



Faculty of Applied Ecology and Agricultural Sciences

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**Master Thesis**

**On the way to independence: Ebbing cohesion  
in Scandinavian wolf family groups**

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# Table of contents

Sammendrag .....	4
Abstract .....	5
1 Introduction.....	6
Predictions.....	10
2 Methods .....	11
2.1 Study area.....	11
2.2 Study animals.....	12
2.3 Identifying wolf territories, natality, extraterritorial and dispersal movements.....	12
2.4 Extracting intra-territory inter-individual spatial relationships.....	14
2.5 Changepoint analyses on time of reproduction.....	15
2.6 Generalized Additive Mixed Model .....	17
3 Results.....	19
3.1 PELT algorithm changepoints on reproduction .....	19
3.2 Cumulative dispersal and movement classes .....	21
3.3 Generalized additive mixed model on pack cohesion.....	23
4 Discussion.....	26
Management implications .....	29
Acknowledgements .....	30
References.....	31

## Sammendrag

Sosial organisering er av stor betydning for å kunne forstå enkeltindividers områdebruk i tid og rom, men også demografiske, fitnessrelaterte, og overordnede populasjonsdynamiske prosesser. Den grunnleggende sosiale enheten hos ulv består av det monogame revirmarkerende paret med en lederhann og en ledertispe, og sammen med deres avkom utgjør de en familiegruppe, eller det som ofte betegnes som en ulveflokk. Familiegruppens flokksamhold og forflyningsmønster i reviret avhenger av ulvenes årssyklus. I denne studien presenterer jeg 14 år med unike GPS-data fra 11 familiegrupper av ulv i den rekoloniserende skandinaviske ulvebestanden. Jeg undersøkte det romlige og tidsmessige flokksamholdet mellom lederhann og ledertispe, mellom valper og lederdyr, og mellom valper og andre kulløsken fra 1. januar til 1. juli eller frem til valpenes utvandringstidspunkt. Jeg standardiserte parkonstellasjonene på firetimersintervaller for totalt 30 forskjellige merkede valper, og 21 lederdyr. Jeg undersøkte avstanden mellom individene som et mål på flokksamhold ved å benytte en ikke-lineær regressiv tidsserieanalyse (GAMM) med justerte referansenivåer og interaksjon på tid. Samholdet var sterkest tidlig på vinteren, men avtagende over tid, preget av at valpene ble stadig mer uavhengige fra resten av familiegruppen før de fleste valper ( $n = 22$ , 76%) utvandret fra hjemreviret på våren før 14 måneders alder. Før spredning identifiserte jeg utforskende forflytninger hos 12 (54%) utvandrende valper, men aldri for hjemmeværende valper som ikke vandret ut. Lederparet forflyttet seg nesten utelukkende sammen før fødselsperioden, og den eneste gangen avstanden mellom lederhannen og -tispa var signifikant forskjellig fra null var rundt fødsel. Avstanden mellom valper og lederdyr og valper og andre kulløsken ble signifikant forskjellig fra avstanden mellom de to lederulvene i paringsperioden, og dette vedvarte til etter fødsel av neste valpekull. Avstanden mellom valper og lederdyr og par av valper var ikke signifikant forskjellige fra hverandre, noe som tyder på at valpene blir uavhengige fra sine foreldre og andre kulløsken mer eller mindre samtidig før utvandring. Mine resultater står i sterk kontrast til myten om at medlemmer av en ulveflokk angivelig går sammen til enhver tid. Mine funn kan ha betydning for overvåkningsprogrammer som har til målsetning å beregne antall ulver og eller antall ynglinger, men også for planlegging samt gjennomføring av en effektiv jakt på familiegrupper av ulv i fremtiden.

**Nøkkelord:** *Canis lupus*, sosial organisering, ulv, utvandring, flokksamhold.

## Abstract

Studying the social organization in animal populations is of primary importance for understanding individual spatial distribution, demography, fitness, and population dynamics. The basic social unit in wolves consists of the monogamous territory-marking pair, and together with their offspring from the contemporary and/or previous litters they form a family group, commonly referred to as the wolf pack. The pack's grouping behavior and movement pattern depends on the wolves' annual cycle. In this study, I present 14 years of unique GPS data of 11 wolf family groups from the recolonizing Scandinavian wolf population. Specifically, I investigated spatial and temporal cohesion between the adult breeding male and female, pairs of pups, and between pups and adult breeders from January 1 to July 1, or until the pup dispersed. I derived simultaneous positions at four-hourly intervals from a total of 30 marked pups and 21 adult breeders. I investigated the paired inter-individual distances as a measure of cohesion by utilizing a regressive non-linear time series analysis (GAMM) with added interaction term on time and adjusted reference levels. The cohesion was strongest in early winter but declining over time, characterized by wolf pups becoming increasingly independent from the rest of their family group, before most pups ( $n = 22$ , 76%) eventually dispersed in the spring before 14 months of age. Prior to dispersal, extraterritorial movements were identified in 12 (54%) dispersing pups, but not for philopatric pups, and these movements were concentrated prior to the birth of the next litter. Adult breeding pairs moved almost exclusively together before denning and the only time the adult breeding pair's cohesion was significantly different from zero was around the time of birth. The cohesion of pups to adult breeders and pairs of pups became significantly different from the cohesion between the adult breeders during the mating season and this effect persisted to past the time of birth of the next litter. The cohesion of pups to adult breeders and pairs of pups was not significantly different from each other, suggesting that pups became independent from their parents and rest of the family group more or less simultaneously before dispersal. My results are in strong contrast to the common belief that members of a wolf pack allegedly operate as a strictly synchronized unit. This may have implications for wolf monitoring programs in terms of calculating the number of wolves and reproductions, and for the planning and implementation of effective culling on wolf family groups in the future.

**Keywords:** *Canis lupus*, Cohesion, Dispersal, Spatial, Social organization, Temporal, Wolf.

# 1 Introduction

Kin selection theory (Hamilton 1964) describes how altruism in group-living animal species is potentially beneficial, highlighting the importance of relatedness in evolution (Smith 2014). Kin selection, also known as inclusive fitness theory, demonstrates how altruistic (i.e. seemingly selfless) behaviors can increase in frequency within a population if the costs to the individual are compensated by increased fitness of related individuals (Eberhard 1975; Gardner, West & Wild 2011). Although affiliation among kin is common in social groups of animals, kinship does not safeguard from negative effects of social competition (Clutton-Brock & Parker 1995; Mock & Parker 1998). In fact, in social groups, the closest competitor is often kin (West, Pen & Griffin 2002; Smith 2014).

The study of social interactions is of primary importance for understanding individuals' temporal space use, gene flow, demography and, resource acquisition as well as population dynamics (Singleton & Hay 1983; Morin *et al.* 1994). Group living can provide several potential direct fitness benefits such as cooperative hunting, resource defense, increased foraging efficiency, predator vigilance, or allo-parental care (Macdonald 1983; Packer & Rutan 1988; Patterson & Messier 2001; Sparkman *et al.* 2011a). These benefits are trade-offs against direct disadvantages related to social competition, disease transmission and increased exposure to parasites (Alexander 1974; Altizer *et al.* 2003; Fuchs *et al.* 2016). The balance between social tolerance, i.e., withholding social aggression, and competition among kin is affected by resource distribution and individuals' spatiotemporal proximity (Alexander 1974; Foster, Wenseleers & Ratnieks 2006). Critical determinants of group formation are diet and the dispersion of food resources (Gittleman 1989). The resource dispersion hypothesis (RDH) suggests that if resources are heterogeneous in time or space, group living is potentially beneficial (Macdonald 1983). If resources are sufficiently patchily distributed in time and space and exceed a critical level of richness, the use of these patches will sustain exploitation by more than just a primary group of occupants. However, secondary occupants could experience lowered food security by exceeding the limits of feeding constraints and social competition (Caraco & Wolf 1975; Nudds 1978; Carr & Macdonald 1986; Bacon, Ball & Blackwell 1991; Johnson *et al.* 2002). Accordingly, the abundance, quality, and distribution of resources can modulate animal movements and behavior, consequently influencing group size and grouping behavior, both spatially and temporally (Macdonald 1983; von Schantz 1984; Carr & Macdonald 1986; Powell 2012).

The wolf (*Canis lupus*) is a good model species for illustrating socio-spatial organization among kin. Wolves follow a relatively rare monogamous mating system (Kleiman 1977; Clutton-Brock 1989) with lifelong breeding exclusivity. The fundamental social unit in wolves consists of the territory-marking pair, and together with their offspring from the contemporary and/or previous litters they form a single family group, commonly referred to as the wolf pack (Mech 1970; Boitani & Ciucci 1995). The pack occupies an exclusive territory to ensure resource security, analogous to their home range (Burt 1943). The cohesion and movement pattern depends on the wolves' annual cycle and climatic factors such as snow conditions (Mech & Peterson 2003). Wolf pups are generally born in late April and early May, preceding or overlapping with the calving periods of their ungulate prey (Jordan, Shelton & Allen 1967; Packard 2003). By fall and early winter, the pups join their parents nomadically, and during this time they reach the size and biomass consumption of adult wolves (Mech 1970; Mech & Boitani 2003; Packard 2003). Wolves' prey menu can be diverse, although the main prey are generally large ungulate species, that in turn are potentially dangerous and hard to catch (Mech & Peterson 2003; Barber-Meyer *et al.* 2016). Young wolves are not particularly successful predators or noteworthy contributors to a pack's kill rate on large prey (Mech & Peterson 2003; Sand *et al.* 2006; Zimmermann *et al.* 2015). Ungulates have a heterogeneous, patchy distribution, and combined with a relatively slow turnover rate they represent a substantial amount of resource per unit effort to share between the pack members (Mech & Boitani 2003). All critical components favoring group living and improving food acquisition (Kleiman 1967; Macdonald 1983; Schmidt & Mech 1997), this may in turn favour larger pack size in wolves (Fuller, Mech & Cochrane 2003; Mech & Peterson 2003). Intrinsically, pack size is regulated by recruitment, mortality, and dispersal rates (Packard & Mech 1980), the latter often negatively related to population size (Murie 1944; Mech 1970). Apart from human-caused mortality (Liberg *et al.* 2012b; Rich *et al.* 2012), the ultimate extrinsic factor that seems to regulate pack size is resource abundance, (Boitani & Ciucci 1995; Fuller, Mech & Cochrane 2003), which in turn can be regulated by wolf population density through intra-specific competition (Peterson & Page 1988).

The maintenance of family structure in socially monogamous species can have direct and indirect fitness consequences (Lukas & Clutton-Brock 2013). Almost exclusively, all wolves will disperse, however the dilemma young wolves face early in life is whether to undergo immediate or delayed dispersal. The ultimate factor for leaving familiar conspecifics is assumed to be the individual's attempt to maximize their reproductive fitness (Lidicker Jr 1962;

Murray 1967). However, this may increase individual mortality risks (Bekoff 1977; Messier 1985). Wolves normally disperse solitarily, as a continuation of single, short departures from the natal pack (Mech & Boitani 2003; Wabakken *et al.* 2007) and dispersal can occur at various ages, some as early as five months, while others may stay with their natal pack until three years of age or longer (Gese & Mech 1991; Ballard *et al.* 1997). Similarly individuals differ considerably in reproductive development, where some may give birth at two years of age (Rausch 1967; Peterson, Woolington & Bailey 1984; Fuller 1989) whereas others do not reach physical and reproductive maturation until three years of age (Mech & Seal 1987).

Wolves are dominant intra-guild competitors, often aggressive to other wolves, including kin (Jordan, Shelton & Allen 1967; Fox 1972; Zimen 1976; Packard, Mech & Seal 1983), and the primary motivation for aggression and social avoidance through natural selection are competition (Brown 1964). In spring, social aggression increases related to reproductive development, mating, parental nurturing of the infant litter, and accumulation of reproductive fat storage (Rabb, Woolpy & Ginsburg 1967; Zimen 1976; Sands & Creel 2004). In fact, pups that disperse from the natal pack the first year typically leave their natal territory between January and May, coinciding with the time at which hormones, maturation, and social resource competition will be the most pronounced (Rabb, Woolpy & Ginsburg 1967; Fuller 1989; Gese & Mech 1991).

In the wolf pack, the new litter receives parental priority above previous years' offspring according to their nurturing needs, while social control by the breeding pair suspends reproduction in adult offspring (Packard, Mech & Seal 1983; Creel 2005). Nevertheless, both wolf parents and offspring may benefit from philopatry (Sparkman *et al.* 2011a; Sparkman *et al.* 2011b), given that the resource availability supports more than the needs of the subsequent litter and the breeding pair (Kleiman 1977; Rodman 1981; Harrington, Mech & Fritts 1983). Prior years' offspring may bear the disadvantage of delayed reproduction by staying in their natal territory, but they may also get the advantage of extended access to secure food sources and increased physical development and knowledge-based experience, which may in turn increase survival during subsequent dispersal (Howard 1960; Schmidt & Mech 1997; Mech & Boitani 2003; Sparkman *et al.* 2011b). Similarly, intensified social competition through increased group size and temporally varying resource availability can affect the relative costs of natal dispersal versus philopatry. Small group sizes could also be unfavorable because of incomplete use of resources, that may subsidize scavengers (Rodman 1981; Vucetich, Peterson & Waite 2004). However, if wolf kills are exploited by inter-specific competitors, scavenging



may also alter the wolves' kill rate (Stahler, Heinrich & Smith 2002; Kaczensky, Hayes & Promberger 2005; Ordiz *et al.* 2015; Tallian *et al.* 2017). Given sufficient resources, philopatric tolerance by parents may facilitate offspring survival and future potential for reproduction, potentially improving the inclusive fitness of both parents and offspring despite delayed onset of reproduction (Rodman 1981; Moehlman 1987; Waser 1996; Mech & Boitani 2003). On the contrary, early individual independence and permanent natal dispersal (Howard 1960; Greenwood 1980) may also be advantageous to offspring and parents if the chances of finding a breeding partner and settling in a new breeding territory are high (Bekoff 1977; Moehlman 1987). Thus, resource abundance and potential of population colonization are likely to influence the benefits and rate of early natal dispersal (Fritts & Mech 1981; Kochetkov 2015).

Cohesion within wolf packs varies, with individual pack members changing between splitting into minor groups, spending time alone or even temporarily leaving the territory on extraterritorial forays (Stenlund 1955; Mech & Frenzel 1971; Haber 1977; Fritts & Mech 1981; Liberg *et al.* 2012a). Spatial and temporal dissociation from the primary social unit is an essential factor for dispersal (Bekoff 1977; Harris & White 1992; Isbell & Van Vuren 1996). Individuals with low fidelity to their social group develop weakened social bonds and are likely to leave their natal territory first (Bekoff 1977; Fuller 1989; Gese, Ruff & Crabtree 1996).

In the Scandinavian wolf population, where predominantly the latest cohort of moose calves is the main prey year round (Sand *et al.* 2008; Zimmermann *et al.* 2015), the largest recorded pack size is 11 individuals, with an average of 5.7 individuals per pack during winter (Supplementary, S3), and an average litter size of 4.8 pups counted, at the den site approx. 3 weeks after birth (Chapron *et al.* 2016). Compared to the review by Fuller, Mech and Cochrane (2003) on pack size across wolf-moose systems, the Scandinavian mean and maximum pack sizes are substantially smaller. Moreover, the studies compiled by Fuller, Mech and Cochrane (2003) reported that most packs consisted of more than 50% of adult or yearling wolves, and the annual dispersal rate across populations ranged 10-40%, with large variation due to irregular dispersal of wolves older than 1 year. Observations in Scandinavia based on long-term series of GPS data and DNA identification from the National Monitoring Program show that packs mainly consist of a breeding pair, the current litter and occasionally yearlings (SKANDULV, unpublished data). This indicates high dispersal rates for pups and yearlings in Scandinavia, similar to those reported by Gese and Mech (1991); Kojola *et al.* (2006), were most wolves dispersed at 11-12 months of age.

Although the wolf is one of the most studied species worldwide (Amori & Gippoliti 2000; Brooke *et al.* 2014; Zimmermann 2014), social behaviour studied simultaneously of several individuals within the same pack are still rare (Miller 2012; Barber-Meyer & Mech 2015). However, advances in global positioning system (GPS) technology have given unique opportunities for following rare, wide-ranging and elusive species (Cagnacci *et al.* 2010). Pioneering studies on social cohesion in wild wolves have recently emerged indicating that wolf pack cohesion is flexible in summer and strong during winter (Metz *et al.* 2011; Barber-Meyer & Mech 2015; Benson & Patterson 2015). This casts doubts on the common views that wolf packs operate as a synchronous unit with strong social cohesion.

In this study, by examining simultaneous paired inter-individual distances between wolves (hereafter used synonymously with cohesion). I aim to quantify the timing of pack dissolution events i.e. extraterritorial movements and dispersal by pups from their natal territories, as well as cohesion among pack members using 14 years of unique long-term GPS data from the transborder recolonizing Scandinavian wolf population.

## Predictions

I predict that **P1)** most pups disperse solitarily before 14 months of age and that **P2)** dispersal coincides with the birth of the subsequent litter in association with social competition and parental priority. Since dispersal is regarded as a solitary departure from the natal territory, I predict that **P3)** extraterritorial movements occur primarily as a solitary pre-dispersal phase, before the birth of the new litter. Moreover, I predict that **P4)** the breeding pair cohesion is predominantly strong, with the pair moving together most of the time except during and after the time of birth to the new litter. Since I expect most pups to disperse solitarily within their first year, I predict **P5)** the highest parent-pup cohesion in early winter, with gradually increasing independence and decreasing cohesion towards the time of dispersal. Since pups are competitors of a common resource provided by the parents, it would be beneficial for pups to associate more with their parents than with litter siblings. Lastly, I therefore predict **P6)** a gradual increase in pup-sibling cohesion, but lower pup-sibling cohesion than parent-pup cohesion.

## 2 Methods

### 2.1 Study area

The study was conducted in the core breeding area of the Scandinavian wolf population in the south-central parts of the Scandinavian Peninsula, a trans-boundary area including Sweden and Norway (59° - 62 °N, 11° - 19 °E; Figure 1). The landscape is dominated by boreal coniferous forest of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) interspersed with bogs, lakes and deciduous trees of birch (*Betula pendula* and *B. pubescens*), aspen (*Populus tremula*), alder (*Alnus incana* and *A. glutinosa*), willow (*Salix spp.*) and rowan (*Sorbus aucuparia*). Extensive forestry practices have generated a vast network of forest gravel roads encompassing the whole region with a density of 0.88 km/km<sup>2</sup> inside wolf territories (Sand *et al.* 2008; Zimmermann *et al.* 2014). Public paved road density is approximately four times lower than the density of gravel roads (Zimmermann *et al.* 2014; Milleret *et al.* 2017). The climate is intercontinental, characterized by cold and dry winters, with 3-6 months of snow cover, mainly between November and April (Zimmermann *et al.* 2015; Milleret *et al.* 2017). While the average human density in Scandinavia is 16 inhabitants per km<sup>2</sup>, it is <1 habitant pr. km<sup>2</sup> in vast areas within the wolf population breeding range (Wabakken *et al.* 2001; Mattisson *et al.* 2013). House density within the wolf territories is on average 3 pr. km<sup>2</sup>, and urbanized and agricultural land covers < 5% of the study area (Zimmermann *et al.* 2014; Milleret *et al.* 2017). Moose (*Alces alces*) is the main prey species for wolves in Scandinavia, and densities are relatively high (average 1-3 per km<sup>2</sup>; range 0.7 – 3.3, Zimmermann *et al.* 2014). Smaller cervid species such as red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and fallow deer (*Dama dama*) are available at low to intermediate densities in restricted parts of the area (Zimmermann *et al.* 2015). The majority of cervid populations undertake seasonal migrations annually imposed by temperature and snow depth (Gundersen 2003; Bischof *et al.* 2012). In winter, generally from November onwards, moose migrate towards valley bottoms and forested lowlands to avoid increasing snow depths and subsequent feeding constraints (Gundersen, Andreassen & Storaas 2004; Storaas *et al.* 2005). This results in a heterogeneous, patchily aggregated distribution of moose during most of the winter period. The spring migration starts in April to May, and the moose ascend to summer habitats at higher altitudes (Gundersen 2003). The recolonizing Scandinavian wolf population was founded by two long-dispersing wolves from the Finnish-Russian source population in the late 1970s. The functionally isolated Scandinavian wolf population suffers severe inbreeding depression (Wabakken *et al.* 2001;

Vilà *et al.* 2003; Liberg *et al.* 2005), but see Åkesson *et al.* (2016). In 2017-2018 the Scandinavian wolf population counted 41 family groups and was estimated to 410 (95% CI 324-533) individuals (Wabakken *et al.* 2018). The population distribution is managed in a geographically differentiated management zone trans-bordering Norway and Sweden, with a low, non-saturated wolf density and mostly large territory sizes (Wabakken *et al.* 2001; Mattisson *et al.* 2013; Chapron *et al.* 2014).

## 2.2 Study animals

Wolves were captured with a CO<sub>2</sub>-powered dart gun from a helicopter and equipped with GPS neck collars (Simplex™ ; Televilt / Followit Positioning AB, Lindesberg, Sweden or GPS – plus ; Vectronic Aerospace, Berlin, Germany) following detailed, standardized biomedical procedures for animal anaesthesia and handling techniques (Arnemo, Ahlqvist & Segerström 2004; Arnemo & Evans 2017) described in detail in Sand *et al.* (2006); Eriksen *et al.* (2011). All captures were approved by the Norwegian Animal Research Authority (FSA), the Norwegian Food Safety Authority, the Norwegian Environmental Agency and the Swedish Committee of Animal Welfare. In this study, a total of 59 wolf captures were conducted, on 51 unique individuals over a 15-year period from 2002 to 2017 (Supplementary Table S1).

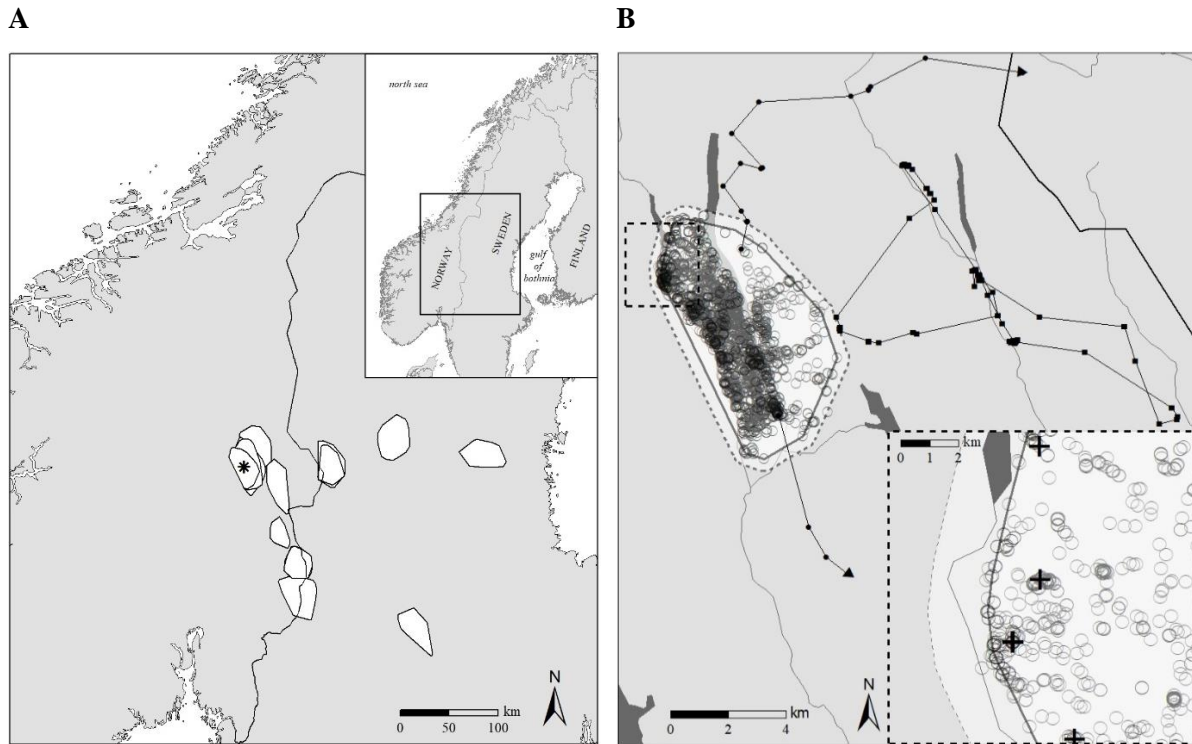
During captures all individuals were aged based on reproductive development, tooth wear, and epiphyseal growth zones according to Von Pfeil and DeCamp (2009). I experienced however that morphological and demographic parameters provided from captures were not always correct, and age based on tooth wear was sometimes overestimated, similar to the findings by Gipson *et al.* (2000). I therefore used the data on DNA provided by the wolf monitoring program (ROVBASE 2018) i.e., the first time an individual was detected in its natal territory to enhance the accuracy of age determination of the marked individuals, and validated this with the DNA obtained at captures and/or from den survey samples on 3-4-weeks-old neonatal wolf pups (H. Sand *et al.* unpublished data). Hence, I was able to reveal full-kinship and specify the age of all offspring, i.e., pups of the year, and yearlings (Supplement Table S1).

## 2.3 Identifying wolf territories, natality, extraterritorial and dispersal movements

Scandinavian wolf territories have an average size of approximately 1000 km<sup>2</sup>, and to calculate sufficiently accurate territory boundaries, a minimum of nine months of position data with > 5 positions in each month is needed (Mattisson *et al.* 2013) (Supplementary Table S2). I therefore defined the study period for territory years from movements by the resident breeding adult or

pair from 1 October to 30 September of each year, using the 100% minimum convex polygon (MCP) method (Mohr 1947) in ArcGIS, ArcMap 10.5.1 (ESRI 2017) to create annual wolf territories. I only retained wolf territories that met requirements by Mattisson *et al.* (2013).

I used data from  $n = 14$  territory years with  $\geq 2$  simultaneously marked wolves to determine movement classes (Supplementary, Table S1). For each territory year I plotted all positions for a given offspring and defined all pup positions within the territory as natal movements. Moreover, I defined extraterritorial pup movements as a sequence of positions outside the territory boundaries, followed by  $\geq 1$  subsequent position inside the territory boundaries. When pups stayed close to the territory borders, many positions were seemingly outside the territory, resulting in a disproportionately large amount of short extraterritorial movements. This may be influenced by several factors such as points of interests in close vicinity to territory boundaries, e.g. carcass remains (Figure 1B), methodological errors such as missing GPS positions from the adults, small delays in positioning or inaccurate positioning. To account for this, I extended the territory borders with a buffer whose width was derived from the adults' movement behavior. I calculated the distances between all consecutive 4-hourly positions of the breeder wolves and divided this number by two, i.e. estimating the distance the adult breeder could reach outside their MCP-defined territory boundary, but still be able to return inside territory boundary before next position was acquired. Due to the right-skewed distribution of this parameter, I conservatively chose the 75% inter-quantile, instead of the mean, as an additional unique buffer for each territory (Supplementary Table S2). Hence, I reclassified pup movement within the buffer as natal movement. I defined dispersal as a sequence of positions outside the territory boundaries with no subsequent position within the territory or buffer. Thus, I used the first position outside the territory buffer from the dispersal trajectory to classify the timing of dispersal. If the pup remained in the territory after 1 July i.e.  $>14$  months of age, as yearlings they were classified as philopatric.

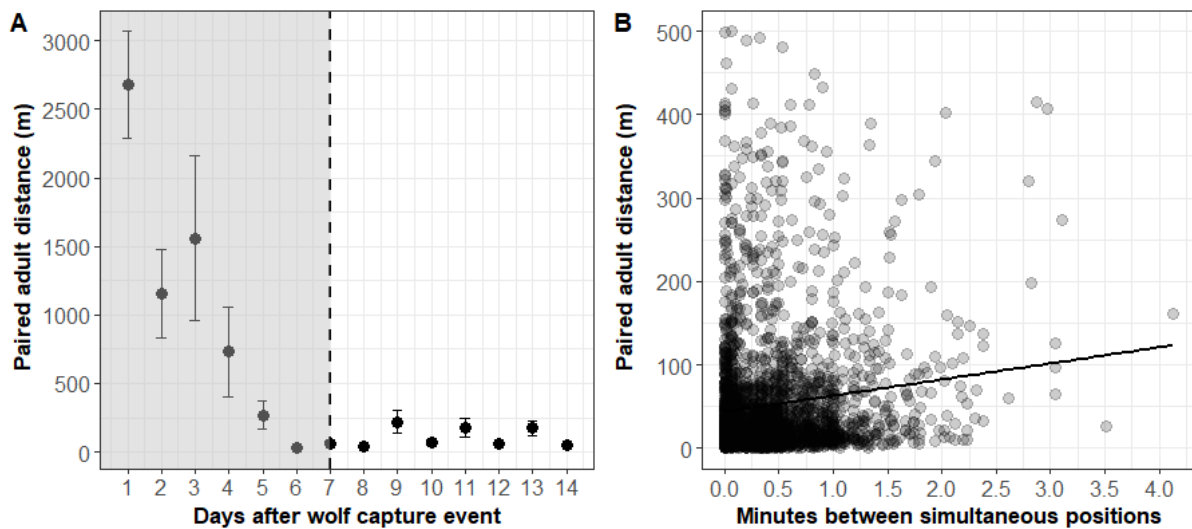


**Figure 1.** **A)** Minimum convex polygon (MCP) in white with black outlines of the 14 territory years in Norway (left) and Sweden (right) where minimum one adult breeder individual and  $\geq 1$  pups were equipped with GPS neck collars in the same year. Asterix (\*) represents the example territory Julussa 2014 in figure **B)**, the dashed black line indicates the additional territory buffer around the MCP extracted from adult breeder individuals' movement distances. The black lines with dots and arrow head show the dispersal trajectories of two male pups: both emigrated to Sweden where one was culled during dispersal (M1406) while the other settled across the Finnish-Russian border (M1408). The black line without arrow head shows the extraterritorial trajectory of a philopatric sibling female (M1407) in the following spring. She later settled in the eastern-most area of Figure 1B and gave birth to pups before she and her partner were confirmed illegally shot in 2017/18. Hollow circles show positions of all three pups while in the natal territory. The partitioned square in the bottom right corner magnifies the pup positions along the north-western territory border and within the additional buffer-zone. Black crosses are confirmed wolf-killed moose ( $n=3$  approx. nine-month-old moose calves and  $n=1$  yearling male moose, 27.03.14 – 19.04.14) (Nordli & Rogstad 2016).

#### 2.4 Extracting intra-territory inter-individual spatial relationships

I paired all individuals with all their marked pack members and standardized positions into 4-hourly positioning intervals. This provided six regular positions per day at 03:00, 07:00, 11:00, 15:00, 19:00, 23:00 (GMT). Furthermore, I derived positions from the position schedule with  $\leq 5$  minutes deviation, similar to Benson and Patterson (2015), to extract positions acquired simultaneously (Figure 2B). I calculated the Euclidean distance between simultaneous positions from adult breeders, pup to adult breeder, and pup to pup. Since I had data from only 2 marked yearlings I removed them from the analyses. Preliminary analyses showed that the

adult breeding pair almost exclusively traveled together during winter. Therefore, I could use data of one adult breeder as a proxy for both adult breeders, allowing me to include territory years where only one adult breeder had a functioning GPS-collar. To avoid pseudoreplication (Hurlbert 1984) in the analyses of pup-adult cohesion, I randomly selected one of the adults in cases where both adult breeders had a functioning collar. Moreover, since captures may have a disruptive influence on the wolves' movement patterns (Teräväinen 2016), I excluded positions that potentially may have been affected by the captures. To find an adequate time threshold after capture for positions to be included, I calculated all inter-individual distances of the adult breeding pair and employed a capture-effect matrix on days after capture after any capture event on the adult breeding pair inter-individual distance in a given territory year. This led me to exclude all positions of all collared pack members by one week (7 days) after capture event of any pack member (Figure 2A, Supplementary, Figure S4).



**Figure 2.** **A)** The distance between adult breeding pairs in relation to days after capture event on all capture efforts in a specific territory. The leftmost shaded grey area with vertical dashed line demonstrates the range of days after capture removed from all subsequent analysis. Black dots represent observed means, and error bars are  $\pm 2$  SE. **B)** The distance between adult breeder pairs in relation to delay in minutes between position fixation, the solid black line from a simple linear regression expose the bias in the distance relative to the deviation between each pair position fixation.

## 2.5 Changepoint analyses on time of reproduction

I used the software R (R Development Core Team 2017) with the integrated development environment R-Studio (RStudio Team 2016) for all statistical analyses. Wolves generally give birth from late April to early May (Jordan, Shelton & Allen 1967), with the lowest daily

movement distances around the time of birth and nurturing of neonatal pups (Boyd *et al.* 1993; Jedrzejewski *et al.* 2001; Eggermann *et al.* 2009). Detailed GPS data allowed me to quantify the timing of these demographic events specific to my study animals. Thus, I estimated the time of birth and mating season by extracting the four-hourly positions for each adult breeder from 1<sup>th</sup> April to 1<sup>st</sup> June to reflect the range of possible birth dates. However, during the time of denning both the breeding female and male were prone to failed position fixation <30%, likely due to satellite coverage and terrain ruggedness near the den site area, as previously reported for wolverine (*Gulo gulo*) and lynx (*Lynx lynx*) in Scandinavia (Mattisson *et al.* 2010). I calculated the daily number of positions each animal should have acquired according to the positioning schedule settings from the GPS collar. I quantified the number of unsuccessful positions and calculated the Euclidian distance for consecutive series of successful positions for each individual to reflect straight-line movement. I applied a pruned exact linear time (PELT) algorithm in both mean and variance with MBIC penalty on 95% CI from the R package ‘changepoint’ to detect whether, and when, a change had occurred (Killick & Eckley 2014). Hence, I used the function *cpt.meanvar* and specified the segment length for change in mean and variance to be at least 72 hours. Consequently, each segmentation length was adjusted in relation to the amount of average successful positions acquired over the period for each individual independently (Table 2). The average kill-rate by wolves on moose calves has been reported to 1.42 days (1.26-1.73) in Scandinavia during summer (Sand *et al.* 2008), and 3.6 - 4 days in winter (Sand *et al.* 2005) with time spent at moose carcasses ranging from 1-57 hours (Zimmermann *et al.* 2007). Even though wolves have been shown to have drastically reduced movement in close vicinity to fresh moose carcasses (Kuzyk, Rohner & Schmiegelow 2005), I considered a 72-hour minimum segmentation as sufficiently broad to segregate between predation events, kill site visits, and day beds versus seasonal variation linked to potential reproductive events. All change point analyses were conducted with the freedom of infinite changes to be able to derive change point lengths. I assessed autocorrelation by the autoregressive function *ACF* for each individual separately. I detected no autocorrelation in the full model set, with a few exceptions for  $n = 3$  individuals with minor auto-correlated lags in post change periods. Moreover, to evaluate normality and residuals in model fit, I applied the Shapiro-Wilk normality test and One-sample Kolmogorov-Smirnov test for each segment of change, if any, independently. The Shapiro-Wilk normality test indicated that my response was not normally distributed. Thus, I reapplied the PELT algorithm with a Gamma distribution for improved fit and reevaluated the residuals for each model. Lastly, I pooled all estimated change points and extracted the earliest and latest date of change detected and established the total



range as the birth period for wolves in this study. Furthermore, since the gestation period of wolves ranges from 61-64 days (Pulliainen 1965; Mech 1970; Packard 2003) I subtracted 64 days from the earliest and latest birth range date to establish the period of mating for the wolves in this study.

## 2.6 Generalized Additive Mixed Model

I wanted to model pack cohesion (i.e., the distances between individuals) through the course of winter until the beginning of summer to test whether the cohesion was significantly different between pups, adult breeding pairs, and pups to adult breeders. I followed the framework provided by Zuur, Ieno and Elphick (2010); Zuur and Ieno (2016) for data exploration and regression type analysis. Prior to the analysis I removed <0.5 % of positions that were either considered improbable or completely impossible movements. Already in the data exploration phase, it was apparent that the response would appear to fit a non-linear function over time. Therefore, I explored the utilities in the statistical software of R (R Development Core Team 2017) to compute time series analysis in GAMs (generalized additive models) implemented in the R package ‘mgcv.’ (Wood 2017). GAMs are a nonlinear regression type analysis relating a univariate response  $y$  to one or more predictor variables  $x_i$ , and compared to an ordinary linear model the predictors in GAMs are replaced with several flexible non-linear smooth functions  $s_i$  to capture the non-linearity in the data (Wood 2017). I evaluated various smoother functions (e.g., adaptive smoother, cubic regression smoothers, and thin plate regression splines) but could only detect minor to no differences in smoother outcome in relation to data points, therefore I applied a default thin plate regression spline for all smoother products (Wood 2003). Since I did not want my estimates to be influenced by the certainty of adult pair’s MCP boundaries, I selected both natal and extraterritorial positions for the analysis. I used the R package ‘itsadug’ in the foreground of ‘mgcv’ to handle the sensitivity of temporal autocorrelation, and to order reference levels for appropriate predictor variables (van Rij *et al.* 2016). Due to the extended time it took to run the analysis on this comprehensive dataset, I used the function *bam* in the ‘mgcv’ package allowing sub-blocks of model matrices to be computed at the time, facilitating modeling complexities with datasets of tens of thousands of observations (Wood, Goude & Shaw 2015). Since the response was heavily tailed and unevenly distributed, I applied a Scaled T distribution (SCAT) for best response fit, specifically accounting for heavy-tailed data points, leaving me with the framework of discretized *bam* models and fREML scores (Wood 2017). Evident in the evaluation of model fit I detected rigid heterogeneity of variance, thus independence problems. Therefore, I used paired wolf\_ID as a

random factor. The desired random structure was determined on the random variable based on a set of candidate models containing distance/cohesion ( $y$ ) in relation to time ( $x_1$ ). I compared the structures of random intercept and slope, versus the optional random factor smooth interaction with the  $fs$  function supplied by the  $m=1$  argument from the ‘mgcv’ package, for appropriate smoother penalty on paired wolf\_ID for each null space, consequently causing pertinent shrinkage to the mean (van Rij *et al.* 2016). Furthermore, I compared these random structures with the Akaike’s information criterion (AIC) (Akaike 1998; Burnham & Anderson 2003) and favored the model with lowest AIC. I selected the random factor smoother interaction structure,  $fs$ , as a fully random effect, exceeding the closest candidate structure containing random intercept and slope by a  $\Delta AIC$  value of 1003.8. When using penalized regression smoothers, determining adequate  $k$  is essential, i.e., the number of knots specified for each parameter basis dimension. I selected basis dimensions of  $k$  by evaluating each term’s effective degrees of freedom from the model fREML computation and compared this to the  $k-1$  index score for each specified basis dimension of  $k$  with the  $gam.check$  function from ‘mgcv’. Furthermore, when  $k$  for each smoother term was considered adequate, I extracted deviance residuals from the model fit and fitted a single smooth for each term to model residuals with substantially increased  $k$  to informally test whether an increased  $k$  could explain the remaining residual pattern for each term. Setting  $k$ , sufficiently large is particularly important to reflect the underlying non-linear nature of the data, while simultaneously keeping  $k$  reasonably small for computational efficiency (Wood 2017). After running the model, residuals were examined for autocorrelation, and I found the data to be heavily autocorrelated. To account for residual autocorrelation, I refitted the model with AR1 model structure, specified with the  $\rho$  parameter on the second lag to rationalize the degree of residuals in the current data point dictated by the residuals in the previous data point. GAMMs (Generalized additive mixed models) including ordered factor terms were fitted with an additional intercept and a smooth term. Since ordered factor smoothers are centered on zero, an intercept difference and a reference smoother are required for the ordered-fixed-effect to obtain necessary flexibility, and to fit overall differences without encountering centering constraints between the reference levels.

To test the prediction of whether cohesion over time for adult breeding pairs (AA), pups to adult breeders (PA) and pups to pups (PP) was significantly different from each other, I ordered factors with adult breeding pair (AA) cohesion as a reference level for pup to adult breeder (PA) and for pup-to-pup cohesion (PP), and lastly with pup to pup (PP) as a reference level for pup to adult breeder (PA). Since GAMMs are simply penalized GLMMs (generalized linear

mixed models), I validated the final model under similar principles (Zuur *et al.* 2009; Wood 2017). I did this by plotting the scaled residuals from the model against the predictor and the fitted values. Hence, I also plotted each smooth term with overlaid residuals. Finally, I applied the *gam.check* function from ‘mgcv’, for the default diagnostic residual plots and final model convergence information. All model predictions were extracted by the functions *get\_predictions* and *get\_difference* in the package ‘itsadug’ and calculated with simultaneous instead of pointwise CI, to reflect appropriate uncertainty estimation in each smoothness parameter over time, similar to Bayesian credible intervals (Simpson 2016; van Rij *et al.* 2016). All plots were generated using the R package ‘ggplot2’ (Wickham 2016) together with dependencies from the packages ‘grid’ (R Development Core Team 2017) and ‘png’ (Urbanek 2013). Combined plot panels were made with ‘ggplot2’ through the package ‘cowplot’ (Wilke 2017).

**Table 1.** Fixed and random factors used to model pack cohesion

Name	Description	Structure	Prediction	Data Source
OFStatus	Pup to adult breeder, pup to pup, adult breeder to adult breeder.	Categorical, ordered factor	P4-6	Collar fix/GSM/store on board
Time	Day in the year from 1 <sup>st</sup> January to 1 <sup>st</sup> July	Continuous, numeric	P4-6	Collar fix/GSM/store on board
PairedWolfID	Paired inter-individual distance ID	Categorical (Random factor)	P4-6	Capture protocols/Rovbase 3.0

## 3 Results

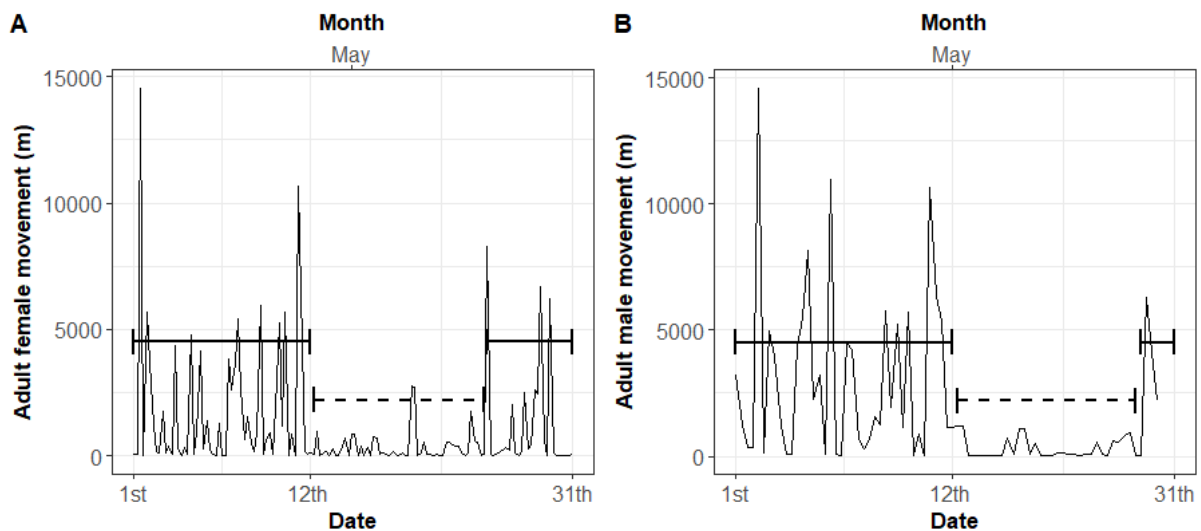
### 3.1 PELT algorithm changepoints on reproduction

Time of reproduction was determined for all territory years with data series available from 1<sup>st</sup> April to 1<sup>st</sup> June (n = 12 out of 14). I always detected a changepoint for breeding females (n = 10; Table 2), but not always for males (n = 6 out of 9; Table 2). However, for all males that failed to produce a reliable change point, I always had the breeding female change point available. Whenever I could detect change points for both female and male in the same territory and year (n = 4), the two change points were  $\leq 28$  hours apart (Table 2, Figure 3). The time of reproduction ranged from 22<sup>nd</sup> April to 12<sup>th</sup> May, with a median of 2<sup>nd</sup> May. Moreover, the mating season ranged from February 17<sup>th</sup> to March 9<sup>th</sup>, with a median of 27<sup>th</sup> February.

**Table 2.** PELT algorithm change points in mean and variance with 95% CI indicating a change in movement for adult breeder males (M) and females (F), corresponding to each territory and year. The minimum segment length inquires a change that is consistent over a minimum of 72 hours by employing an average number of successful positions per day for each individual. Change point date denotes the date when the change in mean and variance became significantly different before and after point of change. Change point length denotes the duration of consistent change in days. Numbers in bold in top and bottom indicates the range of change point dates (estimated birthing period). The territory years Kynna (2007) and Rotna (2012) (Supplementary, Table S1) were omitted from these analyses due to missing data after mid-april.

Territory	Year	Sex	Avg. # positions per day	Min. seg. length	Change point date	Change point length
Graafjell	2003	M	3	9	<b>12.05</b>	9 days
Graafjell	2003	F	4	12	12.05	9 days
Graafjell	2004	M	3	9	12.05	4 days
Ulriksberg	2004	F	2	6	4.05	> 4 days *
Gressmark	2006	F	4	12	25.04	7 days
Galven	2009	M	3	9	6.05	4 days
Galven	2009	F	4	12	7.05	9 days
Fulufjellet	2009	F	6	18	25.04	8 days
Fulufjellet	2010	F	6	18	26.04	4 days
Fulufjellet	2010	M	6	18	N/A	N/A
Tandsjo	2014	F	3	9	26.04	4 days
Tandsjo	2014	M	3	9	28.04	4 days
Rotna	2011	F	2	6	9.05	7 days
Rotna	2011	M	5	15	N/A	N/A
Julussa	2014	F	4	12	12.05	7 days
Julussa	2014	M	3	9	11.05	4 days
Slettaas	2017	F	5	15	26.04	7 days
Slettaas	2017	M	5	15	N/A	N/A
Osdalen	2017	M	4	12	<b>22.04</b>	6 days

\* Insufficient data-series length to detect post change



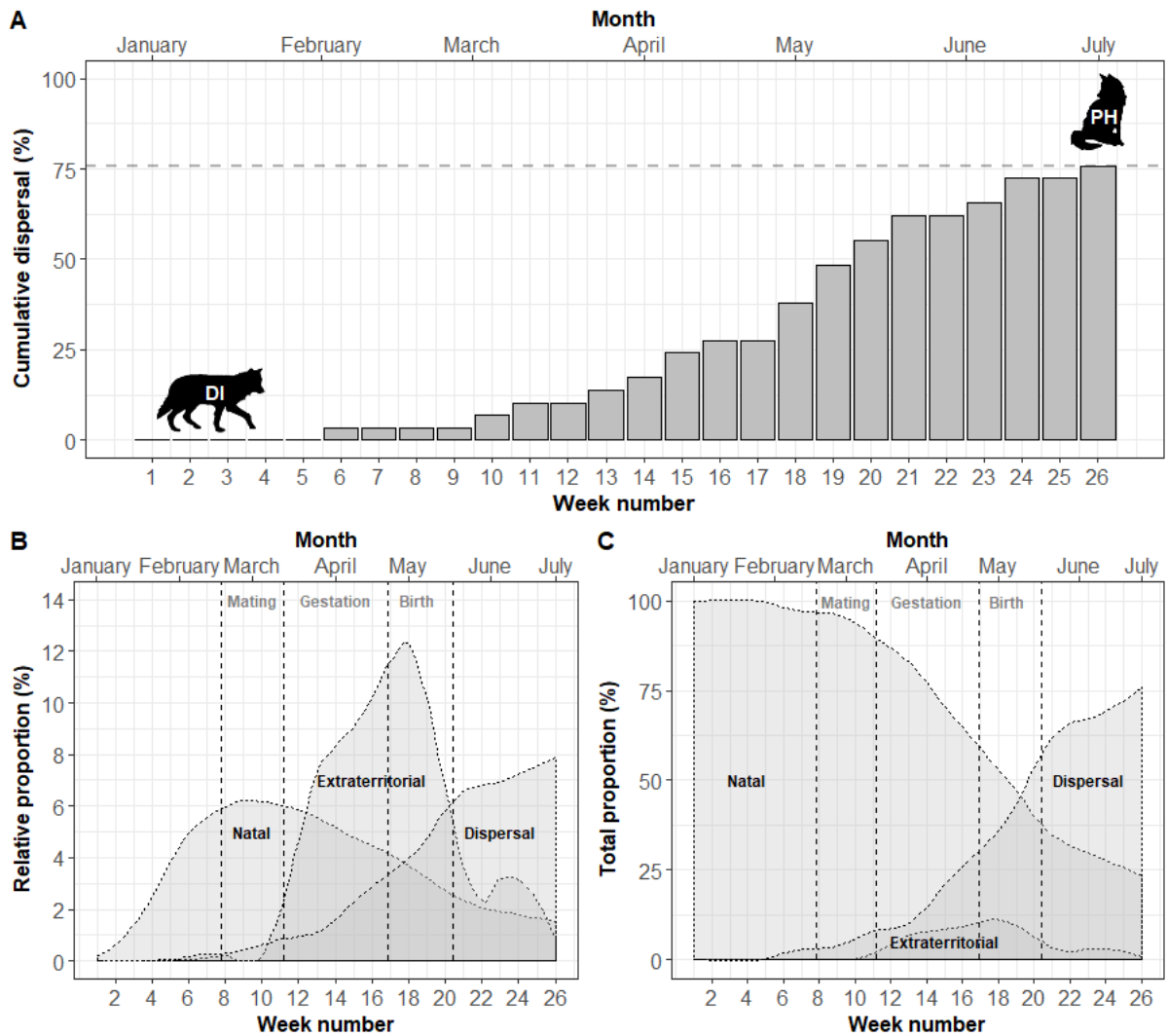
**Figure 3.** 95 % CI PELT algorithm changepoints exemplified by the movement in vertical lines by **A)** the adult breeding female and **B)** the adult breeding male in Graafjell 2003. Solid horizontal bold segments indicate the mean and variance in the movement rates before and after the changed sequence, while dashed bold segments indicate the date of that change (12<sup>th</sup> May), and the length of the change in mean and variance consistent over time.

### 3.2 Cumulative dispersal and movement classes

For 29 of the 30 GPS-collared pups belonging to 14 territory years I was able to determine if the pup dispersed or remained philopatric. The GPS-collar of 2 pups malfunctioned, but DNA monitoring could confirm that at least one of them remained in the natal territory as philopatric. The earliest date of dispersal was 9<sup>th</sup> of February, and by the first week of May 50% of all dispersing pups had dispersed. Moreover, by the first week of July, all 22 dispersing pups (76% of all 29 pups) had permanently left their natal territory (Figure 4A). None of the radio-collared siblings dispersed together or along the same trajectory. The remaining pups (n = 7, 24 %) stayed philopatric at least to the upcoming winter (Figure 4A).

I had access to 22058 positions of the pups in the time period 1<sup>st</sup> January to 1<sup>st</sup> July. Of those, 13058 positions were classified as natal movements, 8176 as dispersal movements and 824 as extraterritorial movements. The proportion of natal positions decreased and inversely the proportion of dispersal positions increased over time (Figure 4 B-C). The number of extraterritorial positions rapidly increased in the middle of March through April and peaked in the beginning of May, in week 18 (Figure 4 B-C). Among all 22 dispersing pups, 12 (54%) conducted extraterritorial movements prior to dispersal. None of these extraterritorial

trajectories were done together with a radio-collared sibling. The radio-collared philopatric pups did not do any extraterritorial movements (Figure 4B-C).



**Figure 4.** **A)** Cumulative dispersal for 29 pups in 14 territory years in relation to week number and month. The dashed grey line ( $y = 76\%$ ) displays the time when all dispersing pups (DI,  $n = 22$ ) had permanently left their natal territory before 14 months of age. Philopatric pups (PH,  $n = 7$ ) that stayed for a minimum another year made up 24 % indicated above the grey dashed line. **B)** Weekly proportion of natal, extraterritorial, and dispersal GPS-positions of all the 29 pups relative to the number of positions in each category per week. **C)** Weekly proportion of natal, extraterritorial, and dispersal positions of all the 29 pups relative to the total amount of all positions per week. Dashed vertical lines indicate the range of birth dates from the PELT algorithm changepoint analyses, including the subtracted gestation period of 64 days and mating period.

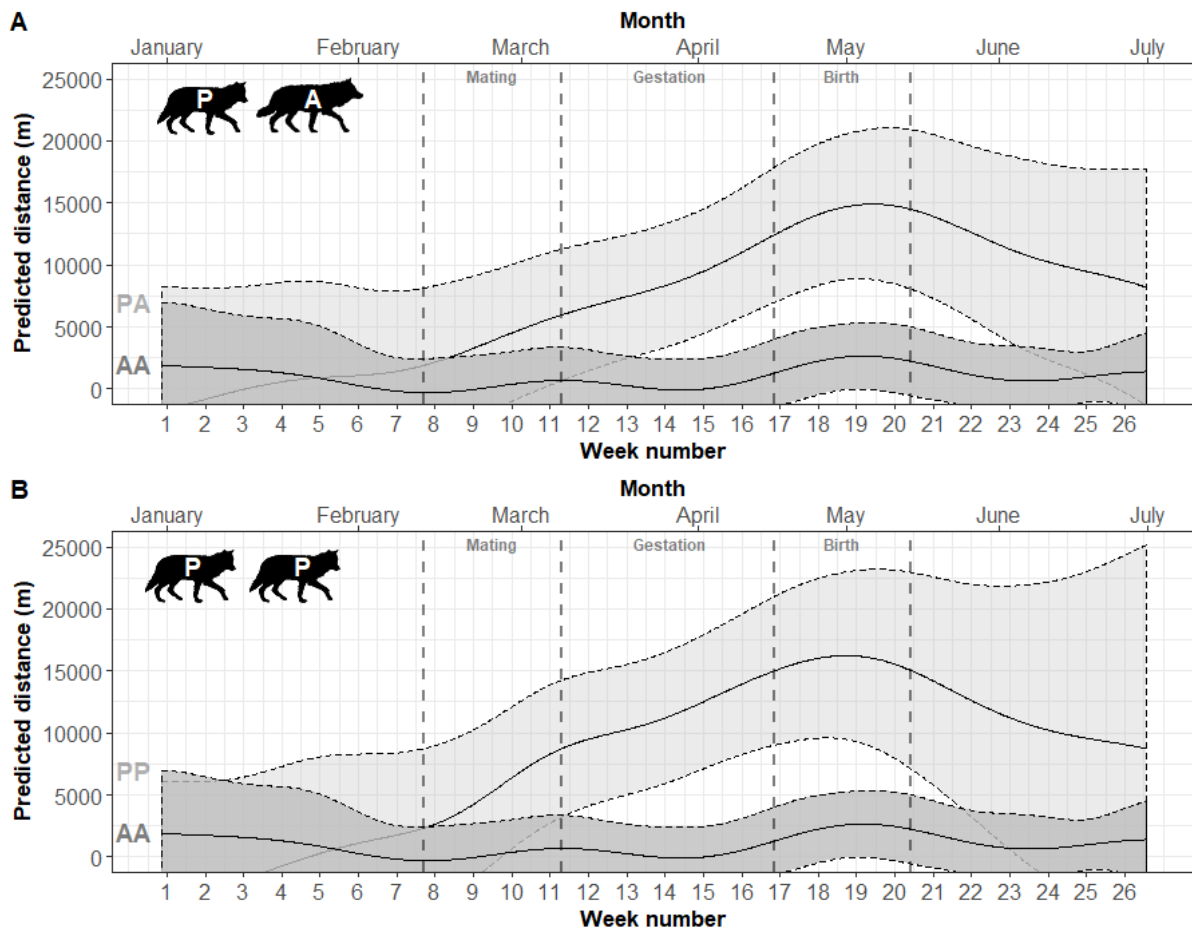
### 3.3 Generalized additive mixed model on pack cohesion

A total of 20285 simultaneous positions was extracted from  $n = 65$  paired inter-individual distances (AA,  $n = 9$ ; PA,  $n = 30$ ; PP,  $n = 26$ ). The adult breeding pair moved almost exclusively together, with a median distance of 26.5 meters. The only time when distance between the breeding female and male was significantly different from zero was during and after the time of birth (Figure 5 A-B; Table 3). Distance between pups and adult breeders was significantly different from zero in late February, and decreased gradually throughout the winter months (Figure 5A; Table 3). Pup to adult breeder distance peaked during early May. Distance between pups significantly differed from zero in mid-late February, with a progressive increase similar to distances between pups and adult breeders (Figure 5B; Table 3). However, from late June onwards, pup distance was no longer significantly different from zero (Figure 5B; Table 3)

**Table 3.** Model summary from the ordered factor cohesion model (GAMM) on inter-individual distances between the adult breeders AA, pup and adult breeders PA, and pairs of pups PP, with adjusted reference levels and interaction term on time. OFstatus indicates the reference level.

<b>A: Parametric coefficients</b>	<b>Estimate</b>	<b>Std.error</b>	<b>t-value</b>	<b>p-value</b>
Intercept	1594	1112	1.434	0.151651
OFstatusPA	6524	1726	3.78	<0.0001
OFstatusPP	7440	2242	3.318	<0.0001
<b>B: Approximate smooth terms</b>	<b>edf</b>	<b>Ref.df</b>	<b>F</b>	<b>p-value</b>
s(time)	1.001	1.001	0.135	0.7137
s(time):OFstatusPA	4.475	5.214	2.631	0.0207
s(time):OFstatusPP	4.697	5.447	2.643	0.0187
s(time,ID)	237.328	518	5.362	<0.0001

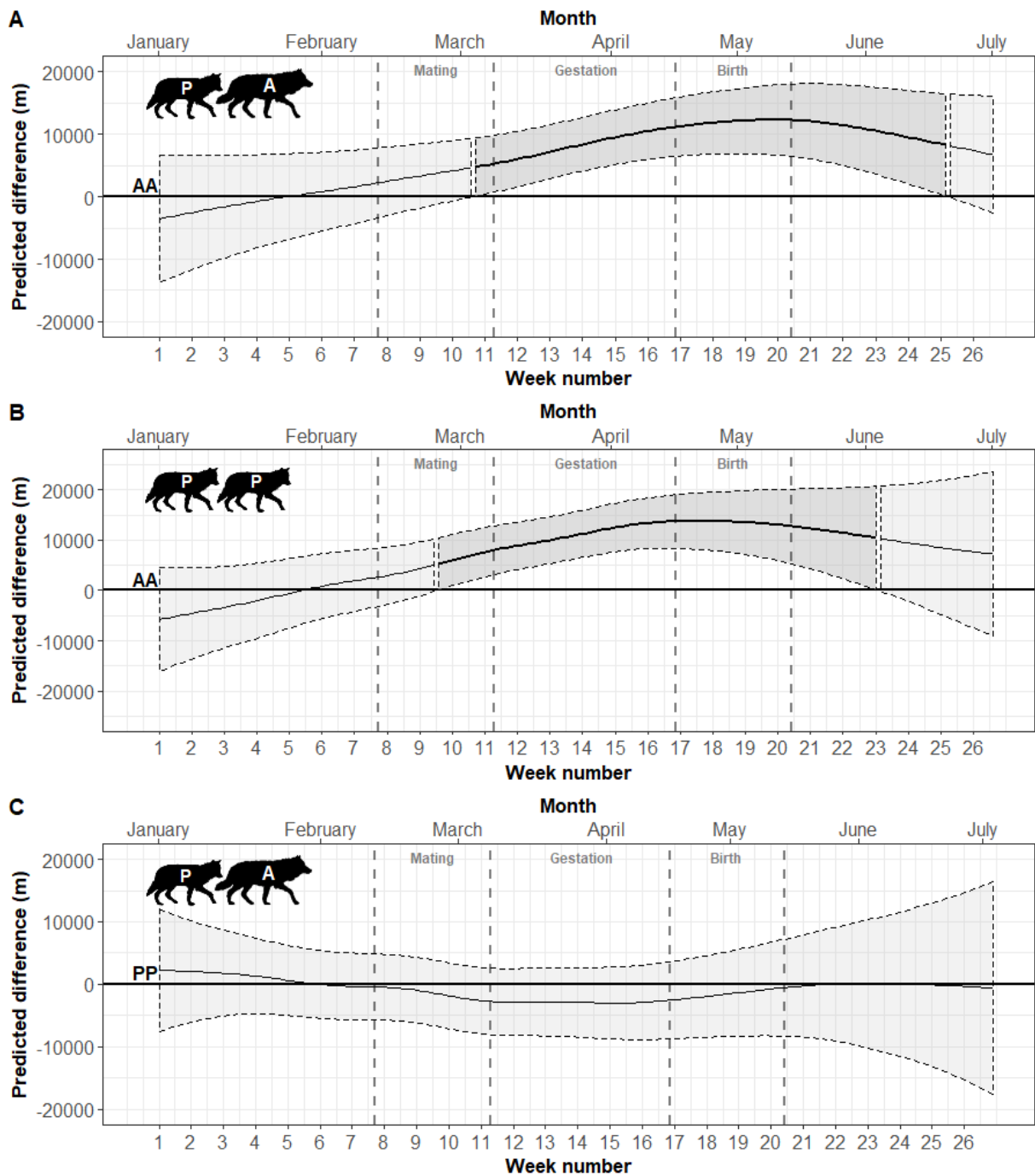
R-sq(adj) = 0.418, deviance explained = 44.7%, fREML 21807.75.



**Figure 5.** The predicted relationship from GAMM models on **A**, **B**) adult breeder distances (AA,  $n = 9$ ) in dark grey **A**) adult breeder to pup distances (PA,  $n = 30$ ) in light grey, and **B**) pup to pup distances (PP,  $n = 26$ ) in light grey in relation to time displayed as months and week numbers. The solid lines are predicted means over time, and the shaded grey areas are the 95% simultaneous CI. Dashed vertical lines indicate the range of birth dates from the PELT algorithm changepoint analyses, including the subtracted gestation period of 64 days and mating period.

By ordering the adult pairs' distance (AA) to the reference level I found that both pups to adults (PA), and pups to pups (PP) distances became significantly different from each other during the mating season and this effect lasted until after the birth of the next litter (Figure 6A-B; Table 4) Similarly, adjusting the pup to pup (PP) distance as the ordered reference level to pups to adults distance (PA), the predicted mean between adults and pups (PA) was lower compared to pup to pup (PP) although I could not detect any period of significant difference (Figure 6C; Table 4).





**Figure 6.** The predicted difference from GAMM model on **A)** pup to adult breeder distance (PA) while adult breeding pairs (AA) is set to zero, **B)** on pup to pup (PP) distance while adult breeding pairs (AA) is set to zero, and **C)** Pup to adult (PA) distance while pup to pup (PP) distance is set to zero. Grey shaded areas show the simultaneous 95 % CI, and dark shaded grey areas indicate, if displayed, in what time the cohesion is significantly different from its reference cohesion at zero. Dashed vertical lines indicate the range of birth dates from the PELT algorithm changepoint analyses, including the subtracted gestation period of 64 days and mating period.

## 4 Discussion

I studied the social cohesion of 11 Scandinavian wolf packs over 14 territory years in the period January to June by means of movement and cohesion analysis of radio-collared pups and adult breeding wolves. Consistent with my first two predictions, the great majority (76%) of the wolf pups dispersed at about one year of age, and probably all of them dispersed solitarily, or at least not together with any of the other GPS-collared pups. The largest proportion of dispersal coincided with the birth of the subsequent litter. In accordance with prediction 3), pups that dispersed by the time they were 14 months old, approx. half did extraterritorial movements before dispersal, but never together with any of the radio-collared siblings. No philopatric pups however did show such explorative behaviour in the same period. My initial predictions 4) and 5) about pack cohesion were also supported, with the adult breeders moving together almost all the time, except of the time during and after birth, while pups gradually weakened the cohesion to the breeding adults and their siblings throughout the period. Philopatric pups however mostly joined up with the adult breeders after birth of their new siblings, and mean inter-individual distance between yearlings and adults was not significant different in June. My last prediction 6) was not fully supported: Mean inter-individual distance between siblings was slightly higher than between pups and parents, but this difference was not significant.

To my knowledge, no other study has quantified, with a sufficient sample how pack cohesion varies over time and among pack members. Nevertheless, to the extent that they are comparable, my findings on cohesion are consistent with earlier pioneer studies on the field (Peterson, Woolington & Bailey 1984; Fuller 1989; Metz *et al.* 2011; Barber-Meyer & Mech 2015; Benson & Patterson 2015). In the following, I discuss the observed ebbing cohesion along the time line from mid-winter to the end of June, from strong pack bonds to dispersal or the decision to stay within the natal territory by philopatry.

Cohesion was strongest in early parts of the winter. In this time period, loose snow is accumulating. It may therefore be advantageous for pups to stay with the pack and move single-filed behind their parents and siblings through deep snow, making their movements more energy-efficient (Mech 1970). Pups and young wolves are not considered successful predators, at least not on large and potentially dangerous prey such as moose (Mech & Peterson 2003; Sand *et al.* 2006; Barber-Meyer *et al.* 2016). Keeping together with the family will therefore increase the access to food for each family member by apportioning the food surplus from a large carcass among kin, instead of facilitating inter-specific competition (Vucetich, Peterson

& Waite 2004; Ordiz *et al.* 2015; Nordli & Rogstad 2016). Even though the difference was not significant, pups seemed to associate more with their parents than with their littermates as hypothesized by Barber-Meyer and Mech (2015). Perhaps the most natural explanation, also shown in other social group living species, is that the next to kin can also be the closest competitor (West, Pen & Griffin 2002; Smith 2014). Hence, associating more with the parents than with other litter mates may increase foraging opportunities and simultaneously avoid limits of social competition (Fox 1972; Zimmermann *et al.* 2007).

Death of one or both parents before or during early winter may affect the movement behavior of pups that are left alone in the natal territory (Ballard & Stephenson 1982; Brainerd *et al.* 2008). Inexperienced pups may therefore approach roads and inhabited houses in search for leftovers to remedy the hunger after the loss of a breadwinner. Anecdotal observations while writing this study, were the numerous visits during broad daylight of two wolf pups of the Julussa-pack that had recently lost their mother, foraging at my compost heap and birdfeeder over a 3-months period during early winter 2016-17 (Supplementary, Figure S5).

The mating season was likely an important trigger for the ebbing cohesion of the pups to their parents and other siblings. At this time hormonally controlled social aggression and hierarchical dominance within the wolf pack is most pronounced (Rabb, Woolpy & Ginsburg 1967; Zimen 1976; Sands & Creel 2004). Reproductive development (puberty) can also be a trigger of dispersal (Howard 1960; Mech & Boitani 2003) and pre-dispersal disruption from the pack bonds. A support for this is the increasing occurrence of extraterritorial movements from mating to mid-birth for more than half of the dispersing pups, while none of the philopatric pups did so.

When the winter is on retreat, the snow is more compact caused by alternating diurnal processes of melting and freezing, and both pups and parents can begin to move more independently from each other without wasting too much energy (Mech & Peterson 2003). The pups may continue to exploit the food surplus made available by the parents, but now they will also utilize old carcasses or other food sources such as bait sites, offal from hunting, and vehicle- or winter-killed ungulates emerging from the melting snow (Forbes & Theberge 1996; Metz *et al.* 2012; Zimmermann *et al.* 2015; Zimmermann *et al.* 2017). Benefits from solitary foraging increases by the supply of smaller and medium-sized prey that in turn are easier and less hazardous to catch than almost full-grown moose (Sand *et al.* 2008; Barber-Meyer *et al.* 2016). For the pups, this means that the potential prey menu is considerably wider.

The adult breeders moved largely together, and the only time the distance between the male and female was significantly different from zero was during the time of birth. As shown in numerous studies (Okarma *et al.* 1998; Mech 2000; Merrill & Mech 2003), at this point the male radiates back and forth from the den while the female nurses the neonate pups (Boyd *et al.* 1993; Jedrzejewski *et al.* 2001; Potvin, Peterson & Vucetich 2004; Demma & Mech 2009; Tsunoda *et al.* 2009). Parental priority is now given to the new pups (Packard, Mech & Seal 1983). At the same time, the parents switch from predominantly killing one-year-old to neonate moose calves (Sand *et al.* 2008), which in turn decreases social foraging opportunities of sharing available biomass surplus among former and current pups. For now, one-year-old, formerly pups, this leads to less attention and food surplus to retrieve from the parents, or to be shared between the nearly twofold sibling group. This may explain why the greatest rate of dispersal occurred during this period, with a sudden increase of the proportion of dispersed animals from 25% to 63%. The fact that the pups did not only increase mean individual distance to the parents, but also to their siblings, indicates that the pups become ever more solitary before dispersal.

By June, most pups had dispersed, and by that time, the mean inter-individual distance of pup to parents and siblings was no longer significantly different from zero. This may well be a result of the relatively small sample size of pups, which remained beyond as philopatric yearlings (n= 7). It could also indicate stronger social bonds of philopatric pups compared to their dispersing siblings. This explanation is supported by the fact that philopatric pups and yearlings did not go for extraterritorial forays. Unfortunately, the small sample size of philopatric pups did not allow for a comparison of the cohesion patterns of dispersing and philopatric pups.

The observed ebbing pack cohesion already before pups were one year old, and the successive dispersal matches some previous studies on wolf dispersal where the largest proportion of the pups left their natal territory 11-12 months of age (Gese & Mech 1991; Kojola *et al.* 2006). In the review by Fuller, Mech and Cochrane (2003) age specific dispersal rates for pups across populations range from 10-35%. The dispersal rate of 50% found in my study is therefore an order of magnitude higher than earlier reported. Because dispersal is regarded as a solitary expedition into an unknown landscape in search for own opportunities for establishment (Fritts & Mech 1981), it is not inconceivable that dispersing individuals prior to dispersal already have become relatively independent from the rest of the family group.

## Management implications

In strong contrast to the common belief that members of a wolf pack allegedly operate as a strictly synchronized unit, the wolf packs in our study displayed an ebbing cohesion of pups to their parents and siblings. This can lead to situations where wolf tracks from the same pack can be observed simultaneously in different parts of a wolf territory, giving rise to suspicion that wolf counts are widely underestimated, and/or that several wolf packs are occupying a given area. In fact, assessing pack size is challenged by the weakened pair bonds, my findings supports the annual monitoring of the wolf population to early parts of winter, when the chance that the pack travels together is higher than later in winter.

To regulate the wolf population, culling of entire packs by license hunt has been implemented in Scandinavia. It may be advantageous to do such culling during mid-winter before mating, while the pack still travels together for most of the time. This would increase efficiency and minimize the risk of 1) surviving pups in the transition of becoming independent, 2) pregnant females being left alone in the territory, and or 3) accidental culling of non-targeted dispersing or extraterritorial young wolves from other packs.

However, the outcome of hunting attempts can be unpredictable, and my results show that parents may sometimes be separated from pups in the natal territory also during early to mid-winter. If hunting leads to parents being culled, pups left alone in their natal territory will be less independent if the hunting happens earlier. It can therefore be argued that culling in late winter may also be advantageous for left behind pups.

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