals (*i.e.* the territorial pair) play an important role in group cohesion (Borg et al., 2014), feeding efficiency (Sand et al., 2006) and offspring survival (Brainerd et al., 2008). Therefore, events occurring at the pack level, especially to the breeding pair, may have direct consequences for the growth of the population. Despite the fact that packs are essential drivers of wolf population dynamics (Vucetich et al., 1997), factors affecting the pack's life history characteristics are still relatively unknown (but see Hinton et al., 2015).

1.2.3 The Scandinavian wolf population as a case study

After being considered functionally extinct in the late 1960's from the Scandinavian Peninsula (Sweden and Norway), the wolf became legally protected in 1966 and 1972 in Sweden and Norway, respectively (Wabakken et al., 2001). In 1983, wolves successfully reproduced in south-central Sweden, and were confirmed present for the first time in more than 80 years in this region (Wabakken et al., 2001). Between 1983 and 1991, the wolf population was founded by only two individuals and included only a single pack (Vila et al., 2003; Liberg et al., 2005). After the arrival of a third immigrant from the neighboring Finnish-Russian wolf population in 1990/1991, the Scandinavian wolf population started to grow exponentially and expand its distribution range (Wabakken et al., 2001; Vila et al., 2003). Wolf population size was estimated to be 365 (95% CI: 300-443) in the

Scandinavian Peninsula during the winter 2014-2015 (Chapron et al., 2016) with a large majority located in Sweden (Anon, 2015). Two main factors may have affected wolf life history in Scandinavia and have been shown to have a significant impact on population recovery: 1) its recolonization process was slowed down by human-related mortality (Liberg et al., 2011) and 2) because the Scandinavian wolf population is spatially isolated, it suffers from inbreeding depression (Liberg et al., 2005; Åkesson et al., 2016).

The management plan of wolves differs between Sweden and Norway. Swedish wolf management is regulated by a Government proposition accepted by the Swedish Parliament in 2013 ('En hållbar rovdjurspolitik', prop. 2012/13:191; Regeringskansliet, 2016) and the European Union Directive (Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora). The Norwegian predator policy is regulated on the national scale by the Nature Diversity Act of June 19, 2009 and internationally by the Bern Convention (Norwegian Environment Agency, 2016). In Norway, a 'wolf zone' to allow reproduction of three wolf litters each year has been established in the south-eastern part of the country (Norwegian Environment Agency, 2016).

Importantly, both countries have defined large parts of their land area as wolf-pack free areas where permanent establishment of packs is not allowed, including areas used for semi-domestic reindeer herding (Sweden and Norway) and domestic sheep grazing (Norway). Here, the establishment of territorial wolves is regularly controlled by culling. Culling of additional wolves inside the Norwegian wolf zone is allowed if the wolf numbers are above the national population goal set by the Parliament. After wolf re-establishment, depredation events on reindeer, sheep, and on domestic dogs (hunting dogs) have occurred (Liberg et al., 2008). To mitigate conflicts between stakeholders, both the Norwegian and Swedish government apply a financial compensation scheme for losses of livestock and domestic dogs due to wolf predation. In this context, understanding how intrinsic and extrinsic mechanisms may affect the life history characteristics of the social unit of the Scandinavian wolf population is important to guide conservation and management decisions.

2 Objectives

This thesis aimed at filling the lack of knowledge on how structural and functional habitat may affect life history characteristics of the group in a social species. More specifically, I linked spatial components of the structural and functional habitat (defined in its broadest sense by including vegetation, landscape structure, species interactions, and human land use), but also intrinsic population factors (*e.g.* inbreeding and population density) to the demography of the Scandinavian wolf population. This was done by studying some important key events of the life history characteristics of the pair; from wolf pair establishment to pair dissolution, and all the way to its consequences for population dynamics.

An individual from a socially-living species, such as the wolf, needs to establish a territory with a mate in order to form a pair, reproduce, and thus contribute to the growth of the population. **In Paper I, I therefore studied the pattern by which wolf pairs select their habitat when they establish a territory**.

After establishment, the second step is to survive and remain with a partner in order to maximize lifetime reproductive success. **Consequently, in Paper II, I quantified wolf pair bond duration, and identified how intrinsic and extrinsic population factors affect the risk of pair bond dissolution**.

The territorial pair is the functional unit of the wolf population and its stability and persistence may have strong benefits for wolf population dynamics. **In Paper III, I studied the extent to which wolf pair bond dissolution and culling mortality rate affect wolf population growth**.

Finally, I found that the presence of a potential competitor for the wolf, the brown bear, negatively affected wolf pair establishment (Paper I). This was in line with previous results suggesting competition between wolf and brown bears in Scandinavia (Milleret, 2011). **In Paper IV, I therefore studied whether spatio-temporal segregation between sympatric wolves and brown bears could be used as a mechanism of coexistence**.

3 Materials and methods

3.1 Study area

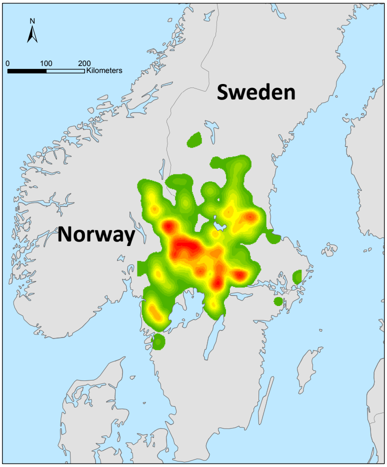

Figure 1: Spatial distribution of all Scandinavian wolf territories detected during the period 1998-2015. A Kernel density estimation was computed on the centroid points of each winter-territory. Colors from green to red represent areas where low to high numbers of territories were detected, respectively.

The study was carried out in the South-central part of the Scandinavian Peninsula (Sweden and Norway) within the wolf breeding range (59°-62°N, 11°-19°E; Figure 1). The landscape is dominated by boreal forests, bogs and lakes. Agricultural and urbanized lands cover <5% of the study area. Due to extensive commercial logging and forest management practices, the average density of gravel forestry roads is high (*i.e.* 0.88 km/km^2 inside wolf territories Zimmermann et al., 2014). However, the density of main roads (paved public roads) is approximately four times lower than the gravel road density (Zimmermann et al., 2014).

Human density is low and the study area encompasses large areas with less than one human per km^2 (Wabakken et al., 2001). The climate is continental and snow covers the ground for 3-6 months annually, mainly during October-April. Moose are the main wolf prey in Scandinavia, and are abundant throughout the study area (average: 1.3/km^2; range 0.7-3.3) (Sand et al., 2005, 2008, 2012; Zimmermann et al., 2015).

3.2 Data collection

I mainly (Paper I, II, and III) used data collected during the annual winter monitoring of the Scandinavian wolf population (Liberg et al., 2012). In the winter (October-April), extensive snow tracking (over a distance of 2200-5600 km each year; see further details in Appendix S1, Paper II) has been conducted through Scandinavia mainly by field personnel employed by the Swedish and Norwegian authorities. The collection of non-invasive samples (feces and urine) was used to genetically identify individuals (Åkesson et al., 2016). This resulted in the re-construction of a near complete pedigree of the population (Liberg et al., 2005; Åkesson et al., 2016). Continuous updates and maintenance to this pedigree was one of the main objectives of the winter monitoring program (Liberg et al., 2012). Therefore, specific effort was made to detect and identify individuals composing territorial wolf pairs. Additionally, I used information and locations gathered from GPS collared individuals (3-21 territorial wolves captured annually by the SKANDULV research project, `http://www.slu.se/skandulv`, Liberg et al., 2012). GPS locations from some territorial wolves were also used in Paper IV to study wolf habitat selection within home ranges. Similarly, I also used GPS locations from collared brown bears (captured by the Scandinavian Brown Bear Research Project; `http://bearproject.info/`)

3.3 Wolf pair establishment (Paper I)

To analyze the type of habitat selected by wolf pairs when establishing a territory *i.e.* second order of habitat selection (Johnson, 1980), I only considered data on the spatial distribution of their territory during their first year (*i.e.* when two new individuals settled together) as recorded during the winter monitoring program. Contrary to the use of simple presence/absence of wolf pairs, this set up allowed me to quantify the rate at which pairs established within a given set of landscape characteristics.

I then identified potential available habitat by constraining the creation of available and randomly located territories (unoccupied by other wolf territories) to the observed distribution of distances from a newly established wolf pair to the closest existing wolf territory.

3.4 Pair bond duration (Paper II)

I counted the number of consecutive winters in which a specific wolf pair was identified in its territory from the winter of establishment until the winter in which no signs of one or both individuals were found (*i.e.* pair dissolution). All pair dissolutions were assigned to one of five classes: 1) death caused by culling (*i.e.* legal control actions or license hunting), 2) verified poaching, 3) natural causes of death (e.g. age, diseases), 4) traffic mortality, and 5) unknown causes, (*i.e.* when a pair dissolution was verified (one or both individuals were missing) but could not be linked to any of the other four categories). Because I could not exclude natural, poaching, and traffic-related causes of dissolution from unknown causes of dissolution I created another category named '*other*' pooling unknown, natural, poaching, and traffic-related causes of dissolution. After a pair bond dissolution event, a replacement occurred when the missing territorial individual(s) were replaced the winter following the dissolution event.

3.5 Spatial characteristics of the territory of wolf pairs (Paper I, II)

I characterized the attributes of the landscape based on factors that have previously been shown to affect large carnivore populations, and, in particular, wolves in Scandinavia, and elsewhere (variables are summarized in Table 1). Precise territory boundaries were only known from a few territorial pairs equipped with GPS collars (Paper I and II). Instead, I used all spatial information available from monitoring and research (*i.e.* VHF/GPS and/or snow tracking locations, DNA-analyses of scats) to compute a centroid point location for each territory and year. I then extracted the large-scale spatial characteristics (Table 1) of these wolf territories within an average circular area of 1000 km^2 centered to this centroid point (Mattisson et al., 2013).

3.6 Intrinsic characteristics of wolf pairs (Paper II)

The level of inbreeding and age were used to characterize the intrinsic characteristics of the wolf pair. An inbreeding coefficient (f) was derived from the pedigree of the population (Liberg et al., 2005; Åkesson et al., 2016). I estimated the most recent possible year of birth (*i.e.* minimum possible age) to obtain a proxy for the age of individuals forming the pair. The latter was estimated using a combination of multiple sources of information, such as the year of first DNA-capture and the last year that the parental pair was known to have successfully reproduced.

Table 1: List of population extrinsic and intrinsic variables used to characterize habitat in this thesis. The name, description and relevance of each variable used are mentioned.

Description	**Proxy of**
Extrinsic	
Total length of paved roads (km per km^2)	Human activity
Total length of gravel roads (km per km^2)	Human accessibility
Percent of roads stretches with $\leq$ 2 buildings per km	Human accessibility & remoteness
Human density, number of inhabitants per km^2	Human activity
Dogs depredation events	Human-wildlife conflict
Sheep depredation events	Human-wildlife conflict
Country in which the wolf territory was located (*Sweden/Norway/Cross-border*)	Characteristics of the countries
Location on the longitude scale	Longitude scale
Location on the latitude scale	Latitude scale
Distance from core area of the wolf population	Effect of management
Annual number of moose shot per km^2 used as an index for local moose density	Food availability
Land cover map describing land cover characteristics (see Appendix 1, Table A1, Paper IV)	Preferences of land cover characteristics
Intrinsic	
Number of winters that wolf pairs occupied the area	Increased tolerance through time, sign of good quality habitat
Number of wolf territories within a 40km radius	Density dependence

3.7 Non-invasive (DNA) individual capture-recapture history data and wolf culling mortality (Paper III)

I used non-invasive (DNA) individual capture-recapture history data with recoveries of dead wolves to estimate demographic parameters, such as survival and transition probabilities between stage classes. I only distinguished among non-territorial and territorial individuals stages. All dead wolves that were legally culled or found dead for various reasons (traffic, natural, poaching) were identified from DNA-analyses. The genetic procedure is fully described in Åkesson et al. (2016).

3.8 Statistical analysis

Survival analysis (Paper I and II)

I used a survival analysis framework to study the factors affecting wolf pair bond duration and wolf-pair establishment. While it is straight forward to study wolf pair bond duration using a survival analysis (*i.e.* time until an event occurs: pair dissolution), it may be counter-intuitive to use a survival analysis to study factors affecting wolf pair establishment. However, the parallel can easily be made. In a survival analysis, an individual is exposed to risk along its life until the event (*e.g.* death) occurs. Similarly, an individual is exposed to different choices (*i.e.* available sites) to select a site to establish (*i.e.* event). This kind of analysis is generally termed conditional logistic regression because it does not include the concept of time until the event occurs. In the two cases, the survival analysis and the conditional logistic regression allow for testing the relationship between a set of factors and the outcome of having an event and a non-event. For the pair bond duration analysis, I also used the Kaplan-Meier method to quantify the probability of persistence of a specific pair over time.

Integrated population model (Paper III)

I developed a Bayesian Integrated Population Model (IPM) that linked demographic parameters and count data through a population model, *i.e.* a Leslie Matrix (Caswell, 2001; Kery and Schaub, 2011; Schaub and Abadi, 2011). The state-space formulation of the IPM allowed disentangling the demographic process from the noise around the observation process. This kind of model has the advantage of making use of multiple datasets. The demographic parameters were estimated with multistate capture-recapture models using information from non-invasive DNA samples, and recovery data from dead wolves. I then developed a state-space formulation to take into account errors in the count data. I used the demographic parameters obtained from the IPM to quantitatively evaluate the effect of culling mortality and wolf pair dissolution on the growth and demographic parameters in the population. Furthermore, I determined to which extent culling was compensatory or additive to other types of mortality in this population.

Habitat selection of sympatric carnivores: the K-select approach (Paper IV)

I quantified habitat selection by sympatric GPS-collared wolves (4 territorial pairs) and bears (53 individuals) within their home range (third order of selection; Johnson, 1980), using a multivariate approach that relied on the concept of ecological niche (Hutchinson, 1957), the K-select (Calenge et al., 2005; Darmon et al., 2012). I then developed a method to quantify their habitat niche overlap in the ecological space of the K-select. This method returned an estimate of the degree of overlap in percentage between wolves and bears. To test whether wolves and bears segregated significantly more than expected by chance, I used randomization techniques, taking into account movement constraints, to create a null model that quantified the expected overlap index under random habitat selection.

4 Results and discussion

4.1 Wolf pair establishment (Paper I)

The establishment of 142 different wolf pairs was detected between 1990 and 2012. Wolf pair establishment in a given site was positively related to previous wolf presence in the area, and was negatively related to main road density, distance to other wolf territories, and bear density (Figure 2). This result confirmed the importance of human-related habitat when a pair selected a site to establish. Avoidance of human-related features has previously been described for Scandinavian wolves (Karlsson et al., 2007; Zimmermann, 2014) and other carnivores (Ordiz et al., 2014).

However, my study focused on the establishment of territorial wolf pairs, which is especially interesting because wolf pairs generate packs, i.e. the functional unit of wolf populations. Furthermore, the avoidance of sites with high brown bear density suggests that mechanisms linked to interspecific competition may also have been important for wolf pair establishment. Brown bears sympatric with wolves have been shown to kleptoparasite on about 50% of the wolf kills in the spring (Milleret, 2011) and alter wolf kill rates Tallian et al., unpublished, which support my results showing the occurrence of interspecific competition between wolves and brown bears. These findings suggest that both human-related habitat modification and interspecific competition have been influential factors modulating the expansion of the wolf population during its recolonization of Scandinavia.

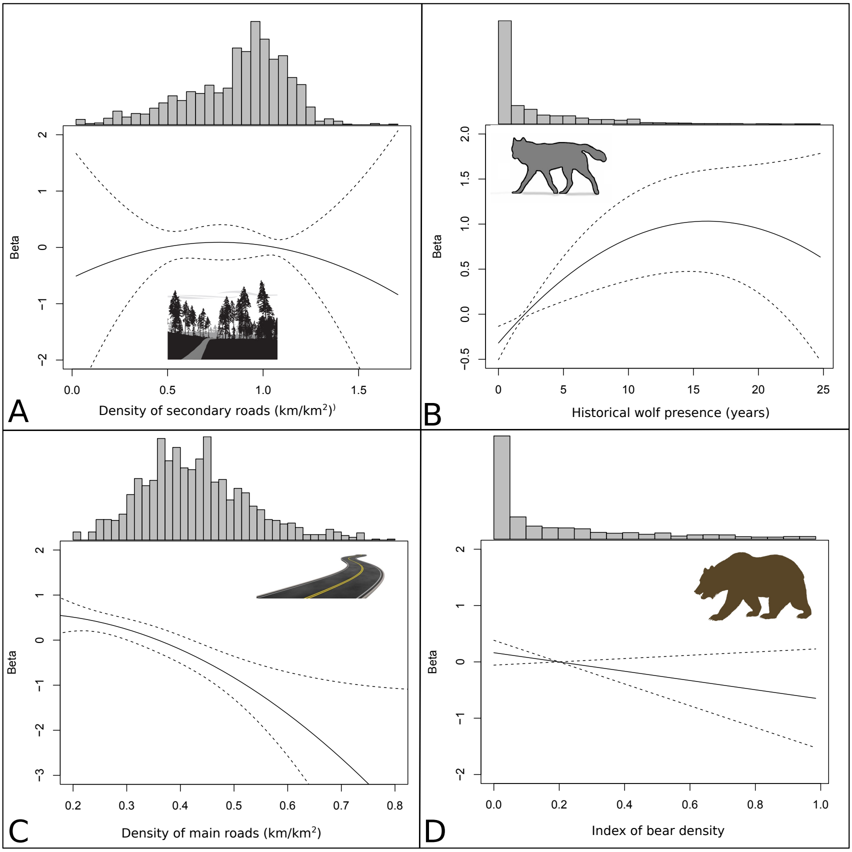

Figure 2: Effect of A) density of secondary (gravel) roads, B) historical wolf presence, C) density of main (paved) roads, and D) bear density on wolf pair establishment in Scandinavia during the period 1990–2012. Beta values > 0 shows selection while values < 0 show avoidance. Dashed lines show 95% confidence intervals and bar plots show the relative availability of both actually used and random sites in the conditional logistic regression.

4.2 Wolf pair bond dissolution (Paper II)

Adult wolf mortality rates are generally low in the absence of human culling (Creel et al., 2015). However, I showed that wolf pair bond duration was short, with a median time of pair persistence of 3 consecutive winters (*i.e.* approximately 2 years, Figure 3), and the dissolution was generally due to a mortality event.

This suggests relatively short pair bond duration for a long-lived species such as the wolf. Approximately 45% of the detected pair dissolution events could be determined with certitude as being caused by human-related factors. For approximately 45% of the remaining dissolution events, the exact cause of dissolution could not be determined. However, assuming that the data from territorial radio-collared wolves showed a representative sample of the population, I argued that a large portion of unknown causes of pair dissolution could be due to an additional source of mortality, such as poaching, and remained cryptic (Liberg et al., 2011).

There was spatial variation in the risk of pair bond dissolution, but it was mostly related to variables characterizing the geographic location of pairs rather than variables describing the landscape structure. Risk of pair dissolution was higher towards the west (*i.e.* towards Norway) and further away from the core area of the population. Although this spatial pattern could reflect the impact of management policies, it could also reflect differences in human attitudes between the two countries (Gangaas et al., 2013). Furthermore, I showed that risk of pair dissolution increased with inbreeding coefficient and age of the male. The mechanisms by which inbreeding may explain pair bond duration remain unclear. However, this suggests that inbreeding and humans might act as intrinsic and extrinsic mechanisms negatively affecting wolf pair bond duration.

Given the importance of the pair as the functional unit of the population, I suggest that this factor is likely to have had a significant impact on the rate and pattern of recolonization of the population. Contrary to the negative effect of intrinsic and extrinsic factors that is usually reported on survival or population growth (Liberg et al., 2011), I provided quantitative estimates of their effect on the functional unit of the population, the wolf pair (Rutledge et al., 2010).

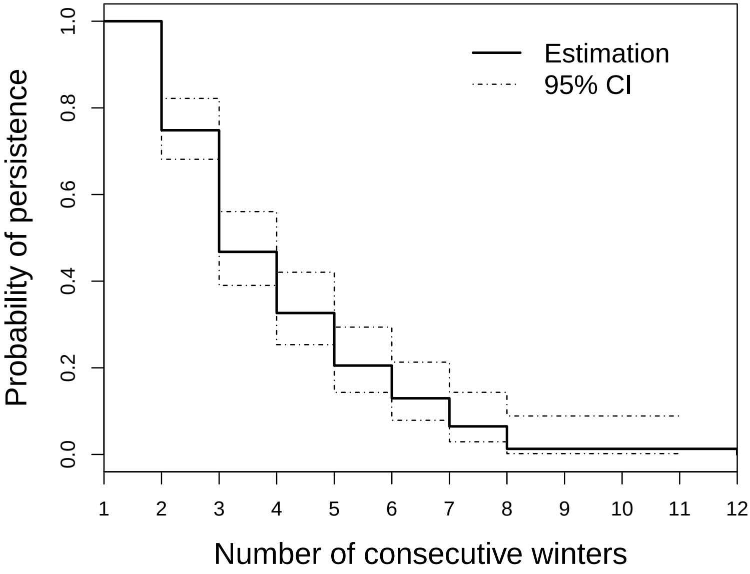

Figure 3: Kaplan–Meier cumulative survival curve with 95% confidence intervals showing the probability of wolf pair bond persistence in Scandinavia during the winters 1998/1999-2011/2012. On the x-axis, winter 1 shows the first winter a pair was detected, winter 2 the second and so on.

4.3 Effect of pair dissolution and culling mortality rate on wolf population dynamics (Paper III)

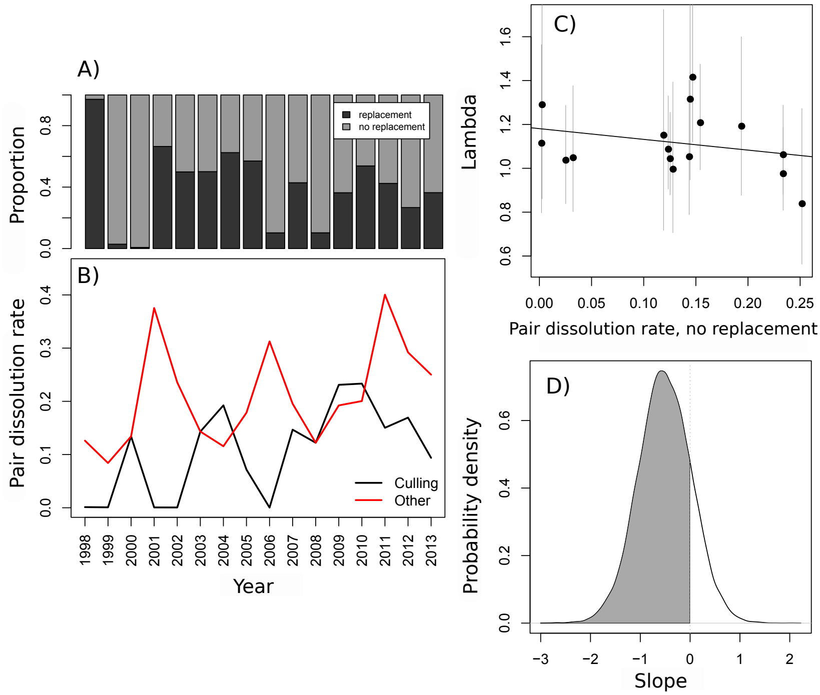

Figure 4: Effect of wolf pair bond dissolution on wolf population growth in Scandinavia during the period 1998-2015. A) Proportion of pair bond dissolution events that were and were not followed by the replacement of new individual(s). B) Temporal variation in pair bond dissolution rate due to culling and other causes. C) The negative effect of pair bond dissolution rate that was not followed by a replacement on the growth rate (lambda) of the population. Grey vertical bars represent 95% CI and the black line the line from the regression on the median values. D) Probability density distribution of the slope of the linear regression between the growth rate and pair bond dissolution rate not followed by a replacement.

The Bayesian integrated population model that I developed for the Scandinavian wolf population highlighted the complexity of the effect of culling on the population dynamics of a socially-living species. I did not detect any effect of culling rate of territorial or non-territorial individuals on population growth. However, pair bond dissolution rate, and especially pair bond dissolution that was not followed by a replacement tended to decrease wolf population growth rate (Figure 4 C, D). This effect tended to occur through a decrease in territorial and non-territorial survival, and recruitment. I found that culling mortality rate of the Scandinavian wolf population during the period 1998-2015 was mainly compensatory.

During this period, culling mortality rate was never greater than 20% of the total population size, which is in the lower range of the level of culling that generally results in a growth rate < 1 (Chapron et al., 2003; Marescot et al., 2012; Creel et al., 2015). This could be one of the reasons explaining why I did not detect any effect of culling mortality rate.

Pair dissolution was generally caused by a mortality event (Paper II). Pair dissolutions due to *other* causes were unknown in most of the cases (i.e. the dissolution was observed but exact cause of dissolution could not be identified). Assuming that the high and unpredictable variation of pair dissolution rate due to *other* causes can be transposed to individual mortality (Figure 4 B), this may explain why I did not detect any effect of culling rate on growth rate. Indeed, when culling mortality was high, mortality due to *other* causes could have been low and vice versa, or even at similar rate than culling. However, I argue that an additional source of mortality, such as caused by poaching, could explain the temporal variation (reaching up to 40%) in pair bond dissolution rate due to *other* causes (Paper II).

When culling interacts with other sources of mortality, such as natural mortality and poaching, and with the intrinsic characteristics of the species, predicting the effect of culling on population growth is even more complicated. According to my results, it is rather challenging to make any prediction about the effect of culling on population growth. For example, while *culling* dissolution rate reached approximately 10% in 2011, pair dissolution rate due to *other* causes was 4 times higher and reached up to 40%. If such a pattern would persist with a higher culling mortality rate, this may have strong negative consequences for the population and its viability.

4.4 Spatio-temporal segregation between wolves and brown bears (Paper IV)

I detected an effect of brown bear presence on wolf pair establishment (Paper I) suggesting the presence of interspecific competition in my study system. A fundamental question of community ecology is to understand the mechanisms allowing competing species to coexist within the same area (Armstrong and McGehee, 1976; Chesson, 2000; Darmon et al., 2012). I found that wolves and brown bears segregated significantly more than expected by chance by selecting different habitat within their home ranges (third order of habitat selection, Johnson, 1980). Wolves tended to select for moose occurrence, young forests, and rugged terrain more than bears did (Figure 5) which likely reflected the different requirements of an obligate carnivore (wolf), and an omnivore (brown bear). Indeed, while moose is by far the main prey for wolves in Scandinavia (Sand et al., 2005, 2008; Zimmermann et al., 2015), the diet of bears is diverse (Stenset et al., 2016) and they mostly prey on young moose neonates during a restricted period in the spring (Swenson et al., 2007; Dahle et al., 2013). Both species also tended to select areas further away from human-related habitat, which likely reflects human avoidance (Ordiz et al., 2012, 2014; Zimmermann, 2014). Altogether, my results suggest that habitat segregation within home ranges between wolves and bears could be used as a key mechanism of coexistence.

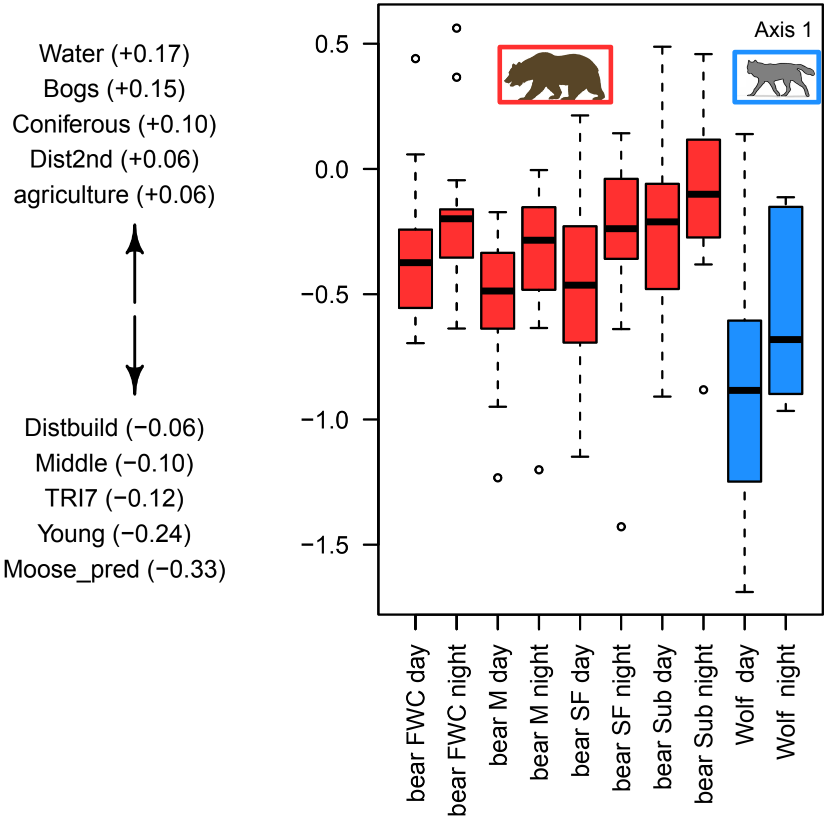

Figure 5: Box plot for habitat selection pattern (within home ranges) of wolves and brown bears during the spring period (1 May – 30 June) on the first axis of the K-select. Values on the y-axis represent marginality scores of the K-select, and the intensity of habitat selection. Wolves mostly obtained negative marginality scores meaning that they selected habitat types described below the arrow, on the left side of the plot. However, bears (FWC=female with cubs; SF= single female; M=Male; Sub= Subadult) obtained marginality scores that were closer from the positive values meaning that they selected less intensively habitats types selected by wolves and described below the arrow, on the left side of the plot. All habitat types are fully described in Paper IV

5 Conclusions

The approach used in my thesis, linking habitat with the functional unit (*i.e.* the wolf pair) of a socially living species was proven valuable. This study revealed key spatial and temporal processes that have contributed to shape the Scandinavian wolf population during its recolonization. I found that a combination of spatially extrinsic, (*i.e.* interspecific competition, human-related habitat features) and intrinsic (*i.e.* historical presence of wolves, inbreeding) factors were major drivers of the Scandinavian wolf population dynamic during its recolonization.

As for many large carnivore species, my thesis confirmed the negative impact of humans on the wolf population. I found that wolf pairs avoided human-related features of the habitat when establishing a territory (Paper I), or when selecting their habitats within home ranges (Paper IV). I also found that wolf pair duration was short and that pair dissolutions were mainly caused by humans (Paper II). Furthermore, spatial heterogeneity in the risk of dissolution was mostly related to variables characterizing the geographic location of pairs in Scandinavia rather than variables describing habitat (Paper II). Because wolf pair stability and events occurring after dissolution (*i.e.* pair replacement or not) were important for population growth (Paper III), the spatio-temporal patterns of pair formation and dissolution detected in Paper I and II have likely been drivers of wolf population dynamics.

There was also a signal suggesting that an additional and cryptic source of mortality, such as poaching, might lie behind the high temporal variation in wolf pair dissolution rate due to other causes (Paper II and III). This would confirm results from previous research in this wolf population (Liberg et al., 2011), and from other large carnivore species (Andrén et al., 2006; Bischof et al., 2009; Persson et al., 2009; Rauset et al., 2016), suggesting that significant poaching of large carnivores does occur in Scandinavia.

Understanding the effect of culling on population dynamics is complex, but even more so when it concerns socially-living species (Creel and Rotella, 2010; Murray et al., 2010; Ausband et al., 2015; Creel et al., 2015). The results presented in my thesis confirmed this complexity (Paper III). Indeed, I found that mechanisms acting on population regulation likely involved a combination of culling-related mortality, complex temporal variation in individual mortality due to causes other than culling, but also intrinsic compensatory mechanisms that were linked to life history characteristics of this socially-living species (i.e. decreased survival of non-territorial individuals after a pair dissolution event and resilience to pair dissolution by replacement). Therefore, it is rather challenging to make any clear prediction of the effect of culling on population growth. However, the stability of wolf territorial pairs was better to predict wolf population growth, suggesting that actions performed at the level of this unit might be more effective to reach management goals.

If pair bond dissolution was better at predicting population growth, it is essentially because the extensive monitoring of this population also allowed identifying pair bond dissolution due to *other* (i.e. especially unknown) causes than *culling*. Although we argue that poaching could explain some of these dissolutions due to other causes, there is the need to better understand the driver of the temporal fluctuation in pair bond dissolution rates. Such knowledge is necessary to develop a sound management and conservation plan for the wolf in Scandinavia.

I showed that territories left vacant after a wolf pair dissolution event (i.e. wolf pair dissolution not followed by a replacement) had a negative effect on population growth (Paper III). Interestingly, my results also suggested that wolf pairs were likely to establish their territories in areas that have been occupied for a long time by wolves (Paper I). Therefore, the culling of territorial wolf pairs in areas of long time occupancy by wolves may have limited effect on population growth because replacement by a new territorial pair may occur relatively quickly.

The social structure of species living in family groups, the pack for wolves, can have important benefits associated with the adaptive evolution of kinship (Lukas and Clutton-Brock, 2013). However, the high impact of humans on wolf pairs detected in this population could prevent the family-based structure from fulfilling its role (Rutledge et al., 2010). The consequences of pack disruption and changes in the social structure on fitness are difficult to measure, but the importance of social organization for feeding efficiency (Sand et al., 2006) and pup survival (Brainerd et al., 2008) suggest that high pair dissolution rate may have strong negative impacts for family-based species (Rutledge et al., 2010). As suggested by Rutledge et al. (2010), conservation policies should look beyond numbers (*e.g.* population size estimates) and should also consider social dynamics of the functional group to evaluate conservation status of a social species.

My results also suggested that interspecific interactions with another large carnivore species, the brown bear, might have been an important factor influencing the dynamics of this wolf population (Paper I and IV). The effect of competition between wolves and bears may be visible at several scales, from direct interactions at feeding sites (Milleret, 2011), to habitat selection within home ranges (Paper IV), and ultimately to wolf pair decisions in settling a territory (Paper I). Therefore, my results support the need for broadening the scope of research and conservation from single species to a wider ecosystem perspective, where species interactions are explicitly integrated (Paper I).

6 Perspectives

This study shows the importance of individual-based data collected from long-term monitoring programs to identify the mechanisms explaining spatial and temporal variation in life history characteristics of a socially-living species. Although I found that risk of pair bond dissolution and pair establishment were spatially variable, I could not identify key areas that could be perceived as sources or sinks. Further studies linking habitat and lifetime reproductive success could be an approach to link the results from Paper I (wolf pair establishment) and II (wolf pair bond duration). For example, it could allow to test whether wolf pairs could be more attracted to poor areas (characterized by short pair bond duration and/or low lifetime reproductive success), and to identify potential ecological traps (Battin, 2004).

This thesis represents an attempt to highlight the relationship between habitat and performance, with performance being measured on the functional unit (the breeding pair for the wolf) of a social species. Because of the scale dependency of the habitat-performance relationships, there is an obvious potential for expanding studies on this topic. Further studies could link how fine-scale behavior and habitat may affect energy intake. At a larger scale, one could link how habitat within a wolf territory may affect another proxy of fitness, such as lifetime reproductive success of the territorial pair.

This kind of spatially-related information could be very useful when projecting population trajectories and estimating viability of populations. For example, spatially explicit modelling of the population using an individual-based model where the events occurring on the territorial wolf pair are explicitly modelled may provide very useful information for management and conservation. Using such tools, one could predict not only a temporal population trajectory, but also the spatio-temporal dynamics by forecasting local persistence, extinctions, and expansions. I recommend that further studies should be conducted in order to capture how spatial variation of the habitat may affect important life stages in a socially living species such as the wolf (*e.g.* the dispersal process; Sanz-Pérez, 2016).

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Paper I

Ordiz, A., Milleret, C., Kindberg, J., Månsson, J., Wabakken, P., Swenson, J. E., and Sand, H. (2015). Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia. *Ecosphere*, 6(12):1–14

esa ECOSPHERE

Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia

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Abstract. Interspecific competition can influence the distribution and abundance of species and the structure of ecological communities and entire ecosystems. Interactions between apex predators can have cascading effects through the entire natural community, which supports broadening the scope of conservation from single species to a much wider ecosystem perspective. However, competition between wild large carnivores can hardly be measured experimentally. In this study, we analyzed the expansion of the Scandinavian wolf (*Canis lupus*) population during its recovery from the early 1990s. We took into account wolf-, habitat-, human- and brown bear (*Ursus arctos*)-related factors, because wolf expansion occurred within an area partially sympatric with bears. Wolf pair establishment was positively related to previous wolf presence and was negatively related to road density, distance to other wolf territories, and bear density. These findings suggest that both human-related habitat modification and interspecific competition have been influential factors modulating the expansion of the wolf population. Interactions between large carnivores have the potential to affect overall biodiversity. Therefore, conservation-oriented management of such species should consider interspecific interactions, rather than focusing only on target populations of single species. Long-term monitoring data across large areas should also help quantify and predict the influence of biotic interactions on species assemblages and distributions elsewhere. This is important because interactive processes can be essential in the regulation, stability, and resilience of ecological communities.

Key words: Brown bears; *Canis lupus*; conditional-logistic regression; habitat selection; human disturbance; interspecific competition; population expansion; Scandinavia; *Ursus arctos*; wolves.

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INTRODUCTION

Interspecific competition holds a central place in ecological and evolutionary theory and has implications for conservation and management. Competition influences the distribution and abundance of species (Wisz et al. 2013), including carnivores (Creel et al. 2001), and it plays an important role in the structure of ecological communities (Schoener 1983) and entire ecosystems, marine and terrestrial alike (Estes et al. 2011, Ripple et al. 2014).

Competition between carnivores can reduce the population size of one of the competitors and affect lower trophic levels (Caro and Stoner 2003). It can lead to spatial avoidance and shifts in habitat use and, in cases of exploitative competition, when predators share the same food resources, kleptoparasitism can force affected species to additional hunting (Elbroch et al. 2015), with its inherent risks and costs. Ultimately, carnivores can also kill each other, sometimes limiting population sizes (Palomares and Caro 1999, Caro and Stoner 2003, Donadio and Buskirk 2006).

Although competition may cause extirpation, it often results in resource partitioning. The outcome may change with environmental conditions and human activities, which can have an overwhelming influence on the population dynamics of the interacting species, their distribution, and the effects of competition (Apps et al. 2006). This may be the case for large carnivores inhabiting human-dominated landscapes, given the long history of human persecution of the carnivores and their avoidance of people (Ordiz et al. 2011, 2013, 2014).

Competition between wild large carnivores can hardly be measured experimentally. However, it may be evaluated by comparing the spatial distribution of each species, while controlling for landscape-related variables (Apps et al. 2006). In a gradient of spatial levels, populations range geographically in a landscape, animals establish home ranges, choose habitat patches, and, finally, select particular sites, such as dens or daybeds (Johnson 1980). Competition may be influential at each level if the presence of a competitor affects where to settle down and/or limits resource use. This is particularly interesting in situations where the recovery of a large carnivore occurs in an area already inhabited by another carnivore and both species have some common requirements of habitat or resources, which can potentially lead to spatial and/or exploitative competition.

Individual interactions have been documented between gray wolves (*Canis lupus*) and brown bears (*Ursus arctos*). Brown bears are omnivorous, but both species prey on ungulates and using the same food resources can lead to exploitative competition. Bears often kleptoparasitize wolf kills in North America (Ballard et al. 2003, Smith et al. 2003) and in Scandinavia (e.g., Milleret 2011). However, wolves can prevail at carcasses and simultaneous scavenging by both species also has been reported (Smith et al. 2003, Lewis and Lafferty 2014). Wolves and bears can also kill each other (Ballard et al. 2003, Gunther and Smith 2004). Therefore, the outcome of individual interactions between these species includes all of the above–mentioned forms of interspecific competition between carnivores. Nevertheless, beyond individual interactions, we lack knowledge about the effects of wolf–bear competition at the population level for both species (Ballard et al. 2003).

Interactions are most relevant if competition reduces the chances that an area is used for breeding (Tannerfeldt et al. 2002). Some individual wolf-bear encounters have been described in this regard, including bears passing by wolf rendezvous sites and a few cases of bear cubs presumably killed by wolves (Ballard et al. 2003, Gunther and Smith 2004). However, the potential effects of interspecific, intraguild competition between bears and wolves on their population recovery and expansion process have not been studied.

In Scandinavia (Sweden and Norway), the recent and ongoing recovery of the wolf population in an area partially sympatric with brown bears and the long-term monitoring of both species offer the opportunity to analyze the spatial relation between these two apex predators, taking also into account intraspecific-, habitat-, and human-related factors. Wolves and bears once occupied most of the Northern Hemisphere, but for as many large mammals they were largely eradicated during the last two centuries due to human persecution (e.g., Morrison et al. 2007). Scandinavia was no exception. Wolves were functionally extinct in the 1960s, but wolf recovery accelerated during the 1990s (Wabakken et al. 2001), with ~11 packs in 2001 (Vilà et al. 2003), 31 packs in 2010 (Liberg et al. 2012), and 43 packs (~400 wolves) in 2014 (Svensson et al. 2014). Regarding brown bears, as few as ~130 were left in Sweden by 1930 (Swenson et al. 1995), but legislation changed

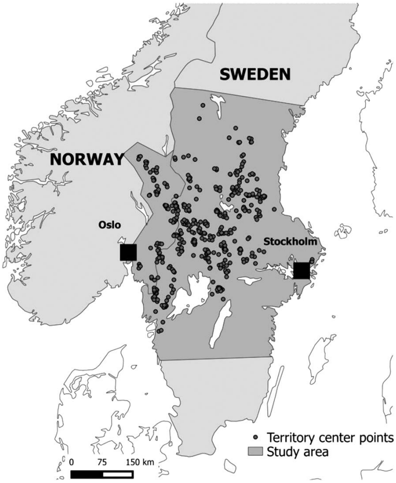

Fig. 1. Study area in south-central Scandinavia (dark gray), showing the center points of all wolf pairs detected between 1990 and 2012.

and the population increased steadily, reaching ~1000 bears in the 1990s (Zedrosser et al. 2001) and ~3,300 by 2008 (Kindberg et al. 2011). Presently most wolves and bears are in Sweden; few inhabit Norway.

We used data on the annual locations of wolf pairs to analyze the factors involved in the expansion of the wolf population in Scandinavia during 1990–2012. Wolf packs originate when a male and female wolf form a pair and reproduce (Rothman and Mech 1979). Packs are the functional, reproductive unit of wolf populations (Mech and Boitani 2003). Scent-marking pairs of wolves establish territories before they breed (Wabakken et al. 2001). Therefore, we used wolf pair establishment as a measure of survival and reproductive performance and linked it to a particular behavior, i.e., home-range establishment. This link between habitat selection and fitness is important, because it allowed us to study wolf habitat selection in terms of breeding performance (Gaillard et al. 2010), i.e., we analyzed habitat selection by wolves during the expansion of the Scandinavian wolf population.

Human factors continue to be a major limitation of large carnivore distribution and habitat use in Scandinavia (Karlsson et al. [2007] for wolves, Ordiz et al. [2011] for bears, May et al. [2008] for the whole large carnivore guild) and elsewhere (Woodroffe et al. 2005, Ripple et al. 2014). Therefore, we predicted a negative effect of human-related variables on wolf establishment. We also predicted that wolf pairs would select areas with lower density of the partially sympatric brown bear when establishing territories, and that previous wolf presence and prey abundance would be positively correlated with the functional selection of territories (Fritts and Mech 1981).

MATERIAL AND METHODS

Study area

Resident wolves currently inhabit over ~100,000 km^2 in south-central Scandinavia (59–62° N, 11–19° E; Liberg et al. 2012; Fig. 1). The area is mainly an intensively managed boreal coniferous forest of primarily Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. Bogs and lakes are common, and agricultural land occurs mostly in the southwestern, eastern, and southern parts. Snow covers the ground from ~December to ~March. In the area where bears occur within the wolf range (Fig. 2), independent estimates of bear density yielded similar values in the 1990s and 2000s; up to ~30 bears/1000 km^2 (Solberg et al. 2006). Moose (*Alces alces*) is the staple prey of wolves in Scandinavia (>95% of the biomass of wolf diet; Sand et al. 2005, 2008), where one the world's largest and most productive moose populations thrives, with a winter population of ~500,000 moose and densities reaching 5–6 moose/km^2 (Lavsund et al. 2003). Human density is generally low within Scandinavian wolf range, with <1 person/km^2 over large areas (Wabakken et al. 2001). The density of primary roads within wolf range is 0.2 ± 0.02/km^2, and gravel road density is on average 4.6 times higher (Zimmermann et al. 2014).

Study period and wolf-related variables

We defined the start of our study period as 1990, when the arrival of an immigrant coincided with a sudden increase in the growth of the

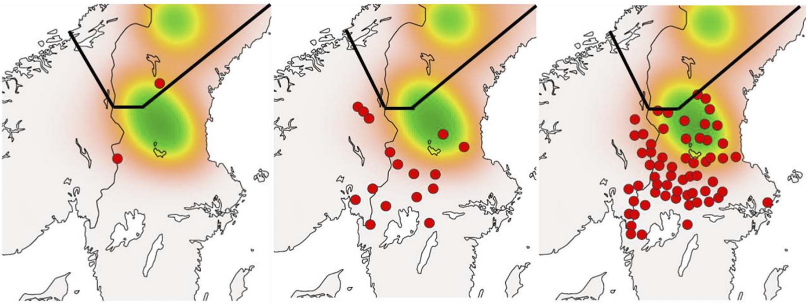

Fig. 2. Location of wolf pairs (red dots) and brown bear density (green color shows the densest bear areas) in south–central Scandinavia, at the beginning (1990, left), middle (2000, central) and towards the end of the study period (2010, right). The black line shows the southern edge of the reindeer husbandry area in Scandinavia.

Scandinavian wolf population (Vilà et al. 2003). Annual censuses were performed every winter by a combination of snow-tracking, genetic pedigrees based on DNA analyses, and radio-tracking methods (Wabakken et al. 2001, Liberg et al. 2005, Svensson et al. 2014). Identifying reproductive territories and updating the pedigree annually were major goals of the monitoring and research (Liberg et al. 2012), thus the genetic identification of new wolf territories and new established wolf pairs received special attention.

When a new territorial pair has been identified by snow-tracking, its identity was confirmed by genetic analyses of scats and estrous blood (Liberg et al. 2005, 2012, Bensch et al. 2006). Beyond mere presence–absence, genetic identification of new wolf pairs allowed us to monitor the rate at which pairs established territories. Wolf packs are territorial and usually occupy a specific area for a long time (Mech and Boitani 2003), with high interannual stability in space use (Mattisson et al. 2013). Therefore, the process of territory selection is especially interesting, because overall quality of the habitat within the territory has a great influence on individual fitness (Gaillard et al. 2010). To analyze the selection of wolf territories from this perspective, we used the first year when each new wolf pair was detected by the winter monitoring program.

Spatial locations of pairs were collected by snow-tracking and when animals were radio-collared for a variety of research and management purposes (Sand et al. 2005, Wabakken et al. 2007, Mattisson et al. 2013; see Liberg et al. [2012] for very detailed information on the monitoring protocol in Sweden and Norway). We used the centroid of all available locations for a specific pair–winter as the center of its territory, because the accuracy of spatial locations varied among pairs. We applied a 1000 km^2 buffer (average wolf home range size; Mattisson et al. 2013) around the centroid to define the territory occupied by a wolf pair.

We used the number of winters that wolf territories were identified in a specific area as an estimate of wolf "historical presence" during the study period. We calculated average longitude and latitude coordinates annually for all wolf territories, and measured the distance from the centroid of new wolf pairs to previously existing wolf territories. We used the number of neighboring territories' centroids within a 40-km radius from an existing territory centroid as a measure of local density (Mattisson et al. 2013). Table 1 summarizes all the parameters we used in the analyses.

Prey-, human- and landscape-related variables within the buffer around wolf territories

Prey density: We obtained moose harvest density (number of moose harvested/km^2) at the municipality and management unit ("älgförvaltningsområde") in Sweden and Norway. Harvest density is a robust, but slightly

Table 1. Summary of parameters used to analyze wolf pair establishment in Scandinavia in 1990–2012 (details in *Methods*).

Parameter, by group	Description	Source
Wolf		Wabakken et al. 2001, Liberg et al. 2012, Mattisson et al. 2013, Svensson et al. 2014
Territory center	Centroid location of all available locations for every specific wolf pair and winter	
Territory size	Buffer of 1000 km^2 around the centroid	
Historical presence	No. winters with identified wolf territories (pairs or packs) in a given area	
Local density	No. neighboring wolf territories' centroids in a 40-km radius around a given territory	
Bear		
Bear density	Kernel density estimator based on records of shot bears	Scandinavian brown bear project, *unpublished data*
Human and landscape, with all layers converted to 200 × 200 m. grid cells		
Main road density	km of main roads per km^2	1:100 000 Lantmäteriet, Sweden; N50 kartdata, Staten-skartverk, Norway
Secondary road density	km of gravel roads per km^2	1:100 000 Lantmäteriet, Sweden; N50 kartdata, Staten-skartverk, Norway
Human density	No. inhabitants per km^2	www.scb.se, Sweden; www.ssb.no, Norway
Remoteness and accessibility	Combination of building and road densities per km^2	C. Milleret et al., *unpublished manuscript*
Altitude	Altitude in meters above sea level	DEM 25 × 25 m; Geographical Data Sweden, Lantmäteriet; Norge digital, Statens kartverk, Norway
Open land	Percentage of open land cover	Mattison et al. 2013; Swedish Corine land cover map Lantmäteriet, Sweden, 25 × 25 m merged with Northern Research Institute's vegetation map, Norway, 30 × 30 m into a 25 × 25-m raster
Prey		
Moose density	Annual harvest density at municipality/management unit	www.viltadata.se, Sweden; www.ssb.no, Norway

delayed estimate of local variation in moose density. The temporal variation in harvest density was better explained by moose density in year $t-1$ than in year t or year $t-2$ (Ueno et al. 2014), so we used harvest density with a one-year time lag (C. Milleret, *unpublished manuscript*). Moose harvest data was unavailable locally in some years before 1998. Thus, we used average moose harvest density in 1998–2000 as a proxy for the 1990–1998 period, which was justified, because moose density was fairly stable within the Scandinavian wolf range during the 1990s (e.g., see Fig. 3 in Lavsund et al. 2003).

Human activities and landscape-related variables: We used the density of both main and gravel roads (km/km^2) as proxies of human disturbance (Ordiz et al. 2014, Zimmermann et al. 2014); human density (inhabitants/km^2) at the municipality level, and also an index of remoteness and accessibility of the landscape, based on combined building and road densities (C. Milleret, *unpublished manuscript*). We also considered altitude (m above sea level), and amount of open, agricultural land cover, which is strongly avoided by wolves (Karlsson et al. 2007).

Brown bear density within the wolf distribution range

Confirmed bear mortality has been shown to be a good proxy of bear distribution and density (Swenson et al. 1998, Kindberg et al. 2009). We used brown bear mortality records in Scandinavia in 1990–2012 (n = 3,083 bears), with legal hunting accounting for 88% of them, to construct a kernel density estimator (Worton 1989) with the "href" procedure in the R package adehabitatHR (Calenge 2006). This estimator yielded a relative probability of finding a dead bear in a given pixel. We created an index of bear density between 0 and 1 by rescaling the values from the kernel estimator across the study area, dividing each obtained value by the maximum observed.

Case-control design

One of the main assumptions of habitat selection studies is that the area defined as available should be entirely available to all animals (Manly et al. 2002). Wolves are a highly mobile species, with a documented strong capacity for long-distance dispersion (Wabakken et al. 2007). However, population management limits the geographical range of the Scandinavian wolf population, i.e., its first-order habitat selection (Johnson 1980), to south-central Scandinavia (Liberg et al. 2012). Therefore, our definition of available space did not include areas where this management prevented wolf establishment. Wolves were killed when they settled within the reindeer husbandry area that covers roughly the northern half of Sweden and Norway, and in Norway wolves establishing outside a specified area along the Swedish border were also killed (Fig. 1). In addition, the area available for spatial expansion of the wolf distribution changed annually, because an area occupied by a wolf pair is, by definition, not available for a new pair. Therefore, we used a longitudinal matched case-control design (Craiu et al. 2004, Fortin et al. 2005). We matched available, random sites at winter t to the actually selected area of newly formed pairs at winter $t + 1$, with a 10:1 ratio for paired randomly selected sites (Thurfjell et al. 2014, Zimmermann et al. 2014).

Definition of random sites

Preliminary analyses showed that the establishment of wolf territories within our study area did not occur randomly, but in close vicinity of existing territories. Due to this "quasi-philopatric" pair establishment pattern, we constrained the creation of available and random territories to the observed distribution of distances from a newly established pair to the closest existing wolf territory. Because a new pair cannot establish within the same area of an existing one, we prevented random sites from occurring within 15 km (distance from center territory points), which corresponded to a 47% overlap. In fact, wolf territories often overlap, with variable buffer zones among study areas (Mech 1994, Mech et al. 1998, Mech and Boitani 2003). It is also unlikely that the center point of a new wolf pair is in a heavily human-dominated area, thus we hindered random sites from falling in human-dominated areas larger than 10 km^2 ($\sim$0.01% of a wolf territory home-range size).

Statistical analyses

We used conditional logistic regression to analyze wolf pair establishment in 1990–2012, contrasting the actual sites where wolves established (1) with random territories (0). We followed a step-selection function procedure with the observed location of a pair as the actual step and 10 random locations as a set of random steps (Fortin et al. 2005, Thurfjell et al. 2014). The 10 random locations and the observed pair location are a "stratum" (Fortin et al. 2005). We used a generalized estimating equation (GEE), including year (winter) as a cluster term of the coxph–command (R package survival; Therneau 2014) to obtain robust standard errors among different years (Fortin et al. 2005).

We performed model selection based on corrected Akaike's information criterion (AIC$_c$) (Burnham and Anderson 2002). We first inspected correlations between variables, with a threshold set at 0.6 (Pearson r coefficient) to avoid inclusion of correlated parameters. Thus, we excluded human density, the index of remoteness and accessibility, elevation, and agricultural land cover from the model selection, due to high correlation with main and/or secondary road densities (r scores > 0.6). We built simple models, including single variables and their quadratic forms, which would reflect a nonlinear relation with the response variable. If the model with the quadratic form had a lower AIC$_c$ (ΔAIC$_c$ ≤ 2), we retained the quadratic form of the variable in the model selection; otherwise we retained the linear form of the variable. We standardized all continuous covariates to 1 SD to facilitate the interpretation and comparison of the relative strength of parameter estimates (Schielzeth 2010, Grueber et al. 2011). All combinations of variables were biologically plausible. There-

Table 2. Multimodel inference based on conditional logistic regression of wolf pair establishment in Scandinavia, 1990–2012. Best models ($\Delta AIC_c < 2$) of all combinations of possible models are ranked in terms of AIC_c and AIC_c weight. The null model is also presented for comparison. Spearman ranks correlation coefficients (r_S) of actually used sites by wolf pairs and random available sites are presented as an index of model robustness; $r_S > 0.6$ indicates robust models.

Variables	df	logLik	AIC_c	ΔAIC_c	AIC_weight	r_S controlled [95%CI]	r_S observed [95%CI]
1/3/4/5/6/7/8	7	−302.27	618.61	0	0.26	0.06 [−0.58;0.69]	0.67 [0.37;0.91]
1/3/4/5/6/7/8/9/10/11	10	−299.32	618.78	0.17	0.24	0.04 [−0.70;0.69]	0.71 [0.47;0.92]
1/3/4/5/6/7/8/9	8	−301.60	619.30	0.69	0.19	0.05 [−0.62;0.65]	0.68 [0.38;0.91]
3/4/5/6/7/8	6	−303.64	619.33	0.72	0.18	0.05 [−0.65;0.64]	0.69 [0.38;0.89]
1/3/4/5/6/7/8/10/11	9	−300.94	620.00	1.39	0.13	0.04 [−0.73;0.76]	0.70 [0.39;0.93]
Null	1	−338.10	676.20	57.6	...	...	...

Note: Variables: Brown bear density = 1; density of wolves = 3, wolf historical presence 1990–2012 = 4; quadratic effect of wolf historical presence = 5; distance to other wolf territory = 6; main road density = 7; quadratic effect of main road density = 8; moose density = 9; secondary road density = 10; quadratic effect of secondary road density = 11.

fore, we computed all combinations of possible models, without interaction terms, and performed model averaging with shrinkage of parameters of the models that had $\Delta AIC_c \leq 2$ (Burnham and Anderson 2002), using the MuMin R package (Barton 2009).

We used 10-fold cross-validation to evaluate the robustness of best models (Boyce et al. 2002). We built a conditional logistic regression using 90% of randomly selected strata. We then used this conditional logistic regression to predict scores for the actually used and random sites of the 10% remaining strata. First, the observed site of each stratum was ranked against its associate random sites from 1 to 11 (i.e., given that a stratum included one observed and 10 random sites, there were 11 potential ranks). Second, we randomly selected one control site and ranked it against the controls only. We used Spearman rank correlation (r_S) to estimate the degree of correlation between the rank of the observed and random sites and their relative frequency. We repeated this process 100 times for each final model and the average r_S, and reported the associated 95% confidence intervals (CI). We rejected all models with $r_S < 0.6$ (Zimmermann et al. 2014). All analyses were conducted in R 3.0.3 (R Core Team 2014).

RESULTS

We detected the establishment of 142 different wolf pairs in 1990–2012. Wolf pair establishment in a given site was positively related to previous wolf presence in the area ($\beta = 0.52$, SE = 0.16), and was negatively related to main road density ($\beta = -0.54$, SE = 0.19), distance to other wolf territories ($\beta = -0.35$, SE = 0.08), and bear density ($\beta = -0.21$, SE = 0.15; Tables 2 and 3). The 95% CI around the effect sizes (β) of these covariates did

Table 3. Effect size (β) and robust standard error (SE) of explanatory parameters of wolf pair site selection in Scandinavia, 1990–2012, estimated from the conditional logistic regression. We performed model averaging (with shrinkage) of best models to estimate the effect size of each parameter. Covariates were all scaled to 1 SD to facilitate comparison and interpretation of effect sizes.

Variable	β	SE	95% CI
Historical wolf presence	0.52	0.16	[0.21; 0.84]
Main road density	−0.54	0.19	[−0.92; −0.17]
Distance to other wolf territory	−0.35	0.08	[−0.51; −0.18]
Wolf density	−0.32	0.16	[−0.63; 0.02]
Brown bear density	−0.21	0.15	[−0.49; −0.03]
Main road density _quadratic	−0.17	0.13	[−0.42; 0.08]
Historical wolf presence_quadratic	−0.07	0.03	[−0.14; 0.00]
Secondary road density_quadratic	−0.08	0.15	[−0.55; 0.12]
Moose density	−0.07	0.11	[−0.40; 0.09]
Secondary road density	−0.06	0.13	[−0.49; 0.15]

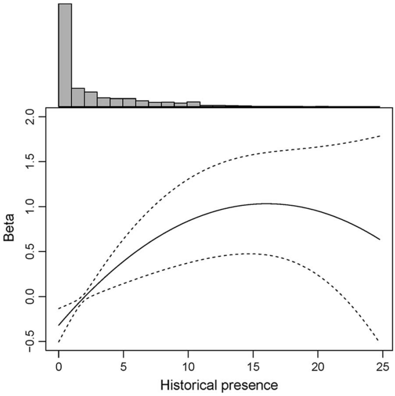

Fig. 3. Beta coefficient of the quadratic effect of wolf pair establishment in Scandinavia, 1990–2012, in relation to the index of wolf historical presence computed from model averaging (Table 3). Dashed line shows 95% confidence interval and bar plots show relative availability of both actually used and random sites.

not include 0 (Table 3), i.e., the sign of their effect on the probability of wolf pair establishment was clear. Wolf density ($\beta = -0.32$, SE = 0.16), moose density ($\beta = -0.07$, SE = 0.11), secondary road density ($\beta = -0.06$, SE = 0.13), and the quadratic form of the variables wolf previous presence ($\beta = -0.07$, SE = 0.03), main road density ($\beta = -0.17$, SE = 0.13), and secondary road density ($\beta = -0.08$, SE = 0.15) also had negative influence on the probability of wolf pair establishment. However, their 95% CI overlapped 0 (Table 3), suggesting a weaker, less conclusive effect than those mentioned previously. Indeed, the effect of the quadratic forms of previous wolf presence and main and secondary road density might just have reflected a lack of data in the tails of their respective distributions (Figs. 3 and 4).

The negative effect of bear density on the probability of wolf pair establishment (Fig. 5) was retained in four of five best models ($\Delta AIC_c = 1.39$ between the top and the fifth model), and the effect of density of wolves, wolf historical presence, distance to other wolf territory, and main road density was retained in all of them (Table 2). Selected models were robust, as shown by the distribution of r_S (averaged $r_S \geq 0.67$), which was higher than the expected by chance alone (averaged $r_S \leq 0.06$; Table 2).

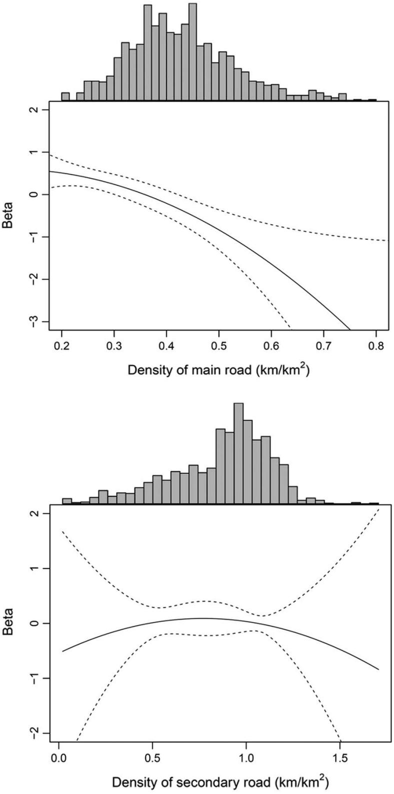

Fig. 4. Beta coefficient of the quadratic effect of wolf pair establishment in Scandinavia, 1990–2012, in relation to the density of main road (top panel) and secondary road (bottom panel) densities, computed from model averaging (Table 3). Dashed lines show 95% confidence intervals and bar plots show the relative availability of both actually used and random sites.

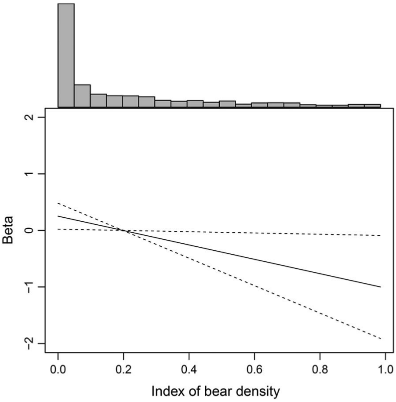

Fig. 5. Beta coefficient of wolf pair establishment in Scandinavia, 1990–2012, in relation with the index of bear density from model averaging (Table 3). Dashed line shows the 95% confidence interval and bar plots show the relative availability of both actually used and random sites.

Discussion

Human-related factors (negative effect of road density), intraspecific factors (positive effect of previous wolf presence and negative effect of increasing distance to other wolf territories), and presence of a competitor species (negative effect of brown bear density) were the most influential factors affecting territory selection by wolf pairs in Scandinavia in 1990–2012, a period of demographic recovery and expansion of the wolf population. Wolf establishment started outside the area with the highest density of bears, which seemed to be progressively occupied by wolves as the population expanded (Fig. 2). The negative effect of bear density on the probability of wolf pair establishment confirmed that pattern (Tables 2 and 3, Fig. 5) and this is the most novel result of our study. Interspecific interactions can affect the species' distributions, but it is rarely possible to incorporate this concept into species distribution models (Godsoe and Harmon 2012). The results suggest that interspecific competition has been one of the influential factors modulating the expansion of the Scandinavian wolf population, reinforcing the role of interspecific competition in shaping ecological communities.

A positive effect of previous wolf presence and negative effect of increasing distance to other wolf territories on the probability of wolf pair establishment has previously been documented. In Minnesota, for instance, edges of parental territories appeared to be preferred sites for wolf establishment, maybe to maximize parental fitness by tolerating the colonization of edges by offspring (Fritts and Mech 1981). The negative effect of main roads on wolf establishment was not surprising. Roads are a good proxy of human disturbance, often even better than human density per se (Ordiz et al. 2014). Main roads are used less by wolves for traveling than gravel roads (Zimmermann et al. 2014), which fits well with our result of a larger negative effect of main road density on wolf establishment, compared to the (also negative) effect of secondary roads (Tables 2 and 3). Regarding prey, wolf pair establishment occurred in areas with varying moose density, even when there was available space in the highest moose density areas, which would explain the negative, yet weak effect (95% CI of the β overlapping 0) of moose density in our study (Table 3). This result reinforces previous findings that wolves in Scandinavia are generally not constrained by moose density, which neither predicted the occurrence of wolf packs (Karlsson et al. 2007) nor influenced wolf home range size (Mattisson et al. 2013). However, it is possible that moose density plays a role at finer scales. In all Scandinavian studies, including ours, moose density estimates have been based on moose data from larger areas than the actual wolf territories.

Scavenging, including kleptoparasitism between carnivores as one of its major forms, is a key ecological process involved in energy flow in ecosystems (DeVault et al. 2003). Brown bears are a primary scavenger in the Northern Hemisphere (Krofel et al. 2012), and the generalized occurrence of bear kleptoparasitism in areas with high bear density (up to ~30 bears/1000 km^2 during the whole study period) might lie behind the negative effect of bear density on wolf establishment. Both wolves and bears feed on moose (Sand et al. 2005, Swenson et al. 2007), and bears are a very efficient predator on newborn moose calves (Barber-Meyer et al. 2008). However, bear predatory efficiency is limited in time, only until the calves are 4 weeks old (Rauset et al. 2012), and bears mainly access larger moose by scavenging other predators' kills (Swenson et al. 2007).

In temperate latitudes with higher densities of predators, brown bears kleptoparasitize up to 50% of Eurasian lynx (*Lynx lynx*) kills during the lynx breeding season, which may ultimately affect lynx fitness (Krofel et al. 2012), and American black bears (*Ursus americanus*) used > 50% of mountain lion (*Puma concolor*) kills (Elbroch et al. 2015). Conversely, additional protein obtained from scavenging kills may increase bear fitness, and wolf kills are particularly important for bears in late winter and early spring (Ballard et al. 2003). Most of the documented individual interactions between wolves and brown bears in North America and Eurasia have occurred near ungulate kills of both predators (Ballard et al. 2003), and it is possible that bears affect wolves and lynx in a similar way. Bears also kleptoparasitize > 50% of the wolf kills in our study area and can displace wolves from their kills (Milleret 2011; A. Ordiz et al., *unpublished data*), i.e., frequency of kleptoparasitism is high also in spring and early summer, when bears also kill moose calves themselves.

In North America 14% of 108 interactions between wolves and bears has been documented to occur near wolf dens (Ballard et al. 2003). As in the lynx case, bear kleptoparasitism could be quite costly during the wolf pup nursing period, when a continuous food supply is needed and fewer members of the wolf pack are available for hunting. Such an effect might be larger for small wolf packs and it has been shown that the effects of kleptoparasitism differ in relation to group size of the affected species (Carbone et al. 2005). Loss of food to scavengers is indeed important for wolf foraging ecology. For instance, wolf pack size increases with increasing scavenging rates by ravens (*Corvus corax*) (Vucetich et al. 2004). In Scandinavia, wolf packs often consist of just an adult pair with or without pups, and wolves >1 year old rarely stay with the pack (Mattisson et al. 2013). Even if prey density is not a limiting factor for Scandinavian wolves, losing food to scavengers may lead to additional hunting effort, which is costly and particularly risky when moose are the target prey (Peterson and Ciucci 2003). This may illustrate the dynamics of intraguild interactions in resource-pulse environments (Greenville et al. 2014), which, in our case, involves wolves as obligate carnivores, bears as facultative predators and scavengers, and moose as their common prey (Moleón et al. [2014] and Pereira et al. [2014] for reviews on the functional complexity of predation and scavenging strategies).

Wolf pairs generate packs, the reproductive, functional units of wolf populations, making habitat selection by wolf pairs especially interesting, because of its relation with breeding performance or fitness (see Gaillard et al. 2010). Genotyped and geo-localized data on both wolf pairs and bears during the entire process of wolf recovery in an area with a gradient of bear density provided the opportunity for this study. Yet quite unique, our approach was necessarily coarse, because the study area was very large ($\sim$100,000 km^2) and the study period very long (22 years). Before a scent-marking pair of wolves can be detected by the monitoring program, both animals must survive during the process of dispersion, meet each other, and settle down. Poaching is a major driver of large carnivore population dynamics in human–dominated landscapes, including wolves in Scandinavia (Liberg et al. 2011). Bears and wolves show preference for forested areas (May et al. 2008), which may facilitate poaching compared to lower altitudes with less persistent snow cover and thus less detectable carnivores. Poaching may be a cryptic factor involved in wolf establishment and therefore may affect our results. Nevertheless, one would expect bears also to be affected by poaching in the same area, but the highest bear density in Scandinavia actually overlaps with the wolf range (Fig. 2). Given these circumstances (large study area, long study period, and potential cryptic factors that may be considered as potentially confounding factors), we suggest that the documented negative effect of bear density on wolf pair establishment is especially remarkable.

Interactions between apex predators can have cascading effects through the entire natural community, which supports broadening the scope of conservation from single species to a much wider ecosystem perspective (Linnell and

Strand 2000). The relative role of top–down and bottom–up processes in ecosystems is a long-lasting ecological debate (e.g., Sinclair and Krebs 2002), but the effects that apex predators have on each other in a broad ecosystem context has gained increasing recognition recently (Estes et al. 2011, Ripple et al. 2013, 2014). Interactions between carnivores have the potential to affect overall biodiversity, e.g., by influencing the structure and composition of the vertebrate scavenger community (Allen et al. 2014). Therefore, the management of large carnivores should consider interspecific interactions (Ordiz et al. 2013), rather than focusing only on target populations of single species. This applies both to marine ecosystems, e.g., for fisheries management (Belgrano and Fowler 2011), and terrestrial ecosystems, e.g., to adjust harvest quotas of game species to account for the return of large, sympatric predators (Jonzén et al. 2013, Wikenros et al. 2015).

Predator kill rates increase as a result of kleptoparasitism by other carnivores and scavengers (e.g., Krofel et al. 2012). Therefore, the effects of predation can be better understood within a whole-community context that takes interactions into account (Elmhagen et al. 2010, Letnic et al. 2011, Elbroch et al. 2015). For instance, wolves provide biomass to scavengers throughout the year (Wilmers et al. 2003, Wikenros et al. 2013), and they also drive changes in the density, distribution, and diet of other predators (Berger and Gese 2007, Kortello et al. 2007). Such interactive processes can be essential in the regulation, stability, and resilience of ecological communities (Ripple et al. 2014). This emphasizes the need of further research at finer scales, i.e., within home-ranges, to disentangle the mechanisms driving interactions and the particular ecological functions of different predators, scavengers, and prey species.

Long-term monitoring data across large areas with environmental gradients, like our case with wolves and bears in Scandinavia, will help quantify and predict the influence of biotic interactions on species assemblages and distributions (Wisz et al. 2013). The current recovery of some large carnivores in Europe and North America (e.g., Chapron et al. 2014), along with the expanded use of GPS-based telemetry, should provide opportunities to study interspecific competition among sympatric apex predators at large, population levels in other ecosystems.

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Paper II

Milleret, C., Wabakken, P., Liberg, O., Åkesson, M., Flagstad, Ø., Andreassen, H. P., and Sand, H. (2016). Let's stay together? Intrinsic and extrinsic factors involved in pair bond dissolution in a recolonizing wolf population. *Journal of Animal Ecology*

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Let's stay together? Intrinsic and extrinsic factors involved in pair bond dissolution in a recolonizing wolf population

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Summary

1. For socially monogamous species, breeder bond dissolution has important consequences for population dynamics, but the extent to which extrinsic or intrinsic population factors causes pair dissolution remain poorly understood, especially among carnivores.

2. Using an extensive life-history data set, a survival analysis and competing risks framework, we examined the fate of 153 different wolf (*Canis lupus*) pairs in the recolonizing Scandinavian wolf population, during 14 winters of snow tracking and DNA monitoring.

3. Wolf pair dissolution was generally linked to a mortality event and was strongly affected by extrinsic (i.e. anthropogenic) causes. No divorce was observed, and among the pair dissolution where causes have been identified, death of one or both wolves was always involved. Median time from pair formation to pair dissolution was three consecutive winters (i.e. approximately 2 years). Pair dissolution was mostly human-related, primarily caused by legal control actions (36·7%), verified poaching (9·2%) and traffic-related causes (2·1%). Intrinsic factors, such as disease and age, accounted for only 7·7% of pair dissolutions. The remaining 44·3% of dissolution events were from unknown causes, but we argue that a large portion could be explained by an additional source of human-caused mortality, cryptic poaching.

4. Extrinsic population factors, such as variables describing the geographical location of the pair, had a stronger effect on risk of pair dissolution compared to anthropogenic landscape characteristics. Population intrinsic factors, such as the inbreeding coefficient of the male pair member, had a negative effect on pair bond duration. The mechanism behind this result remains unknown, but might be explained by lower survival of inbred males or more complex inbreeding effects mediated by behaviour.

5. Our study provides quantitative estimates of breeder bond duration in a social carnivore and highlights the effect of extrinsic (i.e. anthropogenic) and intrinsic factors (i.e. inbreeding) involved in wolf pair bond duration. Unlike the effects of intrinsic and extrinsic factors that are commonly reported on individual survival or population growth, here we provide quantitative estimates of their potential effect on the social unit of the population, the wolf pair.

Key-words: anthropogenic, *Canis lupus*, extrinsic, inbreeding, intrinsic, pair bond duration

Introduction

Population regulation is often described through intrinsic or extrinsic population processes. Species with strong social structures are often more prone to experience some kind of intrinsic population regulation (Odden *et al.* 2014). In such social systems, extrinsic factors (e.g. predation or hunting mortality) may interact with intrinsic factors in such a way that total mortality increases beyond the effect of the actual direct mortality itself (i.e. causing a super-additive effect) (Milner, Nilsen & Andreassen

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2007; Rutledge *et al.* 2010; Andreassen *et al.* 2013; Borg *et al.* 2015). Due to this super-additive effect, it is essential to understand the mechanisms involved in population regulation, as a few accidental deaths may have a disproportionally large effect on the population. For instance, many threatened large carnivore populations are exposed to human-caused mortality events. If these species have strong social bonding between members of a social unit, or experience sexually selected infanticide, such human-caused mortality can result in the social disruption of the group and/or the loss of dependent offspring (Brainerd *et al.* 2008; Rutledge *et al.* 2010; Gosselin *et al.* 2015).

Many species have evolved complex social systems, with a few dominant individuals monopolizing reproduction within the social unit (Macdonald 1983; Jennions & Macdonald 1994; Hatchwell 2009). This is the case for some threatened large carnivore species, from which several have developed a monogamous mating system. In theory, breeders from socially monogamous species repeatedly face the choice of whether to remain together with their current partner or divorce and find another partner. However, lifetime reproductive success of dominant individuals generally increases with the length of their dominance tenure (Hodge *et al.* 2008; Sánchez-Macouzet, Rodriguez & Drummond 2014). The duration of pair bonds has also been suggested to have positive effects on reproductive performance of socially monogamous species by increasing pair familiarity (Sánchez-Macouzet, Rodriguez & Drummond 2014).

Maintaining dominance tenure seems, therefore, to be a primary route to gain fitness in socially monogamous species. However, dominance tenure is threatened by a variety of factors that may vary in space. For instance, recolonization and expansion of large carnivore populations into human-dominated landscapes is often directly affected by human-caused mortality, for example through legal (hunting and trapping) and illegal (poaching and poisoning) actions (Mech 1995; Persson, Ericsson & Segerström 2009; Liberg *et al.* 2011). Indirect effects of human activities, for example habitat fragmentation, habitat loss (Delibes, Gaona & Ferreras 2001) and geographical or management boundaries (Bischof, Brøseth & Gimenez 2015), are also known to restrict large carnivores distribution, leading to genetic structuring and sometimes inbreeding depression with strong consequences for population viability (Keller & Waller 2002; Liberg *et al.* 2005), and possibly also dominance tenure (Kempenaers, Adriaensen & Dhondt 1998; Sparkman *et al.* 2012). In addition, large carnivore populations are also affected by extrinsic factors, such as food availability (Zedrosser, Dahle & Swenson 2006; Cubaynes *et al.* 2014) or population intrinsic factors, such as intraspecific competition (Cubaynes *et al.* 2014), which has also been found to affect dominance tenure (Hodge *et al.* 2008; Berger *et al.* 2015).

In this article, we used data from a long-term monitoring programme of a social carnivore population, the wolf (*Canis lupus*) in Scandinavia (Liberg *et al.* 2012) to examine the causes and the length of an important population demographic trait, pair bond duration. The exhaustive genetic and demographic information collected on the recolonizing Scandinavian wolf population (Wabakken *et al.* 2001, 2012; Liberg *et al.* 2012) offers a unique opportunity to better understand the factors involved in pair dissolution in a large carnivore population that is under strong anthropogenic influence (Karlsson *et al.* 2007; Liberg *et al.* 2011).

Specifically, we aimed at dissociating the effect of intrinsic and extrinsic population factors involved in wolf pair dissolution.

1. First, we quantified pair dissolution and causes of pair dissolution and predicted pair dissolution to be mainly caused by extrinsic (i.e. anthropogenic) factors resulting in short wolf pair bond duration (H1).
2. Then, we quantified to which extent population intrinsic and extrinsic characteristics of the pairs explained risk of pair bond dissolution. We hypothesized that spatial variation in extrinsic factors (mainly anthropogenic) explained spatial variation in pair bond duration (H2). Because the population is still in a recolonization phase, with abundant food resources, we further predicted (H3) that there should be no or small effects of population intrinsic factors, such as intraspecific competition, through food availability or wolf density (Mattisson *et al.* 2013). Finally, (H4) we tested the hypothesis that inbreeding (i.e. intrinsic factor) had a negative role in pair bond duration (Kempenaers, Adriaensen & Dhondt 1998) in addition to the inbreeding depression previously observed in this population (Vila *et al.* 2003; Liberg *et al.* 2005).

Materials and methods

STUDY AREA

The study was conducted in the south-central part of the Scandinavian Peninsula (Sweden and Norway 59°–62 °N, 11°–19 °E; Fig. 1). The landscape is dominated by boreal forest, interspersed with bogs and lakes. Agricultural and urbanized lands cover <5% of the study area. Due to extensive commercial logging and forest management practices, the average density of gravel forestry road is high (i.e. 0·88 km km^{-2} inside wolf territories, Zimmermann *et al.* 2014). However, the density of main roads (tarred public roads) is approximately four times lower than the gravel road density (Zimmermann *et al.* 2014). Human density is low and the study area encompasses large areas with less than one human per km^2 (Wabakken *et al.* 2001). The climate is continental and snow covers the ground for 3–6 months annually, mainly during October–April. Moose are the main wolf prey in Scandinavia and are very abundant (average: 1·3 per km^2; range 0·7–3·3) throughout the study area (Zimmermann *et al.* 2015).

IDENTIFYING WOLF TERRITORIES AND PAIRS

Monitoring of the Scandinavian wolf population was performed by the Norwegian and Swedish management authorities and consisted of tracking wolves on snow from October 1 to April 30 (Wabakken

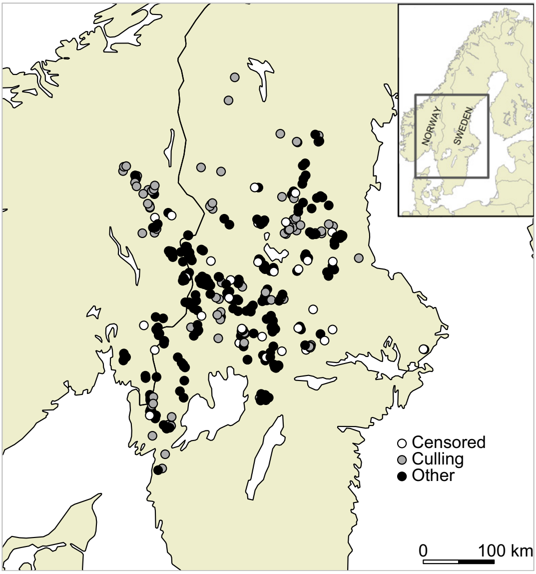

Fig. 1. Centroid location of the 369 wolf territorial pair-winters monitored in Scandinavia during 14 winters, 1998/1999–2011/2012. Grey circles represent pairs that have dissolved due to culling, black circles represent pairs that have dissolved for other reasons, and white circles are for pairs that were censored (i.e. dissolution not observed).

et al. 2001; Liberg *et al*. 2012) over a distance of 2200–5600 km each winter (see further details in Appendix S1, Supporting Information). We also utilized data collected by the cooperative Swedish–Norwegian Wolf Research Project (SKANDULV, Liberg *et al*. 2012) from 3 to 21 territorial wolves equipped with functioning radiocollars each winter. A near complete pedigree of the population has been reconstructed by a combination of individual DNA profiles (samples collected from scats, urine, blood, tissue and hair) and long-term annual snow tracking of territorial individuals (Liberg *et al*. 2005, 2012; Bensch *et al*. 2006). Information on the spatial location of wolf territories during winter was gathered from snow tracking in combination with DNA-analyses of collected samples, or by VHF/GPS location when available. The two main goals of the monitoring programme are (i) to register the annual number and spatial distribution of all reproduction events and territorial pairs (hereafter, we used the term territorial wolf pair for: a pair of two potential breeders or two breeders with their offspring, i.e. a pack) and (ii) maintain and continuously update the pedigree of the population. Special tracking efforts were, therefore, made every winter to detect and genetically identify new potential breeders within territorial pairs. This extensive and long-term monitoring programme provided a near complete description of the annual distribution and dynamics of wolf territories in Scandinavia, including the identities of the territory-marking individuals (Fig. 1). During our study period (1998/1999–2011/2012), the population increased by fourfold–sixfold from 10 to 60 pairs, and, on average, from 70 to 295 wolves (Wabakken *et al*. 1999, 2012).

IDENTIFYING CAUSES OF PAIR DISSOLUTION

All pair dissolutions were assigned to one of five classes: (i) death caused by culling (i.e. legal control actions or license hunting), (ii) verified poaching, (iii) natural causes of death (e.g. age and diseases), (iv) traffic mortality and (v) unknown causes (i.e. when a pair dissolution was verified (one or both individuals were missing), but could not be linked to any of the other four categories). After a pair dissolution event in which one of the pair members went missing, replacement was confirmed when a new wolf started territorial scent marking together with the remaining individual from the previous pair.

EXTRACTING CHARACTERISTICS OF THE TERRITORY AND THE PAIR

In Scandinavia, wolf pair home ranges have an average size of approx. 1000 km^2 (Mattisson *et al*. 2013). However, accurate home range boundaries (i.e. calculated using at least 9 months with location data, each with five or more locations) were unknown for the majority of pairs, which were not radiocollared (Mattisson *et al*. 2013). Instead, we used all available spatial information (i.e. VHF/GPS and/or snow-tracking locations) to compute a centroid point location for each territory and year. We then extracted the large-scale spatial characteristics (Table 1) of the wolf territories within an average circular wolf territory of 1000 km^2 placed around this centroid point (Mattisson *et al*. 2013; Ordiz *et al*. 2015).

Extrinsic characteristics

We used human density (number of inhabitants per km^2), density of gravel roads and main roads (km per km^2) and an index that combined information on the spatial location of roads and buildings to quantify areas that were both highly accessible by humans yet remote (Table 1, Appendix S2). Wolf depredation on

Table 1. List of variables used to model wolf risk of pair bond dissolution in Scandinavia during the period 1998–2011. The name, description and related-hypothesis of each variable used are mentioned. Time series shows whether the variables used varied with time or not. Quadratic effect shows whether a quadratic effect of the variable was tested or not

Name	Description	Hypothesis	Time series	Quadratic effect	Sources
Road1	Total length of paved roads (km per km^2)	(H2) Reflects human activity	No	No	(1:100 000, Lantmäteriet, Sweden; N50 kartdata, Staten-skartverk, Norway)
Road2	Total length of gravel roads (km per km^2)	(H2) Reflects human accessibility	No	No	(1:100 000, Lantmäteriet, Sweden; N50 kartdata Statens Kartverk, Norway)
RoadBuild	Per cent of roads stretches with ≤ 2 buildings per km	(H2) Reflects human accessibility & remoteness	No	No	(Lantmäteriet, Sweden; N50 kartdata, Statens Kartverk, Norway
Hum	Human density, number of inhabitants per km^2	(H2) Reflects human activity	No	No	www.scb.se, Sweden; www.ssb.no, Norway
Conf1	Dogs depredation events	(H2) Reflects potential for conflicts	No	No	www.rovdjursforum.se, Sweden, www.rovbase.no, Norway
Conf2	Sheep depredation events	(H2) Reflects potential for conflicts	No	No	www.rovdjursforum.se, Sweden, www.rovbase.no, Norway
TimePres	Number of winters that wolf pairs occupied the area	(H2) Increase tolerance through time	Yes	No	Wabakken *et al.* (1999, 2001, 2012)
Country	Country in which the wolf territory was located (Sweden/Norway/Cross-border)	(H2) Human attitudes towards wolves differ between Sweden and Norway	No	No	Gangaas, Kaltenborn & Andreassen (2013)
LocEast	Location on the longitude scale	(H2) Longitude scale	Yes	Yes	WGS 84/UTM zone 33
LocNorth	Location on the latitude scale	(H2) Latitude scale	Yes	Yes	WGS 84/UTM zone 33
LocCore	Distance from core area of the wolf population	(H2) Effect of management	Yes	Yes	Wabakken *et al.* (1999, 2001, 2012)
Density	Number of wolf territories within a 40 km radius	(H3) Density dependence	Yes	No	Wabakken *et al.* (1999, 2001, 2012)
Moose	Annual number of moose shot per km^2 used as an index for local moose density	(H3) Food availability	Yes	No	http://www.viltdata.se/, Sweden; www.ssb.no, Norway
Age_F Age_M	Proxy for the minimum age of Female and Male pair members	(H3) Effect of age of pair members	Yes	Yes	Wabakken *et al.* (1999, 2001, 2012)
F_male F_female F	Male, female, potential offspring inbreeding coefficients.	(H4) Inbreeding avoidance	No	No	Liberg *et al.* (2005)

domestic animals and dogs is an important source of conflict with humans in Scandinavia (Herfindal *et al.* 2005; Liberg *et al.* 2010). We therefore quantified the spatial variation of wolf depredation events for domestic sheep and hunting dogs. (Table 1, Appendix S2).

We used descriptors of the geographical location of the territory, such as longitude, latitude and the distance from the core area of the wolf population (here defined as the annual centre of all estimated centroid points of wolf territories) as additional covariates. As tolerance (Gangaas, Kaltenborn & Andreassen 2013) and management of wolves differs between Sweden and Norway, we also included the country in which wolf pairs were located as a covariate in the models.

To map prey density, we created a moose density index based on harvest density (number of moose harvested per km^2) at the municipality level in Norway and at the moose management unit ('älgförvaltningsområde') level in Sweden. Harvest density has been found to be a robust, but delayed, indicator of spatio-temporal variation in moose density (Ueno *et al.* 2014). To account for this delay, we used harvest density figures from the year $t + 1$ to estimate a moose density index in year t.

Intrinsic characteristics

Local density of wolf pairs was used as a proxy of density-dependent effects on pair bond duration (Mattisson *et al.* 2013). Each winter, we counted the number of neighbouring territories having their centroid point within a 40-km-radius buffer (i.e. two times the radius of a large wolf home range) around the centroid location of each pair.

Human tolerance towards carnivores may sometimes increase with time of coexistence (Zimmermann, Wabakken & Dötterer 2001). Based on wolf monitoring data, the centroid location of each winter territory identified was used as the centre of a 1000-km^2 buffer zone (i.e. size of an average wolf home range) and a wolf territory was considered present in pixels covering the buffer. We then created a time series of maps showing the number of winters that territorial wolf pairs had been recorded in each pixel (200 × 200 m, Appendix S2, Supporting information) of the study area since the first wolf pair re-establishment in 1982 (Wabakken *et al.* 2001).

Because age of the individuals forming the pair can affect pair bond duration, we assigned a year of birth to all individuals. However, due to our extensive data set, we could not assign exact year of birth to all individuals. We therefore estimated a latest possible year of birth (i.e. minimum possible age) to obtain a proxy for the age of individuals forming the pair. The latter was estimated using a combination of multiple sources of information, such as the year of first DNA capture and the last year that the parental pair was known to have successfully reproduced. We also assumed that the individual should be minimum 2 years old before the first detected breeding of the individual, and 1 year before first pairing.

Earlier studies have shown that the level of inbreeding may affect fitness traits among Scandinavian wolves (Liberg *et al.* 2005; Bensch *et al.* 2006). We used the reconstructed pedigree to calculate the individual inbreeding coefficient f (Liberg *et al.* 2005), which represents the amount of ancestry shared by parents of an individual (Keller & Waller 2002). To estimate the effect of inbreeding depression on pair bond duration, we used the inbreeding coefficient of the individuals in each pair (i.e. the male and female), and the inbreeding coefficient of their potential offspring as separate variables. Five different Finnish–Russian immigrants that formed a pair were assumed to be outbred (i.e. $f = 0$). For two individuals, with missing pedigree information, we randomly assigned a inbreeding coefficient that was derived from the distribution of inbreeding coefficients calculated from the potential mating of individuals available for mating at the time of birth of the two individuals.

PAIR BOND DURATION

We summarized data from individuals identified during tracking events for each winter. If pair members could not be directly detected during a winter, we used indirect information to confirm their presence, such as the genetic detection of offspring from the non-detected pair member. These multiple sources of information to confirm presence of pair members were combined with a survival analysis framework to quantify the pair bond duration of territorial wolf pairs. Survival analysis refers to statistical procedures for which the outcome variable of interest is time until an event occurs (Kleinbaum & Klein 2011). In our case, each winter monitoring period (October–April) was set as the time unit. A pair detected within a specific territory during each winter was assumed to have been present during that entire winter, because the exact date of dissolution was unknown in most cases. The dissolution event was attributed to the winter in which one or both of the previously identified individuals were no longer detected within a previously defined territory. Thus, we counted the number of consecutive winters in which a specific pair was identified in its territory from the winter of establishment until the winter in which no signs of one or both individuals were found (i.e. pair dissolution). Hence, if a territorial female and male were found together for three consecutive winters, but not during the fourth winter, we considered that the dissolution occurred at the end of the third winter (i.e. the pair persisted for three consecutive winters and for approximately 2 years). Three different criteria for pair dissolution were used as follows: (i) evidence that one or both individuals were dead, (ii) replacement of one or both individuals by another individual the following winter and (iii) failure to record two scent-marking individuals in a previously verified territory, despite large tracking efforts. Censoring (when monitoring stops without the event of interest having occurred; Kleinbaum & Klein 2011) only occurred at the end of our study in 2011/2012.

We used a Kaplan–Meier survivor function to quantify the probability that a specific pair will persist over time (Kleinbaum & Klein 2011). It is a step function that decreases from 1 (all wolf pairs are intact at time t) towards a minimum value of 0 (when dissolution of all pairs has occurred). To model the relative influence of covariates (Table 1) on risk of pair dissolution, we used semiparametric Cox proportional hazard (CPH) models (Kleinbaum & Klein 2011). These models provide hazard ratios (HR) of covariates on the baseline hazards (instantaneous potential of dissolution) for the event to occur at a time t per unit time (Kleinbaum & Klein 2011). We used a counting-process style input, which allows time-varying covariates to be used (Fieberg & DelGiudice 2009). Pair members were identified as correlated groups of observations and were clustered in order to obtain robust sandwich variance estimators (Kleinbaum & Klein 2011).

CAUSE-SPECIFIC PAIR DISSOLUTION

In the case of multiple causes of pair dissolution, a general approach such as Kaplan–Meier is not sufficient because it involves mutually exclusive events in time (i.e. if pair i splits up due to cause k, it is not available to split up from cause j). We therefore estimated specific causes of dissolution using a nonparametric cumulative incidence function estimator (Heisey & Patterson 2006).

To model the impact of covariates (Table 1) on the cause-specific risk of pair dissolution, we re-classified causes of pair dissolution into two main categories, (i) culling (i.e. all legal killing, including control and license hunting) and (ii) other causes (i.e. unknown, natural mortality, verified poaching and traffic related). We created the second category because we could not exclude natural mortality, poaching and traffic-related causes of dissolution from unknown causes of dissolution. We followed methods described by Lunn & McNeil (1995) and Heisey & Patterson (2006) to account for competing risks. We first duplicated the data set as many times as the number of dissolution causes. Then, we used the 'strata()' function to compute different baseline hazard functions for each dissolution cause (Therneau 2014). Finally, we included interaction terms between important covariates obtained after model selection and strata to estimate the potential effects of covariates in relation to different causes of dissolution.

MODEL SELECTION

To determine which factors (Table 1) influenced risk of pair dissolution, we performed CPH model selection based on corrected Akaike's information criterion (AICc) (Burnham & Anderson 2002; Liang & Zou 2008). Before running model selection, we checked for collinearity between all covariates ($r < 0{\cdot}6$). Among two correlated variables, only the variable with the lowest AICc score in a simple model was retained in the model selection process (Appendix S3). We standardized all continuous covariates to 1 SD to facilitate interpretation and comparison of the relative strength of parameter estimates (Schielzeth 2010; Grueber *et al.* 2011). All combinations of additive variables were biologically plausible. Therefore, we considered all possible combinations of models (Table 1), using the 'MuMIn' R package (Barton 2014). We did not consider individual models with more than five variables to avoid over-fitting models (Grueber *et al.* 2011). We considered the quadratic forms of some of the variables (Table 1) in the model selection process, but only included that transformation when a model containing both the linear and quadratic forms of the variable had a lower AICc (i.e. $\Delta\text{AICc} \geq 2$) than a model containing just the linear form. We also considered some interactive terms (age_F × age_M; age_F × F_female; age_M × F_male), but only if the interactive model had lower AICc (i.e. $\Delta AICc \geq 2$) compared to the inclusion of additive model. We then checked for hazard proportionality using the scaled Schoenfeld residuals (Kleinbaum & Klein 2011). We performed model averaging, based on AICc, and calculated confidence intervals for all models with Δ $AICc \leq 2$ (Burnham & Anderson 2002; Grueber *et al.* 2011; Barton 2014). In addition, we used 95% confidence intervals around averaged hazard ratio estimates to help interpret uncertainty in parameters estimation and variable importance (Fletcher & Dillingham 2011; Galipaud *et al.* 2014). Additionally, we also tested whether the replacement of one individual in the pair could be attributed to its degree of relatedness by comparing the inbreeding coefficient of the new individual to the inbreeding coefficient of the replaced individual, using a paired t-test. We also tested the robustness of our method to extract landscape characteristics, by adding some noise to the centroid location of the territory (See Appendix S4 for further details). All analyses were performed using R version 3.0.3 (R Core Team 2014) and the Survival package (Therneau 2014).

Results

PAIR DISSOLUTION

General

Genetic identity of both territorial wolf pair members (i.e. the scent-marking female and male) was determined in 98% of the 442 winter territories documented during 14 consecutive winters from 1998/1999 to 2011/2012. In total, we detected 179 different pairs representing 429 monitored pair-winters and 295 different individuals (140 females, 155 males). Among our 13 winter to winter pair bond duration estimates, we determined the fate of 153 different pairs and documented a total of 119 dissolution events. The winter following most of these dissolution events, a replacement occurred for 70 pairs (58·8%), with one (72·9%, $n = 51$) or both pair members (27·1%, $n = 19$) replaced (Fig. 2). For the remaining 49 (41·2%) dissolution events, no replacement occurred before or during the next winter, and we detected one individual being left alone in 32·7% ($n = 16$) of the cases. However, we could not detect any individuals or pairs within the territory previously occupied by the dissolved pair in 67·3% ($n = 33$) of the cases (Fig. 2). Our proxy for minimum age showed that mean (±SD) age at pair establishment was 2 (±1·61) and 2·4 (±1·90) years old, 3·7 (±2·37) and 4·1 (±2·60) at pair dissolution, and mean age of wolves observed in a pair was 3·2 (±2·21) and 3·64 (±2·50) for males and females, respectively.

Causes of pair dissolution

Altogether, the survival curve indicated that half of the pairs (i.e. median persistence of pairs) have dissolved after three [95% CI = (3–4)] consecutive winters (i.e. after

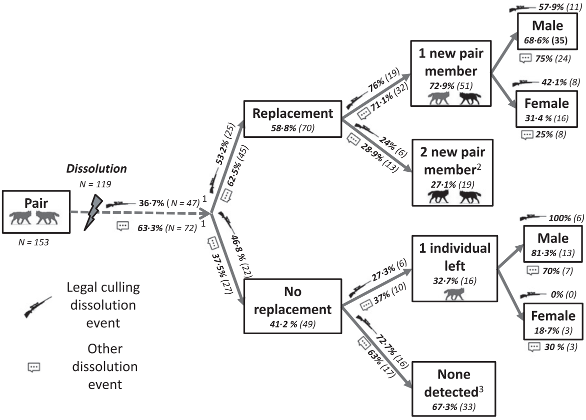

Fig. 2. Flow chart of the consequences of pair dissolution in the Scandinavian wolf population during the period 1998–2011. Among the 153 different wolf pairs included in this study, 47 dissolved due to legal culling (🔫) and 72 pairs due to others causes (💬; i.e. natural, traffic-related, poaching and unknown causes). The winter following a dissolution event, we identified either: (i) a replacement of two individuals (i.e. both the male and the female were replaced) or one individual (i.e. the male or the female was replaced); or (ii) no replacement, meaning that we detected one individual left alone (i.e. the male or the female) or no pairs could be confirmed within the territory. Percentages and number of events are presented to show the extent to which culling and other dissolution events were followed by a replacement or not. ¹Percentages were estimated using nonparametric cumulative incidence function estimator (see methods). ²At least one new pair (two new individuals) detected with a territory overlapping the territory of the previously dissolved pair. ³No pair could be detected overlapping with the territory previously occupied by the dissolved pair.

approximately 2 years) (Fig. 3). The overall probability of a wolf pair bond persisting from one winter to the next (i.e. approximately 1 year) was 0·68 (0·63–0·73). No pair lasted for more than eight consecutive winters, except one that lasted for 12 consecutive winters, with both male and female being at least 13 years old when the pair dissolved. Dissolution due to unknown causes was most common and occurred in 44·3% [95% CI = (37·8–50·8)] of the cases. Causes of dissolution were determined in 55·7% of the cases with 36·7% (25·9–47·5%) of the cases attributed to culling, 9·2% (0–20·1%) to confirmed poaching, 7·7% (0–20·6%) to natural causes of mortality such as disease and age and 2·1% (0–11·9%) to traffic-related accidents.

EFFECT OF INTRINSIC AND EXTRINSIC CHARACTERISTICS OF THE PAIR ON RISK OF PAIR DISSOLUTION

According to the final CPH models based on all wolf pairs, the extrinsic variables *Distance from the core area (LocCore)* and *Longitudinal gradient (LocEast)*, and intrinsic variables *Inbreeding coefficient of the male (F_male)* and *Age of the males (Age_M)* were the most important variables affecting pair bond duration. The low relative variable importance and 95% confidence interval of hazard ratios not overlapping with 1 (Tables 2 and 3) showed that all other variables had considerably less influence on pair bond duration. Risk of pair dissolution increased with the *Distance from the core area*, *Age of the male* and *Inbreeding coefficient of the male*, and pair bond duration was longer with increasing *longitudinal gradient* (Table 3).

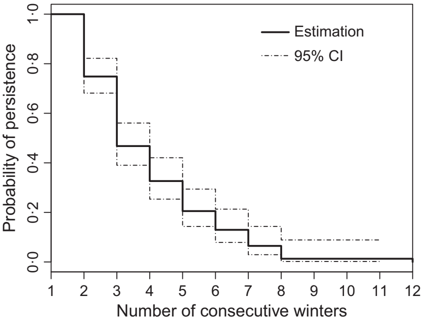

Fig. 3. Kaplan–Meier cumulative survival curve with 95% confidence intervals showing the probability of wolf pair bond persistence in Scandinavia during the winters 1998/1999–2011/2012. On the *x*-axis, winter 1 shows the first winter a pair was detected, winter 2 the second and so on.

On average, pair dissolution tended to occur earlier when dissolution was due to culling compared to other causes (Fig. 4). The competing risk analysis and the 95% confidence intervals revealed that the risk of pair dissolution found for the intrinsic variables; *Inbreeding coefficient* and *Age of the male* were more important for dissolution due to other causes [$HR_{F\_male} = 1{\cdot}35$, 95% CI = (1·04–1·76); $HR_{Age\_M} = 1{\cdot}32$ (0·99–1·76), respectively] than due to culling [$HR_{F\_male} = 1{\cdot}38$ (0·96–1·98); $HR_{Age\_M} = 1{\cdot}27$ (0·89–1·81), respectively]. Concerning the extrinsic variables, the effect of *Longitudinal gradient* was more important for dissolution due to other causes (HR = 0·77, 95% CI = 0·61–0·97) than due to culling (HR = 0·90, 95% CI = 0·69–1·18). Conversely, the effect of *Distance from the core area* was more important for dissolution due to culling (HR = 1·52, 95% CI = 1·12–2·06) than due to other causes (HR = 1·16, 95% CI = 0·91–1·47).

INBREEDING COEFFICIENT OF THE NEW REPLACED MALES

Since the males inbreeding coefficient was retained as an important variable, we checked whether inbreeding coefficient of the new male would be lower after a new replacement. However, new males were on average as inbred as the replaced males (average f new male = 0·266; average f old male = 0·241; t = 0·96, d.f. = 24, P = 0·35), and consequently, the arrival of a new male in the pair had no effect on the inbreeding coefficient of their pups (average

Table 2. Model inferences based on Cox proportional hazard regression models of factors affecting risk of pair dissolution in Scandinavia during the period 1998–2011. Best models based on AICc selection and the null model is also presented for comparison purposes. See Table 1 for variable descriptions

Model set	K	logLik	AICc	ΔAICc	W_i
AgeM + LocCore + LocEast + F_male	4	−475·66	959·37	0	0·27
AgeM + LocCore + LocEast + F_male + AgeF	5	−474·86	959·81	0·43	0·22
AgeM + LocCore + LocEast + F_male + Moose	5	−475·56	961·21	1·83	0·11
AgeM + LocCore + LocEast + F_male + F	5	−475·58	961·25	1·88	0·10
AgeM + Density + LocCore + RoadBuild + LocEast	5	−475·61	961·31	1·93	0·10
AgeM + F_male + LocCore + RoadBuild + LocEast	5	−475·62	961·32	1·94	0·10
AgeM + F_female + F_male + LocCore + LocEast	5	−475·63	961·34	1·97	0·10
Null	1	−485·63	971·26	11·89	0

Only models with Δ corrected Akaike's information criterion (AICc) < 2 are shown. K stands for number of parameters; W_i for the model weight; logLik for log likelihood.

Table 3. Summary of parameter estimates after model averaging the hazard ratios of each parameter on wolf pair bond duration in Scandinavia during the period 1998–2011. A hazard ratio > 1·0 corresponds to an increased risk of pair dissolution for each additional unit of the covariate. All covariates were scaled to 1 SD for comparison purposes. Estimates were calculated from the best models selected after AICc selection (Table 3). See Table 1 for variable descriptions

Parameter	Hazard ratio	95% CI	Relative variable importance
LocCore	1·30	1·10–1·52	1·00
LocEast	0·82	0·70–0·96	1·00
Age_M	1·30	1·09–1·54	1·00
F_male	1·35	1·12–1·63	1·00
Age_F	1·16	0·95–1·42	0·22
Moose	1·05	0·87–1·26	0·11
F_female	0·98	0·84–1·14	0·10
Density	1·03	0·86–1·24	0·10
F	1·04	0·87–1·25	0·10
RoadBuild	0·97	0·81–1·16	0·10

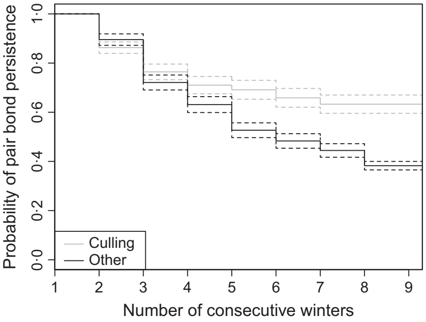

Fig. 4. Nonparametric cumulative incidence estimates with 95% confidence intervals showing the probability of wolf pair bond persistence between the winters of 1998/1999 and 2011/2012, which dissolved due to either legal culling in grey (median pair persistence = 3 winters) and all other causes in black (median pair persistence = 4 winters). On the x-axis, winter 1 shows the first winter a pair was detected, winter 2 the second and so on.

f after new male = 0·285; average f before new male = 0·298; $t = -0{\cdot}54$, d.f. = 24, $P = 0{\cdot}60$).

Discussion

IMPORTANCE OF EXTRINSIC FACTORS IN CAUSES OF PAIR DISSOLUTION

According to our hypothesis (H1), causes of pair bond dissolution were mainly due to extrinsic (i.e. anthropogenic) factors. The death of one or both partners was the typical proximate cause of pair dissolution (Hinton *et al.* 2015), which was supported by data from 98 radio-marked pair members (Liberg *et al.* 2008). No divorces were observed, that is cases in which both individuals were still alive after a pair dissolution event. The cause of pair dissolution could be determined in 55·7% of the cases, and all involved the death of one or both wolves, most of which were caused by humans (culling: 36·7%, verified poaching: 9·2%, traffic: 2·1%) and 7·7% could be attributed to natural factors. Almost half of the dissolution events could not be assigned to any specific cause. If all or most of the unknown causes of pair dissolution were undetected mortality events, there are only two main possibilities: natural deaths or cryptic poaching. Legal culling is by definition reported in all cases, and it is likely that nearly all un-intended traffic mortalities are also reported. Liberg *et al.* (2008) showed that natural causes made up 5·5% of all mortality of radiocollared breeding pair members in the Scandinavian wolf population. In our study, natural causes of pair dissolution amounted to 7·7% suggesting that a large proportion of the dissolution events caused by natural causes were detected, assuming GPS collared individuals were a representative sample of the population. As a consequence, a cryptic source of mortality, such as poaching, could be the main explanation for the remaining part of the unknown cases of dissolution. Poaching could, theoretically, be responsible for approximately half of all dissolution events which would be of the same magnitude as individual mortality caused by poaching in Scandinavia (Liberg *et al.* 2011).

We cannot entirely rule out the possibility that false absences, that is pairs that were considered dissolved but were actually intact, might explain a large number of dissolution events due to unknown causes. However, the continuously updated pedigree of the population reconstructed from DNA profiles, in combination with the comprehensive tracking effort (e.g. in the winter 2008/2009 approx. 100 field workers tracked wolves for >5400 km; Liberg *et al.* 2012) mean that very few reproducing pairs could have remained undetected for more than 1 year. Furthermore, the joined annual survival probability of female and male pair members ($\mathrm{surv}_{\mathrm{female}} \times \mathrm{surv}_{\mathrm{male}} = 0{\cdot}82 \times 0{\cdot}77 = 0{\cdot}63$) obtained from GPS collared animals (Liberg *et al.* 2008), falls within the confidence interval of our estimate of winter to winter pair bond duration (0·68; 95% CI: 0·63–0·73). This gives support to the estimates of pair bond duration obtained in our study.

Large carnivore mortality in human-dominated landscapes is often human-induced, both in Scandinavia (e.g. Bischof *et al.* 2009 for brown bears, Andrén *et al.* 2006 for lynx, Persson, Ericsson & Segerström 2009 for wolverines), and elsewhere (e.g. Jędrzejewska *et al.* 1996; Falcucci *et al.* 2009 in Europe, Smith *et al.* 2010 in North America). Although the wolf is the most studied large carnivores, we are only aware of one study explicitly quantifying pair bond duration (Hinton *et al.* 2015). In this study, mean breeding pair bond duration of red wolves (*Canis rufus*) was estimated to 2 years (mean life span of wolf was 3·2 years) and >65% of pair bond dissolutions were caused by anthropogenic factors (Hinton *et al.*

2015). These estimates are comparable with the estimates obtained in our study and are quite different from the long wolf pair bond duration that seems to be perceived for wolf (e.g. Mech 1997). Adult wolf mortality rates are generally low in the absence of human offtake (Creel *et al*. 2015), which suggests that a median pair bond duration of three consecutive winters is relatively short for a long-lived species such as the wolf (e.g. reported to have reached up to 15 years in the wild Carey & Judge 2000) and may reflect the strong impact of human-related mortality in this population.

IMPORTANCE OF SPATIAL VARIATION IN EXTRINSIC FACTORS ON RISK OF PAIR DISSOLUTION

Our survival analysis revealed that spatial variation in extrinsic factors was an important factor influencing risk of pair dissolution (H2). However, the geographical location of pairs in Scandinavia better explained pair bond duration than the anthropogenic-related variables. Although a consensus exists among scientists to apply management and conservation actions at a relevant biological unit, administrative or jurisdiction boundaries are often used as a basis for management decisions (Bischof, Brøseth & Gimenez 2015). According to official policy in both Norway and Sweden, wolves are not allowed to establish in all areas of the peninsula. For example, Scandinavian born wolves that move into the reindeer husbandry area (i.e. covering approximately the northern half of Scandinavia) and outside the specific Norwegian management zone established for breeding wolves (i.e. along the southern Swedish–Norwegian border) are promptly killed legally. As a consequence, the wolf breeding area is constrained to central Scandinavia (Fig. 1) which likely explains the higher risk of mortality due to culling observed at the periphery of the population. Furthermore, a greater tolerance for poaching exists in Norway than in Sweden (Gangaas, Kaltenborn & Andreassen 2013), which could be the causal mechanism to the longitudinal trend found in pair bond dissolution. Therefore, this could suggest that risk of pair dissolution may not be related to spatial variation in anthropogenic characteristics of the landscape, but rather to variation in tolerance towards carnivores and poaching.

IMPORTANCE OF INTRINSIC FACTORS ON RISK OF PAIR DISSOLUTION

The Scandinavian wolf population currently suffers from severe inbreeding depression that reduces individual fitness (Liberg *et al*. 2005; Bensch *et al*. 2006). We found a negative effect of the male pair member inbreeding coefficient on pair duration (H4), but only for dissolution events caused by 'other' causes. The 'incompatibility hypothesis' suggests that the pairing of two individuals that are of intrinsically good quality, but when paired together result in reduced fitness, would benefit from pairing with a new partner (Choudhury 1995). Thus, the replacement of pair members with a new individual resulting in relatively less inbred offspring could be a mechanism reflecting inbreeding avoidance (Choudhury 1995; Sparkman *et al*. 2012). Interestingly, this pattern could not be confirmed in this population, since no cases of divorce were detected (i.e. where both pair members were observed as a new pair after a dissolution event). In addition, replaced males were not less inbred than their predecessor. However, we could not directly test for the 'incompatibility hypothesis' since this required explicit data on the reproductive success for each pair, and our monitoring did not provide accurate estimates of litter size but only whether reproduction could be confirmed or not. Once wolf pairs started to reproduce, their subsequent reproduction rate was high with >95% of pairs with a confirmed positive reproductive status (SKANDULV unpublished). However, since the proportion of the genome identical by descent, under some circumstances, can vary substantially among individuals with identical pedigree-based ancestry (e.g. full siblings), true differences in inbreeding and fitness between individuals may not have been captured entirely by using pedigree information (Kardos, Allendorf & Luikart 2014). An alternative explanation is that inbreeding depression may cause increased mortality of highly inbred males (Keller & Waller 2002). However, there has not been any effect of inbreeding on adult mortality detected in this population so far.

Although the Scandinavian wolf population has increased fourfold to sixfold during our study, we did not find evidence of density-dependent pair dissolution through an increase in local wolf density or through changes in the density of their main prey (moose), as we hypothesized (H3). This is supported by the lack of home range size response to density-related factors (Mattisson *et al*. 2013) and, so far, there is only one confirmed observation of intraspecific killing among collared Scandinavian wolves (Liberg *et al*. 2008; Wabakken *et al*. 2009). The age of the male was more important than the age of the female for explaining variation in wolf pair bond duration (Table 3). This could be explained by the fact that males tend to have a generally lower survival rate than females in the population (Liberg *et al*. 2008). In another study, males also showed body mass to decline after approximately 5 years, which could be explained by intense intrasexual competition between males causing weak selection for male longevity (MacNulty *et al*. 2009).

CONSEQUENCES OF WOLF PAIR DISSOLUTION

In a socially monogamous species, the maintenance of the family-based social structure can have important fitness benefits associated with the adaptive evolution of kinship (Lukas & Clutton-Brock 2013). For instance, pair bond duration (Sánchez-Macouzet, Rodriguez & Drummond 2014) and the presence of helpers (Sparkman *et al*. 2011) can have positive effects on reproductive success.

Moreover, wolf breeder loss can result in lower pup survival, abandonment of territories, dissolution of social groups (Brainerd *et al*. 2008) or unusual behaviour such as incestuous mating (Vonholdt *et al*. 2008). Although the impact of wolf pair dissolution on population growth is context-dependent (Brainerd *et al*. 2008; Borg *et al*. 2015), the high dissolution rate observed in our study suggests that extrinsic factors (i.e. anthropogenic) could have an impact on the recolonization of the population and would deserve further attention (Liberg *et al*. 2011). While consequences of human impact on populations usually focuses on numerical response (i.e. population size estimates; but see Rutledge *et al*. 2010), we provided quantitative estimates of anthropogenic influence on the dynamics of the social unit of the population, the wolf pair. Additionally, intrinsically linked population factors, such as the high levels of inbreeding observed in this population, also negatively affect the duration of wolf pair bonds and may contribute to inbreeding depression. The mechanisms behind this result are still unclear and further research could help to distinguish whether inbreeding could act on the divorce rate of pairs or lower the survival of highly inbred males. Identifying sources of spatial variation on estimates of fitness related measures, such as pair bond duration, is strongly needed to understand how intrinsic and extrinsic population factors interact to shape the demography of large carnivore populations. This type of information is also essential to provide appropriate recommendations for a conservation-oriented management (Falcucci *et al*. 2009; Gaillard *et al*. 2010).

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Data accessibility

Data available from Dryad Digital Repository http://dx.doi.org/10.5061/dryad.242t8 (Milleret *et al*. 2016).

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Supporting Information

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

Appendix S1. Summary of winter tracking efforts.

Appendix S2. Expanded methods description

Appendix S3. Coefficient of correlation between highly correlated covariates ($r > 0.60$).

Appendix S4. Test of the robustness of the centroid and buffer method.

Appendix S1

We summarized minimum tracking efforts performed each winter during the study period (Wabakken *et al.* 1999; Wabakken *et al.* 2012). These are minimum estimates because only tracking events (actually following a track) were reported. Tracking effort and some opportunistic tracking events were performed and not reported. The lower values for 2003/2004 and 2009/2010 winters correspond to a lack of reporting of kilometers tracked for all tracking events that had occurred in Sweden. For all other winters, kilometers (kms) tracked were recorded for both Sweden and Norway.

Table S1 Tracking efforts for each winter

Winter	Minimum kms tracked
1998/1999	2600
1999/2000	2266
2000/2001	3305
2001/2002	3137
2002/2003	2165
2003/2004	501
2004/2005	3328
2005/2006	3732
2006/2007	4291
2007/2008	3560
2008/2009	5487
2009/2010	436
2010/2011	4938
2011/2012	2411

Appendix S2

To explore the influence of spatial variation in the stability of wolf pair bonds, we used a set of maps describing the large scale spatial characteristics of their territory. We created static maps and time-series grid maps with a fine scale resolution (200m × 200m) for every spatial descriptor (Table 1).

Construction of the spatial variables

Human density was estimated as the number of inhabitants per km^2 in each municipality. We used the density of gravel and paved roads (Basille *et al.* 2013; Mattisson *et al.* 2013; Zimmermann 2014) as an index of anthropogenic impact in terms of human accessibility. First, we obtained and merged national road maps from Sweden and Norway (Mattisson *et al.* 2013; Zimmermann 2014). Then we calculated the total length of paved and forest roads in km per km^2 for each map pixel (Zimmermann 2014). To identify areas that were both highly accessible by humans yet remote, we combined information on the spatial location of roads and buildings. Spatial location of buildings (distinction between inhabited and uninhabited could not be made) within settlement areas were availabi.e.,le for Sweden, but not for Norway. Therefore, we calculated the mean number of buildings per km^2 in Swedish settlements (i.e., 450/km^2) and randomly generated building densities within Norwegian settlements (i.e. minimum density allowed by definition of Norwegian settlements areas = 400 buildings/km^2 http://www.ssb.no) at the same density as observed for Sweden. We then counted the number of buildings per km of road, within a 500m radius buffer zone along each road stretch. A 500 m buffer was chosen to make sure that most of the buildings identified fell within our buffer. For each wolf territory, we calculated the percentage of area available that was both highly accessible yet remote, defined as the area containing <2 buildings per km of road. This covered 25% of the total area occupied by wolf territories.

Wolf depredation

Livestock depredation is one the most important causes of human-large carnivore conflicts (Herfindal *et al.* 2005). In Norway, we used records of wolf depredation events (both ’confirmed‘ and ’supposed‘) concerning sheep (http://www.rovbase.no). In Sweden, we used records of depredation events (https://www.rovdjursforum.se/) in which investigation led to the cause of damage (“besiktigad skadeorsak”) being confirmed, with at least 50% certainty as a carnivore attack and the depredator species being confirmed with at least 50% certainty, as a ’wolf‘. However, the two countries have different sheep farming practices; in Norway sheep are largely left to graze unattended and are free-ranging during the summer grazing season (Zimmermann, Wabakken & Dötterer 2001), while in Sweden sheep are generally kept fenced in and are therefore more protected from predation (Dahle *et al.* 1998). Since we were only interested in the spatial distribution of depredation events and "hot-spot" areas within both countries (independent of the number of attacks in each country) we computed separate maps for Sweden and Norway. We used a kernel density estimator (Worton 1989) to estimate the relative spatial density of all recorded wolf depredation events on sheep during the period 1998-2012, using an average smoothing parameter (h) for each country. Then, we re-scaled values to fall between 0 and 1 by dividing each value obtained by the maximum value observed. This allowed us to conserve the relative intensity of hot-spots depredation areas in each country before merging the two maps.

Wolf attacks on hunting dogs are also an important source of conflicts in Scandinavia (Liberg *et al.* 2010). We used all spatial locations of fatal dog attacks recorded in Sweden and Norway from 1998-2012, and a kernel density estimator (using the ’href‘ method) to create a relative spatial density of wolf attacks on dogs.

Appendix S3

Table S3 shows Spearman coefficient of correlation between highly correlated covariates (r > 0.60). Predictor variables used to run the final models were selected based on the best AICc score, and are shown below in bold. See Table 1 for variable descriptions.

Variables	Variables	r
LocNorth	Road1	-0.78
LocNorth	**RoadBuild**	0.74
LocEast	Road2	0.63
Road1	**RoadBuild**	-0.78
Road1	Hum	0.74
RoadBuild	Hum	0.59

Appendix S4

We tested the robustness of the centroid and buffer methods used to extract geographical landscape characteristics for each territory. Although we performed extensive winter tracking of wolf pairs, we still had uncertainty in the exact home range boundaries. To test whether this could have influenced the values of the extracted landscape characteristics, we randomly added some noise (mean=7.5km, SD=2.5) to the centroid coordinates (i.e., for both X and Y coordinates). This resulted in the creation of new buffers that overlapped, on average, 51.3% (range = 1.5-99%) with the observed buffers. This degree of overlap was in accordance with estimates of inter-annual variability in space use by wolves at the territory level, found in other systems (Uboni *et al.* 2015). We then re-extracted all landscape characteristics as described in the methods section and Table 1 of the main text, and recomputed model selection and model averaging. We repeated this process 100 times and we present the mean Hazard ration and 2.5% and 97.5% quantiles in the Table S4 from all simulations obtained. Hazard ratios obtained using the observed centroid location (Table 3 main text) fall within the 2.5-97.5% quantiles hazard after adding some noise to the centroid location. This shows that errors in the location of the centroid, and the way we determined the landscape characteristics (buffer of 1000km^2), likely had no influence on our results.

Table S4. Mean, 2.5% and 97.5% quantile hazard ratio (HR) obtained from the model averaging of the 100 simulations after random noise was added to the X and Y coordinates of the centroid points for each wolf territory. The column HRo shows the HR estimates obtained using the observed centroid locations (see Table 3 main text)

Parameter	Mean HR	2.5	97.5	HRo
LocCore	1.31	1.27	1.42	1.30
LocEast	0.81	0.79	0.84	0.82
Age_M	1.29	1.28	1.31	1.30
F_male	1.33	1.29	1.35	1.35
Age_F	1.17	1.16	1.18	1.16
Moose	1.05	0.97	1.12	1.05
F_female	0.98	0.96	0.98	0.98
Density	1.12	0.98	1.24	1.03
F	1.05	0.97	1.12	1.04
RoadBuild	0.97	0.89	1.05	0.97

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Paper III

Milleret, C., Chapron, G., Andreassen, H. P., Åkesson, M., Liberg, O., Sand, H., and Wabakken, P. Using an integrated population model to infer the impact of culling mortality and pair dissolution on wolf population dynamics. *Manuscript.*

Using an integrated population model to infer the impact of culling mortality and pair dissolution on wolf population dynamics

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Abstract

The consequences of human exploitation, for example through culling, on population growth of socially-living species are complex because not all individuals contribute equally to population dynamics. Therefore the extent to which the effect of culling is compensatory and/or additive is complex to disentangle. Here, we used the grey wolf (*Canis lupus*), a social large carnivore, as a model species. We specifically estimated the degree to which culling (i.e. caused by legal human harvest) and wolf pair bond dissolution (i.e. the functional unit of the wolf population) affected wolf population dynamics. We used data from the long-term monitoring of the Scandinavian wolf population collected every winter from 1998/1999 to 2014/2015. We constructed a Bayesian Integrated Population Model (IPM) that linked multiple sources of information such as, population counts, individual capture-recapture using non-invasive DNA methods, and dead recovery to simultaneously estimate population trajectory and demographic parameters. Wolf pair bond dissolution, and especially dissolutions that were not followed by a replacement, tended to have a negative effect on the growth of the population. Our IPM revealed that this could have been caused by a decrease in territorial and non-territorial survival, as well as by a decrease in pup recruitment. We did not detect any effect of culling rate measured as the proportion of culled individuals

(territorial and/or non-territorial) in the population. There was also a high temporal variability of pair bond dissolution due to *other* causes that interacted in an unpredictable way with dissolution due to *culling*. If pair bond dissolution rate due to *other* causes can be transposed to individual mortality, this could explain why we did not detect any effect of culling mortality. Indeed, dissolution rate due to *other* causes was sometimes lower, higher or at similar rate than culling dissolution rate. Therefore, we suggest that management actions should be directed at wolf pairs because their stability was a better predictor of population growth than individual culling mortality rate. Due to the importance of wolf pairs for population dynamics, we also suggest that more focus should be given to the stability of the functional unit of socially-living species.

1. Introduction:

A fundamental goal of population ecology is to identify drivers explaining variation in population dynamics. Inter-individual variation in demographic rates (e.g. linked to sex, age or stage classes) can have strong impact on population dynamics (Caswell 2001). As a result, mortality of specific individuals may have larger consequences on population dynamics compared to mortality of other individuals (Coulson et al. 2006). Since human harvest may be a major driver of population dynamics, it is essential to understand how exploited species may respond to variation in harvest rates and harvest selection of specific age and sex groups, especially from a conservation and management perspective.

While harvest mortality may have a direct impact on the population by removing an individual that could carry benefits (e.g. by reproducing) to the population, it may also have more complex and indirect impact on demographic rates. For instance, harvest can disrupt the sex and age structure of a population which can in turn affect reproductive rates (Milner et al. 2007). Harvest mortality can also be compensatory (i.e. harvest doesn't affect overall survival through density-dependence mechanisms and/or heterogeneous individual survival) rather than additive (i.e. survival decrease proportionally with harvest) (Burham and Anderson 1984, Lebreton 2005, Sandercock et al. 2011). In addition, harvest has been shown to have a negative effect on populations by interacting with sexually selected infanticide (Gosselin et al. 2015), facilitating hybridization with other species (Rutledge et al. 2012) or by affecting animal behavior which can also influence their reproductive success and survival (Tolon et al. 2012).

For species living in social groups the consequences of harvest mortality may be especially complex. The family-based social structure has important fitness benefits associated with the adaptive evolution of kinship (Lukas and Clutton-Brock 2013). In the social group, the breeding individuals play an important role in group cohesion (Borg et al. 2014), feeding efficiency (Sand et al. 2006), and offspring survival (Brainerd et al. 2008). The presence of helpers (usually older siblings) has also been associated with an increase in the fitness of offspring (Sparkman et al. 2011a). As a consequence, individuals living in social groups have hetereogeneous reproductive values that are essentialy skewed towards specific individuals. It may therefore be challenging to quantify the effect of individual mortality for species living in social groups. For instance, mortality of breeding individuals could disproportionaly affect population dynamics, by removing a potential breeding opportunity, or by reducing survival of dependent offspring (Brainerd et al. 2008, Borg et al. 2014). In contrast, the mortality of non-breeding group members may only have mariginal effects on population growth. Similarly, the timing of the mortality event or the removal of breeding individuals, resulting in an almost instant replacement of the individual(s) in the group could limit the impact of mortality on population growth (Brainerd et al. 2008, Borg et al. 2014). The inherent complexity in the dynamics of group living species makes it more difficult to predict the actual effect of individual mortality on population growth rate (Borg et al. 2014).

The wolf (*Canis lupus*) is a social species, typically living in family groups (i.e. the breeding pair and their offspring), that has undergone much human persecution, though it is now recovering in areas where it was previously extirpated, such as in Europe (Chapron et al. 2014). Still, wolves are often subjected to strong harvest mortality aimed to control their expansion and reduce conflicts with humans. Several studies have focused on this social species as a case study to explore the effect of harvest mortality on population dynamics. However, the effect of harvest mortality and/or breeder mortality on population growth remains largely unclear. While some studies have claimed that wolf harvest mortality could be to a large extent compensatory (Mech 2001, Fuller et al. 2003, Murray et al. 2010), others have claimed that harvest mortality could be mainly additive (Creel and Rotella 2010, Creel et al. 2015) and even super-additive (Creel and Rotella 2010). The compensatory mechanism to harvest loss was suggested to occur through the resilience of social species to disruption (Borg et al. 2014) or through density-dependent changes in natality, age at maturity, survival or movements (Burham and Anderson 1984, Nichols et al. 1984, Lebreton 2005). On the other hand, a super-additive effect would suggest that harvest mortality increases total mortality beyond the effect of killing itself, through social disruption or the loss of dependent offspring. In this respect, there is a strong need for better quantification of the demographic effects of species-specific harvest, and for disentangling the mechanisms influencing population growth of harvested species, especially for conservation and management persperctives.

Here, we used the Scandinavian wolf population as a case study to investigate the effect of harvest mortality on the population growth of a social species. The wolf naturally recolonized Scandinavia in the early 1980's (Wabakken et al. 2001) and the population size was estimated to be approximately 365 individuals (95% CI: 300-443) in the winter 2014/2015 (Chapron et al. 2016). The population has been continuously monitored through a combination of snow-tracking, radio-tracking and genetic identification, including maintaining a near complete pedigree of the population since founder event (Liberg et al. 2005, Liberg et al. 2012, Åkesson et al. 2016). The detailed demographic and genetic knowledge of the Scandinavian wolf population and the significantly large proportion of human-caused mortality (Milleret et al. 2016) offer a good opportunity to study the consequences of culling mortality on this population. In both Sweden and Norway, protective hunt have been occasionally performed. In January 2010, a license hunt was initiated in Sweden where 28 wolves were legally shot. The hunt was re-conducted in 2011, 2015 and 2016 where 19, 44 and 14 wolves were legally shot, respectively. We further used the term culling as any legal action that directly resulted in wolf mortality.

Our understanding of the forces driving population dynamics is generaly limited by the sample size and uncertainty around field collected data. For example, calculation of demographic rates such as population growth rates, requires that population size is estimated at different time intervals. However, counting individuals is not always trivial, especially not when the species is as elusive as the wolf (Chapron et al. 2016). In order to estimate demographic parameters from the Scandinavian wolf population, we developped a Bayesian Integrated Population Model (IPM) (Kery and Schaub 2011, Schaub and Abadi 2011). The state-space formulation of the IPM allows us to disentangle the demographic process from the noise around the observation process. This kind of model has the advantage of making use of information from multiple datasets. We used an IPM to link population counts and individual capture history, collected through non-invasive DNA sampling. Using this model, we aimed to significantly improve our understanding of the population dynamics of the wolf in Scandinavia, which may also be applied to other social species. More specifically, we predicted that culling mortality had a negative effect on population growth (Creel et al. 2015), especially with increasing culling mortality of breeding individuals. Culling mortality is expected to be a poorer predictor of growth rate than traits more closely linked to the fate of the functional unit of the population, i.e. the reproducing pairs (Milleret et al. 2016). Therefore we also investigated how wolf pair stability (i.e. quantified as pair bond dissolution rate, Milleret et al. 2016) could affect the growth of the population.

Our IPM may help us to isolate the mechanisms, by which culling and pair dissolution rate affect the growth of the population, for territorial wolves as well as non-breeders. So far, analyses of the effect of harvest mortality rate have mainly been conducted across different populations (Fuller et al. 2003, Adams et al. 2008, Creel and Rotella 2010, Murray et al. 2010). Even if general patterns can be inferred from comparisons across populations, heterogeneity among, and temporal variation within study sites could potentially mask the effects of culling mortality on population growth rate. Therefore, we also determined how temporal variation in culling mortality may interact with other mortality causes and tested whether culling was mainly compensatory or additive in this population.

2. Material and Methods

2.1. Wolf monitoring

The main goal of the winter monitoring program of wolves in Scandinavia (Sweden and Norway) was to maintain a pedigree of the population, identify territorial pairs and reproduction events, and provide population size estimates (Liberg et al. 2012). Each winter (October 1st - April 1st), a combination of snow-tracking, genetic sampling, and radio telemetry allowed for the identification of individuals and territorial pairs (Liberg et al. 2012). We identified territorial pairs (i.e. pairs of 2 potential breeders that have not reproduced yet) that were typically <2 years old, or in packs (i.e. pair of 2 breeders with at least one offspring). This resulted in the re-construction of a near complete pedigree of the population (see Liberg et al. 2005, Åkesson et al. 2016). Between winter 1998/1999 and winter 2014/2015, the size of the population has steadily increased (Chapron et al. 2016). The genetic identification from non-invasive samples using methods described in Åkesson et al. (2016), allowed for the construction of an individual capture history from 1339 individuals during the period (May 1st 1998- April 30th 2015). The detailed knowledge obtained for this population from different data sets (counts of individuals and individual capture history) offer good opportunities to combine the different datasets in an integrated population model in order to gain insights into Scandinavian wolf population dynamics.

2.2. The integrated population model

The construction of our integrated population model consisted of several steps. First, we needed a model linking population counts and demographic rates. Second, we needed to formulate specific likelihoods from different datasets. In our case, we wrote the likelihood of a capture-recapture data set and likelihoods of different population counts. Finally, we formulated the joint likelihood of all data sets. Figure S1 represents the conceptual representation of our integrated population model.

Step 1 the population process model

Our integrated population model linked population counts and demographic rates using a female-based, post-breeding, stage-structured population Leslie matrix (Caswell 2001). We created a post-breeding Leslie matrix in an attempt to represent as closely as possible the complex life history characteristics of a social-living species such as the wolf (Chapron et al. 2016). We used a Leslie matrix with four different stages: 1) new born (Nb), 2) transients (Tr), 3) pair member individuals, 4) pack member individuals (Figure 1). The model is formalized as $N_{i+1} = AN_i$ where N_i and N_{i+1} are, respectively, vectors of abundance in each stage at time i and $i + 1$ and A is the projection matrix representing a simplified wolf life cycle:

$$A = \begin{bmatrix} 0 & f.\varphi_{NT}.\psi.P_{repro} & f.\varphi_T & f.\varphi_T \\ \varphi_{NT} & \varphi_{NT}.(1-\psi) & 0 & 0 \\ 0 & \varphi_{NT}.\psi.(1-P_{repro}) & 0 & 0 \\ 0 & \varphi_{NT}.\psi.P_{repro} & \varphi_T & \varphi_T \end{bmatrix}$$

where φ_{NT}, φ_{T}, ψ, P_{repro} are the survival of the non-territorial individuals (NT; i.e. new born and transients), territorial individuals (T; individuals in pairs or packs), the probability to reach the territorial stage, and probability that an individual in a pair reproduces the first year, respectively. The productivity rate is denoted as f, i.e. the number of young produced by a female. Because of the lack of knowledge of the exact stage of each individual when genetically captured (see below), we did not differentiate between new born and transient survival rates. We only distinguished between territorial (in pairs and packs) and non-territorial survival. All parameters present in the matrix were estimated in the IPM, except the probability that a pair reproduce the first year (P_{repro}). We used a prior following a Normal distribution with mean equal to 0.79 and SD equal to 0.05 (Chapron et al. 2016).

For the number of new born individuals (N_{Nb}), we chose a Poisson distribution:

$$N_{Nb,i+1} \sim Pois(f.(\varphi_{\mathrm{NT}}.\ \psi.P_{repro}.N_{tr,i} + \varphi_{\mathrm{T}}.N_{pairs,i} + \varphi_{\mathrm{T}}.N_{packs,i}))$$

We used a Binomial distribution for the number of new transients (N_{Tr1}) and transients remaining transients at time *i+1* (N_{Tr2}). The sum of N_{Tr2} and N_{Tr1} gives the total number of transient individuals(N_{Tr}).

$$N_{Tr1,i+1} \sim Bin(N_{Nb,i}\,, \varphi_{\mathrm{NT}_i})$$

$$N_{Tr2,i+1} \sim Bin(N_{Tr1,i}\;, (1-\psi_i))$$

$$N_{Tr,i+1} = N_{Tr1,i+1} + N_{Tr2,i+1}$$

For the number of individuals in pairs (N_{pairs}), we used a Binomial distribution:

$$N_{pairs,i+1} \sim Bin(N_{Tr,i}\;, \varphi_{NT_i}.\psi_i.(1-P_{repro}))$$

We used a Binomial distribution for the number of transient individuals becoming a pack member (N_{packs1}), the number of individuals in pairs becoming a pack member ($N_{packs\,2}$), and the number of individuals surviving as a pack member (N_{packs3}). The addition of N_{packs1}, N_{packs2}, N_{packs3}, gives the total number of individuals in packs (N_{packs}).

$$N_{packs1,i+1} = (1 - N_{pairs,i+1})$$

$$N_{packs2,i+1} \sim Bin(N_{pairs,i}\;, \varphi_{T_i})$$

$$N_{packs3,i+1} \sim Bin(N_{packs,i}\;, \varphi_{T_i})$$

$$N_{packs,i+1} = N_{packs1,i+1} + N_{packs2,i+1} + N_{packs3,i+1}$$

The sum of N_{packs}, N_{pairs}, N_{Tr}, N_{Nb} gives the total number of individuals in the population (N_{tot}). There was a mismatch between the timing of our population counts (monitoring: January 1st, see below) and results of the projection of the Leslie matrix (post-breeding equals to May 1st). We therefore adjusted our population size estimates obtained from the Leslie Matrix in order to fit the data from the monitoring program. Since we used annual survival estimates, we applied a Binomial distribution with the survival parameters of each stage to obtain population size estimates in January ($Njan$). We used the parameters (φ, ψ) at the power of $\frac{7}{12}$ which represents, for example for the survival parameters, individuals surviving 7 months from 1st May to 1st January. This set of equations describes the population process. To estimate parameters of the model for this population, we had to define the likelihoods of the different data sets.

Step 2 the population counts model

Using a state-space formulation, we modelled three separate population count data sets that were performed each winter and represented the state of the population at approximately January 1st (Chapron et al. 2016). First, we modelled the number of family groups ($Nobs_{pack}$; i.e., typically a pair ≥ 2 years old which has already reproduced, so with ≥ 3 individuals composing the pack) which is the highest priority of the monitoring program. Parentage analyses from DNA genotypes (Åkesson et al. 2016) reveal that most individuals (>98%) are offspring to parents that have been confirmed as a territorial pair (Chapron et al. 2016). This strongly suggests that missing packs in the count are relatively rare. Second, we used the count of territorial pairs ($Nobs_{pair}$; typically a pair <2 years old). According to Anon (2015), more than 88% of the pairs that reproduced for the first time were already confirmed as a pair the year prior to reproduction. Third, we used the minimum ($Nobs_{min}$) number of individuals counted during tracking events for each pack, as an estimation of the number of new born individuals. The number of individuals counted in the pack was used as an estimate of the number of reproductions (Liberg et al. 2012). To confirm a reproduction for packs (territorial pairs that have already reproduced), a minimum of 5 animals counted in different tracking occasions was necessary. Therefore, on each tracking occasion, the minimum number of individuals counted was noted and used as the minimum number of individuals composing the pack. The minimum number of individuals counted minus two (for the two breeders) gives an estimation of the number of non-breeders in each pack i.e. pups (termed new born in our IPM) and yearlings, that have survived until January, which did not disperse and are still present in the pack. In most cases this count represents the minimum number of non-breeders, therefore it is likely an underestimation of the true number of new born pups. However, yearlings are also included in the count which may be similar to double counting new borns. We therefore assumed that the true number of newborn individuals was just as likely to be larger, as it was to be smaller than the counted number of offspring in the pack.

For all count datasets, except for the number of observed packs ($Nobs_{pack}$), the number of wolves at time *i* (*Nobs*) was Poisson-distributed with a rate $\mathit{\Gamma}_t$ Gamma-distributed having itself a mean equals to the prediction of the process model and an SD for observation error. This allowed the uncertainty in the data to exceed the variance of the Poisson parameter ψ_t (Liberg et al. 2011)

$$\alpha_i = \frac{N_i^2}{\sigma_{Nobs}^2}$$

$$\beta_i = \frac{N_i}{\sigma_{Nobs}^2}$$

$$\mathit{\Gamma}_i \sim Gamma\ (\alpha_i\ , \beta_i)$$

$$Nobs_i \sim Poisson\ (\mathit{\Gamma}_i)$$

Since our count data of the number of reproductive packs showed a low apparent number of missing packs, we assumed that the number of packs was normally distributed, with a variance ($\sigma_{Nobs_{pack}}^2$) small enough to minimize the error around the $Nobs_{pack}$ to approximately ±2 packs annually.

The observation process was then linked to the state process (i.e. Leslie population model). The likelihood for the different population counts were written as such:

$$LPS_{pack}\left(\boldsymbol{Nobs_{pack}} \middle| \boldsymbol{Njan_{pack}}, \varphi_T, \varphi_{NT}, \psi, P_{repro,}\ \sigma_{Nobs_{pack}}^2\right) =$$

$$Lobs_{pack}\left(\boldsymbol{Nobs_{pack}} \middle| \boldsymbol{Njan_{pack}}, \sigma_{Nobs_{pack}}^2\right) * L_{Spack}\,(\boldsymbol{Njan_{pack,}}\boldsymbol{Njan_{pair,}}\boldsymbol{Njan}_{,}|\varphi_T, \varphi_{NT}, \psi, P_{repro})$$

$$LPS_{pair}\left(\boldsymbol{Nobs_{pair}} \middle| \boldsymbol{Njan_{pair}}, \varphi_T, \varphi_{NT}, \psi, P_{repro,}\ \mathit{\Gamma}_{pair}\right) = Lobs_{pair}\left(\boldsymbol{Nobs_{pair}} \middle| \boldsymbol{Njan_{pair}}, \mathit{\Gamma}_{pair}\right) *$$

$$L_{Spair}\,(\boldsymbol{Njan_{pair}}|\varphi_T, \varphi_{NT}, \psi, P_{repro})$$

$$LPS_N(\boldsymbol{Nobs_{min}}|\boldsymbol{Njan_{Nb}}, \varphi_T, \varphi_{NT}, \psi, f, P_{repro,}\ \mathit{\Gamma}_{min}) = Lobs_{pair}(\boldsymbol{Nobs_{min}}|\boldsymbol{Njan_{Nb}}, \mathit{\Gamma}_{min}) *$$

$$L_{SNtot}\,(\boldsymbol{Njan_{Nb}}|\varphi_T, \varphi_{NT}, \psi, P_{repro}, f)$$

Step 3 the demographic model

We constructed a ‘genetic capture history’ (CH) for each detected individual by grouping observations within a 1 year period from May 1st (i.e. after reproduction) and April 30th. Specifically, we could distinguish individuals captured as non-territorial, territorial, and found dead. If an individual was found in two different stages within one year, we categorized the stage of the individual using information collected from his last observation. We created a multistate capture-recapture model for the joint analysis of capture-recapture (non-invasive DNA capture) and dead recovery data. Dead recovery data included the genetic identification of individuals that were occasionally found dead and legally culled. Our model had 4 states: 'alive, and non-territorial', 'alive, and territorial', 'recently dead' and 'dead'. Individuals in the state 'alive, non-territorial' can move to the state 'alive, territorial' given they have survived in the non-territorial state (φ_{NT}) with a probability ψ. The state *'recently dead'* is necessary because only individuals recently dead can be recovered (Kery and Schaub 2011). Our survival estimates should be considered as apparent survival. However, because our model includes dead recoveries and the Scandinavian wolf can be considered as a functionnaly closed population, the influence of emigration on our apparent survival estimates can be considered to be marginal (Liberg et al. 2011). We estimated sex-specific survival for territorial individuals, and we assumed no sex differences in survival for non-territorial individuals, in order to use data for individuals that were captured once but where the sex could not be identified. State transition probabilities are defined in the following matrix (row, states of departure; column, states of arrival).

$$\begin{array}{c} \text{alive, non territorial} \\ \text{alive, territorial} \\ \text{recently dead} \\ \text{dead} \end{array} \begin{bmatrix} \varphi_{NT} * (1-\psi) & \varphi_{NT} * \psi & 1-\varphi_{NT} & 0 \\ 0 & \varphi_{T_{sex}} & 1-\varphi_{T_{sex}} & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

Observation probabilities such as probability of capture (P_{NT} and P_T) and probability to find and report a dead individual (P_{FD}) are defined in the following matrix (row: state; column: observation). We also estimated different probabilities of capture according to the country (Norway/Sweden) in which the sample was collected in order to account for differences in the sampling (monitoring) regime.

$$\begin{array}{r|cccc|} \text{alive, non territorial} & P_{NT_{country}} & 0 & 0 & 1-P_{NT_{country}} \\ \text{alive, territorial} & 0 & P_{T_{country}} & 0 & 1-P_{T_{country}} \\ \text{recently dead} & 0 & 0 & P_{FD} & 1-P_{FD} \\ \text{dead} & 0 & 0 & 0 & 1 \end{array}$$

A time effect was used on all parameters to obtain temporal variability of φ , P, and ψ probability estimates. We used a multinomial likelihood to relate the data with φ , P, and ψ probability. The likelihood was:

$$L_{CR}(\boldsymbol{CH}|\varphi_{NT},\varphi_{T},\psi,P_{NT},P_{T},P_{FD})$$

Step 4 Productivity

We did not have access to annual productivity (f) data. However, an important advantage of integrated population models is that they may be used to estimate demographic parameters for which we have no explicit data available (Kery and Schaub 2011). This is possible because the population counts provide information about demographic parameters. However, productivity is not completely unknown in this population. Indeed, counts of pups at den (~ 3 weeks old) have been performed in this population and we gave the same informative prior (mean=5 pups, SD=0.52), following a normal distribution (Chapron et al. 2016).

Step 5 the joint likelihood

The independence of the datasets (i.e. that no animals in the count data may occur in the capture-recapture data) should be an assumption of the model (Schaub and Abadi 2011). However, this assumption is rarely met in practice, since we often only have demographic data from single and sometimes small populations. If independence assumptions are violated, as in the case of our study, precisions of the estimates are likely to be over-estimated. However, Abadi et al. (2010) found that there was almost no effect of dependency between datasets on parameter accuracy, especially with large sample size (e.g. >200 individuals). We therefore wrote the joint likelihood as the product of the component likelihoods:

$$L_{IPM}(\boldsymbol{Nobs_{min}}, \boldsymbol{Nobs_{pair}}, \boldsymbol{Nobs_{pack}}, \boldsymbol{CH} | Njan_{pack}, Njan_{pair}, Njan_{pack}, \varphi_{NT}, \varphi_{T}, \psi, f, P_{T},$$

$$P_{NT}, \Gamma_{pair}, \Gamma_{min,} \sigma^2_{Nobs_{pack}}) =$$

$$LPS_{pack}\left(\boldsymbol{Nobs_{pack}} \middle| \boldsymbol{Njan_{pack}}, \varphi_{T}, \varphi_{NT}, \psi, P_{repro,}\ \sigma^2_{Nobs_{pack}}\right) \text{ x}$$

$$LPS_{pair}\left(\boldsymbol{Nobs_{pair}} \middle| \boldsymbol{Njan_{pair}}, \varphi_{T}, \varphi_{NT}, \psi, P_{repro,}\ \Gamma_{pair}\right) \text{ x}$$

$$LPS_{N}(\boldsymbol{Nobs_{min}} | \boldsymbol{Njan_{Nb}}, \varphi_{T}, \varphi_{NT}, \psi, f, P_{repro,}\ \Gamma_{min}) \text{ x}$$

$$L_{CR}(\boldsymbol{CH} | \varphi_{T}, \varphi_{NT}, \psi, f, P_{T}, P_{NT}, P_{FD})$$

2.3. Culling mortality rate

Legal harvest occurred regularly through protective and license hunting in Sweden and Norway (Chapron et al. 2016). All legally culled wolves were genetically identified and their status (non-territorial or territorial individuals) was identified at their time of death using winter monitoring data and pedigree. We estimated total culling mortality rate at time *t* using the number of wolves that were known to have died from culling causes between time *i* and time *i + 1* ($M_{i \rightarrow i+1}$). Our time step was set from May 1st to April 30th.

The conventional way of calculating mortality rate is to divide the number of individuals that were known to have died from culling between time *i* and time *i + 1* ($M_{i \rightarrow i+1}$) by number of individuals N_i (i.e. m_{1i}=. $M_{i \rightarrow i+1}/N_i$) estimated from monitoring data. However, this approach assumes that N_i is estimated very shortly after reproduction. This does not hold for most populations (including this one) because counts of population size usually occur during winter (i.e. approximately January 1st in our case, i.e. so 7 months after reproduction). Consequently, M_i would be overestimated using this method because it does not include wolves < 6 months old that are also at risk of being killed. We therefore used the estimated population size obtained from our integrated model which provided population size estimates (N_i) shortly after reproduction ($Njan_{tot}$; post-breeding Leslie matrix). Harvest mortality of territorial individuals may have stronger consequences for population dynamics than mortality of non-territorial individuals. Therefore, we calculated three mortality rates in the integrated population model using: 1) only individuals that were known to be territorial individuals (MT_i), 2) non-territorial (MNT_i), 3) and all individuals (M_i; Territorial + Non-Territorial) at the time of death.

2.4. Quantifying wolf pair dissolution rate

Another data set that was built using a combination of information from physically captured individuals (GPS collared individuals), winter snow tracking and genetic identification of wolf territorial individuals was used to estimate winter to winter pair dissolution rate (see Milleret et al. 2016 for further details). We observed whether a wolf pair (i.e. including potential breeders from a territorial pair, or breeders from a pack) that was detected at winter *i* (October 1st - April 1st) could still be detected at winter *i+1*. A pair dissolution event occurred when no signs of one or both individuals were found within their confirmed previous-winter territory. Pair dissolution could be due to culling and other causes i.e., natural, poaching, traffic or unknown (dissolution was observed without knowing the cause). The next winter following a dissolution event (*k*), there could be 1) a turnover (i.e. replacement) of one or both individual in the territory (Figure 2 a), or 2) no replacement (i.e. no territorial pair was detected within the territory previously occupied by the pair, Figure 2 b). These two alternative outcomes are likely to have different consequences for population dynamics. For instance, compared to cases were no replacement occurred, the quick replacement of an individual within a pair could have limited consequences for subsequent reproductive success, or survival of offspring (Brainerd et al. 2008, Borg et al. 2014). We therefore estimated, on an annual basis, the frequency of occurrence of each of these two events following dissolution due to culling or other causes. We reset the start of our wolf-pair survival data each winter *i* and checked whether one of the two events (*k*) occurred after dissolution due to culling or other causes (*j*) from time *i* to time *i+1*. We then used the 1-KM method (which is the complement of the Kaplan-Meir method) to estimate the probability of the events to occur at each time step in the presence of competing risks

(Tai et al. 2001). This approach consists in estimating cause-specific mortality, in our case-specific events following pair dissolution (jk), by treating all events, except those of interest, as censored events. We estimated the frequency of occurrence of each of these events in Bayesian:

$$nb.\,events_{jk} \sim Bin(q, R)$$

$$q \sim Beta(0.001, 0.001)$$

Where R is the number of pairs at risk of dissolution and *nb.events*, the number of *jk* events observed at time *i.* The alpha and beta parameters were set to 0.001 (because they must be positive and cannot be 0) to obtain a non-informative prior bounded between 0 and 1.

2.5. Effect of culling mortality and pair dissolution rate on growth and demographic parameters

We derived the growth rate estimates ($lambda_i = Ntot_{i+1} / Ntot_i$) in the IPM for May 1st (post-breeding Leslie Matrix) and for January 1st (date at which the count data are valid). As a measure of variation of recruitment rate (number of new born, *Nb*), we also derived a growth rate for the new born such as $lambda_{Nbi} = Nb_{i+1}/Nb_{i.}$ However, the growth rate was a derived parameter of the IPM. Therefore, it was not possible to estimate the effect of pair dissolution and culling mortality rate on the growth rate directly within the IPM. We circumvented this issue by performing a linear regression using the posterior distribution of the lambda obtained with the IPM. We then used the median and 2.5% and 97.5% quantiles of the slope to assess the effect of culling mortality and pair dissolution rate on the growth rate. The resulting estimates can then be interpreted in the same way as a slope in a usual regression. We used the same method to identify how demographic parameters ($\varphi_{NT}, \varphi_T, \psi, f$) were affected by culling and pair dissolution rate. We used $lambda_{January}$ to test for the effect of pair dissolution (available on a winter to winter basis) and $lambda_{May}$ to test for the effect of culling rate.

2.6. Additivity/compensatory effect of harvest mortality rate

The equation $S_a = S_o(1 - bK)$ describes the relationship between annual survival (S_a) and harvest mortality (*K*), where S_o is the baseline survival rate in the absence of harvest and b is a slope coefficient linking culling mortality to annual survival (Lebreton 2005, Sandercock et al. 2011). Under additive culling mortality, the effect of culling directly reduces annual survival (*b*=1) while a super-additive effect would cause additional mortality (*b*>1). On the other hand, a compensatory effect of mortality should have no effect on annual survival (*b*=0), up to a threshold. A partially compensatory effect would result in $0< b <1$. We therefore performed a linear regression of annual survival rate on annual harvest mortality rate (MT and MNT) and used the slope of the regression to assess the effect of culling mortality on survival rates. We estimated *b* using $\frac{|slope|}{S_o}$, where S_o denotes the intercept of the regression.

2.7. Monte Carlo Markov chain inference

Priors are summarized in Table S5. We first run three Monte Carlo Markov chains of 10000 iterations discarding the first 3000 in R (Rcore team 2015) with Jags (Plummer 2003) and R2jags (Su and Masanao 2015) . We assessed model convergence by visually checking the trace plot and checking that all $\widehat{\mathrm{R}}$ were less than 1.01 (Brooks and Gelman 1998). We then ran two chains of 150 000 iterations each, with the first 30 000 as a burning and thinned, so that every 10th observation was retained.

3. Results

3.1. General

During the period May 1st 1998 – April 30th 2014, we observed 249 wolves legally culled, including 91 territorial and 158 non-territorial individuals at the time of death (Figure 3). We also observed 204 dissolution events among 629 wolf-pair-years (275 different pairs, Figure 4). Among these events, 125 were followed by a replacement and 79 were not. In order to illustrate the trajectory of the population predicted by our model, we provided population size estimates in January (Figure 5).

3.2. Effect of culling and wolf pair dissolution on population growth rate and demographic parameters

-Culling

The population growth rate was not affected by the rate of legal culling, neither when considering the culling rate of all individuals (median slope= -0.39, 95% Quantiles = -2.50 – 1.67), nor only territorial individuals (slope= -0.69, 95% Q= -5.55 – 3.60), nor non-territorial individuals (slope= -0.61, 95% Q=-3.71 – 2.66).

-Pair dissolution

Total pair dissolution rate tended to negatively affect population growth rate. We found that pair dissolution had an 85.3% probability to have a negative effect on the growth rate with a median Beta= -0.26, and 95% Quantiles= -0.80 – 0.22. As expected, the effect of the rate of pair dissolution that was not followed by a replacement was stronger on the lambda (slope= -0.51, 95% Q= -1.57 – 0.54, Figure 6 A, B) compared to the rate of pair dissolution followed by a replacement (slope= -0.06, 95% Q= -0.74 – 0.63; Figure 6 C, D).

Separating the effect of pair dissolution rate into different causes (culling or other causes), showed that other causes of pair dissolution had a stronger negative effect on the lambda (slope= -0.73, 95% Q= -1.44 – 0.02) compared to dissolution due to culling (slope= -0.05, 95% Q=-1.15 – 1.20).

Pair dissolution rate tended to affect growth rate through a decrease in survival of territorial individuals φ_T (slope= -0.54, 95% Q= -1.13 – 0.16). There was also 82.3% chance that pair dissolution decreased the survival of non-territorial individuals φ_{NT}, (slope= -0.22, 95% Q -0.69 – 0.24; Figure 7 A, B). Additionally, pair dissolution rate that was not followed by a replacement also negatively affected our estimate of recruitment ($Lambda_{Nbjan}$; slope= - 1.12; 95% Q= -2.89 – 0.51; Figure 7 C, D).

3.3. Compensatory vs additive effect of culling

-Culling

The median estimates showed that legal culling rate of non-territorial individuals was partially compensatory on overall survival rate of non-territorial individuals (*b*= 0.89, 95% Q= 0.06 – 1.83; Figure 8, C-D). There was large variation in the estimates from the IPM on culling mortality rate and overall survival rate. Therefore, our measure of compensatory *vs.* additive effect of culling rate (*b*) showed large variation as well. Similarly, the median effect of legal culling of territorial individuals was partially compensatory to the overall survival rate of territorial individuals and also included very large variation of the *b* (*b*= 0.83, 95% Q= 0.04 – 2.59; Figure 8 A-B).

-Pair dissolution

Pair dissolution rate generally increased over our study period (beta=0.02, 95% Q= 0.01 – 0.03), but the causes of dissolution showed large temporal variation and some opposite cyclic pattern (Figure 4). Until 2009, the dissolution rate due to other causes was low while the rate due to culling was high, and vice versa. After 2009, pair dissolution due to other causes mostly stayed above culling rate. Median dissolution rate due to culling of one or both individuals in a pair was partially compensatory to overall pair persistence (*b*=0.90; 95% Q= 0.21 – 1.58; Figure 8 E-F).

4. Discussion

Because of its relevance for wildlife management, the effect of human exploitation (e.g. through culling) on the growth of populations has been studied for many different species (Burham and Anderson 1984, Servanty et al. 2010, Sandercock et al. 2011), and wolves are no exception (Adams et al. 2008, Creel and Rotella 2010, Gude et al. 2012, Creel et al. 2015). However, the mechanisms and the extent by which culling may affect the dynamics of a social species, such as the wolf, remain unclear (Creel et al. 2015). In our study, we did not detect any effect of culling mortality on the growth rate of the population. However, wolf pair dissolution rate, and especially pair dissolutions that were not followed by a replacement, tended to negatively affect the growth of the population. Our IPM revealed that negative population growth may be explained by three different mechanisms. Pair dissolution tended to decrease 1) territorial wolf survival, 2) non-territorial wolf survival, and 3) recruitment. Although there were large uncertainties associated with the effect of culling, we found that the effect of culling mortality was mainly compensatory. Interestingly, there was also a high temporal variation in the rate of pair dissolution due to other causes (i.e. unknown, traffic, natural, verified poaching) than culling (Figure 4).

In social species, reproductive values are skewed towards certain specific individuals. In wolves, the territorial pair has an almost complete monopoly on breeding (Mech and Boitani 2003), giving them a much higher reproductive value than any other members of the population (Vucetich et al. 1997). Therefore, if culling mortality rate had been more directed towards individuals with low reproductive values (i.e. non-territorial animals), this could have explained our results. However, our data allowed us to distinguish between culling rate of territorial and non-territorial individuals, but we were unable to detect an effect of culling rate of territorial individuals (i.e. breeding individuals with high reproductive values) on population growth rate. Additionally, the culling mortality rates observed in this population were mostly below the threshold of mortality rates that has been found to result in a lambda <1 in other studies e.g. ~25% (Creel et al. 2015), ~35 % (Chapron et al. 2003), and between

28-47 % (Mech 2001), or between 15-55% (Marescot et al. 2012). This could be one of the reasons explaining why we did not detect an effect of culling rate on the growth rate of the population.

In contrast, pair dissolution rate (i.e. due to culling and other causes), and especially pair dissolution that was not followed by replacement, tended to have a negative effect on the growth of the population. The number of reproductive units (i.e. the territorial pair in a wolf population), and the demographic events occurring from them should have important consequences for population dynamics (Vucetich et al. 1997, Rutledge et al. 2010, Milleret et al. 2016). However, few studies have used empirical data to test and quantify this relationship (Sparkman et al. 2011b, Borg et al. 2014). Our integrated population model allowed us to disentangle three different mechanisms by which pair-bond dissolution negatively affected wolf population growth rate: 1) Pair bond dissolution rate was negatively correlated with breeder survival. This result is expected since wolf pair dissolution is generally linked to the mortality of one of the pair members (Milleret et al. 2016). 2) More interesting is the fact that non-territorial survival tended to be negatively affected by pair bond dissolution rate. Indeed, the loss of breeders may cause pack disruption and may have an indirect negative effect on pup survival due to a lack of parental and/or helper care (Brainerd et al. 2008, Ausband et al. 2015). However, our model did not include the distinction between pups and transients, which would be necessary to verify this assumption. If such an indirect negative effect of culling existed, this could then increase mortality beyond the effect of direct killing itself and result in a super-additive effect (Creel and Rotella 2010). 3) Pup recruitment was negatively correlated with the rate of pair bond dissolution events that were not followed by a replacement. For social species, the number of offspring produced is dependent on the number of reproductive units (in wolves the territorial pair). Therefore, lost territorial individual(s) in a pair that are not quickly replaced could cause a failure to successfully reproduce during the same season or even during the following seasons, which could also reduce recruitment.

Our Integrated population model revealed that the effect of culling was mainly compensatory. There were large uncertainties in our analysis of compensatory *vs* additive effects of culling, but the effect of culling tended to be mainly compensatory. Pair dissolution events that were followed by a replacement had less influence on growth rate than those not followed by replacement. This suggests that populations of social species, such as the wolf, may have a certain degree of resilience to mortality by swift replacement of lost breeders. A quick replacement may have the capacity to maintain pack cohesion and reproduction, which would function as a compensatory mechanism limiting the impact of mortality (e.g. culling) on population dynamics (Borg et al. 2014). Indeed, Milleret et al. (2016) found that after a pair dissolution event due to culling, replacement of the territorial missing individual(s) was frequent and occurred in approximately 50% of the cases. However, the resolution of their study (i.e. from one winter to another) did not allow the authors to detect how quickly the replacement could occur. The outcome of a dissolution event is likely to be strongly dependent on the timing of the culling event (e.g. pre/post mating or reproduction; Brainerd et al. 2008). In our study, most of the culling events occurred in the winter, with the majority in January (i.e., 40 %, Figure S3). This is a critical period for wolves to lose one of their breeding pair members since it is just before mating season (i.e. late February-early March for Scandinavian wolves, Sand et al. 2014). This gives to the remaining breeder a very limited time to successfully find a new partner, mate, and reproduce.

Culling mortality could also target animals that would die from natural causes. However, wolf mortality in unsaturated populations and in the absence of human offtake is generally low, which gives few possibilities for culling mortality to substitute natural mortality (Creel et al. 2015). In this population, poaching was found to make up about 50 % of all mortality (Liberg et al. 2011). Therefore, our survival estimates and pair dissolution rates included poaching. Poaching is usually cryptic (i.e. remained undetected two-third of the time Liberg et al. 2011) and sometimes results in unexpected temporal variation which challenges its predictability (Chapron and Treves 2016).

Interestingly, our estimates of pair dissolution allowed us to quantify the rate of dissolution due to causes *other* than culling (*other causes*). *Other* causes included *unknown* causes of dissolution (we observed a dissolution event but we could not identify the cause). Pair dissolution was generally linked to a mortality event, and natural and poaching mortality could explain a part of these *unknown* causes of dissolution (Milleret et al. 2016). However, it is unlikely that natural mortality itself could cause such large temporal fluctuations in the rate of *other* causes of pair dissolution (Figure 4). Cause-specific mortality rates from radio-collared individuals showed that natural causes (e.g. age, diseases) accounted for 5.5% of all mortality (Liberg et al. 2008). However, pair dissolution due to *other* causes fluctuated during our study period and reached up to 40% (Figure 3). Disease outbreaks could cause such temporal variation, but has not been detected in this population (e.g. Sarcoptic mange; Fuchs et al. 2016).

Intrinsic population factors such as inbreeding depression could potentially also have affected our estimates of pair bond dissolution (Milleret et al. 2016). However, the recent arrival of new immigrants in the population in 2008 had positive effects on individual fitness which suggest that the effect of inbreeding may have been limited, at least during the last years of our study period (Åkesson et al. 2016). Therefore, temporal variation in the intensity of poaching might be a possible explanation for the large fluctuations in pair dissolution rate due to *other* causes. In particular, our results reveal an interesting pattern where culling dissolutions and other dissolutions are inversely linked (years with high *culling* dissolution show low *other* dissolution and vice versa) until 2009 where *other* causes of dissolutions increased in parallel to the effect of culling (Figure 4). This may indicate that prior to the introduction of license hunting of wolves in 2009 in Sweden, poaching was compensatory to legal culling but license hunting may have sent a signal leading to an increase of poaching. Such a pattern has also been documented elsewhere (Chapron and Treves 2016).

If the temporal variation in pair dissolution rate due to *other* causes can be transposed to individual mortality, this could also explain why we did not detect an effect of culling mortality on growth rate.

Indeed, the temporally fluctuating pattern of pair dissolution rate due to *other* causes, would then be sometimes additive and sometimes compensatory to culling (Figure 4), and would preclude any conclusion on the effect of culling on population growth.

In an attempt to estimate the productivity (*f)* (Schaub and Abadi 2011), we used the formulation of the integrated population model. However, the annual productivity (*f*) parameter was not identified by the model (Appendix S1: Priors equals to posterior distribution). We further attempted to estimate this parameter using the information contained in the count of the minimum number of non-breeders counted in the packs in January (*Nmin*). However, non-breeder individuals in the pack had to survive from their birth in order to be counted during the census in January. Therefore, the model likely integrates information from the count in both the survival and the productivity parameters, making impossible to estimate annual productivity. Additionally, we believe it is important to mention that *Nmin* was a minimum and we made the strong assumption that the true number of newborn individuals was likely to be larger, as counts were likely to be smaller than the minimum number of offspring within the pack. This was our best available count data to estimate annual productivity. However, we ran the IPM without this count, and it provided similar results, but with larger confidence intervals (*Figure S3*). Thus, this confirms the limited impact of our assumption on our results.

It is always a challenge to derive population growth estimates of free-ranging populations, but even more so when it concerns elusive species with complex life histories, such as the wolf (Chapron et al. 2016). Although our IPM considerably simplified the life cycle of wolves, we were able to highlight some of the complexity of the effect of culling on wolf population dynamics. Using a state-space modeling approach, we aimed to disentangle the demographic processes from the observation processes. However, our results showed large parameter uncertainty that prevented us from making stronger inferences on the compensatory and additivity effect of culling. This limitation could to some extent be overcome by increasing the complexity of our Leslie matrix and multistate capture-recapture model. For example, it would be relevant to explicitly account for the complexity of the ecological and observation processes that yielded the capture-recapture data, such as detection heterogeneity (Cubaynes et al. 2010).

In conclusion, previous work has mostly focused on linking the effect of culling on growth rate, or culling mortality on annual survival, without being able to identify by which mechanisms culling may affect population dynamics. Our Integrated population model, linking several data sets, revealed the complexity of the effect of culling in a social living species. When culling may interact with other sources of mortality such as natural mortality, poaching, and intrinsic characteristics of the species, it becomes increasingly complicated to predict the real effect that culling would have on the population. According to our results, we cannot make general predictions about the effect of individual culling mortality rate in the Scandinavian population. Even with a culling rate of approximately 10% in 2011 (which is within the lower range of the culling rate needed to obtain lambda <1; Chapron et al. 2003, Marescot et al. 2012), pair dissolution rate due to other causes was equal to 40%, which is about 4 fold higher than the culling pair dissolution rate. In the case that such a pattern persists with a higher culling mortality rate, this may have strong negative consequences for the population and its’ viability. As long as other causes of mortality fluctuates in such an unexpected way, we recommend keeping the culling mortality rate under a relatively low rate of <20% to avoid dramatic consequences to the Scandinavian wolf population.

Although we argued that a large proportion of unknown causes of pair dissolution might be due to poaching, we cannot be certain. Therefore, we recommend further research to identify the mechanisms causing pair dissolution due *other* causes (especially *unknown* causes). Additionally, management actions and culling rates decisions should be focused at the level of the territorial wolf pair, which tends to be a better predictor of population growth. Furthermore, because of the evolutionary importance of the social unit (Silk 2007), we suggest that its’ stability and structure might be a more relevant measure to assess the effect of culling in socially living species and we generally recommend additional research oriented towards the functional unit of socially-living populations (Rutledge et al. 2010).

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Figures

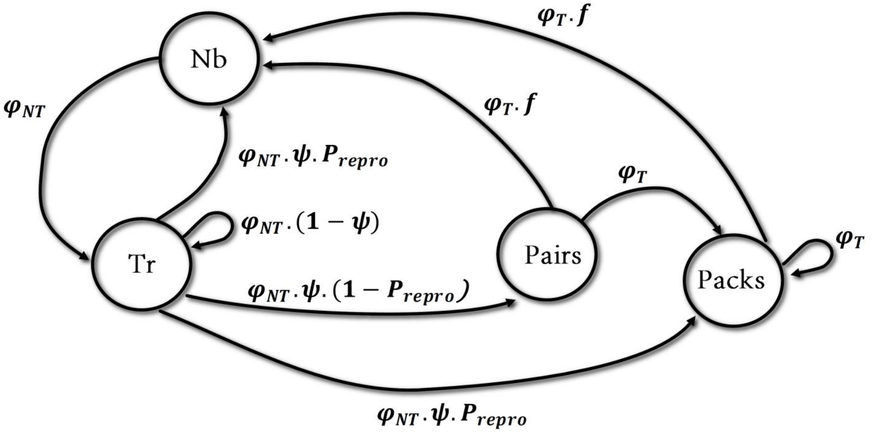


Figure 1. Schematic representation of the wolf cycle used for the Leslie matrix. Circles indicate stages of the individuals (Nb: New born, Tr: Transients, Pairs: a territorial pair member that has not reproduced, Packs: a territorial pair member that has reproduced). Parameters notations are f for fertility rate; φ_{NT}, φ_T, respectively, for survival rate of non-territorial and territorial, ψ for the transition probability from the transient (*Tr*) to the territorial state (*T*), and P_{repro} for the probability that a territorial pair member reproduced during its first year.

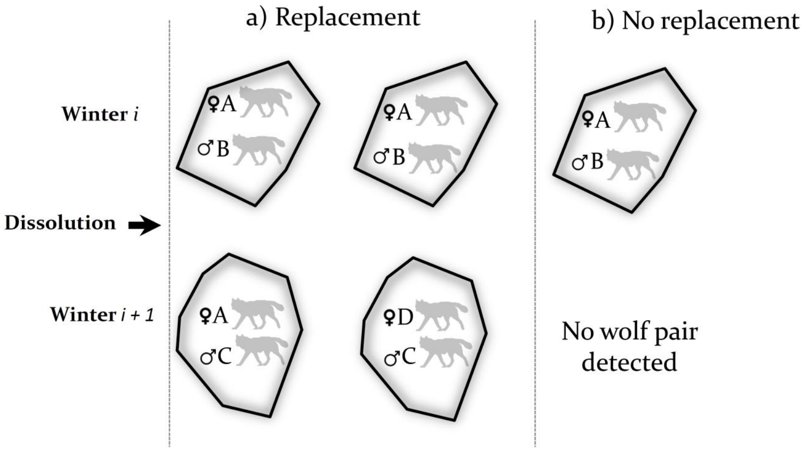


Figure 2. Visual description of the two possible events following a pair dissolution event. The winter *i* represents an example of a wolf pair observed in a specific winter (time *i*) and then during the following winter (time *i* + 1). Black polygons represent the home range location of the wolf pair. A pair dissolution event could result in a) the replacement of one or both individual, or b) no replacement (no territorial pair was detected within the previously detected territory). Capital letters (A; B; C; D) indicate individual ID of males (♂) and females (♀).

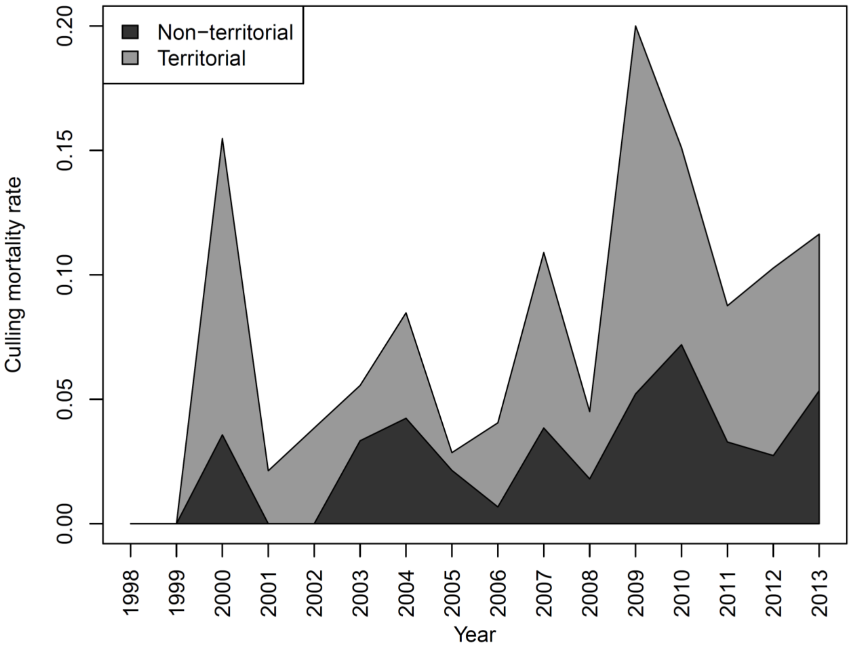


Figure 3. Temporal variation of the culling mortality rate ($M/Ntot_{May}$) of territorial and non-territorial individuals in Scandinavian from May 1st 1998 until April 30th 2014. Year on the x-axis shows the interval in which mortality rate was calculated. Thus, year 1998 shows culling mortality rate during a "wolf year", starting May 1st 1998 until April 30th 1999 and so on. To calculate mortality rate, we used the total number individuals estimated from the Integrated Population Model at May 1st (i.e. shortly after reproduction)

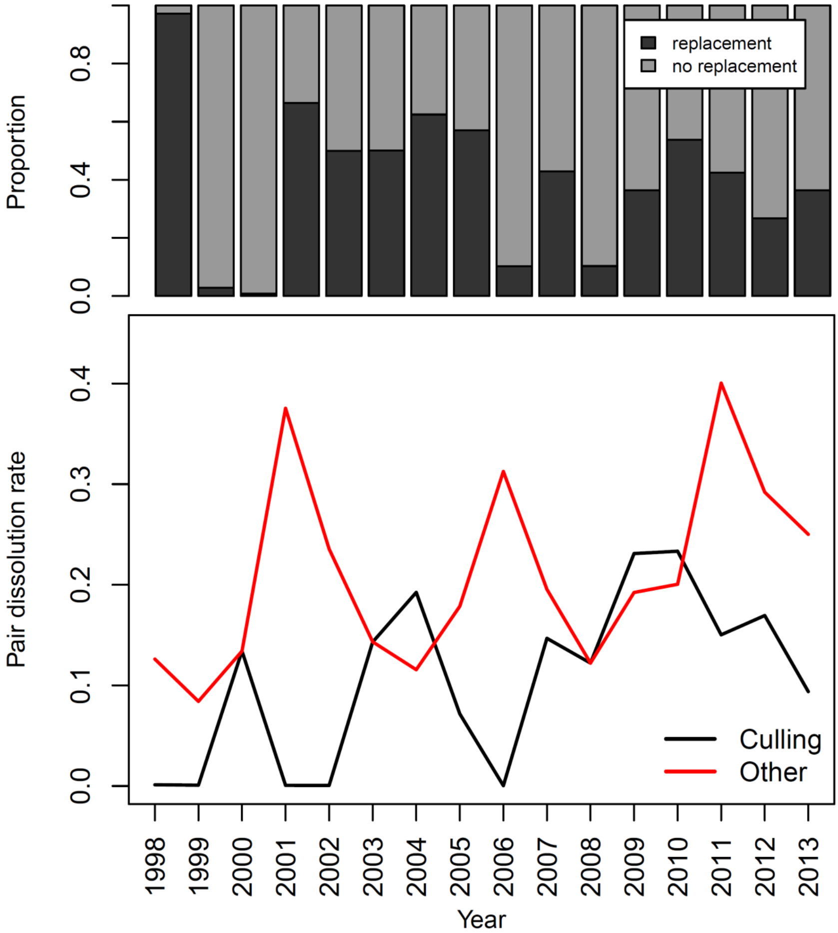


Figure 4. The lower panel shows the changes in pair dissolution rate due to culling and other causes (i.e. unknown, traffic, natural, verified poaching) from 1998-2014. Pair dissolution rates were calculated from one winter to the following one. Therefore, the year 1998 shows pair dissolution rate between the interval 1998/1999 to the winter 1999/2000. The upper panel shows the proportion of pairs that were replaced and the ones that were not replaced after a dissolution event (see details in Figure 2)

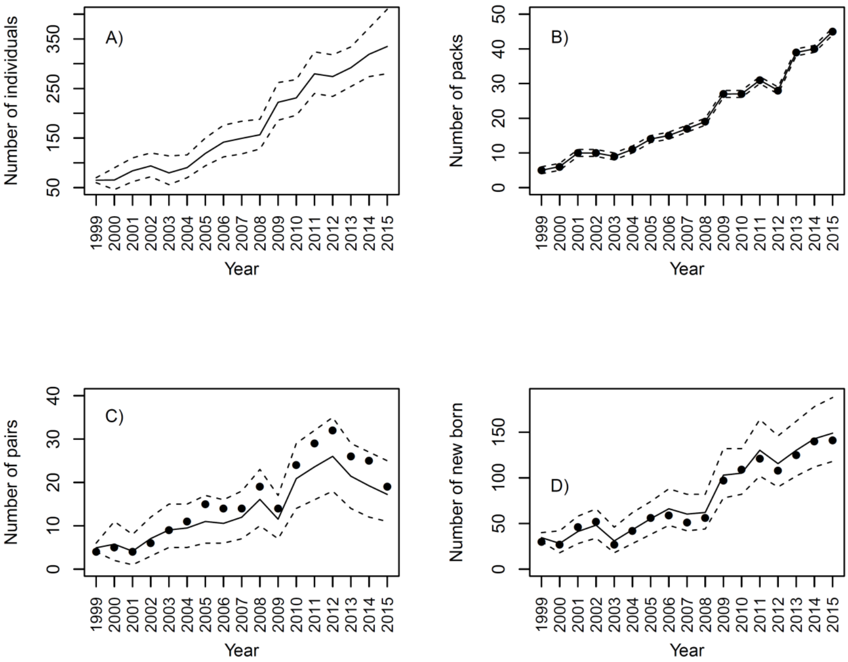


Figure 5. Estimation of A) the number of total individuals, B) individuals in packs, C) in pairs, D) and number of new born for January 1st using the prediction of the integrated population model, for the Scandinavian wolf population from 1999 to 2015. The full line shows the median estimates, the dotted line the 95 % credible interval and the full dots the data from the counts.

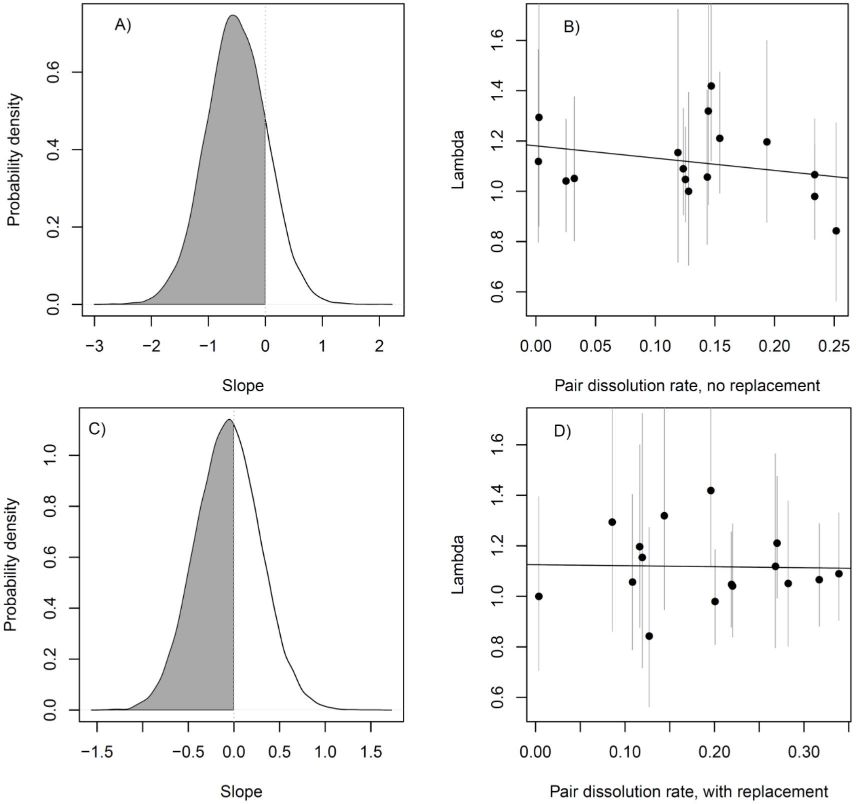


Figure 6. Effect of pair dissolution rate that was not followed (A, B) and followed (C, D) by a replacement on the growth rate (lambda) in January. Graphic A) represents the distribution of the slope of the regression between the posterior distribution of the lambda and pair dissolution rate not followed by a replacement. Graphic B) represents the relationship between the lambda and pair dissolution rate. Grey vertical bars represent 95% CI and the black line the line from the regression on the median values. Graphic C) and D) represents respectively the same than A) and B) but for pair dissolution rate with replacement.

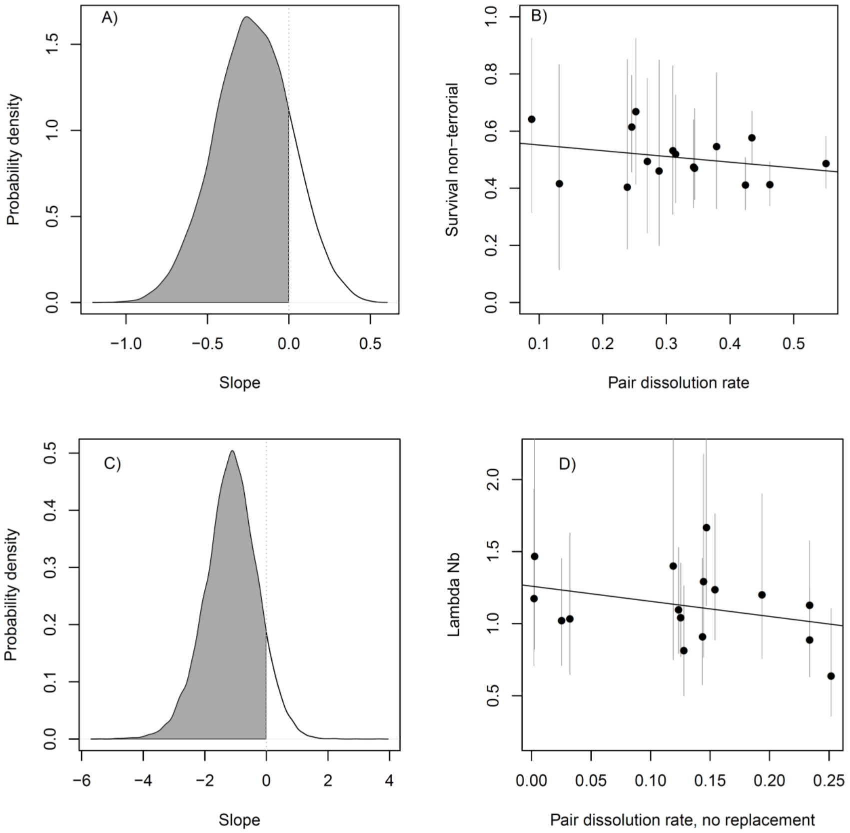


Figure 7. Effect of pair dissolution rate on survival probability of non-territorial individuals (A, B) and on recruitment (*lambda*$_{Nb;}$ *C, D*). Graphic A) represents the distribution of the slope of the regression between the posterior distribution of the survival of non-territorial individuals and pair dissolution rate (followed and not followed by a dissolution event). Graphic B) represents the relationship between the survival of non-territorial individuals and pair dissolution rate. Grey vertical bars represent 95% CI and the black line the line from the regression on the median values. Graphic C) and D) represents respectively the same than A) and B) but between the *lambda*$_{Nb}$ and pair dissolution with no replacement.

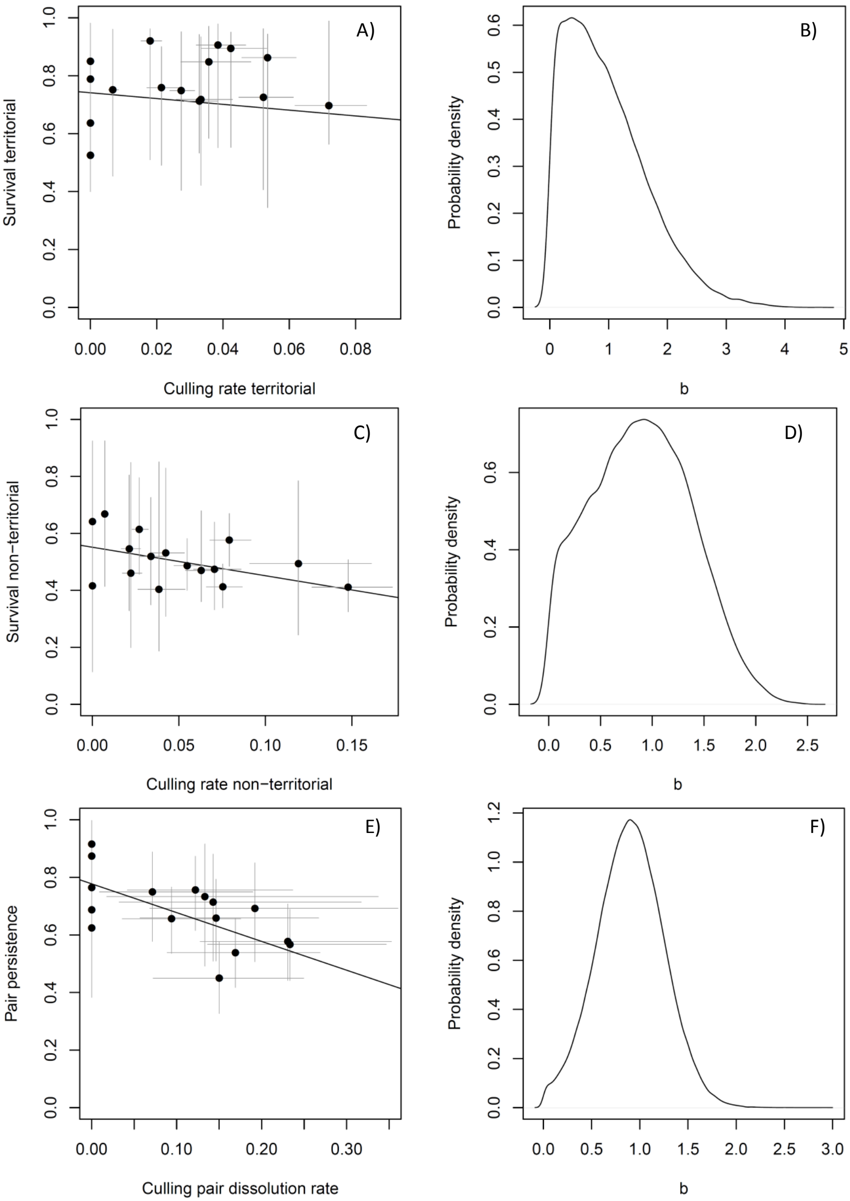


Figure 8. Relationships between culling mortality rate and overall survival for territorial (A-B) and non-territorial (C-D) individuals. Relationships between pair bond persistence and pair bond dissolution rate due to culling rate (E-F). The graphics on the left panel represent the relationships between culling rate and overall survival using the median estimates from the model. The greys horizontal and vertical bars represent the 95% CI. The full line represents the expected slope in the presence of additive mortality (*b*=1) from a baseline mortality rate without the any culling. Baseline mortality rate was estimated using the intercept of the regression between culling rate and overall survival (A, C) and between culling pair bond dissolution rate and pair persistence (E). On right panels, the probability distributions of the b values are represented.

Supporting information

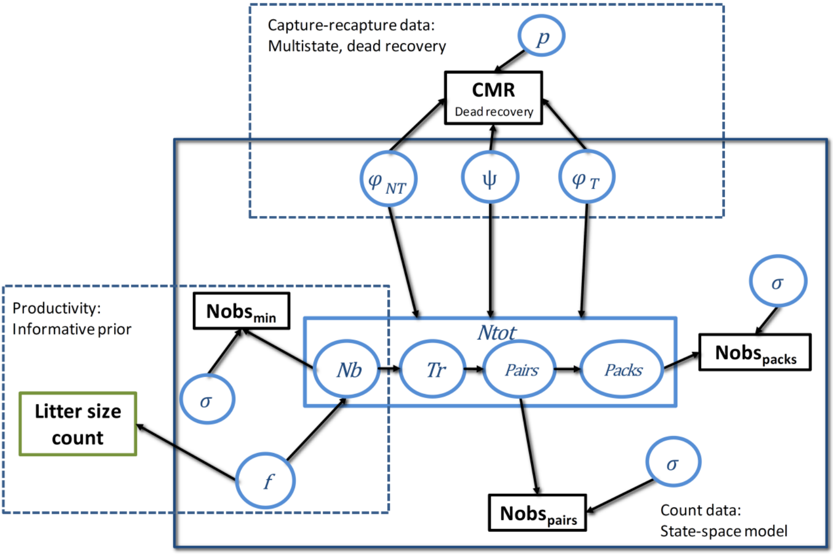
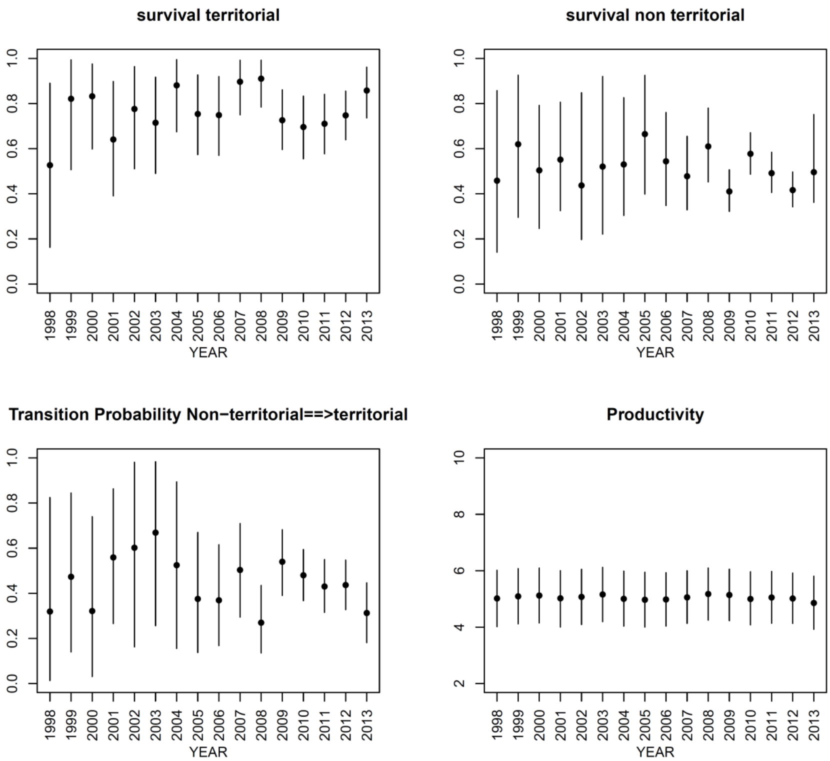


Figure S1. Graphical representation (acyclic directed graph) of the integrated population model without the priors. We only present one informative prior (litter size count, as a green rectangle) which represent an informative prior on the productivity. Small black rectangle represent the data, blue circles the parameters, large rectangles the individual submodels, and arrows the flux of information. The circles present in two submodel indicates that they are informed from two data sources. The σ represents the observation error, f the productivity, p probability of recapture, ψ stage transition probability, φ survival probability. The total number of individuals (*Ntot*) was derived using the number of new born (*Nb*), transient (*Tr*), pairs and packs.


survival territorial

survival non territorial

Transition Probability Non−territorial==>territorial

Productivity

Figure S2. Annual (May 1st – April 30th) median survival (territorial female, non-territorial) and transition probability from non-territorial to territorial stage, and productivity estimates obtained from the IPM. Error bars shows 95% credible confidence intervals.

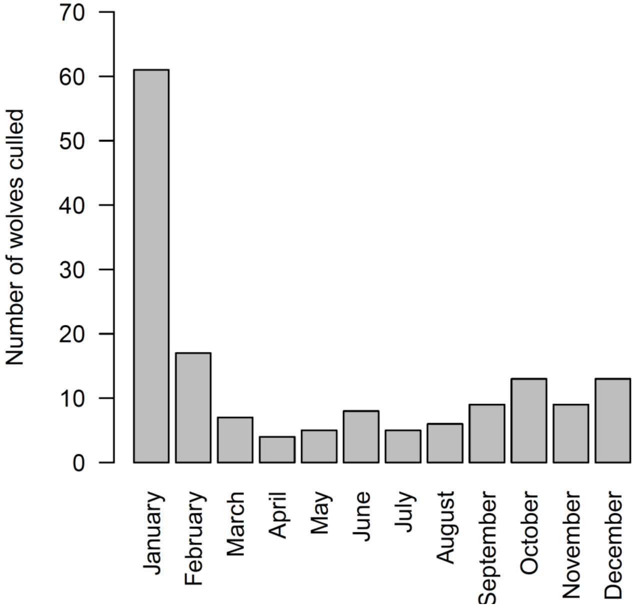


Figure S3. Number of wolves (males and females) legally culled each month.

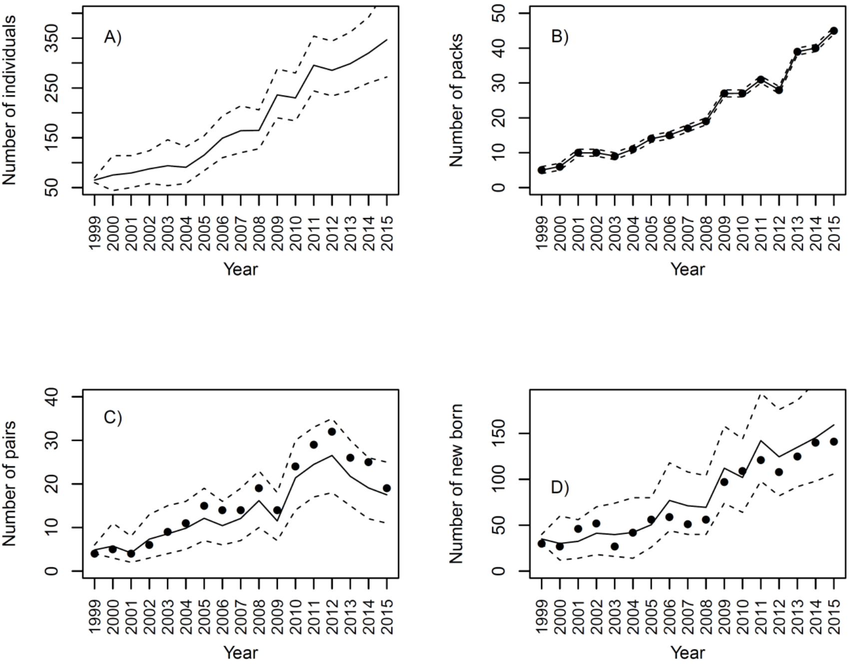


Figure S4. Results of the IPM when we did not integrate the *Nmin* data (Number of new born) as a count data. The results are very similar to those presented in Figure 5. Estimation of A) the number of total individuals, B) individuals in reproducing packs, C) in pairs, D) and number of new born for January 1st using the integrated population model, for the Scandinavian wolf population from 1998 to 2014. The full line shows the median estimates, the dotted line the 95 % credible interval and the full dots the data from the counts. Note that count data of new born in D) were not used in the IPM to obtain those results.

Table S5. List of prior choice used in our integrated population model.

Initial population size in January (note that this is only for females, female-based matrix Leslie model) (Wabakken et al. 1999)	
Nb[1] ~ dnorm(15, 0.0001)I(10,20)	Newborn
Tr[1] ~ dnorm(10, 0.0001)I(5,15)	Transient
Npair[1] ~ dnorm(4, 0.0001)I(2,7)	Number of pairs
Npack[1] ~ dnorm(6, 0.0001)I(5,7)	Number of packs
Other priors	
P_{repro} ~ dnorm(0.79, tau.repro)	P_{repro}; tau.repro represents the tau (SD=0.05) (Chapron et al. 2016)
errorNobs$_{min}$ ~ dunif(0, 15)	Error observation Nobs$_{min}$
sigmaProcNobs$_{min}$ ~ dunif(0, 0.5)	Prior Sigma process Nobs$_{min}$
errorNobs$_{pair}$ ~ dunif(0, 15)	Prior Error observation Nobs$_{pair}$
sigmaProcNobs$_{pair}$ ~ dunif(0, 0.5)	Sigma process Nobs$_{pair}$
phiNT ~ dunif(0.001, 0.999)	Prior φ_{NT}
phiT ~ dunif(0.001, 0.999)	Prior φ_{T}
Psi ~ dunif(0.001, 0.999)	Prior ψ
PFD ~ dunif(0.001, 0.999)	Prior P_{FD}
P_{NT} ~ dunif(0.001, 0.999)	Prior P_{NT}
P_{T} ~ dunif(0.001, 0.999)	Prior P_{T}
f ~ dnorm(5 , tau.f)	Prior f; tau.f represents the tau (SD=0.52)

Paper IV

Milleret, C., Ordiz, A., Chapron, G., Andreassen, H. P., Kindberg, J., Månsson, J., Tallian, A., Wabakken, P., Wikenros, C., Zimmermann, B., Swenson, J., and Sand, H. Not in my back yard; habitat selection and niche overlap between two sympatric apex predators, brown bears and gray wolves. *Under review in Ecography.*

Not in my back yard; habitat selection and niche overlap between two sympatric apex predators, brown bears and gray wolves

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Abstract:

Identifying how sympatric species belonging to the same guild coexist is a major question of community ecology. Niche overlap between two species might lead to interspecific competition and apex predators are of special interest in that context because their interactions can have consequences for lower trophic levels. Spatial segregation is one of the processes allowing coexistence between species, but it has seldom been studied for sympatric large carnivores. Based on monitoring of 53 brown bears (*Ursus arctos*) and 4 sympatric gray wolf (*Canis lupus*) territorial wolf pairs equipped with GPS collars in Sweden, we analyzed the degree of interspecific overlap in habitat selection within home ranges in both late winter and spring, when their diets show the largest overlap. We used the K-select method, a multivariate approach that relies on the concept of ecological niche, to quantify wolf and bear habitat selection. Wolves and bears segregated more than expected by chance. Wolves tended to select for moose occurrence, young forests, and rugged terrain more than bears did, which likely reflects the different requirements of an obligate carnivore (wolf) and an omnivore (brown bear). However, both species generally avoided human-related habitats during daytime. Individual variation in habitat selection detected in our study could not solely be explained by species- and intraspecific characteristics. Individual variation may be a relevant mechanism to overcome intraguild competition and facilitate coexistence.

Keywords – Brown bear (*Ursus arctos*) – Coexistence – Competition – Individual variation- Habitat selection – Niche overlap – Habitat segregation – Gray wolf (*Canis lupus*)

Introduction

One of the main objectives in community ecology is to understand the mechanisms that allow the coexistence of species sharing the same guild. This understanding requires the identification of how sympatric species use and share resources (Armstrong and McGehee 1976, Chesson 2000). Indeed, sympatric species sharing similar resources should demonstrate some degree of niche overlap (sensu Hutchinson 1957), which could lead to interspecific competition (Lotka 1925, Hurlbert 1978, Chesson 2000, Dufour et al. 2015). In turn, interspecific competition can generate difference in habitat use, which has been observed for various taxa in terrestrial (Holt et al. 1994) and aquatic realms (Wellborn et al. 1996). To buffer competition and allow for coexistence, sympatric species may avoid each other either in space and/or time. As niche overlap is determined by the proximity and abundance of competing species (Hutchinson 1957, MacArthur and Levins 1967), long-term monitoring and analyses of spatial and temporal avoidance are important tools for investigating niche overlap (Darmon et al. 2012).

Interspecific interactions between species belonging to the same guild, such as apex predators, may influence the population dynamics of species at other trophic levels (Creel 2001, Caro and Stoner 2003). Because large carnivores are not suitable for experimental approaches in controlled conditions, studies on the effects of interspecific interactions on population level are still scarce (Ballard et al. 2003) and they often report on the relationships between dominant and subordinate species (Belant et al. 2010, Darnell et al. 2014). An alternate approach for identifying the mechanisms allowing carnivore coexistence is to analyze the spatial distribution and niche overlap of carnivores in relation to their habitat used (Apps et al. 2006). Research on fine-scale spatio-temporal interactions is needed to advance our understanding of the mechanisms that allow apex predators to coexist and the magnitude of their interspecific interactions on lower trophic levels (Linnell and Strand 2000, Périquet et al. 2015).

Gray wolves (*Canis lupus*) and brown bears (*Ursus arctos*) are two of the largest and most widely distributed apex predators in Eurasia and North America, where they are sympatric in a large part of their ranges (e.g., see IUCN maps; IUCN 2015; Chapron et al. 2014). Both species are efficient predators of neonate ungulates (Swenson et al. 2007, Barber-Meyer et al. 2008, Sand et al. 2008) and the sharing of this common resource may fuel interspecific competition. In addition, brown bears are known to be efficient scavengers of wolf-killed ungulates (e.g., Ballard et al. 2003). Because of the extensive and largely sympatric distribution and the reported existence of interspecific interactions between wolves and bears (Ballard et al. 2003), they are an interesting duo for evaluating the mechanisms involved in coexistence of apex predators in the Northern Hemisphere.

Wolves are obligate carnivores while bears are omnivores. In Scandinavia, wolves feed primarily on moose (*Alces alces*) (Sand et al. 2008, 2012) , whereas the diet of bears includes a wide range of food items (Stenset et al. 2016). Nevertheless, bears are also efficient predators of neonate moose (Swenson et al. 2007, Dahle et al. 2013), and kleptoparasitize mor than half of wolf kills during spring in central Sweden (Milleret 2011, Ordiz et al. 2015). Also, bear density has a negative effect on probability of wolf pairs to establish in a given area (Ordiz et al. 2015). On the other hand, effects of wolves on brown bears have never been documented at the population level. This findings suggests that wolves and bears may display consumer-resource interactions such as parasitism (bear: +; wolf: -) and exploitative competition (bear: -; wolf: -).

In order to obtain a comprehensive understanding of the mechanisms that allow the coexistence of free-ranging apex predators, it is important to understand how predators avoid each other in space and time. Indeed, the spatial effects of biotic interactions on species distributions have rarely been investigated (Araújo and Rozenfeld 2014). Two species that select similar resources may never interact directly. The spatial scale at which competition becomes visible depends on the nature and strength of the interactions. According to Araújo and Rozenfeld (2014), the effects of parasitism should be visible across all spatial scales, if one species has strong positive benefits on the other, but the effects of competition should only be visible at fine spatial scales. Although wolves and bears are sympatric within similar habitat types at the landscape level (May et al. 2008), segregation could occur at finer spatio-temporal scales (e.g., within different habitats in their home ranges). However, we know of no studies that have examined whether selection of different habitats within home ranges could be used by wolves and bears as a mechanism of coexistence.

We used GPS locations from sympatric radio-marked wolves and bears to quantify their habitat niche overlap in central Sweden. The effect of bears on wolves (i.e., parasitism of wolf kills and exploitative competition on common prey, i.e., neonate moose), may cause wolves to spatially segregate from bears. Therefore, we predict the existence of habitat segregation higher than expected by chance between wolves and bears. We focused our analysis in late winter and spring (i.e., the period when both species prey on moose), which may lead to higher trophic overlap than during the rest of year, thus helping us to infer the degree of interaction between wolves and bears. We used habitat-, prey-, and human-related variables to quantify the habitat niche of wolves and bears, because of the documented influence of these factors on wolf and bear distribution and behavior (e.g., Ordiz et al. 2011, 2014, 2015, Zimmermann et al. 2014). Then, we quantified habitat niche overlap between wolves and bears using a multivariate approach based on the niche concept, and we developed a method to test if they segregated more than expected by chance. Our study may advance current knowledge on the ecological mechanisms that drive interspecific interactions between apex predators and allow their coexistence.

Material and methods

Study area

Our study area was located in central Sweden (Figure 1) (elevation: 100-830 m), mainly composed of boreal forest, with coniferous species Scots pine (*Pinus sylvestris)* and Norway spruce (*Picea abies*) covering ~60% of the area (Appendix 1, Table A1). Human density was low, with 1-7 inhabitants/km^2 in 2012 (www.scb.se, Statistics Sweden, 2012). Snow usually covers the ground from December to March. Bear density approached 30 bears/1000km^2 (Solberg et al. 2006). The first two wolf territories established within the study area were detected during the winter 2000/2001 (Wabakken et al. 2002). Since then, 1 to 8 territories have been recorded annually during systematic snow-tracking surveys (Liberg et al. 2012). Two more members of the large carnivore guild were present in the study area; Eurasian lynx (*Lynx lynx*) and wolverine (*Gulo gulo*). Moose was the most abundant prey species, with average density estimates of 0.6-1.6/km^2; whereas the estimated density of the only alternative ungulate, roe deer (*Capreolus capreolus*), was very low, 0-0.05/km^2 (Zimmermann et al. 2015).

Study animals

Wolves and bears were captured following ethically-appoved and veterinary procedures fully described in Sand et al. (2006) and Arnemo et al. (2012), and were equipped with GPS–GSM neck collars (VECTRONIC Aerospace GmbH, Berlin, Germany). At least one of the breeding adults was collared in the three wolf territories in the core of our study area (Kukumäki, Tandsjön, and Tenskog territories). We used data from 53 radio-collared bears. Wolf collars were programmed to record two locations a day, except during intensive study periods of predation, when collars recorded locations every hour (Sand et al. 2008). Bear collars were programed to record locations every 30 or 60 minutes. During 1 January 2010 -

31 December 2014, we obtained 931,277 GPS locations from 79 bear-years and 25,709 GPS locations from 8 wolf territory-years (Figure 1).

Landscape characteristics

We characterized land cover into twelve categories, according to the ‘Svenska Marktäckedata’ (SMD) land cover map (Lantmäteriet, Sweden; Appendix 1, Table A1) constructed from satellite images taken on 12 September 2002. Because of intensive logging in the study area, we updated the vegetation map using information about forest clearcuts (Nicholson et al. 2014) performed between 12 September 2002 to 1 January 2012 (mid date of the study period). This information was obtained from the Swedish Forestry Agency (http://www.skogsstyrelsen.se). To account for succession of the vegetation, the classes *Clearcuts* and *Young Forest* in 2002 were reconsidered as *Young Forest* and *Mid-age coniferous forest* (Appendix 1, Table A1), respectively, in the updated map (Nicholson et al. 2014).

We also computed distances in km from main (paved) and secondary (gravel) roads. Finally, we used a digital elevation model (GSD-Elevation data, Grid 2+; http://www.lantmateriet.se) to extract elevation and calculate a terrain ruggedness index (TRI) (Sappington et al. 2007). We computed three different TRIs using moving windows of different sizes (3x3; 5x5; 7x7) with a cell resolution of 10 m. A preliminary analysis showed that TRI7 (7x7) was better at explaining wolf and bear habitat selection, and it was therefore retained for the subsequent analyses.

Moose occurrence

Moose are the main ungulate prey of wolves and bears in Scandinavia (Swenson et al. 2007, Sand et al. 2008) and most documented wolf-bear interactions occur near kill-sites (Ballard et al. 2003). We used moose pellet counts (Neff 1968) to compute a moose resource selection function that predicted moose occurrence within the study area. Pellet counts can be used to document moose habitat selection during winter and early spring, and they are the best available data describing moose habitat selection patterns in our study area. We conducted pellet count surveys during spring in each wolf territory: Tenskog (2010; 1960 sample plots), Tandsjön (2012; 2600 plots), and Kukumäki (2014; 1920 plots). The circular sample plots of 100 m^2 were placed along the of 1 x 1 km squares that were systematically distributed within the 100% minimum convex polygon of the wolf territory (Zimmermann et al. 2015). Each square boundary contained 40 sample plots. We searched for moose pellets and determined their age based on their structure, consistency, color, and position in relation to the vegetation, in order to count only pellet groups produced after leaf fall of the previous autumn (Rönnegård et al. 2008, Gervasi et al. 2013).

Based on the pellet survey results, we computed a resource selection function (Manly et al. 2002) with the number of pellets counted in each plot as the response variable (Gervasi et al. 2013). We used all land-use descriptors as explanatory variables (except the variable ‘Water’) and calculated the proportion of land-use characteristics (Appendix 1, Table A1) using a moving window (5 x 5 cells; 20 x 20 m cell size). Due to the high number of zeros in the data, we applied a zero-inflated negative binomial model (Zuur et al. 2009). We started from a fully parameterized model and used Akaike Information Criterion (AIC) to select the most parsimonious model. Models with a $\Delta AIC < 2$ were considered equally supported by the data. We performed a collinearity analysis and detected no excessive level of correlation in the set of explanatory variables (all Pearson’s $r < 0.3$). We used k-fold cross validation to evaluate model performance (Boyce et al. 2002). Performance never exceeded 30% (Spearman’s r), which is in accordance with other studies using similar data and models (e.g., Bouyer et al. 2015) . To predict spatial variation of moose occurrence within our study area, we performed model averaging to obtain coefficients for the variables retained in the best models, using the “MuMIn” package in R (Barton 2014). The predicted values were used as a relative index for moose occurrence (*Moose_pred*) during winter-spring in the subsequent analyses (See Appendix 1, Table A2-A3, and Figure A1 for further information).

Study periods

We defined 2 study periods in late winter and spring to take into account the marked seasonal variation in the annual cycle of wolves and bears. During the late-winter period (1 March - 30 April) male bears start to leave their winter dens (Manchi and Swenson 2005). The spring period (1 May- 30 June) overlaps with wolf reproduction, all bears are out of dens, and also encompasses the bear mating season (Dahle and Swenson 2003). The latter period also includes the birth of moose calves, which are a highly utilized prey by wolves and bears (Figure 2). Within each study period, we selected individual bears with > 500 GPS locations and regular time intervals between locations to ensure that a representative seasonal habitat selection pattern was captured for each individual (Girard et al. 2002). For wolves, we only used GPS locations from intensive predation studies, when locations were recorded every hour. During the late-winter period, we only used GPS locations from one member of the pair (male or female, Appendix 1, Table A3), because both pair members usually travel together outside the reproduction period (Peterson et al. 2002, Zimmermann et al. 2015). During the spring period, we used GPS locations from the males, except for one territory-year, when only the collar of the female was functioning (Appendix 1, Table A3). We prioritized locations from the males over females in the spring period, because the females are more stationary near the den during pup rearing (Alfredeen 2006). Wolf territorial pairs reproduced in all years except one (“Tenskog 2010”, Appendix 1, Table A3).

Habitat selection

We quantified habitat selection by wolves and bears within their home range (third order of selection; Johnson 1980). To quantify habitat niche overlap between the species, we used a multivariate approach that relies on the concept of ecological niche, K-select (Calenge et al. 2005, Darmon et al. 2012). Each habitat variable defines one dimension in the ecological space, and the vector (marginality) of the differences between average available and used habitat quantifies the strength and direction of the selection (Calenge et al. 2005). Therefore, the direction (positive or negative) indicates habitats used, and the marginality ‘score’ indicates the strength of the use. Average conditions were defined using a 95% MCP. In order to extract the relevant aspects of habitat selection, a principal component analysis was computed from the marginality vectors. For further details on mathematical procedures of K-select, see Calenge et al. (2005). Using linear mixed models (Bates et al. 2015), we then tested whether species, bear reproductive status, time of the day, and interactions among these variables could explain differences in the centered marginality values obtained on each axis of the K-select. We included individual identity as a random intercept to account for individual heterogeneity and repeated measures of its habitat selection. We then selected the most parsimonious models using AIC and, when the difference in AIC between competing models was < 2, we retained the simplest model (Burnham and Anderson 2002).

To account for individual variability in habitat selection (Leclerc et al. 2015, Uboni et al. 2015), individuals that were monitored in multiple years were considered as different individuals in each year in the K-select analysis. Because wolves and bears are mostly active from dusk to dawn (Sand et al. 2005, Ordiz et al. 2014), we also separated habitat selection for each individual into day and night, using monthly sunset and sunrise tables. However, we defined the 95% MCP using all GPS locations from both day and night as available for each individual. In brown bears, behavior varies markedly due to sex and reproductive status, e.g., in terms of daily movement patterns (Ordiz et al. 2014) and habitat selection (Steyaert et al. 2013). Therefore, we distinguished habitat selection and niche overlap among the following bear classes: females with dependent offspring, solitary females, adult males, and subadult (< 4 year old) bears of both sexes. We did not make any classes for wolves, because of the low sample size of different categories (only one wolf pair did not reproduce, and locations from one female instead of the male were used in each study period).

Habitat niche overlap

In order to quantify the degree of overlap between bears and wolves, we conducted an *ad hoc* analysis based on scores of the locations obtained for each individual, and on each dimension of the ecological space of the K-select (Figure 3). For the scores of each individual on each dimension, we computed a nonparametric Gaussian kernel density estimation (Geange et al. 2011) using the 'rule of thumb' to obtain the bandwidth value (Silverman 1986). We then paired each kernel estimate with each individual/species and calculated the area of overlap O_{ij_e} between the two distributions of species i and j for each axis *e*, using Equation 1, where $f(x)$ and $g(x)$ are the probability density function of species i and j. Finally, we computed an overall overlap index ($\bar{O}_{ij}$) weighed by the eigen-values (λ) of each dimension e of the K-select (Equation 2). The index (O_{ij}) ranged between 0 (complete segregation) and 1 (complete overlap) between species i and j.

$$O_{ij_e} = \int min[f(x) - g(x)]dx \qquad \text{(Equation 1)}$$

$$\bar{O}_{ij} = \frac{\sum_e^n O_{ij_e} \lambda_e}{\sum_e^n \lambda_e} \qquad \text{(Equation 2)}$$

To test whether or not wolves and bears segregate more than expected by chance, we computed null models describing habitat selection of individuals from both species under random use of their habitat (Figure 3). We followed the methodology used by Martin et al. (2008) to simulate random habitat selection, by randomly rotating the complete trajectory of each individual (i.e., wolves and bears) around the centroid of their respective observed trajectories 1000 times. We then computed the K-select and the overall overlap index ($\bar{O}_{ij}$) as described above for each of the 1000 simulated datasets. We used the 1000 $\bar{O}_{ij}$ values to build a null distribution of niche overlap between wolves and bears under random habitat use. We then used randomization procedures to compare observed overlapping indexes (O_{ij_e}) with the null distribution of overlapping indexes obtained from the simulated data sets. We calculated p-values as the proportion of simulated overlap indexes that were inferior or equal to the observed overlap index. A p-value < 0.05 was used to reject the null hypothesis that there was no niche differentiation between wolves and bears and accept our alternative hypothesis that wolves and bears segregated more than expected by chance. All analyses were conducted using R (R Core Team, 2015) and package “adehabitat” (Calenge 2006).

Results

Late winter (1 March – 30 April)

The first 6 axes of the K-select explained 83% of the marginality and were retained for the analysis (Figure 4A). Wolves and bears segregated from each other more than expected by chance ($\bar{O}_{ij}$= 86.0 %, $p \leq 0.01$). Specifically, wolves segregated more than expected from male bears ($\bar{O}_{ij}$= 85.9 %, $p \leq 0.01$) and females with cubs ($\bar{O}_{ij}$= 72.3%, $p \leq 0.1$) during the day (Table 1). Species and time of day were important variables explaining variation in marginality scores on different axes (Table 2A). Wolves tended to select for moose occurrence, young forests, and rugged terrain more than bears did (Figure 4A, axis 2), as shown by the negative beta values for all bear classes (Table 3A, axis 2). Nevertheless, we also observed similarities in habitat selection among wolves and bears. Both species tended to select mid-age forests and areas further away from secondary roads and buildings during the day compared to the night. For the axes 4, 5, and 6, individual variability in habitat selection was not explained by species-specific or intraspecific (i.e., reproductive status) characteristics (Figure 4A).

Spring (1 May – 30 June)

The first 6 axes explained 75% of the marginality and were retained for the analysis (Figure 4B). Wolves and bears segregated from each other more than expected by chance ($\bar{O}_{ij}$= 79.2 %, $p \leq 0.01$). Wolves segregated more than expected from all bear classes (females with cubs $\bar{O}_{ij} = 77.5\%$, $p \leq 0.01$; males $\bar{O}_{ij} = 80.5\%$, $p \leq 0.05$; lone females $\bar{O}_{ij}$ =78.7%, $p \leq 0.05$; subadults $\bar{O}_{ij}$ =76.7%, $p \leq 0.01$). This segregation pattern was consistent during day and night (Table 1). Species and bear reproductive status were important variables to explain the variation in marginality scores, but only on the first axis of the K-select (Table 2B). Consistently with the late-winter period, wolves tended to select for moose occurrence, young forests, and rugged terrain more than bears did (Figure 4), as shown by the positive beta values for all bear classes (Table 3B, Axis 1).

On all other axes, both species tended to select habitat similarly, with time of day being the best variable to explain individual differences (for both species) in habitat selection. For example, wolves and bears showed a stronger selection for mid-age forest, bogs, and areas farther from building and secondary roads during the day than at night (Figure 4B, Axis 4).

Discussion

Our analyses of habitat selection and niche overlap within home ranges confirmed the hypothesis that Scandinavian gray wolves and brown bears segregated more than expected by chance during late winter and spring. Segregation tended to be more intense as the season advanced, i.e. there was higher niche overlap between wolves and bears in late winter ($\bar{O}_{ij} =$ 86% in 1 March-30 April) than in spring ($\bar{O}_{ij}$=79.2% in 1 May-30 June) and segregation involved more bear classes (i.e., in late-winter, wolves segregated from males and females with cubs, while in spring, wolves segregated from all bear classes). There were both differences and similarities in wolf and bear habitat selection, as shown by the selection on different axes of the K-select analyses. The most distinctive pattern demonstrated that wolves selected for moose occurrence, young forests, and rugged terrain more than bears did, whereas similarities between wolves and bears included the general avoidance of human-related infrastructure during daytime.

The stronger selection of moose by wolves was consistent throughout the two study periods and likely reflects differences in the requirements of an obligate carnivore, compared to those of the omnivorous bear, whose diet is diverse (Stenset et al. 2016). To account for marked seasonal differences in the behavior of wolves and bears, and consider the phenology of the main prey and the progressive green-up of vegetation, we divided our study of habitat selection into late winter and spring (Figure 2). Because ungulate calves are preyed upon efficiently by brown bears in spring, both in Eurasia (Swenson et al. 2007) and North America (Griffin et al. 2011), we might expect wolf-bear habitat segregation to be lower during this period. However, segregation tended to be higher. Wolves segregated from all bear classes in the spring, compared to the late winter period. Wolves rear pups in spring, and all but one of our monitored wolves reproduced, which likely constrained their behavior, including their habitat selection. In addition, interspecific competition between wolves and bears occurs mostly at carcasses and may sometimes result in offspring death for both species (Ballard et al. 2003), which may also help explain larger habitat segregation in spring.

We found that habitat selection of both species was affected similarly by time of the day. Wolves and bears avoided human-related infrastructure during daytime, when outdoor human activities peaked (Ordiz et al. 2011). Large carnivores generally avoid human-dominated habitats and related features (Oriol-Cotterill et al. 2015), and Scandinavian bears and wolves are no exception (Ordiz et al. 2012, Ordiz et al. 2014, Zimmermann et al. 2014, Ordiz et al. 2015). Indeed, most mortality events are human related in Scandinavia for both bears (Bischof et al. 2009) and wolves (Liberg et al. 2011). Therefore, the avoidance of human-related habitats during daytime is not an unexpected result, and may explain similarities in habitat selection.

Although the different diet requirements of wolves and bears might lead to segregation, their use of a common food resource could also lead to similarities in habitat selection, promoting niche overlap. Indeed, wolves and bears actively prey on neonate moose in spring, and bears also feed on wolf-killed moose (Milleret 2011). Whereas neonate moose calves are small and are consumed quickly when preyed upon by either wolves or bears in spring, moose killed by wolves in late winter are larger, providing carcasses that take longer time to be consumed by wolves and bears (Wikenros et al. 2013). Thus, kleptoparasitism of wolf kills by bears in late winter, which is common in our study area (Milleret 2011), could also explain the higher niche overlap, or lower segregation, observed between wolves and bears in late winter than in spring.

Therefore, human avoidance by wolves and bears and predation/scavenging on the same prey likely explain part of the similarities in wolf and bear habitat selection as observed on some axes of the K-select. Similar findings have been reported for Eurasian lynx and wolverines in Scandinavia, where both species are exposed to intensive human-induced mortality and share the same prey (Rauset et al. 2012)

Although overlap on some axes could suggest competition, partitioning on other axes may be sufficient to allow coexistence (Holt 1987). Nevertheless, additional factors must be taken into account to interpret spatial interactions between sympatric species. This includes accounting for intraspecific factors that shape behavioral interactions among individuals (Grassel et al. 2015). We defined two study periods that aligned with seasonal differences in the behavior of both wolves and bears (Figure 2), and explicitly took into account intra-annual and daily individual variation in habitat selection (Uboni et al. 2015). Our K-select analysis highlighted large individual variability in habitat selection that could not solely be explained by species and intraspecific characteristics. The limited sample size prevented us from having the statistical power to distinguish wolf variability in habitat selection. Therefore, reproductive success, sex-specific differences, and den location are factors that could explain the observed habitat selection variation among wolves. Individual variation in habitat selection and daily activity pattern have already been reported for bears (Gillies et al. 2006, Leclerc et al. 2015, Ordiz et al. 2016) and wolves (Hebblewhite and Merrill 2008) and could be explained by differences in personality traits (Réale et al. 2010). The large intraspecific variation found in our study may help wolves and bears to respond to intra- and interspecific competition and may promote coexistence (Vellend 2006). Indeed, several lines of evidence suggest that intraspecific trait variation is important to promote species coexistence (Bolnick et al. 2011, Valladares et al. 2015)

The influence of seasonality on habitat use deserves further research. At the intraspecific level, female bears with offspring segregate from other bears during the mating season in spring, but not during other seasons (Steyaert et al. 2013), and wolves also show seasonal variation in habitat selection (Uboni et al. 2015). Seasonality may also influence interspecific interactions, e.g., with seasonal variation driven by changes in the predator’s diet across the year (Saavedra et al. 2016). Bears are very efficient predators on neonatal moose calves during spring, but not on larger moose (Swenson et al. 2007). Later in the season, most bear populations rely on hard and soft mast (e.g. Naves et al. 2006). Therefore, the degree of trophic overlap between wolves and bears in summer and fall might be lower than in the spring. Accordingly, seasonality could change the degree of niche overlap of wolves and bears we observed. This highlights that seasonal and even shorter (day-night) spatio-temporal patterns may change the observed degree of niche overlap between sympatric species, which deserves further attention to understand the role of species interactions and how this affect their distribution pattern (Araújo and Rozenfeld 2014).

Although wolves co-occur with bears within similar habitat types at the landscape scale (May et al. 2008), wolf pairs avoid areas with high bear density when establishing territories (Ordiz et al. 2015). The spatial scale under consideration is crucial when studying biotic interactions (Araújo and Rozenfeld 2014) and our study shows that habitat segregation between wolves and bears occurs at the home range scale. The patterns observed at different spatial scales (Ordiz et al. 2015 and this study) show that the result of biotic interactions might be visible at several scales and might act as a key mechanism allowing the coexistence between apex predators. Because most of the observed interactions between wolves and bears occur at carcasses (Ballard et al. 2003), fine-scale movements around feeding sites might be an additional mechanism used to reduce the risk of encounters and interactions, as recently described for other carnivores in Scandinavia (López-Bao et al. 2016) and elsewhere. In Africa, for instance, habitat selection by cheetahs (*Acinonyx jubatus*) at the home range scale was similar to that of lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*), but cheetahs avoided immediate risks by occurring farther from lions and hyenas than predicted by a random distribution (Broekhuis et al. 2013).

Conclusions

Habitat niche overlap has been studied at different scales for many coexisting species, from spiders (Thompson et al. 2015) to a variety of mammals, including ungulates (Darmon et al. 2012, Owen-Smith et al. 2015), and medium-sized and large carnivores (May et al. 2008, Pereira 2012, Broekhuis et al. 2013). However, evidence of interspecific competition of two sympatric radio-collared carnivores is just beginning to be explored, in terms of both kill rates (Elbroch et al. 2014) and habitat selection (Ordiz et al. 2015). Our results suggest that wolves and bears spatially segregate within home ranges more than expected by chance, which might be a key mechanism allowing wolves and brown bear to coexist. To obtain a comprehensive understanding of the mechanisms shaping coexistence, it will also be important to understand how habitat selection of each species is influenced by the presence of the other species at large (Ordiz et al. 2015) and finer spatial scales. Disentangling the interactions of such mechanisms at different scales is essential to better understand how sympatric large carnivores coexist, and may affect lower trophic levels. The large intraspecific variability in habitat selection found in our study might also be a relevant mechanism used by both species to coexist and deserves further research (Bolnick et al. 2011, Valladares et al. 2015).

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Table 1. Paired comparisons of weighted habitat niche overlap ($\bar{O}_{ij}$) in percentages between wolves and brown bears in Sweden. Overlap indexes for the late-winter period (1 March - 30 April) are shown on the lower diagonal (i.e., below diagonal line) of the table and the upper diagonal (i.e., above diagonal line) corresponds to the spring period (1 May -30 June). Indexes of overlap between wolves and bears are shaded in gray and unshaded indexes show intraspecific indexes of overlap. The overlap indexes in bold show that segregation is significantly larger than expected by chance. The stars on the right side of the indexes show the degree of significance: * pvalue ≤ 0.05; ** pvalue ≤ 0.01; *** pvalue ≤ 0.001.

	day FWC	**day M**	**day SF**	**day Sub**	**day Wolf**	**night FWC**	**night M**	**night SF**	**night Sub**	**night Wolf**
day FWC		89.9	90.9	87.9	**76.2****	**95.3*****	91.4	89.7	87.8	**83.5***
day M	75.8		91.0	91.0	**79.2***	**87.9****	**93.6*****	**87.5***	**88.2***	86.9
day SF	74.3	81.8		89.7	**77.6***	90.4	92.3	**94.6*****	87.8	86.1
day Sub	72.7	81.9	76.3		**75.5****	87.3	91.5	88.3	**93.4*****	**84.1***
day Wolf	73.3	87.8	83.4	78.2		**75.1*****	**77.4****	**74.9****	**73.6****	**88.3****
night FWC	94.1	76.5	75.2	74.2	74.0		90.9	91.1	88.8	**83.0***
night M	75.1	**93.9*****	80.3	80.9	**86.9***	76.0		90.5	90.3	**86.0***
night SF	73.1	81.4	**93.6***	75.1	82.4	74.1	80.6		88.6	**84.0***
night Sub	72.2	79.9	75.0	94.8	76.0	73.8	79.3	73.6		**82.4***
night Wolf	**71.3***	**84.5*****	81.7	75.8	**91.8*****	**72.3***	**85.9****	81.5	73.9	

Table 2. AIC model selection results for the marginality scores of the K-select for each axis and each study period (A) late-winter period: 1 March- 30 April, and B) spring period: 1 May-30 June) with the variables Time (Day/night), Species (Wolf/bear) and Repro (females with cubs, lone females, adult males, subadult bears of both sexes, and wolf). Number of parameters (K), Akaike information Criteria (AIC), ΔAIC, AIC weight (AICWt) and LogLikelihood (LL) are presented.

A) Late-winter						**B) Spring period**					
Model	**K**	**AIC**	**Delta_AIC**	**AICWt**	**LL**	**Model**	**K**	**AIC**	**Delta_AIC**	**AICWt**	**LL**
		Axis 1						**Axis 1**			
Time	4	93.15	0	0.51	-42.58	Time*Repro	12	82.06	0.00	0.92	-29.03
Species*Time	6	93.60	0.45	0.41	-40.80	Species*Time	6	87.38	5.32	0.06	-37.69
Null	3	98.63	5.48	0.03	-46.31	Time	4	90.08	8.02	0.02	-41.04
Time*Repro	12	99.16	6.01	0.03	-37.58	Repro	7	101.12	19.06	0.00	-43.56
Species	4	99.64	6.49	0.02	-45.82	Species	4	109.19	27.13	0.00	-50.60
Repro	7	102.17	9.02	0.01	-44.08	Null	3	113.93	31.86	0.00	-53.96
		Axis 2						**Axis 2**			
Repro	7	107.30	0	0.88	-46.65	Time	4	33.45	0.00	0.49	-12.73
Time*Repro	12	111.23	3.93	0.12	-43.62	Species*Time	6	34.46	1.01	0.29	-11.23
Time	4	129.56	22.26	0	-60.78	Species	4	36.30	2.84	0.12	-14.15
Species	4	129.79	22.49	0	-60.90	Null	3	37.30	3.84	0.07	-15.65
Species*Time	6	129.99	22.69	0	-58.99	Repro	7	39.23	5.77	0.03	-12.61
Null	3	131.23	23.93	0	-62.62	Time*Repro	12	42.97	9.51	0.00	-9.48
		Axis 3						**Axis 3**			
Repro	7	60.14	0	0.67	-23.07	Time*Repro	12	6.01	0.00	0.42	9.00
Time*Repro	12	61.59	1.44	0.33	-18.79	Time	4	6.43	0.43	0.34	0.78
Null	3	80.49	20.35	0	-37.25	Species*Time	6	8.30	2.29	0.13	1.85
Time	4	82.10	21.95	0	-37.05	Repro	7	9.13	3.13	0.09	2.43
Species	4	82.26	22.11	0	-37.13	Null	3	12.22	6.21	0.02	-3.11
Species*Time	6	85.71	25.57	0	-36.86	Species	4	13.72	7.71	0.01	-2.86
		Axis 4						**Axis 4**			
Repro	7	106.48	0.00	0.38	-46.24	Time	4	-5.39	0.00	0.77	6.70
Null	3	106.77	0.29	0.33	-50.38	Species*Time	6	-2.97	2.42	0.23	7.49
Time	4	108.50	2.02	0.14	-50.25	Null	3	5.82	11.21	0.00	0.09
Species	4	108.75	2.28	0.12	-50.38	Species	4	6.21	11.60	0.00	0.89
Species*Time	6	112.48	6.00	0.02	-50.24	Time*Repro	12	7.17	12.56	0.00	8.42
Time*Repro	12	115.50	9.02	0.00	-45.75	Repro	7	11.45	16.84	0.00	1.27
		Axis 5						**Axis 5**			
Null	3	55.88	0.00	0.46	-24.94	Repro	7	-67.54	0.00	0.50	40.77
Species	4	57.87	1.98	0.17	-24.93	Time	4	-66.25	1.29	0.26	37.13
Time	4	57.88	2.00	0.17	-24.94	Time*Repro	12	-65.29	2.25	0.16	44.64
Repro	7	57.92	2.03	0.17	-21.96	Species*Time	6	-62.30	5.24	0.04	37.15
Species*Time	6	61.56	5.67	0.03	-24.78	Null	3	-62.15	5.39	0.03	34.08
Time*Repro	12	65.51	9.63	0.00	-20.76	Species	4	-60.20	7.34	0.01	34.10

		Axis 6						**Axis 6**			
Repro	7	1.04	0.00	0.28	6.48	Null	3	-64.94	0	0.44	35.47
Null	3	1.27	0.23	0.25	2.37	Time	4	-64.00	0.94	0.28	36.00
Time	4	2.14	1.10	0.16	2.93	Species	4	-63.02	1.92	0.17	35.51
Species*Time	6	2.15	1.10	0.16	4.93	Repro	7	-61.32	3.62	0.07	37.66
Species	4	2.87	1.83	0.11	2.56	Species*Time	6	-60.13	4.81	0.04	36.06
Time*Repro	12	5.47	4.43	0.03	9.26	Time*Repro	12	-52.94	11.99	0	38.47

Table 3. Parameter estimates for each of the fixed effects retained in the best linear mixed models based on AIC model comparison (Table 2). Estimates are presented for each study period (A) late-winter period: 1 March- 30 April, and B) spring period: 1 May-30 June). Beta estimates, standard error (SE) and lower (LCI) and upper (UCI) 95% confidence intervals are presented. FWC: female bears with cubs, F: single female bear, M: adult male bear, S: sub-adult bear. [1]Wolf, [2]Day, [3]Wolf_day and [4]Bear are the respective categorical reference on the intercept.

A) Late-winter

	Beta	SE	LCI	UCI
Axis 1				
Intercept[2]	0.51	0.10	0.30	0.71
Night	-0.15	0.05	-0.26	-0.04
Axis 2				
Intercept[1]	0.64	0.28	0.07	1.21
Bear_FWC	-0.58	0.37	-1.32	0.17
Bear_M	-0.36	0.32	-0.99	0.28
Bear_SF	-0.38	0.32	-1.03	0.27
Bear_Sub	-1.20	0.32	-1.85	-0.56
Axis 3				
Intercept[1]	-0.05	0.37	-0.79	0.69
Bear_FWC	0.32	0.47	-0.64	1.28
Bear_M	0.40	0.40	-0.40	1.21
Bear_SF	0.11	0.41	-0.70	0.93
Bear_Sub	-0.36	0.40	-1.17	0.44
Axis 4				
Intercept	0.26	0.08	0.26	0.52
Axis 5				
Intercept	0.36	0.23	0.19	0.27
Axis 6				
Intercept	-0.01	0.06	0.13	0.19

B) Spring period

	Beta	SE	LCI	UCI
Axis 1				
Intercept[3]	-0.86	0.16	-1.19	-0.54
Wolf_night	0.28	0.14	0.00	0.56
bear_FWC_day	0.57	0.19	0.20	0.94
bear_FWC_night	0.74	0.19	0.37	1.11
bear_M_day	0.28	0.18	-0.08	0.64
bear_M_night	0.50	0.18	0.15	0.86
bear_SF_day	0.34	0.18	-0.02	0.69
bear_SF_night	0.55	0.18	0.20	0.91
bear_Sub_day	0.59	0.18	0.24	0.95
bear_Sub_night	0.76	0.18	0.40	1.12
Axis 2				
Intercept[2]	-0.10	0.04	-0.17	-0.02
Night	0.08	0.03	0.01	0.14
Axis 3				
Intercept[2]	-0.10	0.04	-0.17	-0.02
Night	0.08	0.03	0.01	0.14
Axis 4				
Intercept[2]	0.00	0.04	-0.07	0.08
Night	-0.10	0.03	-0.15	-0.05
Axis 5				
Intercept[2]	0.00	0.03	-0.06	0.06
Night	0.06	0.02	0.01	0.10
Axis 6				
Intercept	0.03	0.03	-0.08	0.02

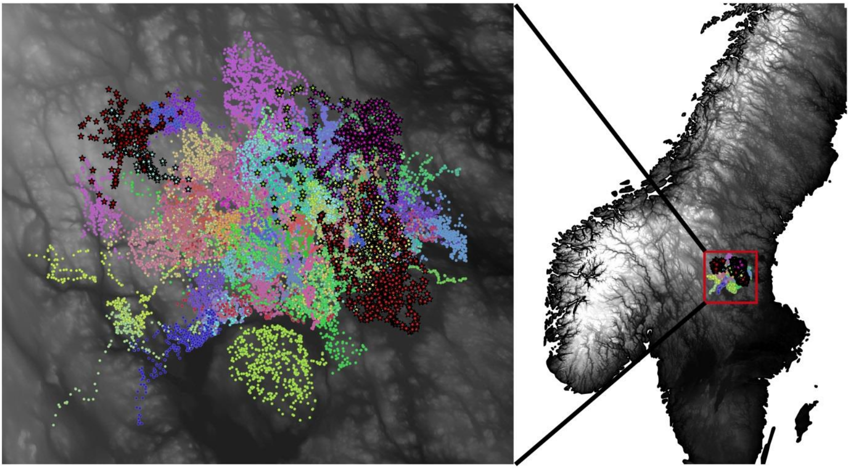


Figure 1. Map of the study area in central Sweden. The elevational gradient is shaded from black (low elevation) to white (high elevation). GPS-locations from brown bears (circles) and wolves (stars with black outline) are shown in different colors for each individual-year.

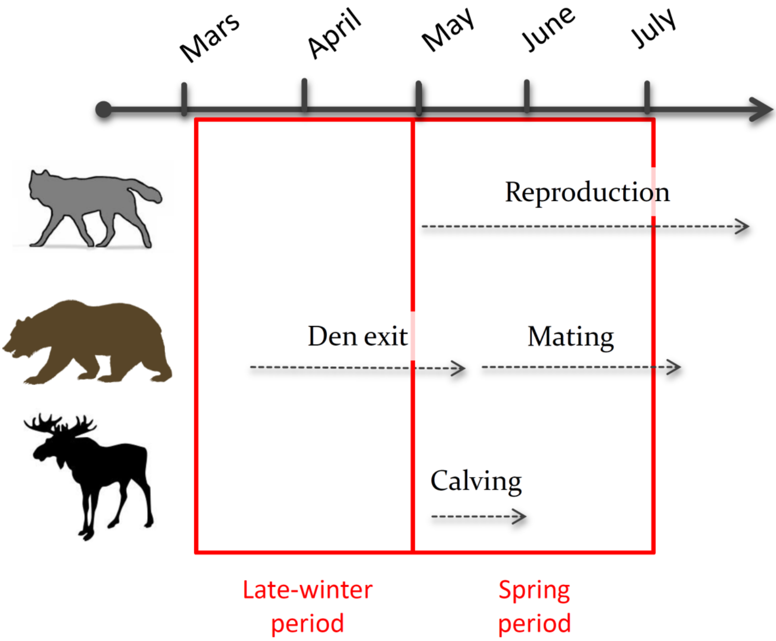


Figure 2. Biological justification of two study periods (red full boxes) in late winter (1 March - 30 April), and spring (1 May - 30 June) to analyze habitat selection of wolves and brown bears in central Sweden. Dashed gray lines illustrate the approximate duration of specific behaviors of wolves, bears and moose, a staple prey of both species.

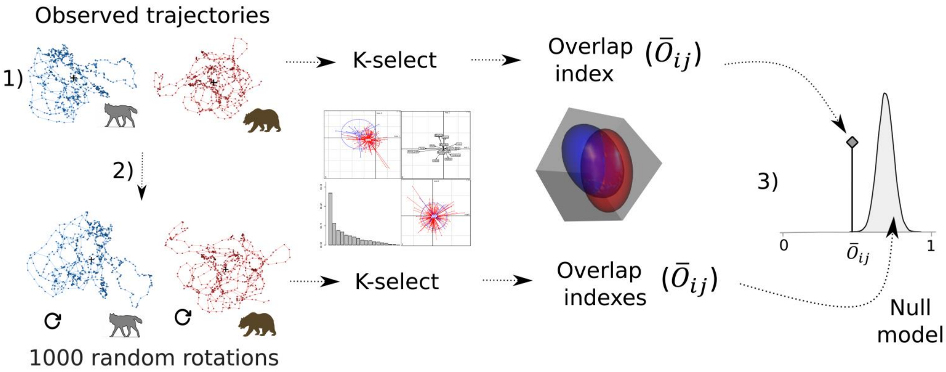
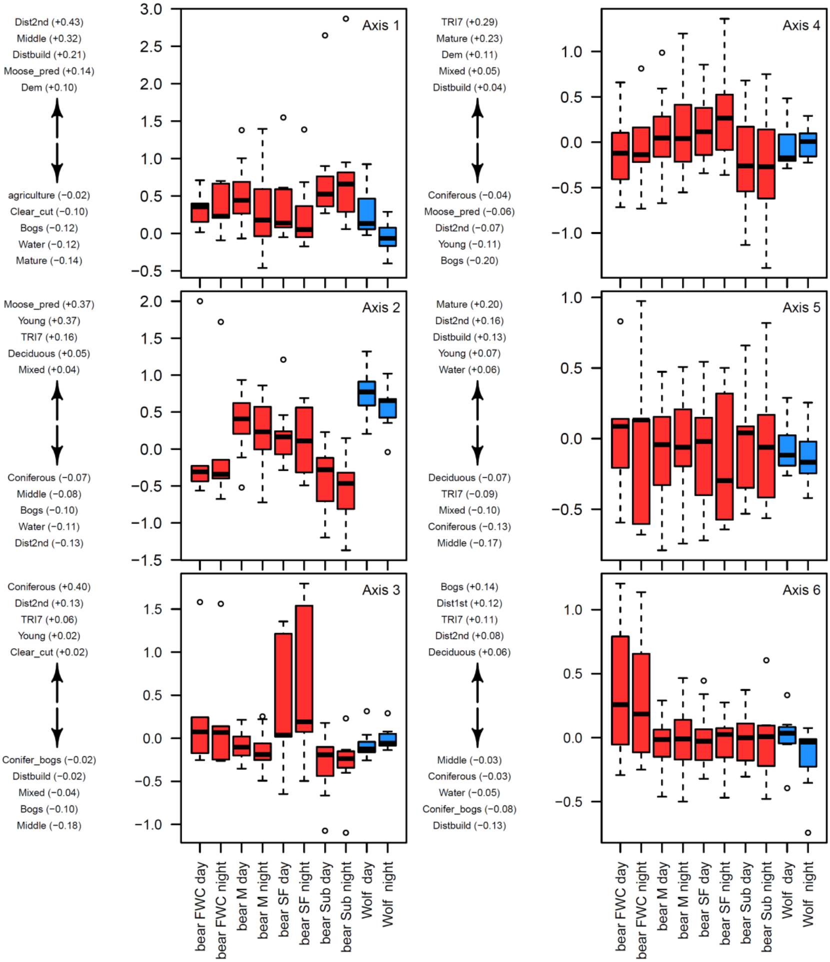


Figure 3. Flow chart illustrating the procedure to analyze wolf and brown bear habitat niche overlap in central Sweden. 1) Observed trajectories from each individual wolf and bear were used to quantify habitat selection with the K-select (See Methods). The 4 plots illustrate results obtained with the K-select (Appendix1, Figure A2-A3) which we used to calculate an overlap index ($\bar{O}_{ij}$ =0-100%) in terms of habitat used by wolves and bears. This overlap index was calculated over all axes of the K-select (i.e., weighted by the respective eigen values obtained on each axis). The 3D plot illustrates the habitat niche (ellipses) of wolves (blue) and bears (red) on only 3 different axes for illustrative purpose ($\bar{O}_{ij}$ was actually performed on 18 different axes identified by the K-select). The area of overlap between the two ellipses illustrates the area of overlap between wolves and bears. 2) To create random use of the habitat by both species, we randomly rotated the complete trajectory from each individual around its centroid 1000 times. The same procedure described in 1) was used for each of the 1000 simulated datasets. 3) The 1000 overlap indexes were used to create the null model (density distribution curve: null hypothesis), the random distribution of the overlap index under random habitat used by both species. If the observed overlap index (vertical line, at the left of the density distribution curve) was ≤ to 95% of the simulated overlap indexes, we rejected our null hypothesis and accepted our alternative hypothesis that segregation between both species was higher than expected by chance.

A) Late winter period



B) Spring period

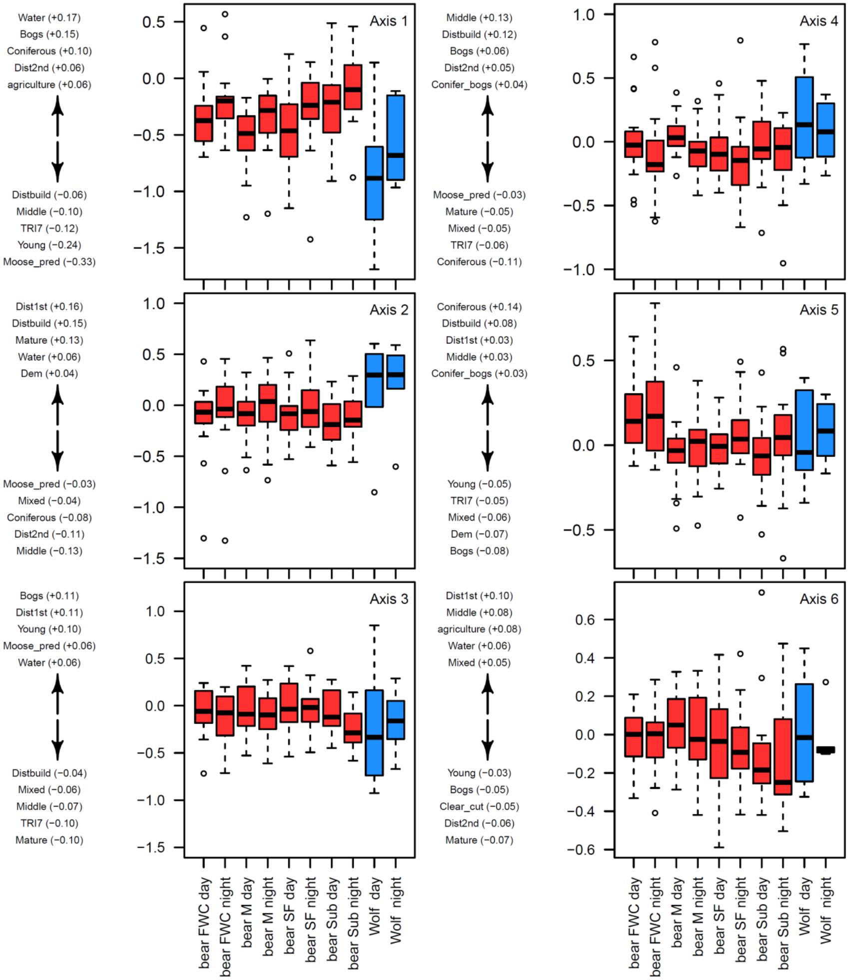


Figure 4. Boxplot of the K-select analysis for habitat selection of wolves (blue) and brown bears (red) in central Sweden for the A) late-winter period (1 March - 30 April) and B) spring period (1 May - 30 June). Boxplots show marginality scores per species and reproductive status for axis 1-6 of the K-select, respectively. The 5 variables contributing the most on each axis are shown on the left side of each box plot, with positive values above the arrow and negative values below the arrow. The scores of the 5 variables contributing the most are represented in brackets.

Appendix 1

Table A1. Reclassification of ‘Svenskt-Marktäckedata’ (SMD) land cover map (Lantmäteriet, Sweden; 25 x 25 m) used in the analysis of wolf and brown bear habitat selection in central Sweden, and percentage represented by each land cover class.

Original ID represented	Reclassification	Abbreviation	%
1.	Human settlements	Human	0.8%
2.	Agricultural fields	Agri	1.5%
3.1.1.1 & 3.1.1.2	Deciduous forest	Deciduous	1.4%
3.1.2.1.1	Coniferous forest on lichen	coniferous	7.1%
3.1.2.2	Coniferous forest on bog	Conifer_bogs	1.9%
3.1.2.1.2.1	Midage coniferous forest	Middle	27.5%
3.1.2.1.2.2 & 3.1.2.3 & 3.3.2	Mature coniferous forest	Mature	23.8%
3.1.3.1 & 3.1.3.2	Mixed forest	Mixed	2.5%
3.2.4.1 & 3.2.4.3	Young forest	Young	10.9%
3.2.4.2	Clear cut	Clear_cut	6%
4.	Bogs	Bogs	11.2%
5.	Water	Water	5.4%

Table A2. AIC model selection results for the moose model (zero-inflated negative model) used to estimate spatial variation in moose density in our study area in central Sweden. Description of the land use characteristics is provided in Table 1 of the main text. Dist1st and Dist2nd show distance (km) to main and secondary roads, respectively. TRI7 is a terrain ruggedness index created using a 7 x 7moving window. Number of parameters (K), Akaike Information Criteria (AIC), ΔAIC, and AIC weight (AIC Wt) are presented.

Models	K	**AIC**	**ΔAIC**	**AIC Wt**
Young + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | coniferous + Mid + Young + Mature + mixed + dist2nd + TRI7 + DEM	17	7174.36	0	0.18
Young + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | coniferous + Mid + Young + Mature + dist2nd + TRI7 + DEM	16	7174.494	0.134	0.17
Young + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | coniferous + Mid + Young + Mature + mixed + Clear_cut + dist2nd + TRI7 + DEM	18	7174.801	0.441	0.14
Young + Mature + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | coniferous + Mid + Young + Mature + mixed + Clear_cut + dist2nd + TRI7 + DEM	19	7175.372	1.012	0.11
Young + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | Mid + Young + Mature + dist2nd + TRI7 + DEM	15	7175.449	1.089	0.1
agri + Young + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | Mid + Young + Mature + dist2nd + TRI7 + DEM	16	7176.084	1.724	0.08
deciduous + Young + Mature + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | deciduous + coniferous + Mid + Young + Mature + mixed + Clear_cut + dist2nd + TRI7 + DEM	21	7176.281	1.921	0.07
deciduous + Young + Mature + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | coniferous + Mid + Young + Mature + mixed + Clear_cut + dist2nd + TRI7 + DEM	20	7177.239	2.879	0.04
deciduous + Young + Mature + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | deciduous + coniferous + Mid + Young + Mature + mixed + Clear_cut + Bogs + dist2nd + TRI7 + DEM	22	7177.341	2.981	0.04
deciduous + Young + Mature + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | deciduous + coniferous + Mid + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + TRI7 + DEM	23	7178.146	3.786	0.03
deciduous + coniferous + Young + Mature + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | deciduous + coniferous + Mid + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + TRI7 + DEM	24	7179.707	5.347	0.01
agri + deciduous + coniferous + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | agri + deciduous + coniferous + Mid + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + TRI7 + DEM	28	7179.944	5.584	0.01
deciduous + coniferous + Young + Mature + mixed + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | deciduous + coniferous + Mid + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + TRI7 + DEM	25	7181.662	7.302	0
agri + deciduous + coniferous + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | agri + deciduous + coniferous + Mid + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + +dist1st + TRI7 + DEM	29	7181.867	7.507	0
deciduous + coniferous + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | deciduous + coniferous + Mid + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + TRI7 + DEM	26	7182.349	7.989	0
agri + deciduous + coniferous + Mid + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + dist1st + DEM | agri + deciduous + coniferous + Mid + Young + Mature + mixed + Clear_cut + Bogs +	30	7183.855	9.495	0

<table>
<tr><td>Conifer_bogs + dist2nd + +dist1st + TRI7 + DEM</td><td></td><td></td><td></td><td></td></tr>
<tr><td>agri + deciduous + coniferous + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + dist1st + DEM |
deciduous + coniferous + Mid + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + TRI7 + DEM</td><td>27</td><td>7184.018</td><td>9.658</td><td>0</td></tr>
<tr><td>agri + deciduous + coniferous + Mid + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + dist1st + TRI7 + DEM +human|
agri + deciduous + coniferous + Mid + Young + Mature + mixed + Clear_cut + Bogs + Conifer_bogs + dist2nd + +dist1st + TRI7 + DEM + human</td><td>33</td><td>7188.157</td><td>13.80</td><td>0</td></tr>
<tr><td>Null</td><td>3</td><td>7567.932</td><td>393.572</td><td>0</td></tr>
</table>

Table A3. Parameter-averaged estimates of the best supported models (zero-inflated negative model) used to estimate spatial variation in moose density in the study area in central Sweden. Description of the land use characteristics is provided in Table 1. Dist1st and Dist2nd show distance (km) to main and secondary roads, respectively. TRI7 is a terrain ruggedness index created using a 7 x 7 moving window. All variables were scaled to facilitate interpretation.

Parameter	**β**	**SE**
Binomial part (zero values)		
Intercept	-2.07	0.75
Young forest	-0.57	0.15
Mixed forest	-0.08	0.11
Coniferous forest on bog	-0.17	0.13
Dist2nd	0.36	0.14
TRI7	-0.26	0.09
Elevation	0.01	0.01
Mid age coniferous forest	-0.82	0.19
Mature coniferous forest	-0.56	0.20
Clear cut	-0.05	0.10
Deciduous forest	-0.04	0.18
Negative binomial part (nonzero values)		
Intercept	-0.14	0.25
Bogs	-0.19	0.09
Young forest	0.30	0.04
Mature coniferous forest	-0.01	0.04
Dist2nd	0.27	0.07
Dist1st	0.19	0.05
Elevation	0.01	0.01
Coniferous forest on bog	-0.18	0.07
Agricultural fields	-0.01	0.03
Deciduous forest	-0.01	0.02

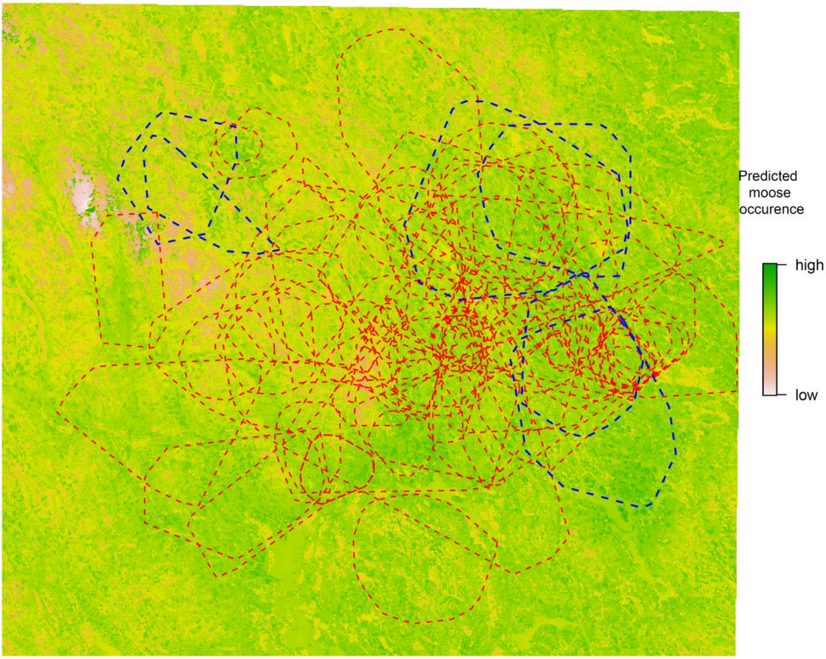


Figure A1. Spatial prediction of moose occurrence in our study area in central Sweden based on pellet counts and zero-inflated negative models. High and low represents high to low number of pellets predicted (Moose_pred) by our best moose model. Red and blue dashed lines show the 95% MCP polygons for each individual bear and wolf, respectively.

Table A3. Summary of GPS locations from each individual wolf and bear included in the study to quantify habitat niche overlap between both species. For wolves, the name of the territory was used as the identification name. Sex of the individual for wolves, i.e. male (M) and female (F), and reproductive status of bears (females with cubs (FWC), lone females (F), adult males (M), and sub-adult bears of both sexes (S) are noted. “Date.begin” and “Date.end” refer the date and time of the first and last position used for each individual, respectively. We show the data for the late-winter (1 March – 30 April) and the spring period of study (1 May – 30 June).

Late-winter Period

Wolf

Territory	Sex	Date.begin		Date.end	
Kukumaki	M	3/5/2013	19:00:13	4/28/2013	23:00:44
Kukumaki	M	3/3/2014	1:00:50	4/25/2014	13:00:47
Kukumaki	F	3/4/2015	4:00:00	4/24/2015	5:00:00
Tandsjon	M	3/1/2012	0:00:44	4/30/2012	23:00:52
Tandsjon	M	3/19/2014	13:00:43	4/25/2014	23:00:39
Tenskog	M	3/1/2010	0:00:50	4/11/2010	3:00:56
Tenskog	M	3/14/2011	0:00:14	4/30/2011	23:00:42

Bear

id	Sex	Date.begin		Date.end	
W0104	FWC	4/1/2013	12:00:00	4/30/2013	23:30:00
W0209	FWC	4/1/2010	2:31:00	4/30/2010	23:30:00
W0217	FWC	4/1/2014	10:02:00	4/30/2014	23:00:00
W0610	SF	4/1/2014	0:00:00	4/30/2014	23:00:00
W0620	FWC	4/1/2014	0:00:00	4/30/2014	23:00:00
W0625	M	4/1/2010	9:33:00	4/30/2010	23:30:00
W0625	M	4/11/2011	11:30:00	4/30/2011	23:30:00
W0625	M	4/18/2013	16:30:00	4/30/2013	23:30:00
W0703	SF	4/11/2011	13:34:00	4/30/2011	23:30:00
W0716	FWC	4/1/2013	0:31:00	4/30/2013	23:30:00
W0719	M	4/1/2011	0:01:00	4/30/2011	23:30:00
W0720	FWC	4/4/2011	10:33:00	4/30/2011	23:30:00
W0802	M	4/1/2011	2:01:00	4/30/2011	23:31:00
W0805	M	4/1/2011	0:00:00	4/30/2011	23:30:00
W0818	SF	4/2/2014	0:33:00	4/30/2014	23:30:00
W0825	SF	4/2/2011	11:31:00	4/30/2011	23:30:00
W0825	SF	4/1/2014	0:00:00	4/30/2014	23:00:00
W1001	M	4/12/2010	13:29:00	4/30/2010	23:30:00
W1001	M	4/1/2011	0:02:00	4/30/2011	23:30:00
W1017	SF	4/1/2014	1:01:00	4/30/2014	23:02:00
W1020	M	4/6/2011	14:59:00	4/30/2011	23:30:00
W1110	Sub	4/1/2012	9:32:00	4/30/2012	23:30:00

W1110	SF	4/5/2014	13:02:00	4/30/2014	23:00:00
W1203	SF	4/1/2014	0:02:00	4/30/2014	23:30:00
W1204	Sub	4/1/2013	0:00:00	4/30/2013	23:30:00
W1204	M	4/1/2014	0:00:00	4/30/2014	23:00:00
W1205	Sub	4/1/2014	0:01:00	4/30/2014	23:00:00
W1206	Sub	4/1/2014	1:02:00	4/30/2014	23:00:00
W1206	SF	4/1/2015	12:00:00	4/30/2015	23:00:00
W1209	Sub	4/1/2014	0:01:00	4/30/2014	23:02:00
W1211	M	4/19/2013	9:30:00	4/30/2013	23:30:00
W1211	M	4/1/2014	0:01:00	4/30/2014	23:00:00
W1211	M	4/1/2015	0:00:00	4/30/2015	23:00:00
W1303	Sub	4/1/2014	0:00:00	4/30/2014	23:00:00
W1306	Sub	4/1/2014	0:00:00	4/30/2014	23:00:00
W1314	M	4/1/2014	13:00:00	4/30/2014	23:00:00
W1314	M	4/1/2015	0:01:00	4/30/2015	23:01:00
W1416	M	4/1/2015	0:00:00	4/30/2015	23:01:00
W9301	M	4/4/2010	19:00:00	4/30/2010	23:30:00
W9403	FWC	4/3/2010	9:33:00	4/30/2010	23:30:00

Spring Period

Wolf

Territory	Sex	date.begin		date.end	
Kukumaki	M	5/19/2014	1:00:46	6/22/2014	23:00:48
Kukumaki	F	5/18/2015	1:01:00	6/29/2015	16:00:00
Tandsjon	M	5/19/2014	1:02:08	6/21/2014	11:00:44
Tandsjon	M	5/1/2012	0:01:19	5/14/2012	0:00:48
Tenskog	M	5/30/2011	0:00:13	6/26/2011	23:00:43
Tenskog	M	5/1/2011	0:00:48	5/15/2011	23:00:41

Bear

id	sex	date.begin		date.end	
W0104	FWC	5/1/2013	0:00:00	5/31/2013	23:30:00
W0104	SF	6/1/2013	0:00:00	6/30/2013	23:30:00
W0104	FWC	5/1/2015	0:00:00	6/30/2015	9:01:00
W0209	FWC	5/1/2010	0:01:00	6/23/2010	14:30:00
W0217	FWC	5/1/2014	2:02:00	6/5/2014	21:01:00
W0425	FWC	5/1/2010	0:01:00	6/30/2010	23:30:00
W0425	FWC	5/1/2011	0:02:00	6/30/2011	23:30:00
W0425	SF	5/1/2014	0:00:00	6/30/2014	23:00:00
W0517	SF	5/1/2012	2:00:00	6/30/2012	23:00:00
W0605	FWC	5/1/2014	0:00:00	6/30/2014	23:02:00
W0610	SF	5/1/2011	0:00:00	6/30/2011	23:30:00
W0610	SF	5/1/2014	0:00:00	6/30/2014	23:00:00
W0611	SF	5/1/2010	0:00:00	6/30/2010	23:30:00
W0611	SF	5/1/2011	0:00:00	6/30/2011	23:30:00

W0620	FWC	5/1/2014	0:00:00	6/30/2014	23:00:00
W0625	M	5/1/2010	0:00:00	6/30/2010	23:30:00
W0625	M	5/1/2011	0:00:00	6/30/2011	23:30:00
W0625	M	5/1/2013	0:00:00	6/10/2013	23:30:00
W0625	M	5/1/2014	0:00:00	6/30/2014	23:00:00
W0703	SF	5/1/2011	0:01:00	6/30/2011	23:30:00
W0716	FWC	5/1/2013	0:00:00	6/30/2013	22:31:00
W0716	FWC	5/1/2014	0:00:00	6/30/2014	23:01:00
W0719	M	5/1/2011	0:00:00	6/30/2011	23:30:00
W0719	M	5/1/2014	0:00:00	6/30/2014	23:00:00
W0720	FWC	5/1/2011	0:00:00	6/30/2011	23:30:00
W0720	FWC	5/1/2014	0:00:00	6/30/2014	23:00:00
W0802	M	5/1/2011	0:00:00	6/30/2011	23:30:00
W0805	M	5/1/2010	0:00:00	6/30/2010	23:30:00
W0805	M	5/1/2011	0:00:00	6/30/2011	23:31:00
W0806	SF	5/1/2014	0:00:00	6/30/2014	23:00:00
W0818	SF	5/1/2014	0:00:00	6/30/2014	21:01:00
W0825	SF	5/1/2011	0:00:00	6/30/2011	23:30:00
W0825	SF	5/1/2014	0:02:00	6/30/2014	23:01:00
W0910	M	5/1/2014	1:00:00	6/30/2014	23:01:00
W1001	M	5/1/2010	0:00:00	6/30/2010	23:30:00
W1001	M	5/1/2011	0:00:00	6/30/2011	23:30:00
W1011	SF	5/1/2014	0:00:00	6/30/2014	23:00:00
W1017	Sub	5/1/2011	0:32:00	6/30/2011	23:30:00
W1020	M	5/1/2011	0:00:00	6/30/2011	23:30:00
W1105	SF	5/1/2014	0:00:00	6/30/2014	23:01:00
W1110	Sub	5/1/2012	0:00:00	6/30/2012	23:30:00
W1110	SF	5/1/2014	0:00:00	6/30/2014	23:01:00
W1203	SF	5/1/2014	0:00:00	6/30/2014	21:00:00
W1204	Sub	5/1/2013	0:00:00	6/30/2013	23:30:00
W1204	M	5/1/2014	0:01:00	6/30/2014	23:00:00
W1205	Sub	5/1/2013	0:00:00	6/30/2013	23:31:00
W1205	Sub	5/1/2014	1:00:00	6/30/2014	23:00:00
W1205	SF	5/1/2015	0:00:00	6/30/2015	23:00:00
W1206	Sub	5/1/2014	0:00:00	6/30/2014	23:00:00
W1206	SF	5/1/2015	0:00:00	6/29/2015	12:00:00
W1209	Sub	5/1/2014	0:02:00	6/30/2014	23:01:00
W1210	M	5/1/2014	0:00:00	6/30/2014	23:00:00
W1211	M	5/1/2013	0:00:00	6/30/2013	23:30:00
W1211	M	5/1/2014	0:00:00	6/30/2014	22:00:00
W1211	M	5/1/2015	0:00:00	6/29/2015	4:01:00
W1301	Sub	5/1/2014	0:00:00	6/6/2014	6:00:00
W1302	Sub	5/1/2014	0:00:00	6/30/2014	22:00:00
W1303	Sub	5/1/2014	0:02:00	6/30/2014	23:00:00
W1304	Sub	5/1/2014	0:00:00	6/30/2014	23:02:00
W1305	Sub	5/1/2014	0:02:00	6/30/2014	23:00:00

W1306	Sub	5/1/2014	1:00:00	6/20/2014	2:00:00
W1307	Sub	5/1/2014	0:00:00	6/30/2014	23:00:00
W1308	Sub	5/1/2014	0:00:00	6/30/2014	23:00:00
W1312	M	5/1/2014	0:00:00	6/30/2014	23:01:00
W1314	M	5/15/2013	14:30:00	6/27/2013	2:00:00
W1314	M	5/1/2014	0:00:00	6/25/2014	20:59:00
W1314	M	5/1/2015	0:00:00	6/30/2015	23:00:00
W1316	Sub	5/1/2014	0:00:00	6/30/2014	23:02:00
W1317	Sub	5/1/2014	0:00:00	6/30/2014	23:00:00
W1319	FWC	5/1/2014	0:00:00	6/30/2014	23:00:00
W1407	Sub	5/1/2014	0:00:00	6/30/2014	23:00:00
W1408	Sub	5/1/2014	0:00:00	6/30/2014	23:00:00
W1416	M	6/4/2014	21:00:00	6/30/2014	22:00:00
W1416	M	5/1/2015	0:00:00	6/30/2015	23:00:00
W1417	SF	6/5/2014	14:00:00	6/30/2014	23:01:00
W1505	SF	5/12/2015	13:00:00	6/30/2015	23:00:00
W9301	M	5/1/2010	0:00:00	6/30/2010	23:30:00
W9403	FWC	5/1/2010	0:00:00	6/30/2010	23:30:00
W9403	FWC	5/1/2014	0:02:00	6/30/2014	23:30:00

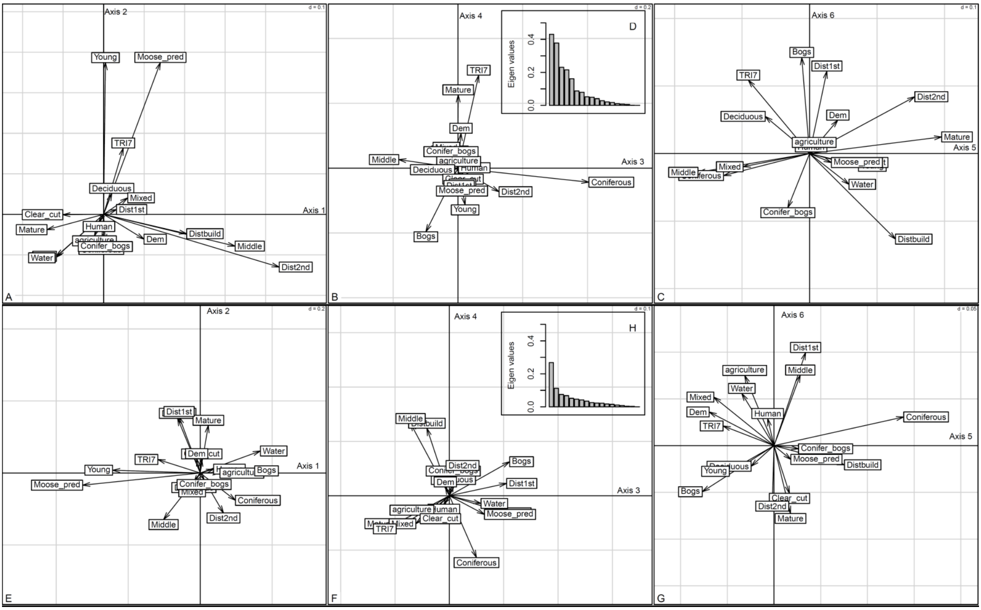


Figure A2. Variable loadings on the factorial axes in our study on wolf and bear habitat selection and niche overlap in central Sweden. Plots in the top panel (A-D) correspond to late-winter period (1 March-30 April) and plots in the bottom panel (E-H) correspond to the spring period (1 May - 30 June). The 3 graphics in each panel show axes 1-2, 3-4, and 5-6, respectively. Graphics D and H shows the bar chart of the K-select eigenvalues, measuring the mean marginality explained by each factorial axis, for the late-winter and spring period, respectively.

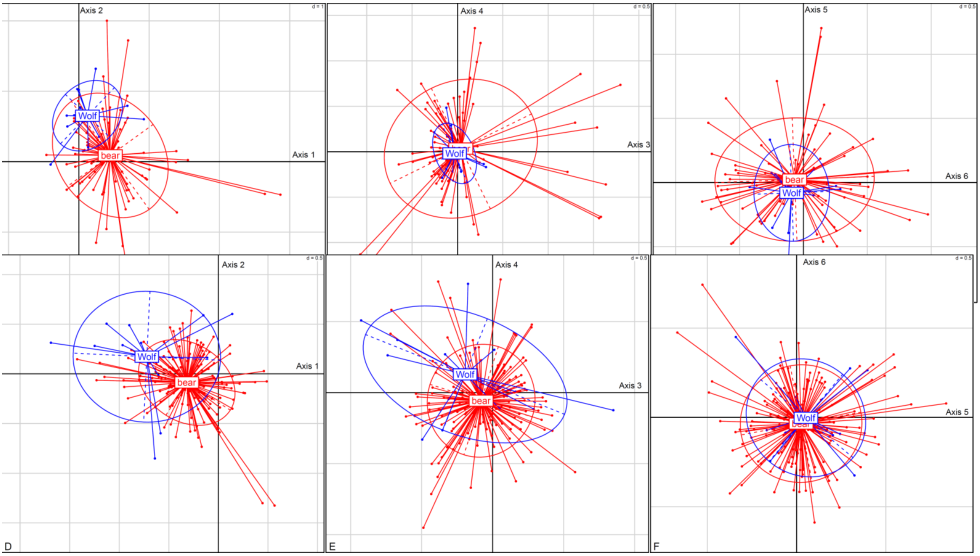


Figure A3 Marginality scores projected on the K-select analysis of each individual wolf (blue) and brown bear (red) in central Sweden, after recentering on each individual home range composition. Each individual-year is represented by 2 points, one for diurnal habitat selection and one for nocturnal habitat selection. Differences in marginality vectors were merged and ellipsed by species. Plots in the top panel (A-C) correspond to the late-winter study period (1 March- 30 April) and plots in the bottom panel (D-F) correspond to the spring study period (1 May-30 June). The 3 graphics in each panel show axes 1-2, 3-4, and 5-6, respectively.