



Spatial and temporal cohesion of parents and offspring in a social large carnivore

Kristoffer Nordli^{a,*}, Petter Wabakken^a, Ane Eriksen^a, Håkan Sand^b,
Camilla Wikenros^b, Erling Maartmann^a, Barbara Zimmermann^a

^a Department of Forestry and Wildlife Management, Inland Norway University of Applied Sciences, Campus Evenstad, Koppang, Norway

^b Department of Ecology, Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Riddarhyttan, Sweden

ARTICLE INFO

Article history:

Received 1 June 2022

Initial acceptance 28 September 2022

Final acceptance 1 November 2022

Available online 23 January 2023

MS. number: 22-00277

Keywords:

Canis lupus

cohesion

dispersal

intraspecific competition

mating

social organization

Social organization in animals is a fundamental factor driving population dynamics and individual spatial distribution. Affiliation among kin is common in social groups, but kinship is no safeguard against intraspecific competition. Within social groups, the closest competitors are often related. In this study, we present 14 years of GPS-position movement data from 65 pairs (i.e. breeding pair, pup–adult breeder and pup–pup) of Scandinavian wolves, *Canis lupus*. We investigated social behaviour by examining spatial and temporal patterns of cohesion through winter to early summer (January to July) including two key reproductive periods, mating and birth, using mixed regressive nonlinear time series analysis (GAMM). During the mating period, breeding wolf pairs remained cohesive, while offspring increasingly dissociated. Offspring became even more solitary until the next birth period, when most permanently left their natal pack and territory. We suggest that the social organization of wolves may be modulated by intraspecific competition related to social aggression during the mating period and food competition around the birthing period. Early independence followed by immediate natal dispersal may be advantageous to both offspring and parents if the chances of finding food and a breeding partner and settling in a vacant area are high.

© 2022 The Author(s). Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Group living may provide several potential direct fitness benefits such as cooperative hunting, resource defence, increased foraging efficiency and predator vigilance (Macdonald, 1983; Packer & Ruttan, 1988; Patterson & Messier, 2001; Sparkman, Adams, Beyer, et al., 2011). According to kin selection theory (Hamilton, 1964), group living with closely related individuals can provide inclusive fitness benefits such as increased provisioning and survival of close relatives, for example helpers at the nest (Russell & Hatchwell, 2001), or delayed natal dispersal (Ekman et al., 1999).

Yet, kinship within social groups does not safeguard individuals from the negative effects of social competition (Clutton-Brock & Parker, 1995; Mock & Parker, 1998). Within most social groups, the closest competitor is often kin (Smith, 2014; West et al., 2002). Benefits of group living are therefore trade-offs against direct disadvantages related to social/intragroup competition, disease transmission and increased exposure to parasites (Alexander, 1974; Altizer et al., 2003; Fuchs et al., 2016). The balance between social

tolerance, for example withholding social aggression, and competition among kin can be affected by resource distribution and individuals' spatiotemporal proximity (Alexander, 1974; Foster et al., 2006). Critical determinants of group formation, size and behaviour include interspecific competition and predation risk as well as diet preferences and the spatial and temporal dispersion, abundance and quality of food resources (Carr & Macdonald, 1986; Gittleman, 1989; Macdonald, 1983; von Schantz, 1984).

In social group-living species, the maintenance of the family structure can have direct and indirect fitness consequences (Lukas & Clutton-Brock, 2013). The ultimate factor for leaving familiar conspecifics (dispersal) is assumed to be the individual's attempt to maximize its own reproductive fitness (Lidicker Jr, 1962; Murray, 1967). However, dispersal not only cuts off access to parental provisioning, but may also increase individual mortality risk (Bekoff, 1977; Messier, 1985). The timing of dispersal may be crucial for timing of first reproduction, individual and newborn survival and subsequent fitness. Population density and resource abundance across the landscape likely increase the rate and success of early versus delayed dispersal (Fritts & Mech, 1981; Mayer et al., 2017).

Studying intraspecific social interactions is crucial for understanding individual temporal space use as well as resource

* Corresponding author.

E-mail address: kristoffer.nordli@inn.no (K. Nordli).

acquisition, population demography and gene flow (Morin et al., 1994; Singleton & Hay, 1983). The wolf, *Canis lupus*, can be used as a model species for illustrating spatiotemporal organization among kin. The fundamental social wolf unit is the monogamous territorial breeding pair, which together with current and/or previous offspring, form a family group, that is, a wolf pack (Mech, 1970). Intrapack cohesion and movement patterns depend on several factors including prey characteristics, climate and likely also social intraspecific competition during periods of mating and birth (Mech & Peterson, 2003; Zimen, 1976).

The primary driver for aggression and social avoidance through natural selection is competition for resources (Brown, 1964; Howard, 1960). Within wolf packs, the reproducing adults are dominant territory holders and often show aggressive behaviour towards conspecifics, including kin (Fox, 1972; Jordan et al., 1967; Packard et al., 1983; Zimen, 1976). In late winter and spring, increased social aggression and social avoidance is suggested to culminate during two specific reproductive events: the mating period and time of birth, that is, the early period of parental care for the newborn pups (Rabb et al., 1967; Sands & Creel, 2004; Zimen, 1976).

During winter–spring, wolf pack cohesion varies, and the individual pack members shift between splitting into smaller groups, spending time alone and even temporarily leaving the territory on extraterritorial forays (Fritts & Mech, 1981; Haber, 1977; Mech & Frenzel, 1971; Stenlund, 1955). Spatial and temporal dissociation from the social unit is common before natal dispersal (Bekoff, 1977; Harris & White, 1992; Isbell & Van Vuren, 1996). Individual offspring with low fidelity to their social group develop weakened social bonds and are likely the first ones to depart (Bekoff, 1977; Fuller, 1989; Gese et al., 1996).

Even though the wolf is one of the most investigated mammal species at a global scale (Amori & Gippoliti, 2000; Brooke et al., 2014; Zimmermann, 2014), studies on social behaviour of several individuals simultaneously within the same pack are still rare for wild populations (Barber-Meyer & Mech, 2015; Miller, 2012). Advances in global positioning system (GPS) technology provide unique opportunities for following rare, wide-ranging and elusive species (Cagnacci et al., 2010). With this technique, pioneering studies on social cohesion in wild wolves have emerged showing that wolf pack cohesion ranges from lower in summer to higher during winter (Barber-Meyer & Mech, 2015; Benson & Patterson, 2015; Metz et al., 2011). However, few quantitative studies on social behaviour of wild, free-ranging wolves outside North America have been published, and none have related cohesion directly to reproductive behaviour.

We examined the social behaviour of wolves from paired individual distances of wolf pack members using temporally synchronized GPS positions (the inverse of which we hereafter use synonymously with cohesion). Our study used 14 years of GPS data from forest-dwelling wolves in Scandinavia to examine the behaviour of pack members from winter to early summer, including the mating and birth period. We quantified the degree of cohesion over time between wolf pack members with both a novel method and a traditional approach for comparative interpretation. The investigated dyads per pack consisted of the adult breeding female and male, pup and adult breeder or pup siblings, and we identified the timing of pack dissolution events and natal dispersal.

We predicted that cohesion of the breeding pair would be strong, except during a few weeks after pups were born (P1). We also predicted pup–adult breeder and pup–pup cohesion would be strongest during the premating period in winter (P2) and would start decreasing during the mating period in February–March (P3). Because only the breeding pair is engaged in reproductive activities, pups may associate more with their litter siblings than with

their parents; therefore, we predicted that pup–pup cohesion would decrease at a slower rate than pup–adult cohesion (P4). Based on an increasing pup–pup independence, we predicted natal dispersal to be solitary (P5), and to coincide temporally with a new litter born within the natal territory (P6).

METHODS

Study Area

The study was conducted within the south-central core breeding range of wolves on the Scandinavian Peninsula, that is, Norway and Sweden (59°–62°N, 11°–19°E). 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, mainly birch, *Betula pendula* and *B. pubescens*, but also aspen, *Populus tremula*, alder, *Alnus incana* and *A. glutinosa*, willow, *Salix* spp., and rowan, *Sorbus aucuparia*. The climate is continental, characterized by cold and dry winters, with 3–6 months of snow cover, mainly between November and April (Milleret et al., 2017; Zimmermann et al., 2015). Moose, *Alces alces*, is the main prey species for wolves in Scandinavia, and densities are relatively high (average in winter: 1–3 per km²; range 0.7–3.3; Zimmermann et al., 2015). The recolonized Scandinavian wolf population is functionally isolated from the Finnish–Russian founder population and experiences inbreeding depression (Liberg et al., 2005; but see Åkesson et al., 2016). Long-term GPS data and DNA identification from the joint Scandinavian wolf monitoring programme shows that the wolf pack structure mainly consists of a breeding pair, the current litter (pups) and occasionally yearlings (Åkesson et al., 2022; Chapron et al., 2016; Liberg et al., 2012).

Study Animals

Wolves were located on snow, immobilized with a CO₂-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 standardized biomedical procedures for animal anaesthesia and handling (Arneimo & Evans, 2017). The GPS data were uploaded into the Wireless Remote Animal Monitoring database system (Dettki et al., 2014) for data validation and management. We darted and GPS-collared 51 individual wolves during 2002–2017, resulting in data from 14 territory-years (Appendix Table A1). For captured wolves, age was determined based on reproductive development, tooth wear and epiphyseal growth zones in the tibia (Wikénros et al., 2021). Kinship and specific age of offspring (i.e. pups of the year and yearlings) of all GPS-collared individuals were classified using an almost complete DNA-based population pedigree provided by the joint Scandinavian wolf monitoring programme (Åkesson et al., 2016; Liberg et al., 2005, 2012).

Ethical Note

Capture and handling of wolves were performed by trained and certified personnel with a veterinarian on site, following standardized biomedical protocols in adherence with international guidelines. Captures and capture-related procedures, for example biomedical sampling and/or GPS-collaring, were approved by the national governing bodies: Norwegian Food Safety Authority (i.e. ethical examination and approval), the Norwegian Environmental Agency and the Swedish Animal Experiment Ethics Board (C 281/6, C 266/99). Mounted GPS-collars did not exceed 2% of the individual wolf body weight and had mechanical drop-off units

preprogrammed to release after 900 days. To our knowledge none of the study animals in this study suffered a capture-related injury or mortality.

Territorial, Extraterritorial and Dispersal Movements

We created annual wolf territories (1 October–30 September) by calculating 100% minimum convex polygons (MCP) in ArcMap 10.5.1 using the GPS positions of adult breeding pairs (ESRI, 2017; Mohr, 1947). We then extended territory borders using a buffer derived from the adult pairs' movement patterns. Here, we calculated the average distance between all consecutive 4 h positions of the adult breeding wolves and divided by two, that is, estimating the mean distance an adult breeder could travel outside its MCP-defined territory boundary, but still be able to return before the next 4 h position was acquired. Owing to the right-skewed distribution of the distances between 4 h positions, we conservatively selected the 75th percentile instead of the mean as a unique buffer for each territory. To classify movement, we used 4 h GPS fixes from 11 unique territories over 14 years, including data from two or more wolves per territory (Appendix Table A1). For each territory and year, we plotted all GPS positions for a given offspring and defined all positions within the parental territory as 'natal movements'. We defined pup 'extraterritorial movements' as a sequence of positions outside the territory boundary buffer, followed by one or more positions inside the territory. We defined the timing of dispersal as the first position outside a territory boundary where no subsequent position was located within the territory or buffer zone. We did not include 'dispersal movements' in the cohesion analysis. If the pup/yearling remained within the territory after 1 July, i.e. > 14 months of age, they were classified as philopatric.

Interindividual Cohesion

We compared distances between all GPS-collared pack members and standardized their positions into 4 h positioning intervals between January and July. This provided six regular positions per day at 0300, 0700, 1100, 1500, 1900 and 2300 (GMT). Similar to Benson and Patterson (2015), we treated positions with ≤ 5 min deviation from the position schedule as simultaneous positions (Appendix Fig. A1a). From simultaneous positions, we calculated Euclidean distances between the breeding pair, pup–adult breeder and pup–pup. Since the breeding pair mostly travelled together (see Results), we randomly used data from one adult breeder as a proxy for both adult breeders to calculate pup–adult breeder distances. This allowed us to include territory-years in which only one adult breeder had a functioning GPS-collar, while avoiding pseudoreplication. Since capture events may influence subsequent wolf movement patterns, we excluded positions from all pack members for 7 days following a capture event (see Appendix and Figs A1b, A2).

Data Analyses

Time of birth

We used the software R, version 4.0.2 (R Development Core Team, 2021) for all statistical analyses. We estimated the time of birth similar to Walsh et al. (2016), but applied change-point analysis to the movement pattern of each adult breeder from 1 April to 1 June to reflect the range of possible birthing dates. We used Euclidean distance as the response variable and applied a gamma-distributed change-point algorithm (PELT) in both mean and variance with 95% confidence interval, CI, from the R package 'changepoint' to detect whether, and when, a change in movement had occurred (Killick & Eckley, 2014). Lastly, we pooled all

estimated change-points and defined the birthing period as the range from the earliest to the latest date of change (Appendix Table A1). In addition, since the gestation period of wolves ranges from 61 to 64 days (Mech, 1970; Packard, 2003; Pulliainen, 1965) we subtracted 64 days from the earliest and latest birth range dates to estimate the mating period.

Pairwise pack member cohesion and dissociation

As a proxy for pack cohesion, we modelled the distances between individual pack members throughout January to July to test whether cohesion varied between breeding wolf pairs, pup–adult breeder or pup–pup. We followed the framework provided by Zuur et al. (2010) and Zuur and Ieno (2016) for data exploration and regression type analysis. We used the function 'bam' implemented in the R package 'mgcv' (Wood, 2017) to build a generalized additive mixed model (GAMM), utilizing flexible nonlinear smooth functions s_i to capture nonlinearity in the data. Because we did not want our estimates to be influenced by the uncertainty of the breeding pairs' MCP boundaries, we selected both natal and extraterritorial positions for the analysis. We 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). Since the response was heavily tailed, we applied a Scaled T distribution (SCAT) for best response fit. To account for heterogeneity of variance, we used pairwise wolf ID (dyad ID) as a random factor smoother interaction, f_s , over time. We selected basis dimensions of k by evaluating effective degrees of freedom from the model computation and compared this to the $k-1$ index score. To account for residual autocorrelation, we fitted the model with an AR1 model structure. We included ordered factor terms to test the prediction that cohesion for breeding pairs, pups–adult breeders and pups–pups were significantly different from each other over time. Ordered factors were fitted with an additional intercept and a smooth term (Van Rij et al., 2016). To compare pack member cohesion, we contrasted ordered factors with the breeding pair cohesion as a reference level for pup–adult breeder and for pup–pup cohesion, and lastly with pup–pup cohesion as a reference level for pup–adult breeder. We validated the final model using the 'gam.check' function from 'mgcv' for diagnostic residual plots and model convergence. All model predictions were extracted by the functions 'get_predictions' and 'get_difference' in the package 'itsadug' and calculated with 95% CI around the mean. All plots were generated using the R package 'ggplot2' (Wickham, 2016).

Pairwise wolf dyad association rate

We analysed mean wolf dyad association rate similar to Barber-Meyer and Mech (2015) and Benson and Patterson (2015) by calculating the proportion of simultaneous positions ≤ 500 m for each week for adult breeding pairs, pups–adult breeders and pups–pups.

Extraterritorial behaviour and natal dispersal

We plotted the frequency distribution of a polynomial model on the onset of pups departing the natal territory on extraterritorial foray and the timing of natal dispersal. We estimated the inflection point of extraterritorial forays and cumulative natal dispersal (i.e. the point on the curve with the maximum derivative) by employing iterative bisection surface estimation (BSE) from the package 'inflection' (Christopoulos, 2012).

RESULTS

Time of Birth

Birthing could be estimated for all breeding females with available data series ($N = 9$; Appendix Table A2), but not for all breeding males ($N = 5$ of 9; Appendix Table A2). The time of birth ranged from 21 April to 12 May, with a median of 1 May, and the mating period ranged from 16 February to 9 March, with a median of 27 February.

Pairwise Pack Member Cohesion

We obtained a total of 20 285 GPS positions from 65 pairs of pack mates (adult breeders: $N = 9$; pup–adult: $N = 30$; pup–pup: $N = 26$) that were temporally synchronized with at least one GPS-collared pack mate. Adult breeding pairs moved almost exclusively together, with a median distance of 26.5 m. The only time period when distance between the breeding pair was significantly different from zero was the first month after the estimated time of birth (Fig. 1a, b, Table 1). This was also evident from the association rate (Fig. 2), as adult breeders dissociated more after time of birth.

Distance between pups and adult breeders was significantly different from zero from late February, increased gradually throughout the winter months and peaked during early May (Fig. 1a, Table 1). Association rate between pups and adult breeders yielded similar results, as pups increasingly dissociated from adult breeders during and after the mating period (Fig. 2). Distance between pups differed significantly from zero in mid-late February, with a progressive increase similar to distances between pups and adult breeders (Fig. 1b, Table 1). However, from late June onwards, distance between pups that turned 1 year old was no longer significantly different from zero (Fig. 1b, Table 1).

Comparing Pack Member Cohesion

By ordering the breeding pairs' distance as the reference level, we found that both pup–adult breeder and pup–pup distances became significantly different from adult–adult distances during the mating period, and this effect lasted until after the birth of the next litter (Fig. 3a, b, Table 1). Similarly, adjusting the pup–pup distance as the ordered reference level, the predicted mean distance between pup and adult breeder appeared lower compared to pup–pup distances prebirth, although we could not statistically

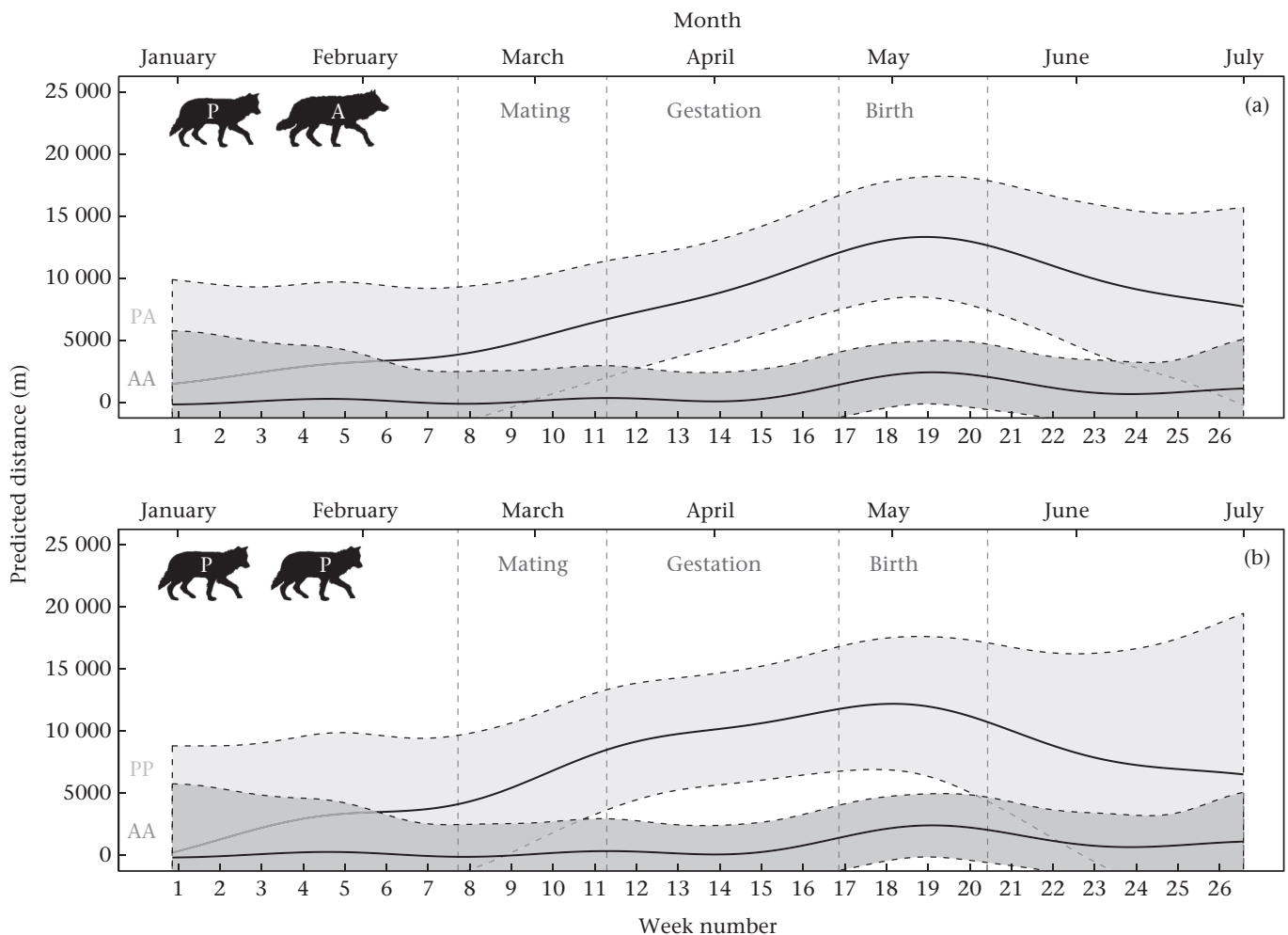


Figure 1. Predicted distances of Scandinavian wolves between (a, b) breeding pairs (AA, $N = 9$, dark grey), (a) pup–adult breeder (PA, $N = 30$, light grey) and (b) pup–pup (PP, $N = 26$, light grey), in relation to time displayed as months and week numbers. Distances were estimated using a mixed regressive nonlinear time series analysis (GAMM). The solid lines are predicted means over time, and the shaded grey areas present the 95% confidence interval. Dashed vertical lines indicate the range of birth dates from the PELT algorithm change-point analyses and the mating period given by subtracting the gestation period of 64 days.

Table 1

Model summary obtained from GAMM model on interindividual distances of Scandinavian wolves between breeding pairs (AA), pup–adult breeders (PA) and pup–pup (PP), with adjusted reference levels and the interaction term on time

	Estimate	Estimate df	Reference df	SE	t/F ¹	P
Parametric coefficients						
Intercept	515			1161	0.44	0.657
OFstatusPA	7079			1528	4.63	<0.001
OFstatusPP	6835			1875	3.64	<0.001
Approximate smooth terms						
s(time)		1.001	1.001		0.036	0.849
s(time)*OFstatusPA		3.868	4.343		2.906	0.017
s(time)*OFstatusPP		3.944	4.422		2.334	0.043
s(time, paired_wolf_ID)		202.2	517.0		2.803	<0.001

$R^2(\text{adj}) = 0.46$, deviance explained = 40%, $\text{fREML} = 21\,488$, $N = 20\,284$. OFstatus indicates the reference level. 's' is a smoother parameter allowing constructs of nonlinear relationships (in this case through time).

¹ Statistics are *t* for approximate smooth terms and *F* for parametric coefficients.

verify any period of significant difference (Fig. 3c, Table 1). Association rate between sibling pups showed a similar pattern, compared to that found for pups and adult breeders (Fig. 2).

Extraterritorial Forays and Timing of Natal Dispersal

We were able to classify 29 of the 30 GPS-collared pups as either dispersers or philopatric. The GPS-collar of two pups

malfunctioned, but DNA monitoring confirmed that at least one of them was philopatric, remaining in the natal territory. The extraterritorial predicted inflection point was on 18 March, followed by a predicted inflection point for dispersal on 1 May, i.e. the highest rate of dispersal coincided with the birth of the new litter (from 25% to 63%; Fig. 4). The earliest date of dispersal was 9 February, and by the first week of May, 50% of all dispersing pups had dispersed, which was equal to an annual dispersal rate of 38% for pups.

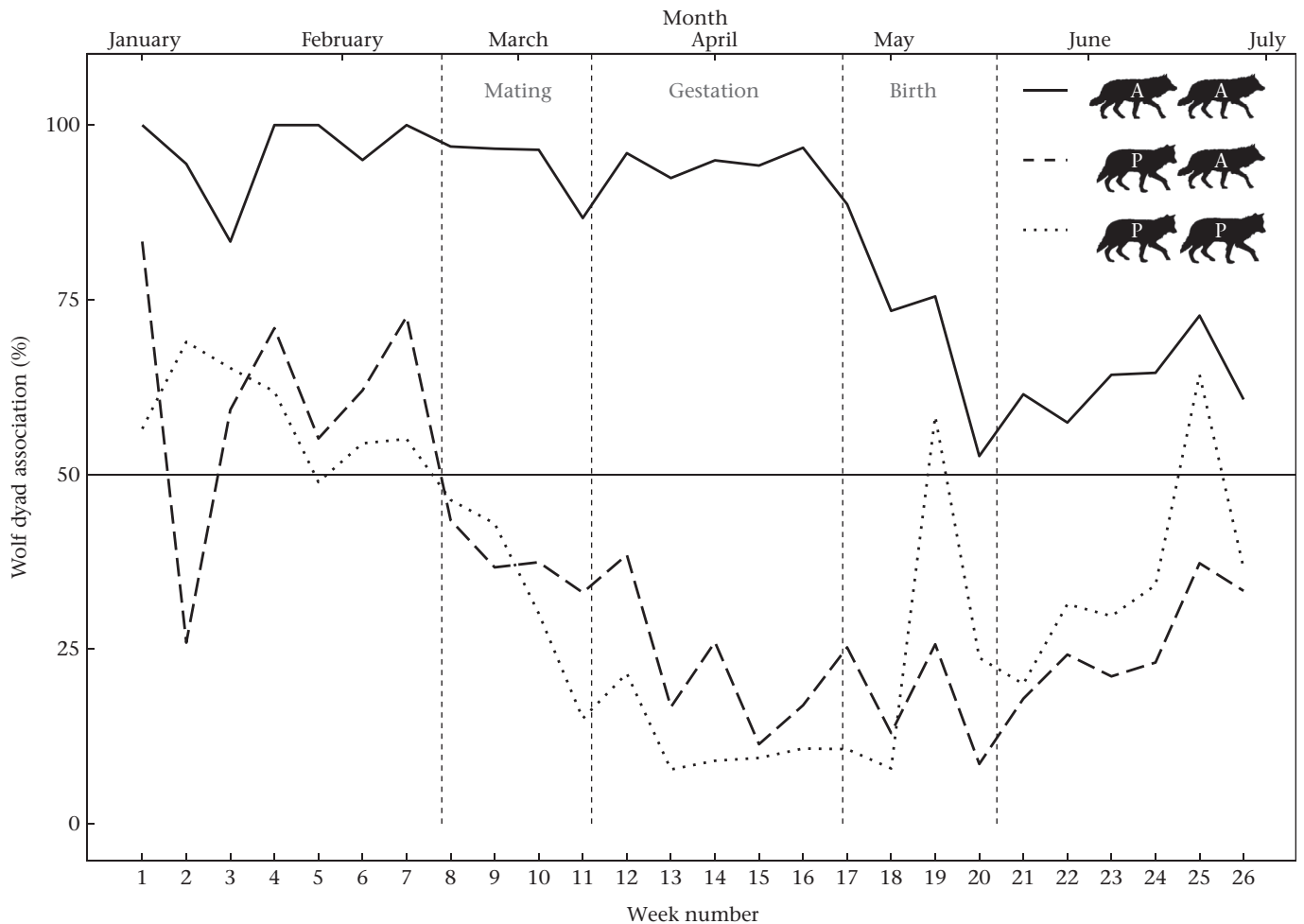


Figure 2. Mean dyad association rates (% of fixes ≤ 500 m) of Scandinavian wolves by weeks between adult breeding pairs (AA, $N = 9$, solid line), pup–adult breeder (PA, $N = 30$, dashed line) and pup–pup (PP, $N = 26$, dotted line). Dashed vertical lines indicate the range of birth dates from the PELT algorithm change-point analyses and the mating period given by subtracting the gestation period of 64 days.

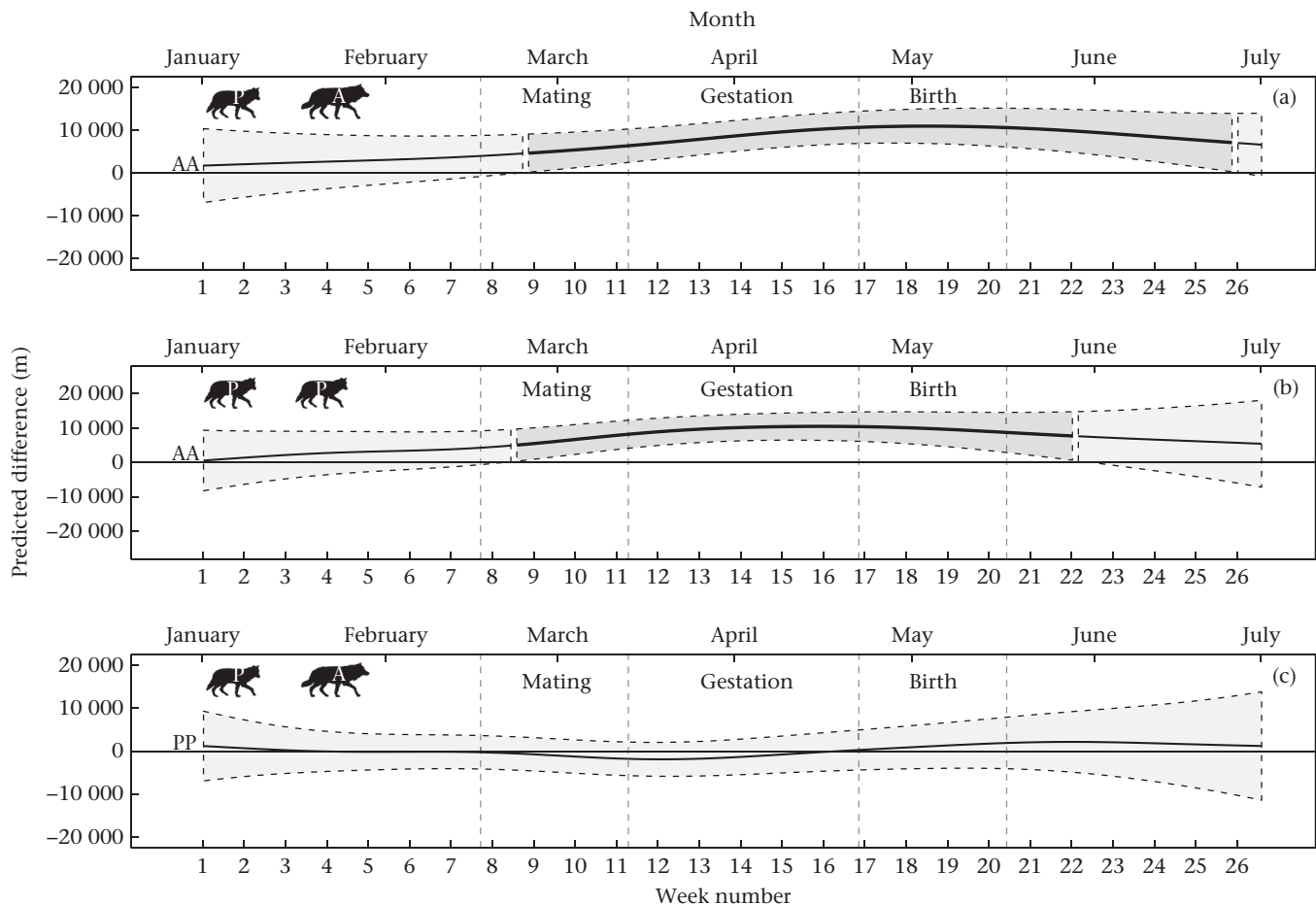


Figure 3. Predicted differences in distance of Scandinavian wolves between (a) pup–adult breeder (PA) while cohesion of adult breeding pairs (AA) is set to zero, (b) pup–pup (PP) while cohesion of adult breeding pairs (AA) is set to zero and (c) pup–adult breeder (PA) while pup–pup (PP) cohesion is set to zero. Distances were estimated using a mixed regressive nonlinear time series analysis (GAMM). Grey shaded areas show the 95% confidence interval and dark shaded grey areas indicate time periods in which the cohesion is significantly different from its reference cohesion. Dashed vertical lines indicate the range of birth dates from the PELT algorithm change-point analyses and the mating period given by subtracting the gestation period of 64 days.

Moreover, by the first week of July, all 22 dispersing pups (76%) had permanently left their natal territory. Among those, 12 (54%) showed extraterritorial predispersal behaviour (Fig. 4). None of the GPS-collared siblings dispersed together or along the same trajectory. The remaining seven pups (24%) were philopatric at least until the start of the subsequent winter (Fig. 4).

DISCUSSION

We have demonstrated how cohesion among wolf pack members changes over time, specifically during two main reproductive events, with pack dissociation starting during the mating period in winter (February–March) and the highest rate of natal dispersal coinciding with the birthing period of the subsequent litter in spring (April–May), respectively. Based on our findings, we suggest that behavioural processes related to mating and food competition around the time of birth are important factors modulating social organization in wolves, emphasizing the role of intraspecific competition in population dynamics of group-living species. Our study adds to a handful of earlier studies in the field (Barber-Meyer & Mech, 2015; Benson & Patterson, 2015; Fuller, 1989; Metz et al., 2011; Peterson et al., 1984) but provides considerably more detail.

Our results confirm earlier findings of high but seasonally variable cohesion within the primary social unit of wolf packs, that is,

the breeding pair (Barber-Meyer & Mech, 2015; Benson & Patterson, 2015). Consistent with our first prediction (P1), the breeding pairs moved largely together, except during the birthing period. From the time of birth, the male attempts to maximize food provision to the nursing female at the den (Mech, 2000). Hence, lower cohesion during the birthing period, as well as a lack of an identifiable change-point in the movement data from about half of the breeding males, likely resulted from sex-specific roles in biparental care of newborn pups. We also found support for our second (P2) and third (P3) predictions, that pup–adult and pup–pup cohesion would be strongest during the premating period and would decrease from mating onwards. Strong pack cohesion during mid-winter is likely to be advantageous for pup survival and parental fitness, as pups are not particularly successful predators of large and dangerous prey, such as moose (Barber-Meyer et al., 2016; MacNulty et al., 2009; Mech & Peterson, 2003; Sand et al., 2006). Mid-winter cohesion would not only increase access to food provided by the adults, but also increase potential protection against territorial neighbours, and allow for single-file movement through deep snow, which reduces energy expenditure (Mech, 1970).

However, during the mating period, pack cohesion appeared to dissolve, except for the breeding pair which remained together. Intraspecific competition, including competition for mates, is

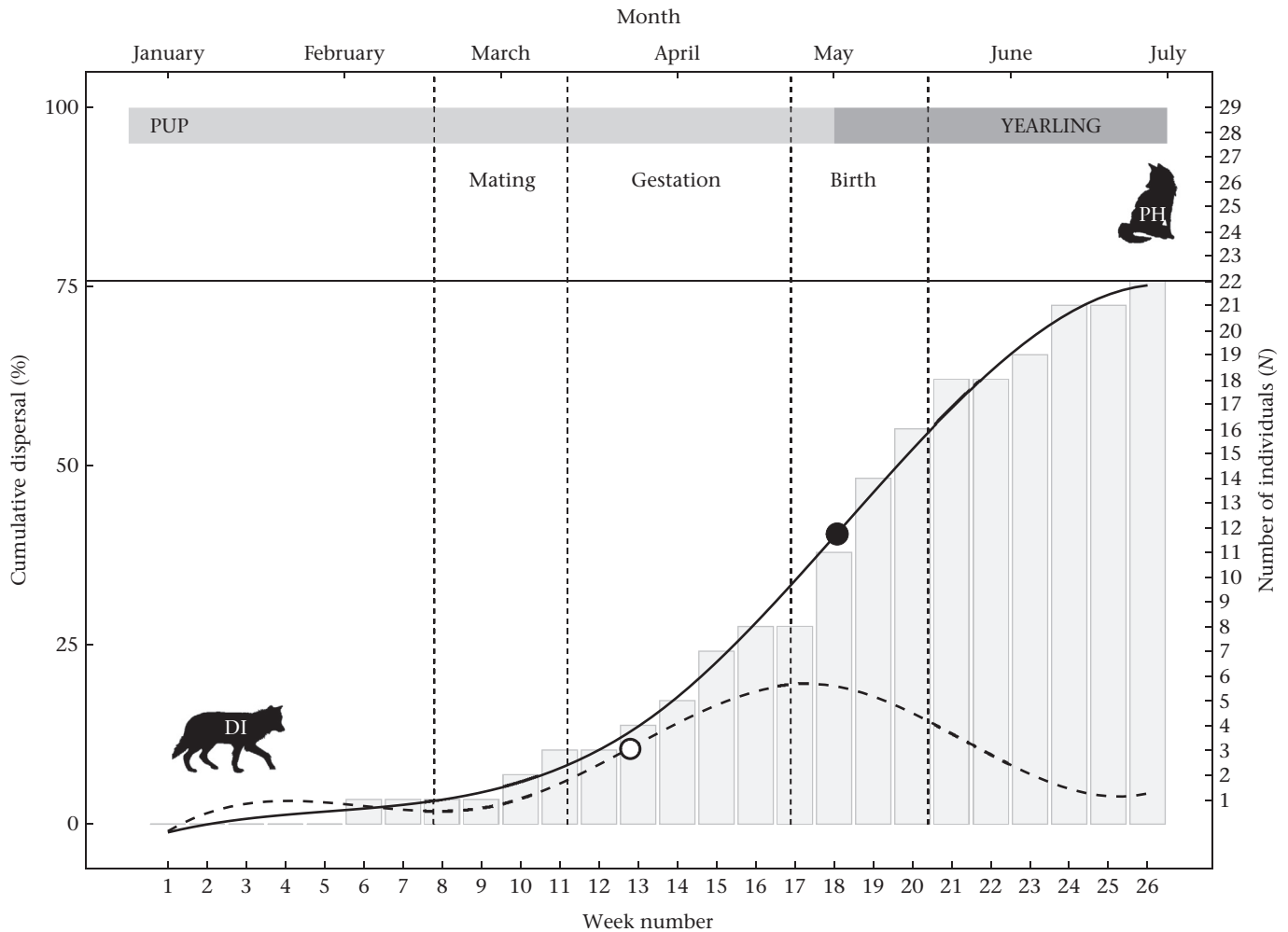


Figure 4. Cumulative frequency distribution of the time of dispersal (displayed as months and week numbers) for 29 Scandinavian wolf pups in 14 territory-years. The upper shaded area indicates when offspring are regarded as pups (light grey, < 1 year) and yearlings (dark grey, > 1 year), based on the median birth date at 1 May. The horizontal line ($y = 76\%$) displays the time when all dispersing pups/yearlings (DI, $N = 22$) had permanently left their natal territory before 14 months of age. Philopatric pups (PH, $N = 7$) that stayed in the natal territory made up 24%, indicated above this line. Dashed vertical lines indicate the range of birth dates from the PELT algorithm change-point analyses and the mating period given by subtracting the gestation period of 64 days. The dashed curved line shows the frequency distribution of extraterritorial offspring and the white circle indicates the predicted inflection point bisection surface estimation (BSE) of extraterritorial behaviour at 18 March. The solid black curved line shows the cumulative frequency of dispersal and the black circle indicates the predicted inflection point BSE at 1 May.

proposed as the primary driver for aggression and social avoidance within groups (Brown, 1964). Hormonally controlled aggressive behaviour linked to reproductive development is thought to be an important trigger for leaving familiar conspecifics (Howard, 1960). From observational studies on captive wolves, Rabb et al. (1967) and Zimen (1976) hypothesized that the time of mating seemed to be the key event influencing social organization in packs of wolves, as social aggression and hierarchical dominance peak during that time. Similarly, Sands and Creel (2004) reported that, during the period of mating, social aggression, along with elevated levels of glucocorticoids, a class of stress hormones, increased for wolf pack members in Yellowstone National Park, independent of sex or social status. Our results corroborate this pattern of social interactions between adults, pups and siblings during this reproductive event, lending support to the hypothesis that social organization in group-living species may be driven by intraspecific competition related to mating, that is, the first phase of pack member dissociation is triggered during the mating period.

Our fourth (P4) prediction that pup–pup cohesion would decrease at a slower rate than pup–adult cohesion was not

supported, as it was lower than, although not significantly different from, the cohesion between pup and adult breeder before birthing. These results correspond to Barber-Meyer and Mech's (2015) findings indicating temporarily stronger cohesion between pups and parents before compared to after birthing. Pups contribute little or nothing to a pack's kill rate on large prey (MacNulty et al., 2009; Zimmermann et al., 2015), making them competitors for food provided by their parents, as manifested in an inverse relationship between pack size and body weight of siblings (Zimmermann et al., 2015). This may explain why pups could benefit more from associating with their parents than with littermates.

However, our results suggest that pups became increasingly isolated from both parents and littermates in the same time period, as both pup–adult breeder and pup–pup cohesion decreased simultaneously. Progressive disruption of predispersal pack bonds by pups becoming increasingly independent while still in the natal territory corresponds to observations made by Bekoff (1977) that dispersing individuals dissociate spatially and temporally from the social group prior to dispersal. This may well provide subsequent benefits during dispersal, as it allows cognitive learning and

physical development in a more familiar and secure environment. Our results on extraterritorial behaviour support these findings, as we detected such behaviour in about half of the dispersing pups.

Our results on predispersal solitary behaviour supports our fifth prediction (P5), as none of the pups dispersed together with any other GPS-collared littermates. In accordance with our final prediction (P6), all dispersing offspring dispersed before 14 months of age, and the highest rate of dispersal coincided with the birth of the new litter. Interestingly, Behr et al. (2020) found that African wild dogs, *Lycaon pictus*, started to disperse at 13 months of age. Our results match findings from earlier studies on wolves showing that dispersing pups typically leave their natal territory between March and May, with the highest rate of dispersal at about 10–12 months of age, that is, prior to the birth of the new litter (Fuller, 1989; Gese & Mech, 1991; Kojola et al., 2006). The annual dispersal rate of 38% found for pups is slightly higher than the 10–35% reported in Fuller et al.'s (2003) review.

After the birthing period, most of the previous years' pups in our study had already dispersed, and by that time the cohesion no longer differed between the remaining pack members. Reduced cohesion may be a result of the relatively small number of pups that remained after the peak of dispersal or that stayed as philopatric yearlings. Alternatively, this may also indicate stronger social bonds of philopatric pups/yearlings compared to their dispersing littermates. However, the small sample size of philopatric pups did not allow us to compare the cohesion patterns of dispersing versus philopatric pups.

Disrupting social bonds during two periods in which hormonal influence (i.e. mating period) and food competition (i.e. birthing period) are most pronounced may increase foraging opportunities as it reduces social competition and aggression. For the Scandinavian wolves, moose calves are their main prey year-round (Sand et al., 2008; Zimmermann et al., 2015). Thus, approximately a month after a litter is born, the breeding pair switches from killing predominantly 1-year-old moose to killing neonate calves (Sand et al., 2008). The adult breeders prioritize feeding the new litter and reduce provisioning to the previous years' offspring (Creel, 2005; Jordan et al., 2022; Packard et al., 1983). Intensified social competition through increased group size and/or temporally varying resource availability may increase the relative cost of delayed versus early natal dispersal. In addition, the continued social suppression by the breeding pair, preventing offspring in their second year from breeding, may pose a disadvantage for philopatric offspring.

Leaving the natal territory around the time of birth of a new litter coincides with the prey community's birth pulse, as well as potential scavenging opportunities emerging in the winter snow or from brown bears, *Ursus arctos*, killing moose after den emergence (Dahle et al., 2013). Benefits of solitary foraging may increase with the supply of smaller/medium-sized prey, which are easier and less risky to catch than large moose (Barber-Meyer et al., 2016; Sand et al., 2008). Early independence followed by immediate natal dispersal may therefore be advantageous to both offspring and parents if the chances of finding food, a breeding partner and settling in a vacant breeding territory are high (Bekoff, 1977; Moehlman, 1987).

In contrast, given sufficient resources in the natal territory to support more than the needs of the newest litter and the breeding pair (Harrington et al., 1983; Kleiman, 1977; Rodman, 1981), the whole pack may benefit from philopatry (Sparkman, Adams, Beyer, et al., 2011; Sparkman, Adams, Steury, et al., 2011). Tolerance of philopatric yearlings by parents may extend their access to secure food sources and increase physical development and knowledge-based experience prior to dispersal (Howard, 1960; Mech & Boitani, 2003; Schmidt & Mech, 1997; Sparkman, Adams, Steury,

et al., 2011). This may in turn increase both survival during delayed dispersal and future potential for reproduction, while younger offspring may benefit from helper effects provided by their older siblings (Mech & Boitani, 2003; Moehlman, 1987; Rodman, 1981; Waser, 1996). Thus, resource abundance (prey density) combined with the level of intraspecific competition (wolf density) is likely to influence the timing and rate of natal dispersal in wolves.

Author Contributions

Kristoffer Nordli: Conceptualization, Methodology, Data analyses, Writing—original draft, Writing—review & editing. **Petter Wabakken:** Conceptualization, Methodology, Supervision, Funding acquisition, Writing—review & editing. **Ane Eriksen:** Methodology, Supervision, Writing—review & editing. **Håkan Sand:** Methodology, Funding acquisition, Writing—review & editing. **Camilla Wikenros:** Methodology, Writing—review & editing. **Erling Maartmann:** Methodology, Writing—review & editing. **Barbara Zimmermann:** Conceptualization, Methodology, Supervision, Writing—review & editing.

Data Availability

The data set generated and analysed during the current study is not publicly available as it contains potential sensitive information about den site and rendezvous locations of wolves. Data can be made available from the corresponding author upon reasonable request.

Declaration of Interest

The authors declare no conflicts of interest.

Acknowledgments

We are indebted to the veterinary team, J. M. Arnemo, A. L. Evans, P. Ahlqvist, P. Segerström, B. Fuchs, L. Gangås, and T. H. Strømseth, who captured and handled the wolves, pilot U. Grinde for outstanding helicoptering, S. E. Bredvold, B. Fuchs, F. Holen, P. Larsson, M. Rogstad and O-K. Steinset, along with the Norwegian Nature Inspectorate (SNO), and numerous volunteers and students at Campus Evenstad, who participated in captures and other field work, and O. Devineau for advice on statistics and data management. We also thank A. Tallian, Z. Walton, A. Thiel, the editor and three anonymous referees for valuable comments on the manuscript. This study was supported by the Scandinavian Wolf Research Project (SKANDULV) network. Financially, the SKANDULV project has been funded primarily by the Norwegian Research Council, Norwegian Environment Agency, Inland Norway University of Applied Sciences, Norwegian Institute for Nature Research, NOR-SKOG, County Governor of Innlandet, Swedish Research Council Formas, Swedish Environmental Protection Agency, Swedish University of Agricultural Sciences, Swedish Association for Hunting and Wildlife Management and Worldwide Fund for Nature (Sweden).

References

- Åkesson, M., Liberg, O., Sand, H., Wabakken, P., Bensch, S., & Flagstad, Ø. (2016). Genetic rescue in a severely inbred wolf population. *Molecular Ecology*, 25(19), 4745–4756.
- Åkesson, M., Svensson, L., Flagstad, Ø., Wabakken, P., & Frank, J. (2022). Wolf monitoring in Scandinavia: Evaluating counts of packs and reproduction events. *Journal of Wildlife Management*, Article e22206.
- Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics*, 5(1), 325–383.

- Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., Dobson, A. P., Ezenewa, V., Jones, K. E., Pedersen, A. B., Poss, M., & Pulliam, J. R. C. (2003). Social organization and parasite risk in mammals: Integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 517–547.
- Amori, G., & Gippoliti, S. (2000). What do mammalogists want to save? Ten years of mammalian conservation biology. *Biodiversity & Conservation*, 9(6), 785–793.
- Arnemo, J. M., & Evans, A. (2017). *Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx*. Inland Norway University of Applied Sciences.
- Aronson, Å., Wabakken, P., Sand, H., Steinset, O. K., & Kojola, I. (2000). *Varg i Skandinavien: Statusrapport for vinteren 1999–2000* [Wolves in Scandinavia: Status report for winters 1999–2000]. Hedmark University College.
- Aronson, Å., Wabakken, P., Sand, H., Steinset, O. K., & Kojola, I. (2001). *Varg i Skandinavien: Statusrapport for vinteren 2000/2001* [Wolves in Scandinavia: Status report for winters 2000–2001]. Hedmark University College.
- Barber-Meyer, S. M., & Mech, L. D. (2015). Gray Wolf (*Canis lupus*) dyad monthly association rates by demographic group. *Canadian Wildlife Biology and Management*, 4(2), 163–168.
- Barber-Meyer, S. M., Mech, L. D., Newton, W. E., & Borg, B. L. (2016). Differential wolf-pack-size persistence and the role of risk when hunting dangerous prey. *Behaviour*, 153(12), 1473–1487. <https://doi.org/10.1163/1568539x-00003391>
- Behr, D. M., McNutt, J. W., Ozgul, A., & Cozzi, G. (2020). When to stay and when to leave? Proximate causes of dispersal in an endangered social carnivore. *Journal of Animal Ecology*, 89(10), 2356–2366.
- Bekoff, M. (1977). Mammalian dispersal and the ontogeny of individual behavioral phenotypes. *American Naturalist*, 111(980), 715–732.
- Benson, J. F., & Patterson, B. R. (2015). Spatial overlap, proximity, and habitat use of individual wolves within the same packs. *Wildlife Society Bulletin*, 39(1), 31–40.
- Brooke, Z. M., Bielby, J., Nambiar, K., & Carbone, C. (2014). Correlates of research effort in carnivores: Body size, range size and diet matter. *PLoS One*, 9(4), Article e93195.
- Brown, J. L. (1964). The evolution of diversity in avian territorial systems. *Wilson Bulletin*, 76, 160–169.
- Cagnacci, F., Boitani, L., Powell, R. A., & Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550), 2157–2162. <https://doi.org/10.1098/rstb.2010.0107>
- Carr, G., & Macdonald, D. (1986). The sociality of solitary foragers: A model based on resource dispersion. *Animal Behaviour*, 34(5), 1540–1549.
- Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andren, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Baly, V., Bedó, P., Bego, F., Blanco, J. C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., ... Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346(6216), 1517–1519. <https://doi.org/10.1126/science.1257553>
- Chapron, G., Wikenros, C., Liberg, O., Wabakken, P., Flagstad, Ø., Milleret, C., Månsson, J., Svensson, L., Zimmermann, B., Åkesson, M., & Sand, H. (2016). Estimating wolf (*Canis lupus*) population size from number of packs and an individual based model. *Ecological Modelling*, 339, 33–44.
- Christopoulos, D. T. (2012). Developing methods for identifying the inflection point of a convex/concave curve. *arXiv preprint arXiv:1206.5478*.
- Clutton-Brock, T. H., & Parker, G. A. (1995). Punishment in animal societies. *Nature*, 373(6511), 209–216.
- Creel, S. F. (2005). Dominance, aggression, and glucocorticoid levels in social carnivores. *Journal of Mammalogy*, 86(2), 255–264. <https://doi.org/10.1644/bhe-002.1>
- Dahle, B., Wallin, K., Cederlund, G., Persson, I.-L., Selvaag, L. S., & Swenson, J. E. (2013). Predation on adult moose *Alces alces* by European brown bears *Ursus arctos*. *Wildlife Biology*, 19(2), 165–169.
- Dettki, H., Brode, M., Giles, T., & Hallgren, J. (2014, June 18). *Wireless Remote Animal Monitoring (WRAM) - A new international database e-infrastructure for management and sharing of telemetry sensor data from fish and wildlife* [Conference presentation]. San Diego, CA, U.S.A: International Congress on Environmental Modelling and Software <https://scholarsarchive.byu.edu/cgi/viewcontent.cgi?article=1019&context=iemssconference>.
- Ekman, J., Bylin, A., & Tegelström, H. (1999). Increased lifetime reproductive success for Siberian jay (*Perisoreus infaustus*) males with delayed dispersal. *Proceedings of the Royal Society B: Biological Sciences*, 266(1422), 911–915.
- ESRI. (2017). *ArcGIS desktop release 10.5.1*. Environmental Systems Research Institute.
- Foster, K. R., Wenseleers, T., & Ratnieks, F. L. (2006). Kin selection is the key to altruism. *Trends in Ecology & Evolution*, 21(2), 57–60.
- Fox, M. W. (1972). Socio-ecological implications of individual differences in wolf litters: A developmental and evolutionary perspective. *Behaviour*, 41(3), 298–313.
- Fritts, S. H., & Mech, L. D. (1981). Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildlife Monographs*, 80, 6–79.
- Fuchs, B., Zimmermann, B., Wabakken, P., Bornstein, S., Månsson, J., Evans, A. L., Liberg, O., Sand, H., Kindberg, J., Ågren, E. O., & Arnemo, J. M. (2016). Sarcoptic mange in the Scandinavian wolf *Canis lupus* population. *BMC Veterinary Research*, 12(1), 156.
- Fuller, T. K. (1989). Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs*, 3–41.
- Fuller, T. K., Mech, L. D., & Cochrane, J. T. (2003). Wolf population dynamics. In L. D. Mech, & L. Boitani (Eds.), *Wolves: Behavior, ecology, and conservation* (pp. 161–191). University of Chicago Press.
- Gese, E. M., & Mech, L. D. (1991). Dispersal of wolves (*Canis lupus*) in Northeastern Minnesota, 1969–1989. *Canadian Journal of Zoology*, 69(12), 2946–2955. <https://doi.org/10.1139/z91-415>
- Gese, E. M., Ruff, R. L., & Crabtree, R. L. (1996). Social and nutritional factors influencing the dispersal of resident coyotes. *Animal Behaviour*, 52, 1025–1043. <https://doi.org/10.1006/anbe.1996.0250>
- Gittleman, J. L. (1989). Carnivore group living: Comparative trends. In J. L. Gittleman (Ed.), *Carnivore behavior, ecology, and evolution* (pp. 183–207). Springer.
- Haber, G. C. (1977). *Socio-ecological dynamics of wolves and prey in a subarctic ecosystem* (Ph.D. thesis). University of British Columbia.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, 7(1), 17–52.
- Harrington, F. H., Mech, L. D., & Fritts, S. H. (1983). Pack size and wolf pup survival—their relationships under varying ecological conditions. *Behavioral Ecology and Sociobiology*, 13(1), 19–26. <https://doi.org/10.1007/bf00295072>
- Harris, S., & White, P. C. (1992). Is reduced affiliative rather than increased agonistic behaviour associated with dispersal in red foxes? *Animal Behaviour*, 44(6), 1085–1089.
- Howard, W. E. (1960). Innate and environmental dispersal of individual vertebrates. *American Midland Naturalist*, 152–161.
- Isbell, L. A., & Van Vuren, D. (1996). Differential costs of locational and social dispersal and their consequences for female group-living primates. *Behaviour*, 133(1), 1–36.
- Jordan, N., Golabek, K., Behr, D., Walker, R., Plimpton, L., Loström, S., Claase, M., Van der Weyde, L. K., & McNutt, J. (2022). Priority of access to food and its influence on social dynamics of an endangered carnivore. *Behavioral Ecology and Sociobiology*, 76(1), 1–15.
- Jordan, P. A., Shelton, P. C., & Allen, D. L. (1967). Numbers, turnover, and social structure of the Isle Royale wolf population. *American Zoologist*, 7(2), 233–252.
- Killick, R., & Eckley, I. (2014). changepoint: An R package for changepoint analysis. *Journal of Statistical Software*, 58(3), 1–19.
- Kleiman, D. G. (1977). Monogamy in mammals [Review]. *Quarterly Review of Biology*, 52(1), 39–69. <https://doi.org/10.1086/409721>
- Kojola, I., Aspi, J., Hakala, A., Heikkinen, S., Ilmoni, C., & Ronkainen, S. (2006). Dispersal in an expanding wolf population in Finland. *Journal of Mammalogy*, 87(2), 281–286.
- Liberg, O., Andren, H., Pedersen, H. C., Sand, H., Sejberg, D., Wabakken, P., Åkesson, M., & Bensch, S. (2005). Severe inbreeding depression in a wild wolf (*Canis lupus*) population. *Biology Letters*, 1(1), 17–20. <https://doi.org/10.1098/rsbl.2004.0266>
- Liberg, O., Aronson, Å., Sand, H., Wabakken, P., Maartmann, E., Svensson, L., & Åkesson, M. (2012). Monitoring of wolves in Scandinavia. *Hystrix, the Italian Journal of Mammalogy*, 23(1), 29–34. <https://doi.org/10.4404/hystrix-23.1-4670>
- Lidicker, W. Z., Jr. (1962). Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. *American Naturalist*, 96(886), 29–33.
- Lukas, D., & Clutton-Brock, T. H. (2013). The evolution of social monogamy in mammals. *Science*, 341(6145), 526–530. <https://doi.org/10.1126/science.1238677>
- Macdonald, D. W. (1983). The ecology of carnivore social behaviour. *Nature*, 301(5899), 379–384.
- MacNulty, D. R., Smith, D. W., Vucetich, J. A., Mech, L. D., Stahler, D. R., & Packer, C. (2009). Predatory senescence in ageing wolves. *Ecology Letters*, 12(12), 1347–1356.
- Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J. D. C., Rauset, G. R., & Pedersen, H. C. (2013). Home range size variation in a recovering wolf population: Evaluating the effect of environmental, demographic, and social factors. *Oecologia*, 173(3), 813–825. <https://doi.org/10.1007/s00442-013-2668-x>
- Mayer, M., Zedrosser, A., & Rosell, F. (2017). When to leave: The timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. *Animal Behaviour*, 123, 375–382.
- Mech, L. D. (1970). *The wolf: The ecology and behavior of an endangered species*. University of Minnesota Press.
- Mech, L. D. (2000). Leadership in Wolf, *Canis lupus*, packs. *Canadian Field-Naturalist*, 114(2), 259–263.
- Mech, L. D., & Boitani, L. (2003). Wolf social ecology. In L. D. Mech, & L. Boitani (Eds.), *Wolves: Behavior, ecology, and conservation* (pp. 1–35). University of Chicago Press.
- Mech, L. D., & Frenzel, L. D. (1971). *Ecological studies of the timber wolf in north-eastern Minnesota* (Vol. 52). US North Central Forest Experiment Station.
- Mech, L. D., & Peterson, R. P. (2003). Wolf-prey relations. In L. D. Mech, & L. Boitani (Eds.), *Wolves: Behavior, ecology, and conservation* (pp. 131–160). University of Chicago Press.
- Messier, F. (1985). Social-organization, spatial-distribution, and population-density of wolves in relation to moose density. *Canadian Journal of Zoology*, 63(5), 1068–1077.
- Metz, M. C., Vucetich, J. A., Smith, D. W., Stahler, D. R., & Peterson, R. O. (2011). Effect of sociality and season on gray wolf (*Canis lupus*) foraging behavior: Implications for estimating summer kill rate. *PLoS One*, 6(3), 10. <https://doi.org/10.1371/journal.pone.0017332>. e17332.

- Miller, J. A. (2012). Using spatially explicit simulated data to analyze animal interactions: A case study with brown hyenas in northern Botswana. *Transactions in GIS*, 16(3), 271–291.
- Milleret, C., Wabakken, P., Liberg, O., Åkesson, M., Flagstad, Ø., Andreassen, H. P., & Sand, H. (2017). Let's stay together? Intrinsic and extrinsic factors involved in pair bond dissolution in a recolonizing wolf population. *Journal of Animal Ecology*, 86(1), 43–54.
- Mock, D. W., & Parker, G. A. (1998). *The evolution of sibling rivalry*. Oxford University Press.
- Moehlman, P. D. (1987). Social organization in jackals: The complex social system of jackals allows the successful rearing of very dependent young. *American Scientist*, 75(4), 366–375.
- Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *American Midland Naturalist*, 37(1), 223–249.
- Morin, P. A., Moore, J. J., Chakraborty, R., Jin, L., Goodall, J., & Woodruff, D. S. (1994). Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science*, 265(5176), 1193–1201.
- Murray, B. G. (1967). Dispersal in vertebrates. *Ecology*, 48(6), 975–978.
- Packard, J. M. (2003). Wolf behavior: Reproductive, social, and intelligent. In L. D. Mech, & L. Boitani (Eds.), *Wolves: Behavior, ecology, and conservation* (pp. 35–65). University of Chicago Press.
- Packard, J. M., Mech, L. D., & Seal, U. S. (1983). Social influences on reproduction in wolves. In L. N. Carbyn (Ed.), *Wolves in Canada and Alaska: Their status, biology, and management* (pp. 78–85). Canadian Wildlife Service.
- Packer, C., & Rutman, L. (1988). The evolution of cooperative hunting. *American Naturalist*, 132(2), 159–198. <https://doi.org/10.1086/284844>
- Patterson, B. R., & Messier, F. (2001). Social organization and space use of coyotes in eastern Canada relative to prey distribution and abundance. *Journal of Mammalogy*, 82(2), 463–477. [https://doi.org/10.1644/1545-1542\(2001\)082<0463:soasuo>2.0.co;2](https://doi.org/10.1644/1545-1542(2001)082<0463:soasuo>2.0.co;2)
- Peterson, R. O., Woolington, J. D., & Bailey, T. N. (1984). Wolves of the Kenai peninsula, Alaska. *Wildlife Monographs*, 3–52.
- Pulliaainen, E. (1965). Studies on the wolf (*Canis lupus* L.) in Finland. *Annales Zoologici Fennici*, 2, 215–259.
- R Development Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Rabb, G. B., Woolpy, J. H., & Ginsburg, B. E. (1967). Social relationships in a group of captive wolves. *American Zoologist*, 7(2), 305–311.
- Rodman, P. S. (1981). Inclusive fitness and group-size with a reconsideration of group sizes in lions and wolves. *American Naturalist*, 118(2), 275–283. <https://doi.org/10.1086/283819>
- Russell, A. F., & Hatchwell, B. J. (2001). Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate. *Proceedings of the Royal Society B: Biological Sciences*, 268(1481), 2169–2174.
- Sands, J., & Creel, S. (2004). Social dominance, aggression and faecal glucocorticoid levels in a wild population of wolves, *Canis lupus*. *Animal Behaviour*, 67, 387–396. <https://doi.org/10.1016/j.anbehav.2003.03.019>
- Sand, H., Wabakken, P., Zimmermann, B., Johansson, Ö., Pedersen, H., & Liberg, O. (2008). Summer kill rates and predation pattern in a wolf-moose system: Can we rely on winter estimates? *Oecologia*, 156(1), 53–64. <https://doi.org/10.1007/s00442-008-0969-2>
- Sand, H., Wikenros, C., Wabakken, P., & Liberg, O. (2006). Effects of hunting group size, snow depth and age on the success of wolves hunting moose. *Animal Behaviour*, 72, 781–789. <https://doi.org/10.1016/j.anbehav.2005.11.030>
- von Schantz, T. (1984). Spacing strategies, kin selection, and population regulation in altricial vertebrates. *Oikos*, 42, 48–58.
- Schmidt, P. A., & Mech, L. D. (1997). Wolf pack size and food acquisition. *American Naturalist*, 150(4), 513–517. <https://doi.org/10.1086/286079>
- Singleton, G. R., & Hay, D. A. (1983). The effect of social organization on reproductive success and gene flow in colonies of wild house mice, *Mus musculus*. *Behavioral Ecology and Sociobiology*, 12(1), 49–56.
- Smith, J. E. (2014). Hamilton's legacy: Kinship, cooperation and social tolerance in mammalian groups. *Animal Behaviour*, 92, 291–304.
- Sparkman, A. M., Adams, J., Beyer, A., Steury, T. D., Waits, L., & Murray, D. L. (2011). Helper effects on pup lifetime fitness in the cooperatively breeding red wolf (*Canis rufus*). *Proceedings of the Royal Society B: Biological Sciences*, 278(1710), 1381–1389. <https://doi.org/10.1098/rspb.2010.1921>
- Sparkman, A. M., Adams, J. R., Steury, T. D., Waits, L. P., & Murray, D. L. (2011). Direct fitness benefits of delayed dispersal in the cooperatively breeding red wolf (*Canis rufus*). *Behavioral Ecology*, 22(1), 199–205. <https://doi.org/10.1093/beheco/arq194>
- Stenlund, M. (1955). *A field study of the timber wolf (Canis lupus) on the Superior National Forest*. Minnesota: Minnesota Department of Conservation.
- Svensson, L., Wabakken, P., Maartmann, E., Åkesson, M., & Flagstad, Ø. (2017). *Inventering av varg vintern 2016-2017 [Monitoring of wolves in winter 2016-2017]*. Rovdata, NINA and Viltskadecenter, SLU.
- Van Rij, J., Wieling, M., Baayen, R. H., & van Rijn, H. (2016). *itsadug: Interpreting time series and autocorrelated data using gamms*. R package version 2, 2 <https://cran.r-project.org/web/packages/itsadug/itsadug.pdf>.
- Wabakken, P., Aronson, A., Sand, H., Rønning, H., & Kojola, I. (2004). *Ulv i Skandinavia: Statusrapport for vinteren 2002-2003 [The wolf in Scandinavia: Status report of the 2002–2003 winter]*. Hedmark University College.
- Wabakken, P., Aronson, A., Sand, H., Steinset, O. K., & Kojola, I. (1999). *Ulv i Skandinavia: Statusrapport for vinteren 1998-99 [The wolf in Scandinavia: Status report of the 1998–99 winter]*. Hedmark University College.
- Wabakken, P., Aronson, A., Sand, H., Steinset, O., & Kojola, I. (2002). *Ulv i Skandinavia: Statusrapport for vinteren (2001-2002) [The wolf in Scandinavia: Status report of the 2001–2002 winter]*. Hedmark University College.
- Wabakken, P., Aronson, A., Sand, H., Strømseth, T. H., Kojola, I., & Norsk Institutt for Naturforskning, & Sverige, N. (2004). *Ulv i Skandinavia: statusrapport for vinteren 2003-2004 [The wolf in Scandinavia: Status report of the 2003–2004 winter]*. Hedmark University College.
- Wabakken, P., Aronson, A., Strømseth, T. H., Sand, H., & Kojola, I. (2005). *Ulv i Skandinavia : statusrapport for vinteren 2004-2005 [The wolf in Scandinavia: Status report of the 2004–2005 winter]*. Hedmark University College.
- Wabakken, P., Aronson, A., Strømseth, T. H., Sand, H., Maartmann, E., Svensson, L., Åkesson, M., Flagstad, Ø., Liberg, O., & Kojola, I. (2011). *Ulv i Skandinavia: Statusrapport for vinteren 2010-2011 [The wolf in Scandinavia: Status report of the 2010–2011 winter]*. Hedmark University College.
- Wabakken, P., Aronson, A., Strømseth, T. H., Sand, H., Maartmann, E., Svensson, L., Flagstad, Ø., Hedmark, E., Liberg, O., Kojola, I., & Sverige, N. (2010). *Ulv i Skandinavia: Statusrapport for vinteren 2009-2010 [The wolf in Scandinavia: Status report of the 2009–2010 winter]*. Hedmark University College.
- Wabakken, P., Aronson, A., Strømseth, T. H., Sand, H., Maartmann, E., Svensson, L., & Kojola, I. (2009). *Ulv i Skandinavia: Statusrapport for vinteren 2008-2009 [The wolf in Scandinavia: Status report of the 2008–2009 winter]*. Hedmark University College.
- Wabakken, P., Aronson, A., Strømseth, T. H., Sand, H., Svensson, L., & Kojola, I. (2006). *Ulv i Skandinavia: Statusrapport for vinteren 2005-2006 [The wolf in Scandinavia: Status report of the 2005–2006 winter]*. Hedmark University College.
- Wabakken, P., Aronson, A., Strømseth, T. H., Sand, H., Svensson, L., & Kojola, I. (2007). *Ulv i Skandinavia: Statusrapport for vinteren 2006-2007 [The wolf in Scandinavia: Status report of the 2006–2007 winter]*. Hedmark University College.
- Wabakken, P., Aronson, A., Strømseth, T. H., Sand, H., Svensson, L., & Kojola, I. (2008). *Ulv i Skandinavia: Statusrapport for vinteren 2007-2008 [The wolf in Scandinavia: Status report of the 2007–2008 winter]*. Hedmark University College.
- Wabakken, P., Sand, H. (n.d.). [Captured and GPS-collared wolves within the Scandinavian wolf research project (SKANDULV).] Unpublished raw data.
- Wabakken, P., Svensson, L., Kojola, I., Maartmann, E., Strømseth, T. H., Flagstad, Ø., Åkesson, M., & Zetterberg, A. (2012). *Ulv i Skandinavia og Finland: Sluttrapport for bestandsovervåking av ulv vinteren 2011-2012 [The wolf in Scandinavia and Finland: Status report of the monitoring of wolves for the 2002–2003 winter]*. Hedmark University College.
- Wabakken, P., Svensson, L., Maartmann, E., Åkesson, M., & Flagstad, Ø. (2016). *Inventering av varg vintern 2015-2016 [Inventory of wolves in winter 2015-2016]*. Rovdata, NINA and Viltskadecenter, SLU.
- Wabakken, P., Svensson, L., Maartmann, E., Flagstad, Ø., & Åkesson, M. (2015). *Bestandsovervåking av ulv vinteren 2014-15 [Monitoring of wolves in winter 2014-15]*. Rovdata, NINA and Viltskadecenter, SLU.
- Walsh, P. B., Sethi, S. A., Lake, B. C., Mangipane, B. A., Nielson, R., & Lowe, S. (2016). Estimating denning date of wolves with daily movement and GPS location fix failure. *Wildlife Society Bulletin*, 40(4), 663–668.
- Waser, P. M. (1996). Patterns and consequences of dispersal in gregarious carnivores. In J. L. Gittleman (Ed.), *Carnivore behavior, ecology, and evolution* (Vol. 2, pp. 267–295). Cornell University Press.
- West, S. A., Pen, I., & Griffin, A. S. (2002). Cooperation and competition between relatives. *Science*, 296(5565), 72–75.
- Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*. Springer.
- Wikenros, C., Gicquel, M., Zimmermann, B., Flagstad, Ø., & Åkesson, M. (2021). Age at first reproduction in wolves: Different patterns of density dependence for females and males. *Proceedings of the Royal Society B: Biological Sciences*, 288(1948), Article 20210207.
- Wood, S. N. (2017). *Generalized additive models: an introduction with R*. Chapman and Hall/CRC.
- Zimen, E. (1976). On the regulation of pack size in wolves. *Ethology*, 40(3), 300–341.
- Zimmermann, B. (2014). *Predatory behaviour of wolves in Scandinavia* (Ph.D. thesis). Evenstad: Hedmark University College.
- Zimmermann, B., Sand, H., Wabakken, P., Liberg, O., & Andreassen, H. P. (2015). Predator-dependent functional response in wolves: From food limitation to surplus killing. *Journal of Animal Ecology*, 84(1), 102–112. <https://doi.org/10.1111/1365-2656.12280>
- Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, 7(6), 636–645.
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3–14.

Appendix

To find an adequate time threshold for positions to be included after capture, we calculated all interindividual distances of the adult breeding pair. We then employed a capture effect matrix on days after any capture event within the territory. This led us to exclude all positions of all collared pack members in the first week (7 days) after a capture event of any pack member (see Figs A1, A2).

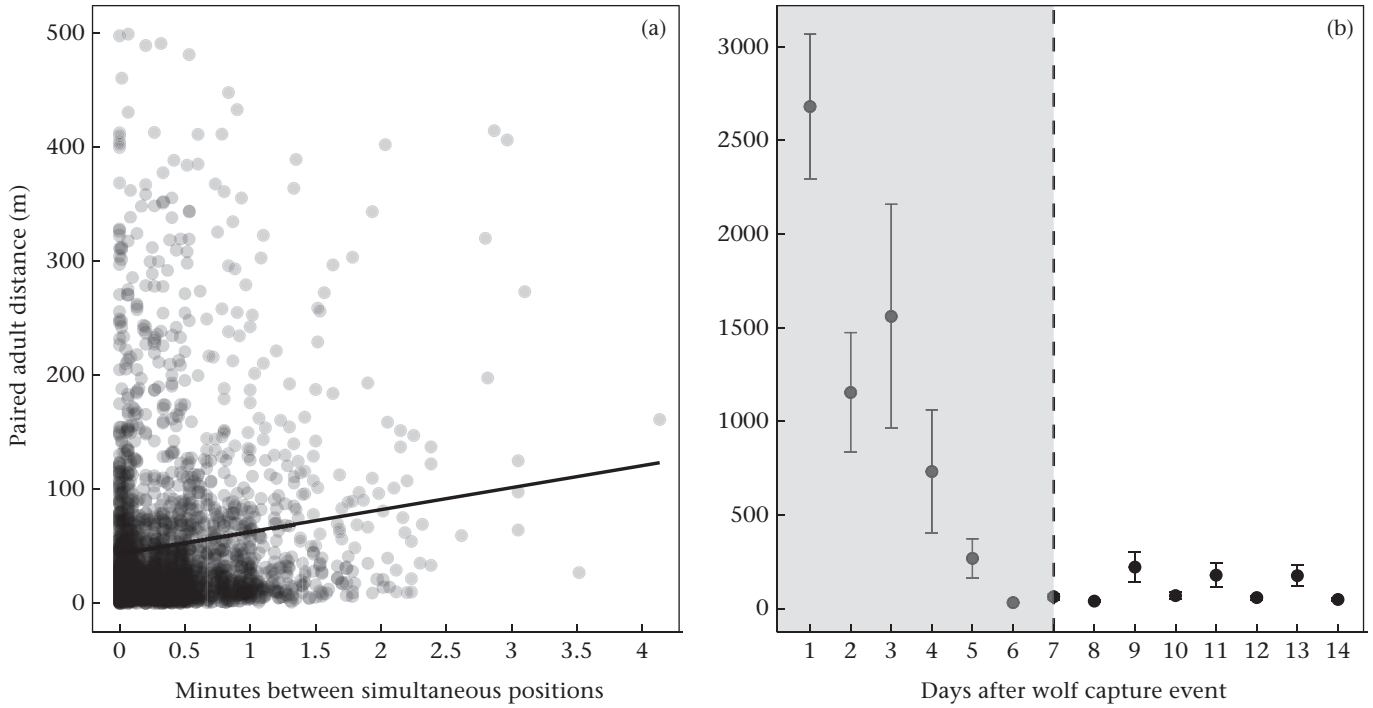


Figure A1. (a) The distance between adult breeders in relation to the time (min) between positions. The black line from a simple linear regression shows the bias in the distance relative to the deviation between each pair’s positions. (b) The distance between adults in a breeding pair in relation to days after a capture event for all capture efforts in a specific territory. The grey shaded area to the left of the vertical dashed line demonstrates the range of days after capture removed from all subsequent analysis. Black dots represent observed means and error bars are ± 2 SE.

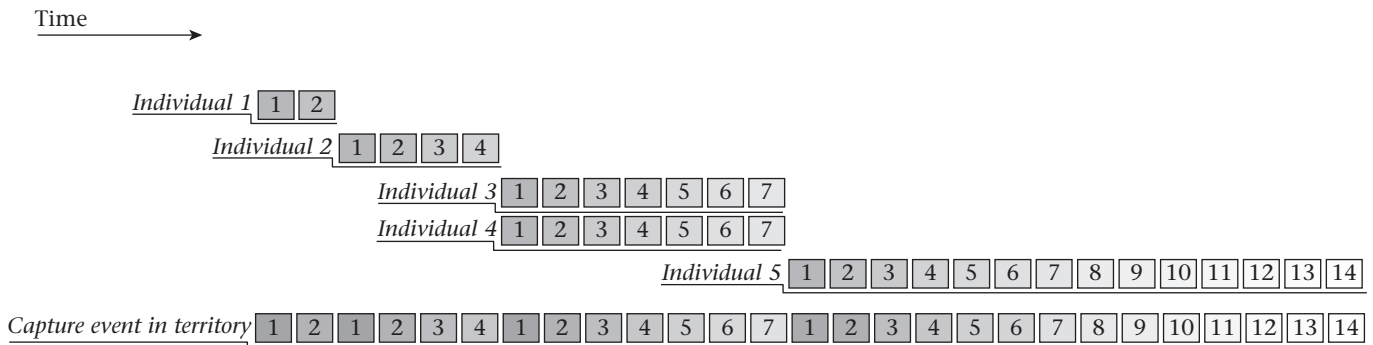


Figure A2. Schematic example of the number of days after capture of individuals in a wolf territory before the next capture event occurred. Numbers in squares indicate the days post capture for each individual. The bottom line shows the summary matrix for days since capture events for all individuals captured in a territory that territory-year. All positions of individuals before day 8 in the bottom line were removed from the analyses (i.e. 1 week after a capture event).

Table A1
Information about GPS-collared individuals in territory–years

Territory–year	Wolf ID	Status	Age	PH/DI	Pack size	% Collared
Graafjell–2002/2003	M0109	Adult breeder ♂	N/A	N/A	6(4)	66
	M0110	Adult breeder ♀	N/A	N/A		
	M0301	Offspring ♀	0	DI		
	M0302	Offspring ♀	0	DI		
Graafjell–2003/2004	M0109	Adult breeder ♂	N/A	N/A	7(5)	42
	M0110	Adult breeder ♀	N/A	N/A		
	M0406	Offspring ♂	0	DI		
Gressmark–2005/2006	M0611	Adult breeder ♂	N/A	N/A	5(3)	60
	M0610	Adult breeder ♀	N/A	N/A		
	M0609	Offspring ♀	0	DI		
Kynna–2006/2007	M0704	Adult breeder ♀	3–4	N/A	6/7(4/5)	42
	M0703	Offspring ♂	0	DI		
	M0705	Offspring ♀	0	PH		
Ulriksberg–2007/2008	M0602	Adult breeder ♀	3	N/A	1	33
	M0801	Offspring ♀	0	N/A		
Fulufjellet–2008/2009	M0904	Adult breeder ♂	4	N/A	5/6(4/5)	83
	M0906	Adult breeder ♀	3–4	N/A		
	M0907	Offspring ♀	0	DI		
	M0908	Offspring ♀	0	DI		
	M0909	Offspring ♀	0	DI		
Fulufjellet–2009/2010	M0904	Adult breeder ♂	5	N/A	9/10(7/8)	30
	M0906	Adult breeder ♀	4–5	N/A		
	M1011	Offspring ♂	0	DI		
Galven–2008/2009	M0903	Adult breeder ♂	FRI	N/A	7/8(5/6)	50
	M0914	Adult breeder ♀	2–3	N/A		
	M0901	Offspring ♂	0	DI		
	M0902	Offspring ♀	0	DI		
Tandsjø–2013/2014	M1103	Adult breeder ♂	4–5	N/A	8(6)	50
	M0909	Adult breeder ♀	4	N/A		
	M1402	Offspring ♀	0	DI		
	M1403	Offspring ♂	0	DI		
Rotna–2010/2011	M1109	Adult breeder ♂	3–4	N/A	5(3)	80
	M1110	Adult breeder ♀	N/A	N/A		
	M1108	Offspring ♂	0	PH		
	M1111	Offspring ♀	0	PH		
Rotna–2011/2012	M1110	Adult breeder ♀	N/A	N/A	7(5)	28
	M1206	Offspring ♂	0	DI		
Julussa–2013/2014	M1410	Adult breeder ♂	3	N/A	10(8)	50
	M1409	Adult breeder ♀	4–5	N/A		
	M1408	Offspring ♂	0	DI		
	M1407	Offspring ♀	0	PH		
	M1406	Offspring ♂	0	DI		
Osdalen–2016/2017	M1710	Adult breeder ♂	4–5	N/A	2	3
	M1705	Adult breeder ♀	5	N/A		
	M1706	Offspring ♀	0	PH		
	M1707	Offspring ♂	0	PH		
	M1708	Offspring ♂	1	DI		
	M1709	Offspring ♀	0	PH		
	M1711	Offspring ♂	0	DI		

Table A1 (continued)

Territory–year	Wolf ID	Status	Age	PH/DI	Pack size	% Collared
	M1712	Offspring ♀	1	PH	³	
	M1713	Offspring ♀	0	DI		
Slettaas–2016/2017					10(6)	90
	M1503	Adult breeder ♂	3–4	N/A		
	M1714	Adult breeder ♀	8	N/A		
	M1701	Offspring ♂	0	DI		
	M1702	Offspring ♀	0	DI		
	M1703	Offspring ♀	0	DI		
	M1704	Offspring ♀	0	DI		
N = 14 territory years	51 unique individuals			22DI:7PH	9/10(7/8)	60

Territory-year, individual wolf ID, status (offspring or adult breeder and sex), age, whether offspring were philopatric (PH) or dispersing (DI), pack size and litter size (in parentheses) were extracted from the wolf monitoring programme. Percentage of marked individuals is based on the minimum total pack size, using territory-year individual ID. FRI: Finnish/Russian immigrant. Source: Wabakken and Sand (n.d.) and the joint Scandinavian wolf monitoring programme: (Aronson et al., 2000, 2001; Chapron et al., 2014; Mattisson et al., 2013; Svensson et al., 2017; Wabakken, Aronson, Sand, Rønning, et al., 2004; Wabakken et al., 1999, 2002, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2015, 2016; Wabakken, Aronson, Sand, Strømseth, et al., 2004).

¹ Collar malfunction (M0801); unknown fate.

² Collar malfunction (M1706); confirmed philopatric by DNA in the subsequent winter.

³ As M1708 and M1712 were yearlings at the time of capture, they were included in capture effect matrices but not cohesion, pup–pup or pup–adult analyses.

Table A2

Birthing period estimated from adult breeders' movement rates

Territory	Year	Sex	Average no. of positions per day	Minimum segment length	Change-point date
Graafjell	2003	F	3	9	12 May
Graafjell	2003	M	3	9	07 May
Graafjell	2004	M	3	9	12 May
Ulriksberg	2004	F	2	6	4 May
Gressmark	2006	F	2	6	24 April
Galven	2009	M	3	9	6 May
Galven	2009	F	4	12	7 May
Fulufjellet	2009	F	5	15	25 April
Fulufjellet	2010	F	6	18	26 April
Fulufjellet	2010	M	6	18	N/A
Tandsjo	2014	F	4	12	28 April
Tandsjo	2014	M	3	9	N/A
Rotna	2011	M	5	15	N/A
Julussa	2014	F	4	12	12 May
Julussa	2014	M	5	15	11 May
Slettaas	2017	F	5	15	26 April
Slettaas	2017	M	5	15	N/A
Osdalen	2017	M	4	12	21 April

A change-point algorithm (PELT) was used to detect a change in movement for adult breeder males (M) and females (F) in each territory and year. The minimum segment length indicates a change that is consistent over a minimum of 72 h 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 the point of change. Numbers in bold indicate the range of change-point dates (estimated birthing period). The territory-years Kynna (2007) and Rotna (2012) (Table A1) were omitted from these analyses due to missing data after mid-April.