

Wolf monitoring in Scandinavia: evaluating counts of packs and reproduction events

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Abstract

Large carnivores are elusive and use large areas, which causes monitoring to be challenging and costly. Moreover, management to reduce conflicts and simultaneously ensure long-term population viability require precise population estimates. In Scandinavia, the monitoring of wolves (*Canis lupus*) is primarily based on counting packs, identifying reproduction, and genetically identifying territorial wolves from noninvasive DNA samples. We assessed the reliability of wolf monitoring in Scandinavia by estimating the detectability of territorial pairs, packs, and reproduction. Our data, comprising snow-tracking data and DNA-identified individuals from 2005–2016, covered 11 consecutive winter monitoring seasons (Oct–Mar). Among 343 cases where we identified a wolf pack, territorial wolves were also detected in the same area during the previous season in 323 (94.2%) cases. In only 6 of the remaining 20 cases, there was no prior knowledge of territorial wolves in the area. Among the 328 detected reproduction events (litter born to a pack), we detected 97% during the monitoring period and identified the rest ≥ 1 year later from kinship assessments of all DNA-detected individuals. These results suggest that we failed to detect only few packs with reproduction events during the monitoring season that followed breeding. Yearly monitoring of territorial individuals and continuous updates

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of the pedigree allowed us to retrospectively identify reproduction events and packs that were not identified earlier.

KEYWORDS

Canis lupus, large carnivores, non-invasive survey, pedigree, population monitoring, reproduction, Scandinavia, wolf

Several large carnivore species are recolonizing parts of their historical distribution in Europe and North America (Chapron et al. 2014, Ripple et al. 2014). In some areas, wildlife-related conflicts have increased because of predation on livestock, pets, and hunting dogs (Naughton-Treves et al. 2003), or because of fear of large carnivores among people (Johansson et al. 2017, Støen et al. 2018). Large carnivores are also highly appreciated and attract the interest of many people, including tourists and hunters (Kränge et al. 2017).

Because of the polarizing response from people, there is need for reliable estimates of reproductive performance and size of large carnivore populations for appropriate political decisions, management, and the public debate, but monitoring large carnivore populations is challenging because of low population densities and elusive behavior (Thompson 2004). With limited funding, managers also need monitoring solutions to be justified and cost-efficient (Walters 2007, McDonald-Madden et al. 2010, Allen and Gunderson 2011, Keith et al. 2011).

Since 2005–2006, the main objectives of the Scandinavian annual wolf (*Canis lupus*) monitoring program have been to locate and count territorial pairs, packs, and reproduction events; genetically identify every scent-marking territory-holding individual within pairs and packs; estimate inbreeding among the breeding pairs; and estimate the population size. These data are used in the decision process of wolf management in Scandinavia, with the primary goals to maintain a viable wolf population that is genetically connected with neighboring populations and to reduce conflicts and livestock damages (Naturvårdsverket 2016, Stortingsforhandling 2016).

The wolf population in Scandinavia has been monitored annually since 1978; the number of pairs, packs, and reproduction events were first estimated primarily based on information from snow tracking, including locations of territorial scent-markings that are typical of adult resident and breeding wolves (Mech and Boitani 2003). In 1998–1999 radio-telemetry was added to the monitoring program and in 2001–2002 DNA samples became an important source of information (Wabakken et al. 2001, Liberg et al. 2012). Non-invasive sampling techniques have become increasingly useful to efficiently monitor a significant proportion of the individuals in a population, without affecting the animals themselves (Waits 2004, Mackay et al. 2008, Kelly et al. 2012, Rich et al. 2013, Whittington et al. 2015). In monitoring wolves in Scandinavia, DNA-based individual identification and parentage (e.g., from scats and urine) provided means to separate neighboring territories and confirm reproduction. Moreover, the DNA identification of breeding wolves has enabled the reconstruction of a pedigree used to estimate and monitor inbreeding on an annual basis (Liberg et al. 2005, 2012; Åkesson et al. 2016). Monitoring wolves in Scandinavia is thus an integrated approach combining snow tracking and individual identification and relatedness from DNA analyses. After repeated snow tracking in wolf areas, all acquired data (individual identification and relatedness from DNA, location data, tracking data) are combined to determine the presence of territorial pairs and packs, if reproduction has occurred, and parentage.

The information used to estimate wolf population size in Scandinavia has undergone a few changes over the years, primarily to make the monitoring more cost-efficient (Chapron et al. 2016). The annual number of packs is a segment of the population that is used to estimate reproductive success and population size (Marucco and Boitani 2012, Chapron et al. 2016). Researchers have reported that multiplication factor-based approaches can be precise and reliable, assuming that all packs and reproduction events in the population are counted (Chapron et al. 2016, Bischof et al. 2019). Management decisions, including those of culling quotas and compensation to livestock owners in areas with wolf packs, are generally based on the population count from the most recent monitoring season.

In these situations, management relies on the accuracy of the most recent population counts. Still, there has been no assessment of the accuracy of the population counts of packs and reproduction events.

Our objective was to evaluate the wolf monitoring in Scandinavia. Specifically, we estimated the detectability of territorial wolves and births under the current monitoring approach and address management implications of pairs or packs that we did not detect.

STUDY AREA

We conducted the study on the Scandinavian Peninsula (~750,000 km²; Figure 1). Even though wolves have been observed throughout the Peninsula, the breeding part of the population has primarily been in the south-central segment of Sweden and Norway (i.e., 59° to 62°N and 11° to 19°E; Figure 1). The forest cover of the area was about 50% and was dominated by boreal forest managed for logging purposes. Most areas were highly accessible from main roads (0.35 km/km²) and forest roads (1.14 km/km²). Less than 5% of the area containing territories with reproducing pairs was covered by agricultural or urbanized land. Human density in the study area was low and often <1 person/km² (Zimmermann et al. 2014). During the monitoring period in winter (1 Oct–31 Mar), temperature ranged between 0° and –25°C. Snow covered the area for 3–6 months each year and the maximum snow depth (measured from 9 weather stations in the study area 2005–2013) ranged between 6 cm and 90 cm (Wern 2015). Other large and medium-sized predators were also inhabiting the study area, including red fox (*Vulpes vulpes*) and Eurasian lynx (*Lynx lynx*), which were found in the entire study area, while brown bear (*Ursus arctos*) and wolverine (*Gulo gulo*) occupied the northern parts of the study area.

METHODS

Population monitoring approach

From 1 May 2005–30 April 2016 the County administrative boards had the responsibility for monitoring wolves in Sweden, while Statens Naturoppsyn together with Inland Norway University of Applied Sciences had the responsibility in Norway (see details on the monitoring system in Supporting Information). Observers conducted annual monitoring during winter between 1 October and 31 March. Observations from the public were usually reported directly to field personnel or via a public website (www.skandobs.se). Trained personnel verified all observations in the field before they included them in the monitoring data. Trained field personnel searched for wolf tracks on snow or for scats on bare ground, mainly within the wolf breeding area but also outside of the breeding area when observations of wolves were reported by the public.

We back-tracked wolves on snow and collected information of scent-markings (raised-leg urination and scratching) and number of wolves, and DNA samples from scats, urine, or blood throughout the monitoring season. We determined territory status from territorial pairs, packs, or other resident wolves. The search effort in finding tracks and sampling DNA was not systematically recorded. Some areas had poor snow cover for prolonged periods during winter. In these areas, we collected DNA samples on bare ground by driving on forest roads to search for scats. Additionally, we obtained DNA samples from all wolves that were found dead, legally harvested, or dead from vehicle collisions. Samples from dead wolves were collected upon necropsy by the Swedish Veterinarian Institute or Norwegian Institute for Nature Research, Norway.

By collecting DNA from territory markings (urine from raised leg urination) found during snow tracking, we identified territorial males and females in each pack or pair genetically and consequently confirmed the number of different territories, all in accordance with criteria set in the current guidelines of wolf monitoring (Table S2, available in Supporting Information). We identified a territory when we followed tracks from ≥1 wolf ≥3 km,

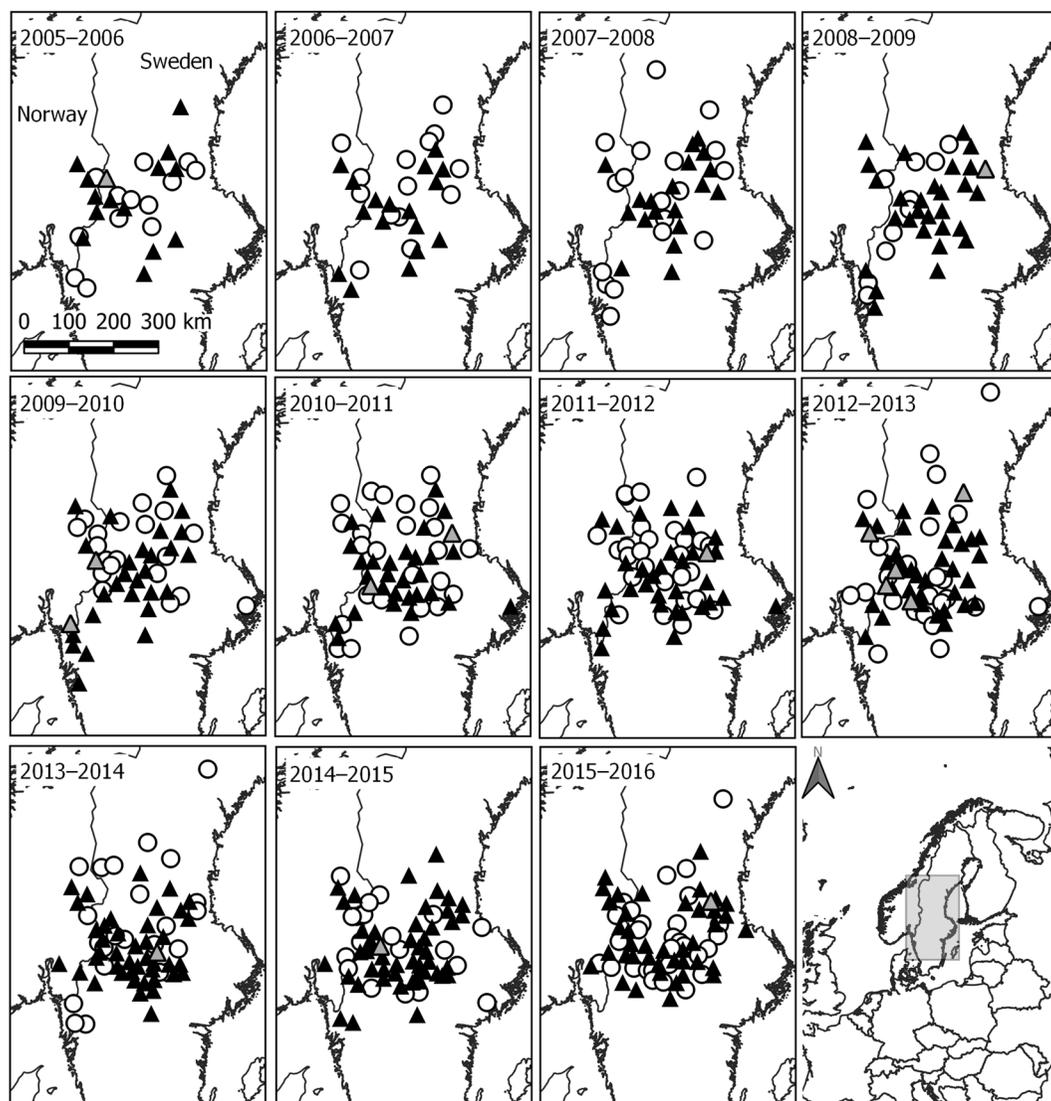


FIGURE 1 The spatial distribution of territorial wolf pairs (open circles) and packs, with confirmed (black triangles) or unconfirmed (grey triangles) territorial pairs or packs the previous year during 11 monitoring seasons, 2005–2016, with the study area highlighted with the grey box in the map showing Scandinavia.

normally on several occasions, and where we observed scent-markings along the tracks. We distinguished neighboring territories using DNA samples collected along the tracks, where genetic identity from scent-marking individuals of the opposite sex from the same track identified them as a pair and differentiated them from other pairs. Moreover, by determining the parents for individuals in a territory, we distinguished scent-marking wolves from their offspring.

We classified the status of wolves in a territory annually as one of the following: a territorial pair (2 wolves, a scent-marking male and female), a pack (≥ 3 individuals of which ≥ 1 was a scent-marking adult wolf), and other resident wolves (resident scent-marking wolves that could not be classified as a pair or a pack such as a stationary wolf or a group of pups that have lost both parents; Table S2. We confirmed successful reproduction after genetic

identification of ≥ 1 pup from a new wolf pair in a territory, after sightings of pups by authorized personal or on photos from motion-sensitive cameras, or when tracking ≥ 4 wolves in the territory (Table S2).

Individual identification using DNA analysis

We used DNA samples (scats, urine, hair, tissue, blood) that were collected during the study period and analysed in the laboratory for identification and sexing as described in Åkesson et al. (2016). All samples were distinguished from other canids, including red fox and domestic dogs. The genetic differentiation between wolves in Scandinavia and the neighboring Finnish-Russian population enabled us to detect immigrant wolves by using Bayesian individual assignment (Rannala and Mountain 1997, Åkesson et al. 2016). Using a reference sample consisting of 92 wolves from Scandinavia, 64 wolves from Finland, 34 domestic dogs, and 9 foxes, we calculated the most likely population origin using the program GeneClass 2 (Piry et al. 2004). We based assignments on a threshold assignment score of 0.001. This resulted in 449 samples assigned with a score >0.001 to either domestic dogs or foxes, which we consequently excluded from further analysis.

We used CERVUS version 3.0.3 to determine and match individual identity from samples (Waits et al. 2001, Kalinowski 2004). We considered genotypes to be individually unique with probability of identity of siblings (PID_{Sib}) <0.001 and with ≥ 2 mismatches to other samples, thereby taking the occurrence of allelic dropout into account. We combined matching genotypes to 1 consensus genotype that we used for further analysis.

Parentage and reproduction

To determine parental identities of individuals, we used a 2-step process based on microsatellite genotypes and field observations (Åkesson et al. 2016). First, we determined individual parents by genetic exclusion of putative parents (i.e., a pair of identified wolves that scent-marked in the same territory). If all putative parents could be excluded assuming no more than 2 mismatches, we used parental assignment in CERVUS version 3.0.3 using the entire database of individuals identified between 1983 and 2016. Using CERVUS, we ran a simulation based on allele frequencies from the Scandinavian population to estimate the critical values of the difference in log-likelihood values between different pairs (i.e., putative parents). In the simulations we assumed the parental sexes to be known, with 200 candidate mothers and 200 candidate fathers and 95% of the parents sampled. Moreover, we assumed that 73.5% of the loci were typed (which corresponds to the average success rate of the non-invasive samples in the data set), and 2% of the loci were mistyped. We checked matching parents manually for deviations from Mendelian inheritance.

Using ML-RELATE (Kalinowski et al. 2006), we addressed the genealogical relationship of individuals for which neither parent could be identified or reconstructed. By estimating full sibling relationships (10,000 simulations; significance level = 0.05), we were able to identify the number of full-sibling groups (i.e., missed litters) among these individuals.

We used the parentage of identified individuals to categorize if 1) a wolf was an offspring in a litter (i.e., reproduction event) that was detected during the same or previous monitoring seasons or if 2) a wolf was an offspring in a litter that remained undetected for ≥ 1 year after birth but where the parents were identified or reconstructed at a later stage from the DNA profiles of their progeny. Among these failed real-time detections of reproduction events, we specified if ≥ 1 parent was known to have scent-marked but not given reproductive status or none of the parents were not known to have scent marked. We categorized individuals with unknown parentage as 3) wolves from litters that remained undetected during the monitoring season following the reproduction event and where the parents were not identified or possible to reconstruct at a later stage, or 4) wolves from an unknown natal territory with several possible parent pairs, among those that were known to scent-mark.

Because the monitoring protocols prioritized for efficiency reasons the analyses of samples from areas with tracks of >1 wolf, we investigated vehicle-killed wolves ($n = 82$) separately to obtain an independent sample. This segment likely picks up a higher proportion of solitary individuals, individuals temporarily split from their pack mates, and individuals from unknown territories not prioritized or not detected by the field personnel.

Statistical analysis

For each territory that contained a pack, we determined whether a pair or pack was detected in the area the year before. We tested the probability of pair or pack detection the previous year for effects of year, number packs the previous year, and number of pairs the previous year using a general linear models approach in R (R Core Team 2020), with the `glm` function in the R package `lme4` (Bates et al. 2015) assuming a binomial distribution. Using a chi-squared test, we also tested if the detection or failed detection of a pair or pack in a territory the previous year was different between packs that reproduced for the first time or those that had reproduced before.

RESULTS

Territory status the previous year

Between 1 May 2005 and 30 April 2016, we identified 343 packs in the wolf population in Scandinavia (Figure 1). We detected reproduction in 318 of these packs and in 159 (50.0%) cases the DNA of offspring confirmed the reproduction of a new parental pair. Out of the 343 packs, 226 were also classified as packs the previous year (65.9%) and 97 were classified as territorial pairs the previous year (28.3%). In 20 cases we had not detected the pack the previous year either as a pack or pair (Table 1). Among these instances, we observed resident wolves in the area in 14 cases but without fulfilling the predefined criteria for a territorial pair or pack (Table S2). All 20 cases with an undetected pair or pack the previous year occurred in territories where the pair had not been observed to reproduce before ($\chi^2_1 = 21.3$, $P < 0.001$). Based on a logistic regression approach, there was no effect of year (likelihood ratio test; $\chi^2_{10} = 14.4$, $P < 0.155$), number of packs the previous year ($Z = -0.19$, $P = 0.85$), or number of pairs the previous year ($Z = 1.284$, $P = 0.20$).

During the 11-year study, we detected 225 territorial pairs. We later determined, based on the identification of offspring to the pairs after the monitoring season, that 4 (1.7%) of these pairs were probably mis-classified packs, consisting of a scent-marking pair and ≥ 1 offspring.

Individual parental assignment and reproductive status

Based on 7,461 DNA samples collected during the study, we identified 1,329 wolf individuals that were born in Scandinavia (Figure 2), after removing 30 genotypes that had `PIDsib` >0.001 to another genotype in the final data set and 17 that assigned with the Finnish-Russian wolves. For 1,320 individuals (99.3%) it was possible to genetically identify both parents ($n = 1,296$) or reconstruct the genotypes of the parents well enough to determine their genealogy ($n = 24$). For 6 wolves (0.5%), although assigning with wolves in Scandinavia, we could not determine the identities of the parents or the parental genealogy. For the remaining 3 wolves (0.2%) we did not have enough genetic information to differentiate between ≥ 2 potential parental pairs.

Among the 1,329 individuals, 1,310 (98.6%) were offspring to a pair that reproduced at a time that was not temporally in conflict with the individual's first observation date. For 5 (0.4%) individuals we documented ≥ 1 parent scent-marking the previous year but did not observe any pups within a year after the breeding event. For

TABLE 1 Yearly number of wolf packs (≥ 3 animals) in Scandinavia counted during the monitoring period and the inferred status the previous year including number of territorial pairs and packs and those not detected or confirmed as a territorial pair or pack (i.e., had other status). The percentage of the number of packs that were not detected or had other status is given within parenthesis.

Year	n packs	Status previous year			
		Pack	Pair	Not detected (%)	Other status (%)
2005	15	8	6	1 (6.7)	0 (0)
2006	17	11	6	0 (0)	0 (0)
2007	20	13	7	0 (0)	0 (0)
2008	28	13	14	0 (0)	1 (3.6)
2009	28	23	3	1 (3.6)	1 (3.6)
2010	31	21	6	1 (3.2)	3 (9.7)
2011	33	21	10	0 (0)	2 (6.1)
2012	38	22	10	2 (5.3)	4 (10.5)
2013	43	29	13	0 (0)	1 (2.3)
2014	49	36	11	0 (0)	2 (4.1)
2015	41	29	11	1 (2.4)	0 (0)
Sum	343	226	97	6 (1.7)	14 (4.1)

11 individuals (0.9%) neither parent was known to have been scent-marking (5 with known parentage but no evidence of scent-marking, 6 with unknown parentage), and 3 individuals (0.2%) had several possible parents among the known territorial pairs. In summary, we found that only 16 (1.2%) of the DNA-identified individuals were born from parents that we had not previously confirmed scent-marking or with pups in the field (i.e., evidence of reproduction was from DNA only). We identified 10 full-sibling litters among the 16 wolves that were not detected within a year from the breeding event (Table 2). Because we previously detected reproduction in 318 packs, we concluded that we had identified 97% of the minimum number of packs that reproduced ($n = 328$).

Among 82 wolves killed by vehicles during the study period, 81 were Scandinavian born (based on population assignment and parentage analysis) and 1 was assigned to the Finnish wolf population. Among the 81 Scandinavian-born wolves, 1 was born from unknown parents (D-10-63 in Table 2).

DISCUSSION

Eleven years of wolf monitoring in Scandinavia, resulted in the detection of 328 reproductive events, of which 318 (97%) were confirmed during the monitoring season following directly after the birth of pups in May. This strongly suggest that our integrated approach, combining snow tracking and DNA analyses, is associated with a very high detectability of wolf packs.

Nevertheless, abundance estimates based on the count of individuals or territories should be interpreted with some caution because such an attempt is likely to give negatively biased values and it is generally difficult to evaluate and take the level of inaccuracy into account (Krebs 2006). Still, many monitoring programs aim at conducting a minimum or total count of individuals or segments of the population such as territories or packs (Kaczensky et al. 2009, Stenglein et al. 2010, Chapron et al. 2016, Kojola et al. 2018). Although the accuracy of these population estimates are rarely evaluated or even mentioned, they are used as the basis for scientific studies

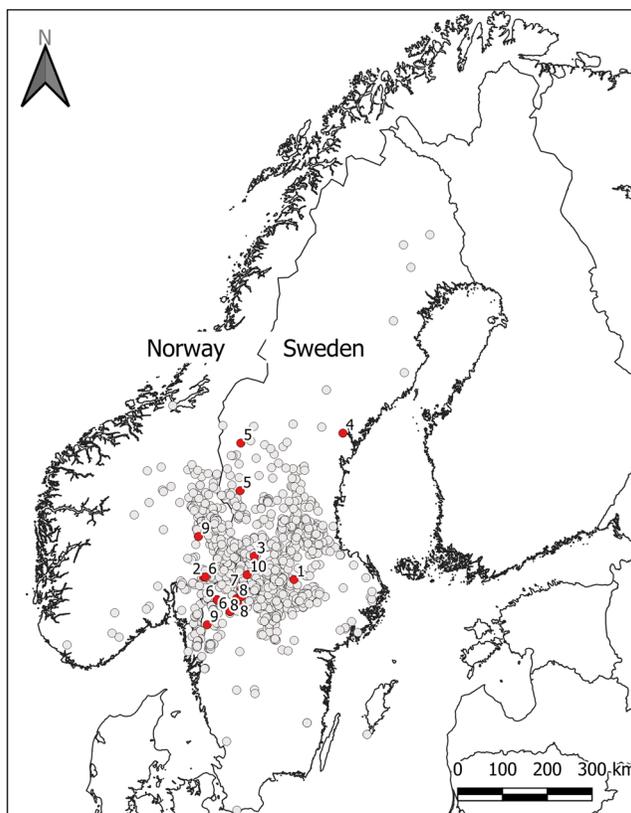


FIGURE 2 The first known position of 1,329 individual wolves identified in Scandinavia, 1 May 2005–30 April 2016. The map highlights (in red circles) the 16 individuals, with number corresponding to siblings, born from reproduction events that we did not detect during the subsequent monitoring period.

(Jansson et al. 2012, Åkesson et al. 2016). In this context, our study represents an important and rare possibility to evaluate the precision of direct count estimates.

While monitoring the wolf population in Scandinavia, observers did not search for wolf tracks and wolf activity over the entirety of the Scandinavian Peninsula but mainly focused on areas where there was prior knowledge of wolf presence (Figure 1) and areas with spontaneously reported observations of wolves and wolf tracks during the monitoring season. Partly, this knowledge was based on reports from the public using internet-based reporting in Skandobs (www.skandobs.se). Furthermore, the search effort was not regularly recorded during the study period. These limitations of the monitoring design emphasize the difficulties in obtaining reliable unbiased uncertainty estimates of the population size (Chapron et al. 2016, Bischof et al. 2020). That said, our long-term data on scent-marking wolves in territorial pairs and packs, together with DNA-based individual and parental identity allowed us to evaluate the occurrence of packs and reproduction events not detected during the monitoring season.

During 11 years of monitoring wolves in Scandinavia, our data strongly suggest that only a few wolf reproduction events were undetected within a year after the breeding event. We identified 343 territorial wolf packs and confirmed reproduction occurred during the preceding spring in 318 packs. During the same period we identified 10 full-sibling groups that were born in territories that could not be linked to any of the confirmed packs and reproductions. This suggests that we failed to detect at least 3% of the reproduction events (10 out of 328) during the following monitoring season throughout the study period, averaging approximately 1 undetected reproduction event per year.

TABLE 2 Full-sibling litters (sibships, $n = 10$) of individuals ($n = 16$) in Scandinavia, 1 May 2005–30 April 2016 with parents that were not confirmed as a reproducing pair. We also provide year of first observation, if both parents have been genetically sampled and identified, and if the parents were confirmed as a scent-marking pair.

Sibship ^a	Identification	Year of first observation	Parents identified	Scent-marking parents confirmed
1	M-10-07 ^b	2009	Yes	Yes
2	D-10-62	2010	No	No
2	D-10-63	2010	No	No
2	D-11-20	2010	No	No
3	G39-11	2010	No	No
3	G123-11	2011	No	No
4	G109-14	2014	Yes	No
4	G13-16	2015	Yes	No
4	G63-15	2015	Yes	No
5	G204-13	2013	Yes	Yes
6	G38-14 ^c	2013	Yes	Yes
7	G11-14	2013	Yes	No
7	G163-13	2013	Yes	No
8	G49-13	2012	Yes	Yes
9	G101-16	2016	No	No
10	G80-14	2014	Yes	Yes ^d

^aThose with the same sibship number indicate we confirmed a close relationship (full-sibling or parent-offspring) with 95% confidence.

^bBorn at the latest in 2008. Parental pair was confirmed to reproduce the first time in 2009.

^cBorn at the latest in 2012. Known parental pair was never confirmed to reproduce.

^dMultiple paternity.

The identification of individuals from reproduction events that were not detected during the monitoring season following the breeding event (1.2%, $n = 1,329$) may have been negatively biased from spatial variation in tracking and sampling effort during the study period. Because the search effort was not fully registered, we also investigated a subsample of individuals. We used vehicle-killed wolves born in Scandinavia ($n = 81$), where only 1 individual (1.2%) was born from a undetected reproduction event. But subsampling of vehicle-killed wolves may not fully account for the potential spatial bias in search effort and they may themselves be spatially biased (e.g., with a higher risk of being killed in areas with higher density of roads used for traveling; Zimmermann et al. 2014). As such, the natal origin of vehicle-killed individuals may have been associated with road density and traffic load, especially when the individual is killed close to its natal territory. The vehicle-killed wolves comprised juveniles and adults and when using only adults ($n = 58$), 1 individual was born from an undetected reproduction. These observations support the conclusion that the frequency of undetected reproduction events was low during the study.

In addition, failure to detect reproduction when the territorial pair is known is also possible. During the study, we identified 343 packs and in 25 of these cases we did not detect reproduction in the monitoring season. Twenty of these cases represented situations where we detected a partner switch the previous year, indicating that a breeding partner may have been missing during the mating period and that the pack the following winter may have been composed of scent-marking adults together with older offspring and no yearling pups. In the other 5 cases, the

scent-marking pair in the pack was identical to the pair that reproduced prior to or after the focal year, thus indicating that the pair might not have been successful in their breeding, or that the monitoring failed to detect offspring during the following winter (e.g., because of bad snow conditions, small litter size, low pup survival; Table S2).

Twenty of 343 territories with packs did not have a confirmed detection of a pair or pack in the same area the previous year and in all cases the pair was classified as first-time reproducers. In 14 of the cases, we detected ≥ 1 territorial wolf (i.e., scent-marking) in the area, so it is unlikely that there was a pack and that a reproduction event had occurred. In the remaining 6 cases, there was no knowledge of the territory and territorial individuals the year before. Even though these situations could suggest possible undetected reproduction events, they could also be explained by the timing of pair formation. The later a pair is formed during the monitoring season, the smaller the temporal window for detection.

Some reproduction events were not detected in the monitoring season following the breeding event, even in cases where the parents were tracked. Among 225 territorial pairs with no documented pups, we confirmed reproduction in 3 cases from offspring DNA collected at a later stage. This shows that it was possible, although rare (1.3%), for reproduction to have occurred even though we did not detect a pack or reproduction event the following monitoring period.

The monitoring of reproduction events in Scandinavia is based on the assumption that they are exclusive to 1 pair in each territory. Although it has been frequently documented in other parts of the world that multiple breeding events can occur within a pack (Mech and Boitani 2003) it is unlikely to be common in Scandinavia because pack sizes rarely exceed 10 wolves (Liberg et al. 2012, Chapron et al. 2016). Even if there were cases of territorial overlap, there were no indications of multiple parent pairs within the same home range.

That said, we identified 1 likely case of polyandry, where a female appeared to have been reproducing with 3 different males during 2012 and 2013. This could indicate a case of multiple paternity in 1 litter (most likely in 2013) and would then explain 1 of the confirmed undetected reproduction events in the study (G80-14 in Table 2). There are few if any documented cases of multiple paternity in wolf litters, but it has been observed in Ethiopian wolves (*Canis simensis*; Sillero-Zubiri et al. 1996), and polyandry can be common in red foxes (Baker et al. 2004). Even though the case of multiple paternity presented in this study is not based on DNA-sampled pups from the den, which would lead to stronger conclusions, it is unlikely that it could be explained by an undetected reproduction event by the female. If a reproduction event would have been undetected in 2011, the year previous to the first confirmed reproduction event, the mother would be only 1 year old. Wolves are rarely reproducing during their first year (Medjo and Mech 1976, Kreeger 2003) and in Scandinavia these cases are so far exclusive to males (Wikenros et al. 2021). Moreover, 2 of the fathers were identified from DNA in 2003 during the time of mating in February (Mech and Boitani 2003) inside or near the female territory, further supporting a case of polyandry in the territory.

MANAGEMENT IMPLICATIONS

Accurate population estimates are key to understanding and evaluating how wildlife populations respond to changes in the environment and different management actions. Our study demonstrates that the applied methods for wolf monitoring in Scandinavia worked well, suggesting that virtually all wolf packs, territorial pairs, and reproduction events were detected. Compared to the estimates of many other wildlife species, this yields an extremely low level of uncertainty regarding number and distribution of wolves, which in turn give decision makers and managers the possibility to set very specific goals for population numbers and distribution of wolves.

A major strength of the Scandinavian monitoring program is the combination of field observations from snow tracking and the collection of samples for DNA analyses. Identification of resident scent-marking individuals in territorial pairs and packs provide information about social status and reproduction, which allow for a better understanding of the drivers behind population dynamics and change in genetic variation, both important aspects

for wildlife management to be successful in achieving its goals. As such, the Scandinavian monitoring program could serve as a model for the design of monitoring programs in other wolf populations.

Admittedly, snow is an important factor for this kind of integrated methodological approach. Without snow, managers would have to rely on alternative approaches for identifying wolf reproduction events. Relying more heavily, or even solely, on DNA analyses is an alternative in areas without snow, as in areas with poor snow conditions in Scandinavia.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

All procedures, including capture and handling of wolves, fulfilled ethical requirements and have been approved by the Swedish Animal Experiment Ethics Board (permit number C 281/6) and the Norwegian Experimental Animal Ethics Committee (permit number 2014/284738-1).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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