

# WILDLIFE BIOLOGY

## Research article

## Wolverine denning behaviour and its implications for monitoring reproductive females

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Knowledge about the number of reproductive females is important for monitoring population dynamics, and can be critical for managing human–wildlife conflicts. For wolverines *Gulo gulo*, counts of reproductive females is the basis for estimates of population size in Scandinavia, as well as a key measure for compensation payments to Sámi reindeer-herders in Sweden. However, documenting wolverine reproductive events in the field is challenging and requires knowledge of female denning behaviour. Furthermore, females may shift den sites, presenting difficulties in determining whether two den sites belong to the same or two neighbouring females. In this study, we used data from 18 GPS-collared wolverine females, monitored intensively during the denning season (15 February–31 May) in 2004–2014, to provide baseline information on denning behaviour. We documented reproductive events in 32 of 54 potential denning seasons, and identified a total of 245 den sites. Females used  $8.8 \pm 8.5$  (mean  $\pm$  SD) den sites per denning season (median = 6, range: 1–28). The number of den site shifts, the distance between subsequent den sites, and the time and distance females spent away from a den site increased during the denning season; while distances between neighbouring females' den sites remained constant. From late April, the distance between consecutive den sites used by the same female overlapped with distances between neighbouring females' den sites, resulting in increased uncertainty regarding whether two den sites belonged to one or two females. Using Bayesian modelling we calculated probabilities that two den sites belonged to the same female, or neighbouring females, conditional on the time of season and the distance between den sites. These findings will allow the monitoring program to adapt its methods for determining if multiple den sites belong to one or two reproductive events, using seasonally-dynamic threshold based on an understanding of wolverine denning behaviour.

Keywords: adaptive management, conservation performance payment, *Gulo gulo*, large carnivore



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## Introduction

Large carnivore populations are recovering in human-dominated landscapes across Europe (Chapron et al. 2014). This raises the importance of reliable population size estimates to assess population status, evaluate the effect of management measures and mitigate human–carnivore conflicts within an adaptive management framework (Walters and Hilborn 1978). Monitoring large carnivores is challenging and costly as these species are often elusive and range over large areas. The wolverine *Gulo gulo* is a typical example: a solitary and territorial carnivore inhabiting alpine tundra and boreal forest at low densities (Persson et al. 2010, Inman et al. 2012a). In Europe, wolverines occur in Sweden, Norway, Finland and Russia (Chapron et al. 2014). In the European Union, the wolverine is listed in the Habitat Directive, Annex II, as requiring the designation of special areas of conservation (www.ec.europa.eu). There are only two wolverine populations in Europe, the Scandinavian and the Karelian populations (Chapron et al. 2014); thus Sweden, Norway and Finland have the responsibility for wolverine conservation in Europe. The Scandinavian wolverine population is shared between Sweden and Norway (Chapron et al. 2014) where the countries have separate national management goals but a joint wolverine monitoring program to assess conservation status (Gervasi et al. 2016). The main unit for the monitoring program and population goals are annual counts of reproductive events, which are also used to estimate population size (Hedmark et al. 2021).

In northern Scandinavia, wolverines primarily prey on free-ranging, semi-domestic reindeer *Rangifer tarandus* managed by indigenous Sámi reindeer-herding communities (Mattisson et al. 2016). In Norway, wolverines also prey upon free-ranging domestic sheep *Ovis aries* during summer (Landa et al. 1997, Mattisson et al. 2016). Thus, the resulting depredation conflicts are a central management issue (Hobbs et al. 2012, Tveraa et al. 2014), which is mitigated mainly through economic compensation, lethal control and licensed hunting (Persson et al. 2009, 2015). In Sweden, a conservation performance payment (CPP) system is implemented within the reindeer husbandry area, where compensation is paid in relation to wolverine presence to offset predation losses (Zabel and Holm-Muller 2008). Like the national population goal and monitoring program, the main unit for the CPP is the annual number of reproductive events (i.e. 200 000 SEK per reproductive event within each reindeer herding district, Persson et al. 2015). Since its implementation in 1996, the CPP has contributed to a population increase through indirect protection of reproductive females (Persson et al. 2015). Consequently, the accuracy of and trust in the monitoring program is critical for assessing the population status, for management decisions and conservation payments, and therefore has socioeconomic consequences and influences the credibility of wolverine management (Zabel and Holm-Muller 2008, Aronsson and Persson 2017).

The Scandinavian wolverine monitoring program is largely based on snow-tracking where authorized personnel

register wolverine activity indicating reproductive events (i.e. documented active reproductive den sites or observations of young) and collect DNA-samples from wolverine scats (Aronsson and Persson 2017). Wolverine females give birth to 1–4 young (mean 1.9 young, Persson et al. 2006), mainly in February, and the young are kept in a den during the spring (Inman et al. 2012b). Within the monitoring program, active reproductive den sites and observations of females with cubs are documented from 1 February to 31 July, following predefined criteria, to determine the annual number of unique reproductive events (Aronsson and Persson 2017, SEPA 2021). Den sites are often located in steep and rugged terrain (May et al. 2012, Makkonen 2015), and usually consist of one or several tunnels in snowdrifts or are linked to snow-covered structures such as boulders, cliffs or fallen trees (Magoun and Copeland 1998, May et al. 2012, Makkonen 2015). As wolverines are solitary and territorial, and each female occupies a large territory (mean female territory size = 170 km<sup>2</sup>, Persson et al. 2010), it is a challenge for the monitoring personnel to find the den site. Thus, knowledge of female denning behaviour and activity patterns during the denning period (i.e. time and distance spent outside the den site) would facilitate planning of monitoring activity to improve the chance of detecting tracks leading to or from den sites, and to fulfil the criteria needed for documentation of active reproductive den sites (Aronsson and Persson 2017). Furthermore, wolverine females may move their young between multiple den sites during the spring (Inman et al. 2012b), either by carrying the young (early denning season) or the young following the mother (late denning season). This behaviour poses additional challenges in terms of assessing if multiple documented den sites belong to one unique reproductive event (i.e. one female moving her young between den sites) or two separate reproductive events in neighbouring female territories (Fig. 1d, Persson et al. 2012). The current monitoring program uses a pre-defined distance criterion of 10 km to separate reproductive events, i.e. if two or more den sites are registered within the same area. Thus, all den sites within 10 km are classified as the same reproductive event unless DNA samples collected at both sites identifies separate breeding females, or if females with young are observed (visual observation or snow tracks) at both sites within 12 h (SEPA 2021). However, the reliability of using this static distance criterion throughout the entire monitoring season needs to be evaluated with empirical data on wolverine female denning behaviour, including information on den site use of neighbouring females (Persson et al. 2012).

In this study, we use location data from 18 wolverine females, monitored intensively with GPS-collars during a total of 54 potential denning seasons (15 February–31 May) in 2004–2014, to present baseline information on female denning behaviour. We assess the number of den sites used within the same denning season, how often and how far females move when switching den sites, and how females use their territory in relation to the location of their den site. In addition, we used observed distances between den sites used

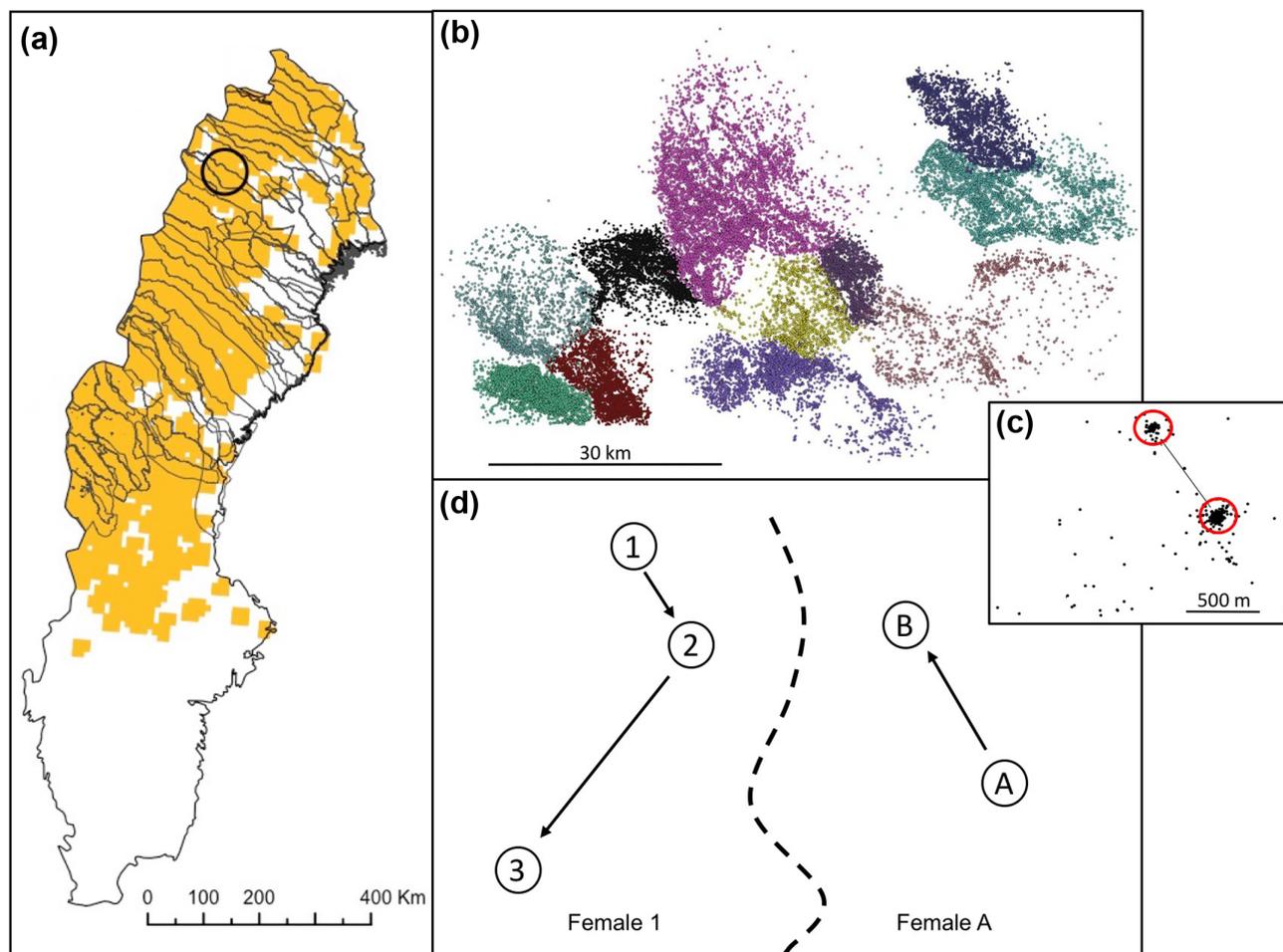


Figure 1. (a) Wolverine distribution in Sweden (yellow; from Chapron et al. 2014), the reindeer husbandry area (grey lines show borders for all the 51 reindeer management units), and the location of the study area (black circle). (b) Example of wolverine female GPS-location data from the study area (different colours show different females). (c) Example of how cluster of GPS-locations (black dots) are used to identify wolverine female den sites (red circles). (d) Schematic representation of two neighbouring females changing den sites during the denning season (circles; 1–3 for female 1; A–B for female A), and their territory border (dashed line; not known during population monitoring of uncollared females). If two of these den sites are found within the monitoring program, the challenge is to assess if the two den sites belong to the same female (e.g. den sites 1 and 3, or A and B) or two neighbouring females (e.g. den sites 2 and B, or 3 and A), when only the locations of the two den sites and when during the denning season they were found is known.

by the same female and between neighbouring females' den sites to calculate the following: 1) the daily probability that a single female will switch den site further than predefined distance thresholds, 2) the probability that the distance between den sites used by a single female is above predefined distance thresholds at different time periods during the denning season, and the probability that the distance between neighbouring females' den site is below these threshold distances and 3) the probability that two den sites belong to the same female or to neighbouring females based on the distance between them and the time period when the latter den site was observed. This assessment of wolverine denning behaviour provides important information to improve the monitoring program, an evaluation of the use of distance criteria to separate reproductive events during the denning season, and thus the reliability of both the CPP system and population size estimates.

## Material and methods

### Study area

The study was carried out in and around Sarek National Park in northern Sweden (Kvikkjokk: 67°00'N, 17°45'E) (Fig. 1). The area consists of deep valleys from about 300 m a.s.l. to alpine peaks up to 2000 m a.s.l. The main vegetation at lower elevations consists of mixed conifer forest (Scots pine *Pinus sylvestris*, Norway spruce *Picea abies*) interspersed by mires and lakes, followed by hillsides and high-elevation downy birch forest *Betula pubescens* which form the tree line at 600–700 m a.s.l. (Rauset et al. 2013). The higher parts of the hillsides include low alpine tundra with dwarf birch *Betula nana* and willow shrubs *Salix* spp., succeeded by lower growing heaths, grass and meadows, and high plateaus of bare rock

and glaciers. The climate is continental with average temperatures of  $-13^{\circ}\text{C}$  in January and  $5^{\circ}\text{C}$  in May ([www.smhi.se](http://www.smhi.se)). The ground is usually snow covered from November to May. The study area includes important spring–autumn grazing land for semi-domestic reindeer, although some reindeer remain in the area every winter ([Mattisson et al. 2011](#)).

The human population density is very low, limited to one minor village (<10 permanent settlements) and a few cabins. There are two dead-end roads in the outskirts of the study area, and a hydropower plant ([Rauset et al. 2013](#)). Within the National Park there are restrictions for access, with strict regulations regarding snowmobiling, flying and landing, fishing, hunting and the use of dogs ([SEPA 2013](#)). Outside the National Park, the main human activity is seasonal reindeer herding, but the area hosts a limited number of tourists, mainly concentrated to a few larger valleys in March–April and hiking in July–August.

### Wolverine capture, monitoring and identification of den sites

All capture and handling of wolverines followed pre-established protocols ([Arnemo et al. 2012](#)) approved by the Animal Ethics Committee for northern Sweden and fulfil the ethical requirements for research on wild animals (protocol no. A13-09). We captured wolverines by darting from helicopter or from the ground, immobilised them with a mixture of ketamine and medetomidine and equipped them with GPS-collars (2004–2006: Televilt Posrec C300; TVP positioning, Lindesberg, Sweden, and 2008–2014: GPS plus mini, Vectronic Aerospace GmbH, Berlin, Germany) and intraperitoneally implanted VHF-transmitters (iMP/400/L, Telonics inc., Mesa, Arizona, USA). The fix-rate programming for GPS-collars was 8–48 locations per day.

We used location data from 18 adult wolverine females monitored intensively with GPS-collars during 54 potential denning seasons (15 February–31 May) in 2004–2014 to evaluate whether they displayed behaviours revealing a reproductive event ([Persson et al. 2006](#), [Rauset et al. 2015](#), [Aronsson 2017](#)). Den sites used by each female were identified by detection of distinct clusters of GPS locations ([Fig. 1c](#)) using GIS software (ArcMap 9.3, ESRI), complemented with VHF radio-tracking from the ground ( $\geq 500$  m) or occasionally from helicopter. We classified a cluster as a den site if it was characterized by concentrated consecutive locations predominantly during daytime ([Walton and Mattisson 2021](#)) and we investigated identified clusters in the field to separate den sites from other activities, such as feeding sites, cache sites or daybeds (c.f. [Mattisson et al. 2011](#), [Mattisson et al. 2016](#), [van der Veen et al. 2020](#)). To avoid disturbance at suspected den sites, field visits were done  $\geq 1$  week after the female last used the site, and often during early summer after snowmelt. Furthermore, den sites were not visited in the field by the personnel from the national monitoring program, as the GPS locations provided sufficient information to be included in the annual count of reproductive events within the monitoring program. The natal den site (i.e. where the cubs were

born), was defined as the first place where GPS location data showed that a female remained within a restricted area ( $\leq 50$  m radius) for several consecutive days, sometimes in combination with an increase in unsuccessful fixes, which indicate that the female is at a place with obstructed satellite contact ([Mattisson et al. 2010](#), [Walton and Mattisson 2021](#)). It became increasingly difficult to confidently identify den sites with time during the denning season, often from late-May, because females switched den site more frequently and spent shorter times with cubs at each site. Therefore, we did not include any sites used after 1 June in this study.

In total, females reproduced in 32 (59%) of the 54 potential denning seasons (1–4 reproductions per unique female). The reproductive events were confirmed by cubs observed or captured together with the mother ( $n=28$ ), or by cubs found dead at the den site ( $n=2$ ). In the remaining two cases we lost contact with the denning female (evident from GPS-locations) due to collar failure ( $n=1$ ) and suspected poaching ( $n=1$ ) before reproduction could be confirmed by observations of cubs.

### Denning behaviour

For den sites of uncollared females documented within the population monitoring program, the parturition date is unknown. Therefore, to represent the limited information available for monitoring personnel, we separated the denning season into seven ~ two-week time periods (i.e. 15–28 February, 1–15 March, 16–31 March, 1–15 April, 16–30, 1–15 May and 16–31 May); hereafter referred to as time periods 1–7. We obtained den site information during all of the seven time periods for 13 of the 32 female denning seasons with confirmed reproductive events. For the remaining 19 female denning seasons with confirmed reproductive events, we did not obtain den site information for all time periods due to several reasons: one female gave birth in March and was hence only monitored during time periods 2–7); it was not possible to locate den sites within the last time period [ $n=5$ ]; transmitter failure (1 March–9 April [ $n=6$ ]); the female lost the cubs (19 and 21 February, 4 and 11 May [ $n=4$ ]); the female died (20 March and 4 May [ $n=2$ ]); one female was captured together with young on 6 May and was hence only monitored during time periods 6–7.

We defined that a female changed den site when her GPS-locations started creating a new cluster at a new den site, and did not return to the previous den site. We excluded the first and last day at each den site, to avoid including locations when the cubs were moved between den sites. When a female changed den site, we calculated the moving distance as the distance from the new den site to the most distant of all the previous den sites used during the same denning season (i.e. maximum moving distance). Distances were measured from the centre point of each den site using the ‘rgeos’ package ([Bivand and Rundel 2016](#)) in R ([www.r-project.org](http://www.r-project.org)). To assess if distances between den sites were influenced by home range size (i.e. females with larger home ranges also had longer distance between den sites) we fitted linear

mixed models using the ‘lme4’ package (Bates 2015) in R ([www.r-project.org](http://www.r-project.org)) with log-transformed maximum moving distances as the response variable and yearly home range size as explanatory variable, for each of the seven time periods. Annual home range sizes were estimated using the fixed kernel method (Worton 1989) using the ‘adehabitatHR’ package (Calenge 2006) in R ([www.r-project.org](http://www.r-project.org)), following Aronsson and Persson (2018). Individual female denning season was included as a random effect in all models to account for repeated measurements.

To assess the amount of time each female spent at each den site, we recorded the proportion of locations within 100 m from the central point of the current den site (hereafter ‘denning area’) for each time period. Because the location frequency varied between females and years, we used the daily proportion of total location attempts that resulted in a location inside or outside of the denning area, as well as the proportion of failed fix attempts. To assess the amount of time the female spent at different distances from the den site, we calculated the cumulative proportion of total locations (failed fixes excluded) outside of the denning area that were within 1, 2, 4, 6, 8 and 10 km from the den site for each time period. Furthermore, we calculated the daily mean distance from the centre point of the den site to all locations outside of the denning area for each time period.

### Den sites belonging to the same or neighbouring females

Within the Scandinavian wolverine monitoring program, there is a need to consider distances between den sites found at different times during the denning season to determine whether they belong to the same reproductive event (i.e. one female moving her young between den sites) or two separate reproductive events by two neighbouring females. This study is conducted within the Swedish wolverine research project, where one major goal has been to monitor all resident wolverine females within the study area during 1993–2015 (Rauser et al. 2015), resulting in a known distribution of female territories (Aronsson 2017, Aronsson and Persson 2018). For this study, we define neighbouring females as females for which the GPS locations show that their territories are bordering each other (Fig. 1b), resulting in a total of 23 yearly pairs of neighbouring females (17 unique females).

In the field, it is often impossible to identify the natal den site or the order of den use by uncollared females. Further, often the only information available in the monitoring program are the dates that the different den sites are found and the distance between them, as reproductive events can only be merged (to the same female) or separated (between neighbours) if DNA is analyzed from the different sites or if females with young are observed simultaneously at both sites (SEPA 2021). Therefore, to provide information that is applicable for the monitoring program, we compiled daily den site distances within individual females (i.e. den sites used by the same female within the same denning season), as well as between den sites of neighbouring female pairs. For individual females,

the daily den site distance is zero while she remains at the natal site, thereafter it is the distance between the new den site and furthest of the former den site throughout the season (maximum moving distance as described above). Daily den site distances for neighbouring females were only calculated for days when we had information on the location of the den sites for both females in the pair.

We used the daily den site distances within individual females to assess the daily probability that a female would move to a new den site further away than six threshold distances (i.e. 0.5, 1, 2, 3, 4 and 5 km) from a previous den site. We limited the maximum threshold distance to 5 km because our dataset contained few distances exceeding this threshold ( $n = 121$ , 5% of total daily distances, Fig. 2). We modelled the daily probability ( $p$ ) of moving to a new den site beyond each threshold distance, with the daily maximum distance categorised as a binary variable relative to the threshold distance (i.e. below = 0 or above = 1) following a Bernoulli distribution in a Bayesian framework. See the Supporting information for model description and interpretation.

To assess the probability that two den sites belong to the same female or a neighbouring female pair, we compiled distances between all pairwise combinations of den sites per time period for within-individual females, as well as between neighbouring female pairs. For individual females, this represents the distances between all pairwise combinations of den sites from the same denning season, grouped into the time periods (as defined above) based on when the latest den site in the pair was first used (e.g. if den site number 4 was first used at 10 April, the distances from den site 4 to the previous den sites 1, 2 and 3 were assigned to time period 1–15 April). For neighbouring female pairs, the distances between pairwise combinations of den sites were assigned to the time period when the latest den in the pair was first used. We used a Gamma distribution to calculate the posterior probability distributions representing den site distances for within individual females and between neighbouring female pairs for each two-week time period. From these probability distributions, we used 11 threshold distances (0.5, 1–10 km) to assess the probability that the distance to a previous den site for an individual female exceeded each threshold distance, and the probability that the distance between neighbouring females’ den sites were within each threshold distance, for each of the seven time periods (i.e. the proportion of the probability distributions above or below each threshold distance). See the Supporting information for model description and interpretation.

Finally, we used the area of overlap between the probability distributions for den site distances within individual females and den site distances between neighbouring female pairs to calculate the probability of whether an observed den site belongs to the same female or a neighbouring female, dependent on in what time period, and how far away from a previous den sites it was observed. This was done for 15 distance ranges spanning 1 km (i.e. 0.1–1, 1–2, 2–3... up to 14–15 km between den sites). These probabilities were calculated by comparing the probability distribution for individual females versus neighbouring females within each distance range, to

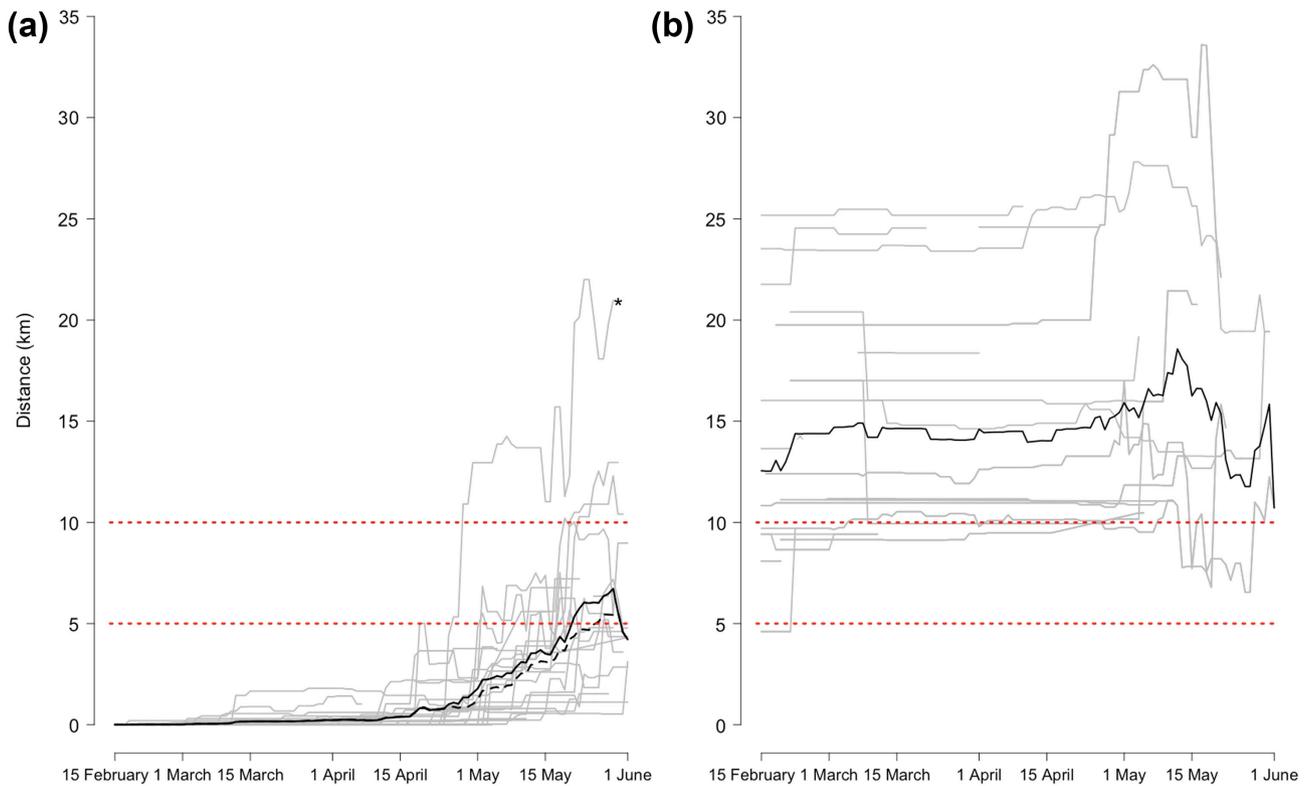


Figure 2. Daily distances between den sites used by (a) individual females and (b) between neighbouring females during the denning season. Grey lines show individual distances, bold black lines show the daily mean distance (dashed black line in (a) shows the mean distance when one outlier female [marked \*] is excluded). For individual females, daily distances are measured from the current den site to the most distant previous den site (i.e. maximum distance; distance=0 until the first den site change). For neighbouring females, daily distances are only calculated for days with information on the location of both females' den sites. Dotted red lines indicate 5 and 10 km reference thresholds.

calculate the relative probability of the new den site belonging to the same individual female (probability of belonging to a neighbouring female =  $1 - \text{probability for belonging to the same female}$ ). Please note that probabilities are conditional on a second den site being found within each distance range category. See the Supporting information for model description and interpretation.

For all modelling and calculations of associated probabilities we used a Bayesian framework implemented in JAGS (Plummer 2003) called from R ([www.r-project.org](http://www.r-project.org)) using the 'rjags' package (Plummer et al. 2016). For each model we ran two independent chains with different starting values and after discarding the first 100 000 iterations we extracted parameter estimates at every 25th step from a total of 200 000 accumulated samples from each chain. Convergence was assessed by visual inspection of trace plots to assure stability and homogeneous mixing and by using the Gelman and Rubin diagnostic ( $<1.1$ , Gelman and Rubin 1992).

## Results

### Denning behaviour

We identified 245 den sites used in the 32 denning seasons when reproducing wolverine females were monitored, with

228 of the sites (93%) used for  $> 1$  day. The mean number of den sites per female and denning seasons was  $8.8 \pm 8.5$  (mean  $\pm$  SD, median = 6, range: 1–28,  $n=32$ ). If we restrict the data to the 13 female denning seasons where we have complete information from all seven time periods,  $14 \pm 8.3$  den sites were used by each female (range: 4–28). The location of the natal den was known in 31 of the 32 female denning seasons (not for one female captured with young on 6 May). In 22 female denning seasons the female was monitored until she moved from the natal den site, the mean date for this first den switch was 30 March, ranging from 17 February and 3 May. The remaining nine female denning seasons were interrupted before the female moved from the natal den (interrupted between 19 February–4 May, due to transmitter failure [ $n=5$ ], female lost her young [ $n=2$ ], or death of the female [ $n=2$ ]).

The number of den site changes, the inter-den moving distances and the daily distance between den sites increased during the denning season (Fig. 2, Table 1, 2a). We only recorded three den site shifts during the first time period (15–28 February), with the maximum moving distance being 200 m. Even though females occasionally change their den site already in the following three time periods (1 March–15 April), the distances between currently used den sites and the most distant of the previous den sites remained short (mean 260 m, range: 0–2.1 km in early April). Thereafter, from early

May, females changed den sites more frequently and moved longer distances (Fig. 2, Table 1, 2a). Females with larger home ranges did not switch den sites over longer distances (Supporting information). One female moved exceptionally large distances in one denning season (2009), starting in April (13 km); however, when this same female reproduced in 2011, she behaved similar to other females (i.e. maximum moving distances were 3.6, 6.8 and 6.8 km during time two-week time periods 5, 6 and 7, respectively).

The amount of time females spent outside the denning area (>100 m from the den site centre) was low during the first two time periods (15 February–15 March). In February, only 12% of the GPS-fixes were outside of the denning area, and 40% of these were within 1 km of the den site (Fig. 3a, Supporting information). However, from mid-March (time period three) females spent more time away from the denning area, and at the end of May (two-week time period seven) 44% of GPS-locations were outside the denning area. From mid-March, denning females also started to travel further from the denning area: from this time females travelled on average 5 km from the den site, and average maximum distances during this time was 10–15 km with individual females travelling up to 25 km from the den site (Fig. 3b, Supporting information).

### Den sites belonging to the same or neighbouring females

For the 22 yearly neighbouring female pairs, the daily distances between den sites did not change during the denning season (mean daily distances ranged between 14 and 18 km, Fig. 2, Table 2b). The minimum distance between neighbouring females' den sites during the entire denning season was 4.6 km; this distance was only recorded in time period two as one of the females lost her young on 22 February. In the following time periods, the minimum distances between neighbouring females den sites ranged between 6.5 and 9.5 km (Table 2b).

The probability that a female would switch to a den site further away than the different threshold distances (i.e. 500 m, 1, 2, 3, 4 and 5 km) increased during the denning season, and this increase was more pronounced after April 15 (Fig. 4, Supporting information). During the initial time periods, the predicted upper 95% credible interval (CRI) probability for movement between den sites was low (1.6 and 0.4%

probability that a female moved to a new den site  $\geq 500$  m and  $\geq 1$  km at 16 March, respectively). By 16 April the upper 95% CRI probability that a female moved to a new den site  $\geq 500$  m or  $\geq 1$  km away had increased to 53 and 24%, respectively, while the probability that a female moved to a new den site  $\geq 5$  km away remained low (0.55%). However, by 31 May the probability that a female would move to a new den site  $\geq 5$  km away increased to 83% (Fig. 4, Supporting information).

As females rarely move between den sites during the first part of the denning season, it was not until May (two-week time period six) that the probability of a new den site being located > 500 m away from any previously used den site approached 90% (Table 3, Supporting information). Furthermore, it was first in early May, when movement and distance between den sites increased for all wolverines, that daily den site distances and the pairwise combination of den distances within individual females started to overlap with neighbour females (Fig. 2 and 5, Table 1). Yet even during May, the distance between current den and previous den sites for individual females and distances between neighbouring females den sites were not equally probable for the different distance categories (Table 3). For example, in early May, the probability of neighbouring female's nearest den site distance being < 10 km was 25%, while the probability of the same female having a new den site > 9 km from her previous den sites was only 1.6% (Table 3). Thus, there is value in also calculating the relative probability of two den sites belonging to the same female or two neighbouring females, conditional on the distance between the two den sites and in which of the seven time periods the second den site is found (Table 4, Supporting information). This means that levels of certainty can be assigned to each observation as to whether each new den site is more likely to belong to the same female, a neighbouring female, or that it is uncertain to whom it belongs (Table 4). For example, if a second den site is found < 2 km away from a previous den site at any time during the denning season, or < 3 km away later than mid-March (from time period three), or < 5 km away later than mid-April (from time period 5); it very likely belongs to the same female ( $\geq 89\%$  probability; Table 4). On the contrary, if a second den site is found > 9 km away from a previous den site before 16 May, or > 8 km away before 1 May, or > 6 km away before 16 April; it very likely belongs to a neighbouring female (> 90% probability; Table 4). In between these

Table 1. Number of times each female changed den site during the denning period. Only females that were monitored for the entire time period (ca 15 days) are included, and are represented as a female denning season.

| Time period    | Min | Max | Median | Female denning seasons (n) | Total den site changes | Den site changes/denning season |
|----------------|-----|-----|--------|----------------------------|------------------------|---------------------------------|
| 15–28 February | 0   | 2   | 0      | 29                         | 3                      | 0.10                            |
| 1–15 March     | 0   | 6   | 0      | 28                         | 15                     | 0.54                            |
| 16–31 March    | 0   | 4   | 0      | 24                         | 14                     | 0.58                            |
| 1–15 April     | 0   | 4   | 1      | 23                         | 23                     | 1                               |
| 16–30 April    | 0   | 5   | 1      | 23                         | 36                     | 1.56                            |
| 1–15 May       | 0   | 11  | 3      | 20                         | 69                     | 3.45                            |
| 16–31 May      | 0   | 10  | 5      | 16                         | 78                     | 4.87                            |

Table 2. Daily distance (km) between (a) individual females' den sites and (b) neighbouring females den sites, separated by seven time periods (ca 15 days) during the denning season. For individual females, daily distances are measured from the current den site to the furthest den site used during the same denning season (i.e. maximum distance; distance=0 until the first den site change). For neighbouring females, daily distances are only calculated for days with information on the location of both females' den sites. From period five (16–30 April) results include the one female that moved exceptionally large distances between den sites during denning season 2009. For daily den site distances excluding this female, see the Supporting information.

| (a) Individual females   | Mean | Median | Min  | Max  | SD   | Daily distances (n) | Denning periods (n)    |
|--------------------------|------|--------|------|------|------|---------------------|------------------------|
| 15–28 February           | 0.01 | 0      | 0    | 0.20 | 0.04 | 343                 | 30                     |
| 1–15 March               | 0.07 | 0      | 0    | 1.7  | 0.20 | 393                 | 28                     |
| 16–31 March              | 0.18 | 0      | 0    | 1.8  | 0.38 | 389                 | 25                     |
| 1–15 April               | 0.26 | 0      | 0    | 2.1  | 0.45 | 346                 | 24                     |
| 16–30 April              | 0.90 | 0.27   | 0    | 13   | 1.5  | 329                 | 23                     |
| 1–15 May                 | 2.8  | 2.0    | 0    | 14   | 3.1  | 305                 | 24                     |
| 16–31 May                | 5.2  | 4.2    | 0.52 | 22   | 4.5  | 237                 | 20                     |
| (b) Neighbouring females | Mean | Median | Min  | Max  | SD   | Daily distances (n) | Neighbouring pairs (n) |
| 15–28 February           | 16.1 | 13.6   | 4.60 | 29.2 | 7.21 | 193                 | 19                     |
| 1–15 March               | 17.6 | 17.0   | 8.65 | 29.6 | 6.69 | 214                 | 18                     |
| 16–31 March              | 16.7 | 16.0   | 9.12 | 29.5 | 6.17 | 236                 | 16                     |
| 1–15 April               | 14.9 | 12.8   | 9.44 | 26.9 | 5.19 | 175                 | 14                     |
| 16–30 April              | 14.9 | 14.0   | 9.48 | 26.2 | 4.86 | 151                 | 11                     |
| 1–15 May                 | 15.1 | 13.5   | 7.71 | 27.8 | 5.59 | 115                 | 11                     |
| 16–31 May                | 13.9 | 13.1   | 6.54 | 25.6 | 5.29 | 58                  | 6                      |

distances and time periods (1 April–31 May), the certainty of whether the two den sites belongs to the same female or a neighbouring female is lower (i.e. ranging between 78–13% probability for the same female, Table 4).

## Discussion

### Denning behaviour

Our results show that both the frequency of denning females moving to a new den site, and the distance between den sites progressively increased during the denning season. Hence, the female wolverines changed den sites earlier and more often than previously suggested (Magoun and Copeland 1998, Inman et al. 2012b). Female denning behaviour is a part of wolverine ecology where available information is scant, and largely based on relatively few females with VHF-transmitters (Inman et al. 2012b). The use of GPS-collars to intensively monitor denning females enabled us to identify short distance movements between consecutive den sites. Furthermore, as active dens were not approached by field personnel, and the study was conducted in a remote area with limited human activity, we provide new detailed knowledge about denning behaviour of undisturbed females. This information is needed as a step towards empirical baseline data for future studies on the effect of disturbances, which is highly relevant for wolverine conservation and management across much of their range. For instance, there is an increasing focus on potential sensitivity of wolverines to human disturbance, especially denning females (Scrafford et al. 2018, Heinemeyer et al. 2019).

During late February and early March, wolverine females spent most of their time at the den site, and only travelled short distances; this period corresponds to the first 1–3 weeks after parturition (mean birth date 15 February,

Aronsson 2017). Also, the proportion of unsuccessful GPS fixes most likely represents time spent at den sites (Walton and Mattisson 2021), as dens are usually located under snow covered boulders or cliffs (i.e. objects obstructing the GPS-receiver, Magoun and Copeland 1998, Mattisson et al. 2010, May et al. 2012, Makkonen 2015). However, already in late March, the time away from the denning area and distances travelled had increased to similar levels as during the remaining part of the denning period. The increased time spent travelling far from the den site in the latter part of the denning season, together with the frequent den shifts over longer distances, highlights that increased movements of the female cannot necessarily be used as an indication of a non-reproducing female, nor that the reproduction failed. For example, the female that changed den sites 28 times during one denning season was later captured together with one cub.

Mean female territory size in the study area was 170 km<sup>2</sup> (Persson et al. 2010), but the variation among individuals was large and ranged between 80 and 410 km<sup>2</sup>. Still, we did not detect any effect of annual home range size on the distance between den sites in any of the time periods, including the female that moved exceptionally large distances in one denning season. This should be expected, especially during the first part of the denning season when females have to carry their cubs or they are too small to move far (Inman et al. 2012); thus, distances between den sites should be limited by cub mobility and not home range size. Until 15 April, the maximum distance between den sites used by the same female was 2.1 km, which was shorter than the radii of the minimum territory (5 km, assuming a circular territory). Even in the last three time periods (from 16 April), when females change den sites more frequently and over longer distances, only 37, 22 and 11% of all the distances between den sites were longer than the radius of the minimum (5 km), mean (7 km) and maximum (11 km) territory, respectively.

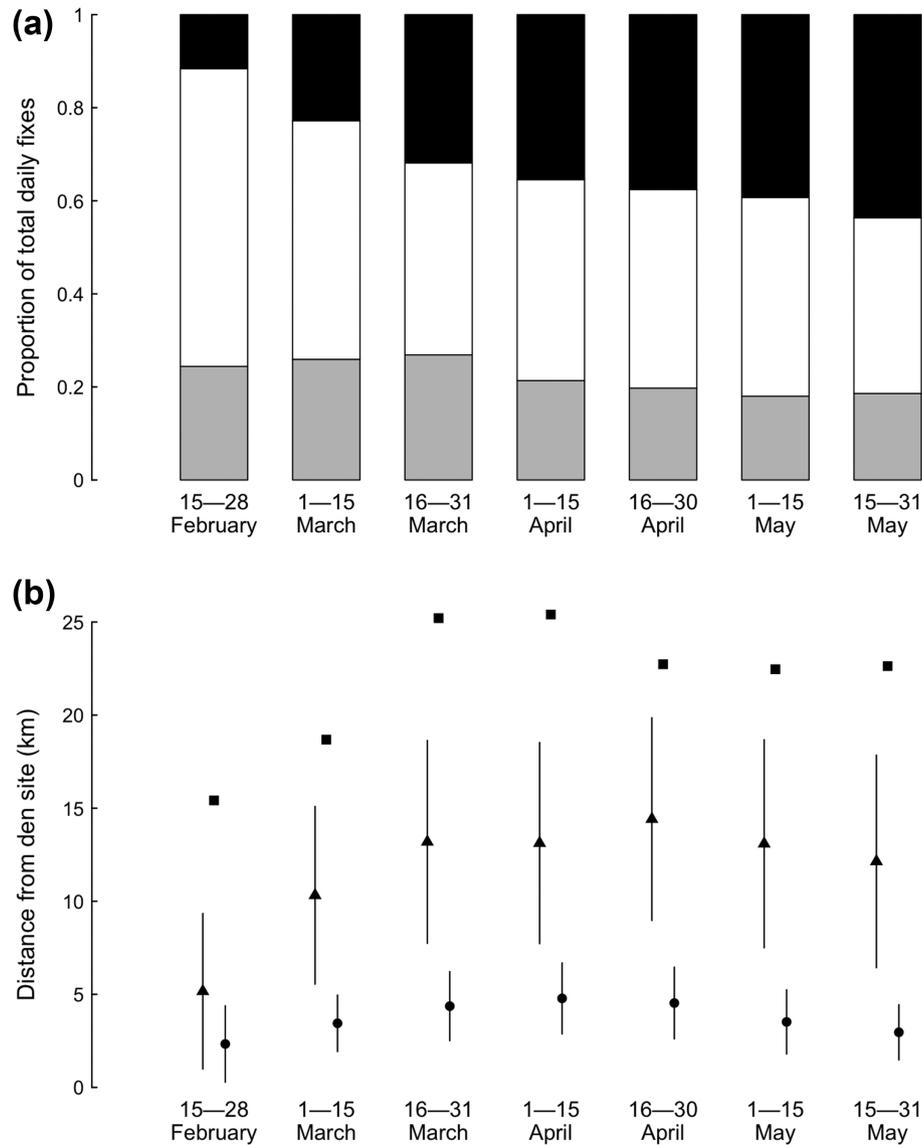


Figure 3. (a) Proportions of total number of GPS fix attempts that were at the denning area ( $\leq 100$  m from den centre; grey), outside of the denning area ( $> 100$  m from den centre; black) and unsuccessful fixes (white; assumed to be largely from time spent in the den where the GPS-receiver is blocked), separated per time period. (b) Mean distances females travel away from her den site based on all locations outside of the denning area, separated by time period. Dots (●) show mean  $\pm$  SD of all mean distances for females and denning seasons, triangles (▲) show mean  $\pm$  SD of all max distances, and square (■) show the absolute max distance. Only females monitored for the entire time period are included.

### Finding den sites

Female denning behaviour presents several challenges for locating wolverine den sites during population monitoring. The chance to detect snow tracks to and from a den site is relatively low in the early part of the denning season (15 February–15 March), due to the females' restricted movements. However, as females start to regularly travel outside the denning area within weeks of parturition, our results suggest the likelihood of finding tracks from females travelling to or from the den site increases already in early to mid-March. Also, females still use a limited number of den

sites in mid-April, even though the distance between den sites starts to increase. From May onwards, the frequent change of den sites, and increasing distances between successive den sites, may influence both the likelihood of finding the den sites, and to document concentrated and regular wolverine activity at the site (i.e. for the site to be classified as a reproductive event within the monitoring program). However, in areas with consistent spring snow cover, as in our study area, the increased movement between den sites in late-April–May might be favourable to document tracks from the young together with the female, as they become more mobile and move between den sites.

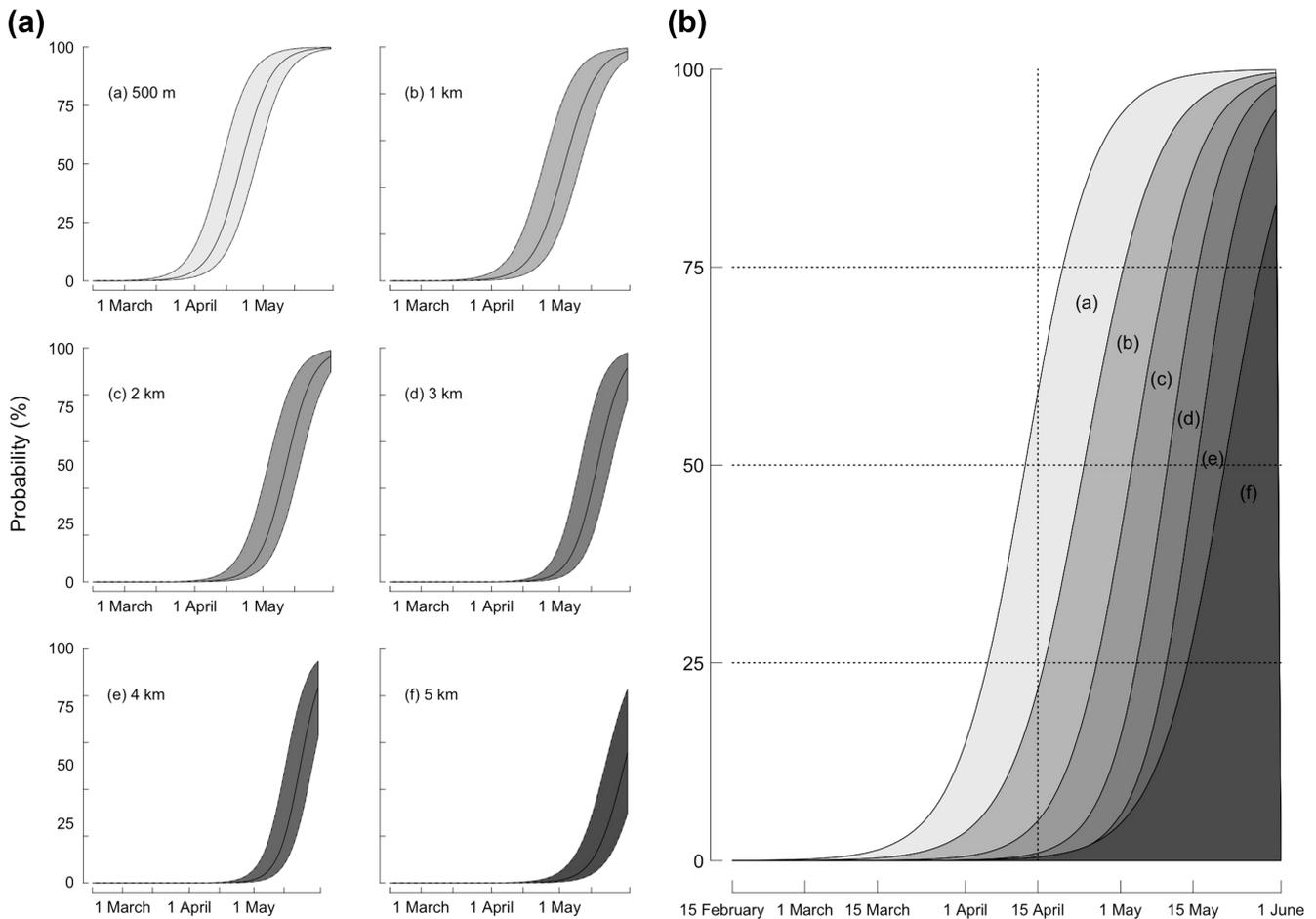


Figure 4. (a) The daily probability (%) (mean with associated 95% credible intervals) that a female will move to a new den site further away than six predefined threshold distances (i.e. 500 m, 1, 2, 3, 4 and 5 km, indexed a–f), based on daily maximum distances between all den sites for individual females. (b) Visual comparison of the upper 95% credible intervals (from a–f) to represent the earliest expected time in the season that a new den site distance would cross each threshold.

### Den sites belonging to the same or neighbouring females

The average distance between neighbouring females' den sites did not change during the denning season; however, the distances varied greatly between pairs. As both the frequency of den site changes and distances between den sites for individual females were low for the first four periods, it was not until time period five (16 April–30 April) that the maximum distance between den sites for the same female began to exceed the minimum distance between neighbouring den sites (4.6 km). With the exception of the outlier female, it was not until time period six (1 May–15) that the daily maximum distance for the same female approached the daily minimum distance between neighbouring females. Accordingly, our analysis of daily distances between den sites predicted the probability of a female moving to a new den site more than 4 or 5 km away to be < 1% up until 16 April (using the conservative upper 95% CRI, or < 0.1% using the mean estimate). It is worth noting that because the estimated probability distributions for distances between neighbouring females' den sites

extended well below their observed range until 16 April (time periods 1–4), comparisons of den site information for the same and neighbouring females based on these distributions should be interpreted with caution. Based on only observations, the shortest distance between combinations of den sites for neighbouring females are close to 5 km in all except one time period (time period three); while the probability of a female moving to a new den site more than 5 km, or that two den sites from the same female are found further apart than 4–6 km, is negligible before 16 April.

Also, because the rate of den site shifting increases as the denning season progresses, the number of den site pairs increase within the 5–10 km interval for both the same female and neighbouring females. Thus, the possibility of accurately separating wolverine reproductive events belonging to the same or neighbouring females based solely on the distance between them becomes increasingly difficult within this mid-distance range (Table 3). Despite this increasing overlap, our Bayesian modelling allows us to make probabilistic estimates of whether two den sites belong to the same reproductive event or not, and can show when this is reliable based solely on distance

Table 3. (a) The probability (%) that a second den site belonging to an individual female is further away than a specified distance from a previous den, for different time periods during the denning season. (b) The probability that neighbouring female's den sites are located closer than the specified distance. These probabilities are assessed from the posterior distributions based on distances between all combinations of den sites belonging to the same individual female, and all combinations of den sites belonging to neighbouring females in the dataset (Fig. 5). Time periods are assigned based on when the second den site occurred in the dataset. Note that the probabilities for individual female den sites are conditional on the female shifting to a new den site during the different time periods. Because these probabilities are calculated from a fitted gamma distribution, some estimates may differ from that expected based purely on the observational data (Fig. 5). Because females almost never change den sites in February (only three changes were observed), we did not estimate a posterior for individual females during time period 1 (15–28 February). Because the estimated probability distributions for distances between neighbouring females den sites extends below their observed range in time periods 1–4 (15 February–15 April), these probabilities should be interpreted with caution and are hence not presented here, but are included in the Supporting information. For model description see the Supporting information.

|                          | Distance |      |       |      |      |      |      |      |      |       |       | n   |
|--------------------------|----------|------|-------|------|------|------|------|------|------|-------|-------|-----|
|                          | 500 m    | 1 km | 2 km  | 3 km | 4 km | 5 km | 6 km | 7 km | 8 km | 9 km  | 10 km |     |
| (a) Individual females   |          |      |       |      |      |      |      |      |      |       |       |     |
| 1–15 March               | 35       | 12   | 1.9   | 0.36 | 0.06 | 0.03 | 0    | 0    | 0    | 0     | 0     | 35  |
| 16–31 March              | 40       | 16   | 2.4   | 0.48 | 0.09 | 0.02 | 0    | 0    | 0    | 0     | 0     | 74  |
| 1–15 April               | 55       | 32   | 11    | 3.7  | 1.4  | 0.51 | 0.14 | 0.06 | 0.02 | <0.01 | <0.01 | 114 |
| 16–30 April              | 76       | 57   | 31    | 17   | 9.3  | 4.9  | 2.6  | 1.4  | 0.75 | 0.43  | 0.23  | 243 |
| 1–15 May                 | 89       | 76   | 50    | 32   | 19   | 12   | 7.5  | 4.6  | 2.6  | 1.6   | 0.95  | 537 |
| 16–31 May                | 95       | 89   | 75    | 62   | 50   | 41   | 32   | 26   | 21   | 17    | 13    | 929 |
| (b) Neighbouring females |          |      |       |      |      |      |      |      |      |       |       |     |
| 16–30 April              | 0        | 0    | 0     | 0.04 | 0.18 | 0.76 | 1.9  | 3.7  | 6.2  | 9.9   | 15    | 201 |
| 1–15 May                 | 0        | 0    | <0.01 | 0.03 | 0.15 | 0.68 | 2.2  | 5.1  | 10   | 17    | 25    | 400 |
| 16–31 May                | 0        | 0    | 0.01  | 0.06 | 0.4  | 1.5  | 4.2  | 8.3  | 14   | 22    | 31    | 694 |

criterion. For example, in our analysis conditional on a second den site being found in time periods five and six (16 April–15 May), there is a > 90% probability that it belong to the focal female up until the 4–5 km distance range from a previous den site, and > 90% that they belong to a neighbouring female first from the 9–10 km distance range (Table 4). From mid-May however, even at the distance range 10–11 km, it is difficult to determine if the newly found den site belongs to the focal or a neighbouring female (23 vs 77% probability).

### Implications for the Scandinavian monitoring program

Our detailed documentation of wolverine denning behaviour has important implications for the Scandinavian wolverine monitoring program. Monitoring of reproductive events appears to be most efficient from early March until late-April, when females regularly travel in and out of their denning area. This movement facilitates den-site detection without the complication of frequent den shifts over larger distances, which likely reduces the chance of documenting consistent activity at specific den sites. If young wolverines are not documented (observed or tracked) in the field, the criteria for 'long-term activity' needs to be fulfilled at a site for it to be classified as a reproductive event within the monitoring program (i.e. wolverine activity registered at the site during 3–4 visits by the monitoring personnel, over at least 3–4 weeks, Aronsson and Persson 2017, SEPA 2021). Consequently, the chance to document such long-term activity is highest from early March to late-April, and might become increasingly difficult during May when females change den sites on average 3.5–4.9 times.

The fact that wolverine females change den sites more frequently during the latter part of the denning season,

complicates accurate counts of the number of reproductive events within the monitoring program. If multiple wolverine den sites are documented in the same area during the same denning season and cannot be separated or merged by field observations or DNA-identification, it becomes necessary to use the distance-criterion to decide if these den sites correspond to one or two reproductive events (SEPA 2021). Under the current monitoring protocols, a focal female moving > 10 km between den sites will be erroneously counted as two separate reproductive events, while neighbouring female den sites ≤ 10 km apart will be erroneously merged into a single reproductive event. Such errors in classification could have two negative outcomes: biased population estimates, and reduced trust in the monitoring and compensation program. Misclassifications of reproductive events, in either direction, can have large economic consequences (200 000 SEK to the reindeer herding district per reproduction; from 2017–2021, the mean number of reproductive events registered per reindeer herding district was 2.1 [range 0–9], rovbases30.miljodirektoratet.no). Thus, we recommend incorporating context-dependent denning location data that is related to the probability of a female switching to a new den site against that new den site belonging to a neighbouring female across the denning season. Here it is important that these probabilities between individual and neighbouring female den sites are balanced to achieve a compromise that minimises decision errors in both directions, and is understood by all parties involved in wolverine management.

Based on our results, we suggest that the distance-criterion in Scandinavian wolverine monitoring need to be updated to meet this goal. As a minimum, we recommend separating the early and latter part of the denning period to reflect the different probabilities of overlap between focal and neighbouring females. Until mid-April, the distance-criterion defining

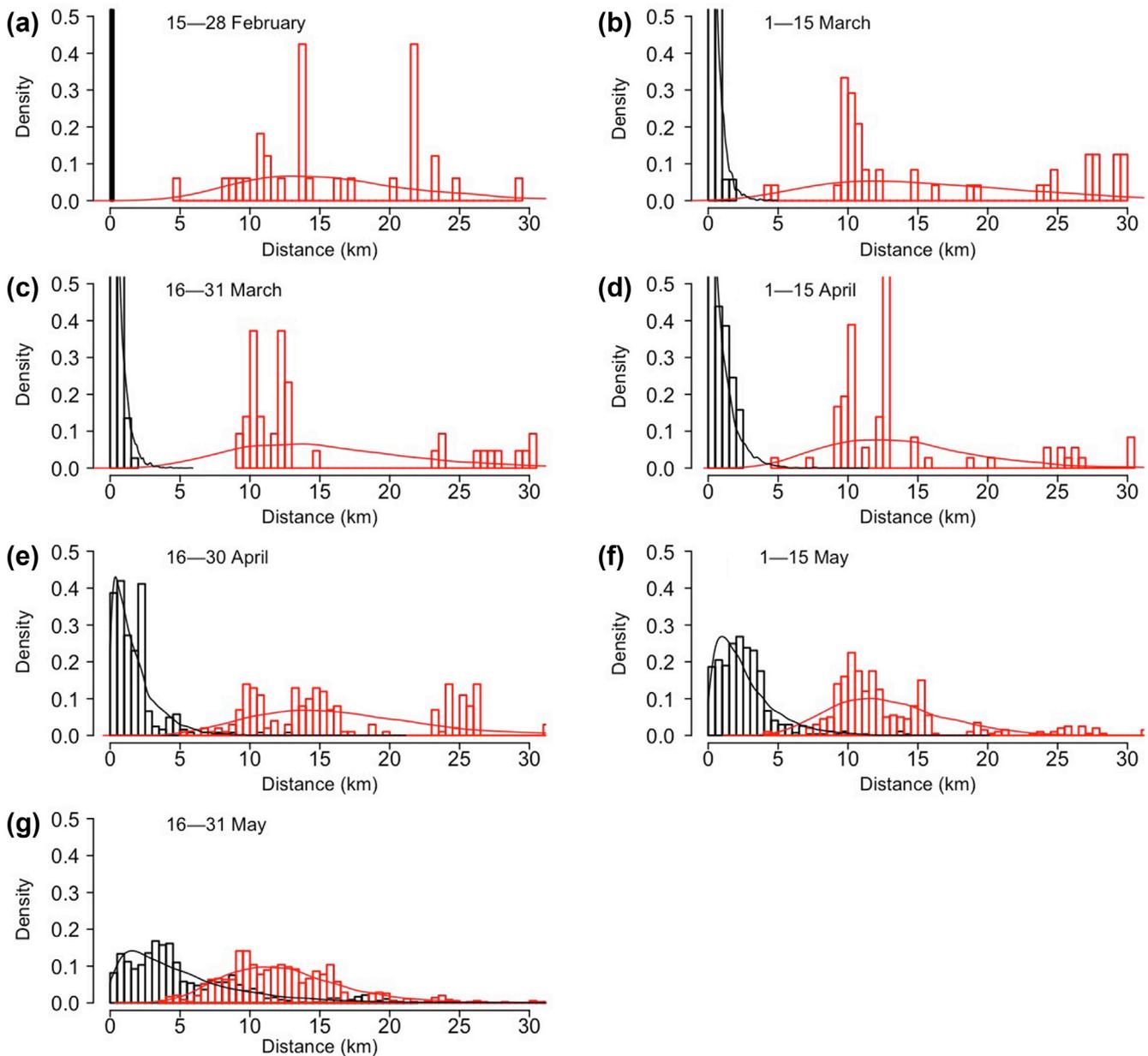


Figure 5. Histogram showing the frequency distribution of distances between all combinations of den sites belonging to one individual female (black) and neighbouring females (red) per time period (a–g). The distances between den sites are assigned to time periods based on when their second den site in the pair occurred in the dataset. Lines are the posterior probability densities of a gamma distribution based on the distances per time period. Because females almost never change den sites in February (only three changes were observed), we did not estimate a posterior for individual females during the first period. The y-axes are the same in all figures to simplify comparison between the periods, resulting in some cropping for periods a–d. For sample sizes see the Table 4.

separate reproductive events should be decreased, to reduce the risk that two separate reproductive events are merged into one using the current 10 km distance. If a second den site is found during this period, the current distance-criteria could be reduced to at least 5 km, as the probability that a female will move > 5 km from her current den site is very low. Furthermore, as the distance moved between den sites is not influenced by home range size, but rather limited by the

mobility of the young, a reduced distance criterion should not increase the risk of misclassifications where home range sizes are larger than in our study, or where females change den sites more often. Importantly, this would ensure that in areas with relatively small wolverine home ranges, the risk of misclassifying a neighbouring female's den site as belonging to a focal female is low; since the approximate radii of the minimum home range in our study area was 5 km.

Table 4. Probability (%) that two den sites belong to the same female, depending on the distance between den sites (distance range) and the time period when the second den site was found (time period). These probabilities are calculated from the overlap of the posterior probability distributions shown in Fig. 5. Note that these estimated probabilities are conditional on a second den site being found within the distance range category (e.g. den site distances between 3 and 7 km are rare in the data before 16 April, and thus some of these categories may represent a hypothetical situation rather than something that is ever likely to be observed). Probability that two den sites belong to neighbouring females = 1 – probability same female. Because the estimated probability distributions for distances between neighbouring females den sites extends below their observed range in periods 1–4, these probabilities should be interpreted with caution and are hence not presented here, but are included in the Supporting information. For model description see the Supporting information.

| Distance range (km) | 16–30 April | 1–15 May | 16–31 May |
|---------------------|-------------|----------|-----------|
| 0.1–1               | 100         | 100      | 100       |
| 1–2                 | 100         | 100      | 100       |
| 2–3                 | 100         | 100      | 99        |
| 3–4                 | 98          | 99       | 97        |
| 4–5                 | 89          | 93       | 90        |
| 5–6                 | 67          | 75       | 78        |
| 6–7                 | 32          | 52       | 58        |
| 7–8                 | 21          | 27       | 45        |
| 8–9                 | 7.9         | 13       | 33        |
| 9–10                | 4.0         | 7.2      | 28        |
| 10–11               | 1.9         | 3.2      | 23        |
| 11–12               | 0.83        | 2.0      | 18        |
| 12–13               | 0.39        | 1.8      | 17        |
| 13–14               | 0.18        | 0.80     | 16        |
| 14–15               | 0.18        | 0.65     | 13        |

From mid-April to mid-May, the distance-criterion would need to be increased, either as a function based on the changing denning behaviour of individual females in relation to the static relationship between neighbours (i.e. using information in Table 3 and 4), or by simply using the current 10 km threshold. As it becomes increasingly difficult to separate reproductive events based on distance later in the denning season, there is an increasing trade-off for management authorities during this time between the risk of overestimating or underestimating the number of reproductive events. If a new den site is found from late-May onwards, even a distance criterion of 10 km will not be able to definitely separate if it belongs to the same or a neighbouring female. Thus, DNA corroboration to differentiate reproductive events becomes increasingly important later in the season. Also, as den site distance criteria become increasingly uncertain in June and July, there needs to be a reassessment of how to change the focus of monitoring from den site use to other criteria based on factors such as observations of young or their tracks, and movements by females and territory size. This is to aid differentiation of reproductive events in late-spring early-summer rather than by movements between specific den sites used earlier in the spring.

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*Permits* – Wolverines were captured and immobilized using strict handling protocols (Arnemo et al. 2017 Biomedical protocols for free-ranging brown bear, wolves, wolverines and lynx) and approved by the Swedish Animal Ethics Committee (permit permits A40-2018). Wolverines were captured under a permit from the Swedish Environmental Protection Agency (permit NV-07775-16).

## Author contributions

**Malin Aronsson:** Conceptualization (equal); Data curation (equal); Formal analysis (lead); Funding acquisition (supporting); Methodology (equal); Project administration (supporting); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Henrik Andréén:** Formal analysis (supporting); Methodology (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Matthew Low:** Formal analysis (supporting); Methodology (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Jens Persson:** Conceptualization (equal); Data curation (equal); Funding acquisition (lead); Project administration (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

## Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1002/wlb3.01079>.

## Data availability statement

Restrictions apply to availability of wolverine den site information, as it is defined as classified information by the Swedish Environmental Protection Agency. Non-classified data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cz8w9gj7j> (Aronsson et al. 2023).

## Supporting information

The Supporting information associated with this article is available with the online version.

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