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Research Article

Recruitment probability in a large carnivore: the role of biological and human-related factors in early-life

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To reach reproduction, individuals must survive the juvenile stage, a critical period of low survival rates in large carnivores. Early-life conditions during this stage can have lasting effects on survival, reproductive maturation, growth, physiology and behaviour. We assessed recruitment probability in Scandinavian wolves, i.e. the probability that a wolf reaches the reproductive stage and has pups surviving at least five months of age. To unravel human-related and biological factors within the natal territory that could affect recruitment probability, we analysed life-history data from 582 Scandinavian wolves *Canis lupus* identified by DNA as pups or juveniles in their birth territory. Factors considered included main prey density, road density, human density, and proximity to non-breeding zones, as well as sex, inbreeding level and collaring. Among the 582 wolves analysed, 122 produced at least one surviving pup, corresponding to a recruitment probability of 0.21. Recruitment probability was more than twice as high (0.5) for juvenile wolves fitted with GPS-collars compared to non-collared individuals (0.22), and was positively correlated with human population density in the natal territory. We found no significant effects of other biologically or human-related predictors. These results suggest that in this large carnivore population, managed below carrying capacity, individual recruitment probability is primarily influenced by human-related factors, potentially reflecting poaching risk.

Keywords: *Canis lupus*, juvenile stage, life-history traits, natal territory, reproduction

Introduction

Life-history theory seeks to explain the general features of an organism's life cycle, including both intra- and interspecific variation, by exploring how organisms allocate resources to growth, survival and reproduction throughout their lives (Stearns 1976, Brommer 2000). A key component of an organism's life-history strategy is its

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ability to survive the juvenile stage and reach reproductive maturity. The juvenile stage is particularly crucial as it is often characterized by low and variable survival rates (Stearns 1976, Garratt et al. 2015). Favourable early-life conditions, often linked to low population density with reduced competition for resources, can enhance an individual's chances of survival and increase the probability of reaching reproductive maturity, thereby contributing positively to population growth. In contrast, adverse early-life conditions can lead to reduced body growth, alter behaviour or physiological processes – such as delaying reproduction – and reduce overall fitness (Lindström 1999, Berger et al. 2015, Tung et al. 2016, Gicquel et al. 2022).

Recruitment can also be influenced by human activity – either directly through disturbance or mortality, and/or indirectly via habitat modification and changes in prey, predator or competitor populations. Indeed, there is ample evidence that humans can act as ecological keystone species, functioning as 'super predators' (Darimont et al. 2015). Tuomainen and Candolin (2011) highlights how individuals behaviourally respond to various types of human disturbances. These responses can be direct or indirect, often resulting from changes in factors that affect fitness, such as resource availability, opportunities and success in dispersal, access to free space, and the presence of other interacting species.

Over the past few decades, large carnivores have made a notable recovery, establishing in anthropogenic landscapes (Chapron et al. 2014). This can lead to conservation conflicts, particularly in rural areas where livestock depredation becomes a pressing concern for farmers and herders (Wabakken et al. 2001, Gangaas et al. 2013, Chapron et al. 2014, Morehouse and Boyce 2017). In addition, as many large carnivore populations remain small and isolated, they are more exposed to threats affecting the long-term viability of populations such as loss of genetic variation, inbreeding depression and reduced adaptive potential (Kardos et al. 2018, 2021, Khan et al. 2021).

One of the most remarkable large carnivore recoveries in Europe is that of the wolves *Canis lupus*, a highly adaptable species able to settle along the entire gradient from low to high human impact (Chapron et al. 2014, Di Bernardi et al. 2025). Cohabitation with humans impacts both wolf behaviour and population dynamics (Rich et al. 2012, Milleret et al. 2019) with known effects of human infrastructures (Theuerkauf et al. 2003b, Kaartinen et al. 2005), especially of roads (Kaartinen et al. 2005, Whittington et al. 2005, Person and Russell 2008, Zimmermann et al. 2014). In addition, the fitness and performance of wolves later in life can also be influenced by the resource availability during their early life which can depend on intra-specific competition, prey density and hunting success (Mech and Boitani 2003, Monaghan 2007, Wikenros et al. 2009). Wolf density may also have a positive impact on the recruitment probability by increasing the chances to find a mate, which can be challenging at low population densities (Wabakken et al. 2001, Hurford et al. 2006, Wikenros et al. 2021, Stenglein and Deelen 2022).

Recruitment probability may also correlate with intrinsic characteristics such as sex, size, body condition or inbreeding level. Inbreeding, known for its detrimental effects across many species (Amos et al. 2001, Keller and Waller 2002, Randi 2011, Trask et al. 2021) including wolves (Laikre and Ryman 1991, Fredrickson and Hedrick 2002, Liberg et al. 2005, Åkesson et al. 2016), has been shown to have a significant impact on juveniles (Keller and Waller 2002, Huisman et al. 2016). Inbreeding depression can lead to malformations (Fredrickson and Hedrick 2002, Räikkönen et al. 2006, 2013), increase the age of first reproduction (Wikenros et al. 2021), as well as decrease pairing and breeding success (Åkesson et al. 2016). Furthermore, the recruitment probability can differ among sexes, with juvenile male mammals commonly exhibiting higher mortality rates than their female counterparts (Clutton-Brock et al. 1985, Kraemer 2000, Kraus et al. 2013). While radio tagging animals can give insight into intrinsic characteristics (Cagnacci et al. 2010), the negative impact of external devices on bird survival and reproduction is well-documented (Bodey et al. 2018). However, their effect on mammals remains understudied, with contrasting results. For example, some studies report a higher survival of collared wolverines *Gulo gulo* (Milleret et al. 2021b) and wolves (Schmidt et al. 2015, Treves et al. 2017a) whereas others link collars to a higher risk of mortality for wolves (Borg et al. 2016, Suutarinen and Kojola 2017).

The recovery of the Scandinavian wolf population serves as a well-documented example of the re-establishment of wolves in Europe. In 2021, the entire population of an estimated 460 (CI: 439–483) wolves (Milleret et al. 2021a) could at that point be traced back to only six unrelated founders, and inbreeding levels were extremely high (Liberg et al. 2005, Åkesson et al. 2016). Compared to other regions worldwide, the population was still at a relatively low density with a high ratio of moose *Alces alces* to wolf (Eriksen et al. 2009, Sand et al. 2012), with moose being the primary prey species in this population (Sand et al. 2008, Zimmermann 2014, Di Bernardi 2022). Due to extensive monitoring efforts of the wolf population, which has allowed for the identification of 97% of all reproductive events, the natal territory and the inbreeding level are known for almost all individuals from the re-establishment of the population in 1983 to date (Åkesson et al. 2022). The population also serves as a good example of the conservation challenges linked to wolf recovery due to the historical bottleneck during re-establishment and the severe inbreeding (Liberg et al. 2005). Similar to other regions worldwide, the recovery of wolves in Scandinavia has resulted in conflicts within local communities (Wabakken et al. 2001, Gangaas et al. 2013) that pose challenges for the conservation of the wolf population. Poaching has been estimated to account for half of the total wolf mortality (Liberg et al. 2012). Beyond poaching, wolves have been legally culled in Scandinavia for damage control and through quota systems (Liberg et al. 2020), maintaining the population well below the carrying capacity (Recio et al. 2018).

In this study, we specifically address the juvenile life history stage of wolves, testing the effect of intrinsic predictors and environmental factors in the natal territory on the recruitment probability of wolves in Scandinavia. While early-life conditions are known to significantly influence an organism's biology and fitness, the specific effects of human-related factors alongside biological factors from the early-life stage remain under-documented. By utilizing a comprehensive long-term dataset that includes detailed intrinsic data, such as inbreeding levels, as well as data on environmental and anthropogenic conditions including the effect of collaring during early-life, we aim to address such gaps. Increasing our understanding of the role of early-life conditions is crucial for managing conservation challenges, including inbreeding depression and poaching. We examined the influence of biological and human-related factors in the natal territory on recruitment probability, i.e. producing pups that survives to at least five months of age. The factors included in our study and the associated hypotheses are summarized in Table 1.

Table 1. Hypotheses on the effects of biological intrinsic (inbreeding coefficient, sex) and extrinsic (moose density, wolf density, snow depth) factors, and human-related factors (collaring, gravel road density, human density, birth country, and distance to non-breeding zones) on the recruitment probability of wolves in Scandinavia.

Hypothesis	Parameter	Rationale	References
Inbred wolves have a lower recruitment probability	Inbreeding	Inbreeding depression on reproductive traits	Åkesson et al. 2016, Keller and Waller, 2002, Liberg et al. 2005, Wikenros et al. 2021
Females have a higher recruitment probability than males	Sex	Juvenile females often exhibit lower mortality rates than males in mammals and stay less long in the dispersing phase, which exposes them to lower mortality risk	Clutton-Brock et al. 1985, Kraemer 2000, Kraus et al. 2013, Wabakken et al. 2015
Females have a lower recruitment probability than males		Males start reproducing on average earlier than females in this population	Wikenros et al. 2021
Moose density in the natal territory increases the recruitment probability	Moose density	Moose is the primary prey species in this population	Sand et al. 2008, Zimmermann 2014
Wolf density in the natal territory increases the recruitment probability	Wolf density	Increased probability to find a mate	Wabakken et al. 2001, Eriksen et al. 2009, Wikenros et al. 2021
Snow depth in the natal territory increases the recruitment probability	Snow depth	Increase of wolf hunting success in deep snow	Haber 1977, Nelson and Mech 1986, Huggard 1993, Kunkel et al. 2004, Wikenros et al. 2009
Snow depth in the natal territory decreases the recruitment probability		Increased risk of poaching	Suutarinen and Kojola 2017, Santiago-Ávila and Treves 2022
Collared wolves have a higher recruitment probability	Collared	Potential protection against poaching	Schmidt et al. 2015, Treves et al. 2017b, Milleret et al. 2021b
Collared wolves have a lower recruitment probability		collars haves been linked to a lower survival mainly in bird species, but also in some wolf populations	Schmidt et al. 2015, Suutarinen and Kojola 2017, Bodey et al. 2018
Gravel road density in the natal territory increases the recruitment probability	Gravel road density	Roads facilitate travelling and hunting for wolves	James and Stuart-Smith 2000, Eriksen et al. 2009
Gravel road density in the natal territory decreases the recruitment probability		Roads increase traffic mortality, disturbances and facilitate poaching	Mech 1989, Kaartinen et al. 2005, Person and Russell 2008
Human density in the natal territory increases the recruitment probability	Human density	Less poaching in more human-populated areas	Suutarinen and Kojola 2018
Human density in the natal territory decreases the recruitment probability		Higher human disturbance might impact wolves' behaviour as they tend to avoid humans	Theuerkauf et al. 2003a, 2003b, Kaartinen et al. 2005
Wolves born in Sweden haver higher recruitment probability than those born in Norway	Birth country	Lower social acceptance of large carnivores in Norway	Gangaas et al. 2013
Distance to non-breeding zones of the natal territory increases the recruitment probability	Distance to non-breeding zones	Lower probability to survive in areas where management authorities do not allow wolves to breed	Liberg et al. 2012

Material and methods

The wolf population on the Scandinavian peninsula

After being declared functionally extinct in 1966, the wolf population has re-established on the Scandinavian peninsula in the 1980s with the immigration of a few wolves coming from the Finnish–Russian population (Wabakken et al. 2001, Vilà et al. 2003, Liberg et al. 2005). The population has been increasing, reaching approximately 460 (CI: 439–483) wolves in Scandinavia at the beginning of the monitoring season 2020–2021 with less than 20% of the wolves ranging in Norway and the rest in Sweden (Milleret et al. 2021a). The population is legally culled in Scandinavia for damage control with management goals and wolf policy differing between Sweden and Norway, e.g. in population size and distribution (Bull et al. 2009, Liberg et al. 2010). In Sweden, wolves are allowed to settle outside the reindeer husbandry area (approximately 55% of the total country area of 447 425 km^2), and in Norway, wolves are allowed to settle in a 'wolf zone' (approximately 5% of the total country area of 324 220 km^2) (Eriksson and Dalerum 2018) (Fig. 1). Social acceptance of large carnivores is generally lower in Norway than in Sweden (Gangaas et al. 2013).

Every year since 1998, a monitoring programme has been conducted during the winter period (1 October–31 March) for individual identification, sex and parentage analysis. It was originally based only on snow tracking, but from the early 2000's DNA analyses of non-invasive samples (scat, urine, hair) was also included. Based on these data, territorial pairs and packs can be identified in order to determine the annual number of reproduction events, confirmed as described by Åkesson et al. (2022). The DNA analyses for individual identification and relatedness enable the reconstruction and annual update of the pedigree of the population, which provides annual estimates of inbreeding of virtually all individuals in the Scandinavian population (Liberg et al. 2005, Åkesson et al. 2022).

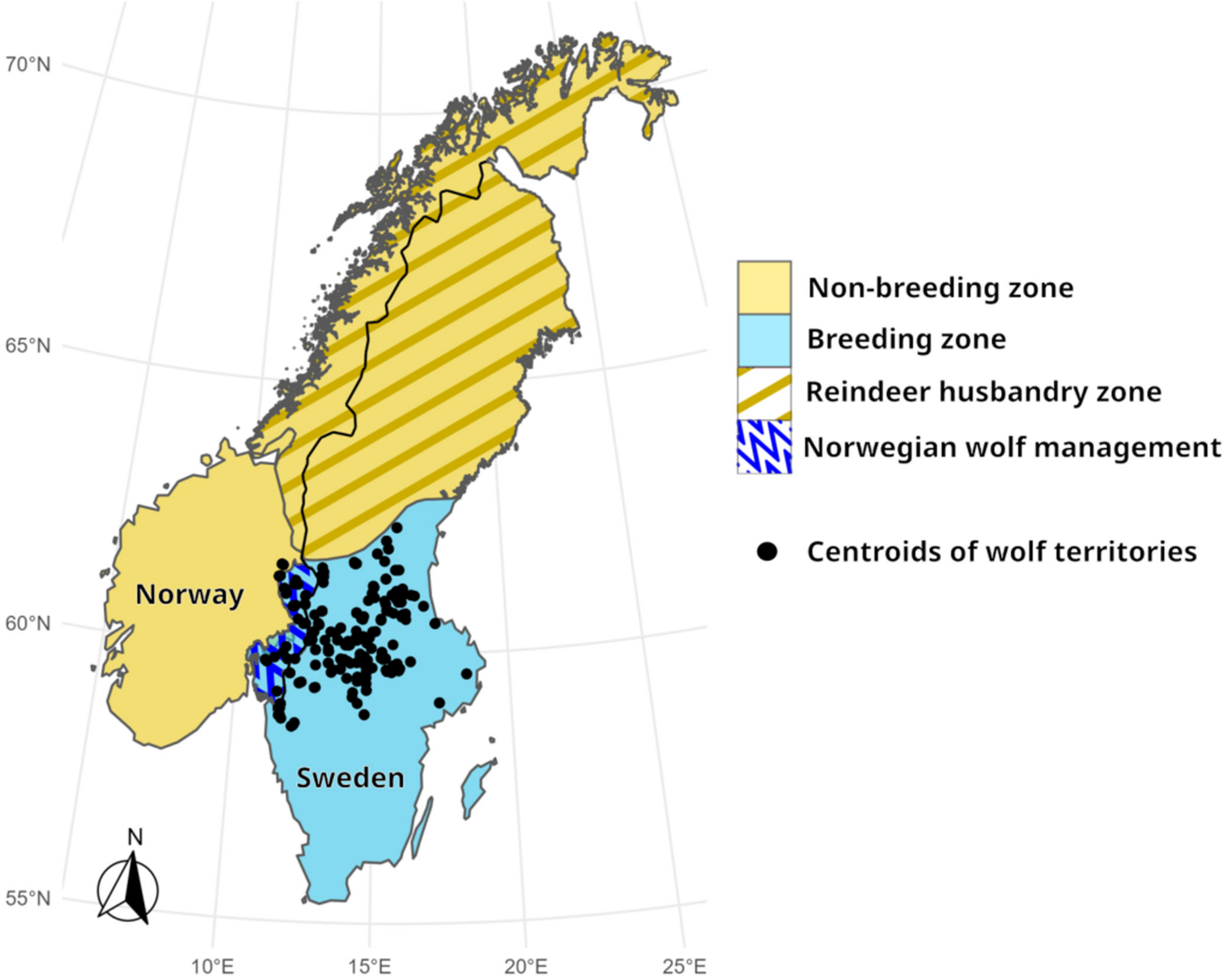

Figure 1. Map of the study area with the Norwegian wolf management zone (blue waves) and the Scandinavian reindeer husbandry zone (yellow stripes). The blue part represents the area where wolves are legally accepted to settle and reproduce (the breeding zone) and the yellow one is the non-breeding zone. The black dots represent the centroids of the wolves' natal territories used in this study from 2003 to 2016.

Selection of target wolf individuals

The identification of wolf individuals in this study was based on DNA sampling from 1) scats, urine, or oestrus blood collected during the monitoring season, 2) saliva from depredation events, or 3) blood sampled from live-captured wolves. We utilized data from 2003 to 2021, including individuals born in Scandinavia between 2003 and 2016. A previous study has shown that 95% of the surviving wolves had reproduced by the age of five years and that the median age at first reproduction in this part of the population was three years for females and two years for males (Wikenros et al. 2021). Thus, to avoid misclassifying wolves as non-breeders before they had the opportunity to reproduce, our study included only wolves born up to 2016.

To minimize bias towards individuals that successfully bred and to maintain consistency in our data, our study included only those individuals that were detected alive during their first monitoring season (Åkesson et al. 2022), which spans from 5 to 11 months of age (1 October–30 March). This approach was taken because older individuals exhibit a higher recruitment probability. Our sample included 340 individuals for which the birth year was known, either because they were sampled and individually identified during the first year after their parents' first reproduction event (n = 310) or they were captured and identified as pups (<1 year old, n = 30). Additionally, 242 individuals with an unknown age were included if their first identification was within their natal territory during the monitoring season which resulted in a total dataset of 582 wolves (Table 2). It is likely that the majority of these individuals were less than one year old, i.e. identified during the first monitoring season after birth, as 76% of the pups permanently leave their natal territory before their second monitoring season, i.e. before the age of 1 year and 5 months (Wabakken et al. 2015, Nordli et al. 2023).

Across the whole dataset of 582 wolves, 126 had been legally killed before five years of age (Table 2). Wolves legally killed before 5 years of age have lower recruitment probability due to management decisions, and were therefore excluded from the main analysis. We conducted a separate analysis where these individuals were kept in the dataset (Supporting information). To ensure consistency, we applied the same threshold of five years of age for legally killed wolves, regardless of whether the wolf had reproduced, i.e. if a wolf was killed before reaching five years of age, we assumed it may not have had the time to breed yet and therefore was removed from the separate analysis.

Biological and human-related factors

The factors included in this analysis were measured for the natal territory of each wolf, representing the condition experienced during early-life. The extent of natal territory was defined as a circular area of 1000 km^2, corresponding with the average size of a Scandinavian wolf territory (Mattisson et al. 2013). The circle was a buffer with 18 km radius around the centroid of all DNA samples of wolves belonging to a given territory, as registered during the annual monitoring.

Biological factors

The biological factors related to individual wolves were both intrinsic (inbreeding coefficient and sex), and extrinsic (wolf density, moose density and snow depth). The inbreeding coefficient of each individual is based on the pedigree of the Scandinavian wolf population (Liberg et al. 2005, Åkesson and Svensson 2022). The sex of individuals was determined either from morphological characteristics of captured individuals or from genetic analysis of biological samples (Seddon 2005, Åkesson et al. 2022). Wolf density was estimated as the number of bordering neighbouring territories, i.e. the number of territories overlapping with the natal territory. As moose harvest size has been shown to correlate with the population density of moose in Scandinavia (Ueno et al. 2014), we used the yearly hunting bag records as an index of moose density (number of moose killed/10 km^2 for counties in Sweden www.algdata.se and Norway https://www.ssb.no/). Data on hunting bag records was generated as a weighted average of the moose density of the counties overlapping with the territory. Yearly average of snow depth was estimated from daily snow depth data extracted from the database SMHI for the weather stations in Sweden (https://www.smhi.se) and from website seklima (https://seklima.met.no/) using the data from met.no (https://www.met.no) for Norway. Corrections for missing values (4% in Sweden and 1% in Norway) were implemented according to the SMHI recommendations (Supporting information). As we were interested in the effect of snow depth during the first year of life of wolves, we used the yearly average of snow depth data from 1 October of the year of birth of the pups to 30 April next year, for each weather station. Consequently, for each individual, the average snow depth during its first year of life in its natal territory was estimated using a kriging interpolation model including the effect of altitude as this factor improved the model accuracy (Pebesma and Graeler 2023).

Human-related factors

The human-related factors included in this study were human density, gravel road density, the birth country, the distance to non-breeding zones, and the effect of collaring. Human density was calculated as the yearly number of inhabitants per km^{2}for each municipality for Sweden (https://www.scb.se/) and Norway (https://www.ssb.no/). For each natal territory, human density was extracted as the average human density of the municipalities overlapping with the natal territory. Since this factor was highly skewed, we applied a logarithmic transformation. Gravel road density was calculated as the average length of gravel roads (km per km^2). We further included two geographical factors of the natal territory, i.e. the birth country (Norway or Sweden according to the location of the territory centroid), as well as the distance between the natal territory centroid and the closest area where the wolves were not allowed to establish (non-breeding zone), i.e. outside of the Norwegian wolf zone and inside the reindeer husbandry area (Fig. 1). As the objective was to study the effect of collaring during the early life stage of wolves, we considered

Table 2. Number of individuals in the Scandinavian wolf population that reached reproduction in the different datasets (2003–2021).

	Total no. of individuals	No. of individuals that reached reproduction
Main analysis (Table 3)	456	108 (0.24)
Post hoc analysis (Table 4)	456	108 (0.24)
Including legally killed (Supporting information)	582	122 (0.21)
Excluding collared individuals (Supporting information)	437	99 (0.23)

as collared individuals only those wolves collared before 1 year of age (n = 19 excluding legally killed individuals and n = 27 including them). We also conducted a separate analysis excluding these collared wolves (Supporting information).

Statistical analysis

We defined whether an individual recruited or not as a binary response factor in our model, assigning a value of 1 to individuals with pups confirmed alive during the following monitoring season and 0 for those without. We employed a generalized linear mixed-effects model (GLMM) using the 'glmmTMB' R package ver. 1.9.14 (Brooks et al. 2024), with a binomial distribution (logit link) that included ten fixed effects (sex, birth country, and collared as binary factors, while inbreeding, log(human density), gravel road density, snow depth, moose density, distance to non-breeding zones for wolves, and wolf density as scaled continuous factors) (see the Supporting information for the minimum, maximum and average values of these factors). The birth year and ID of the parental pair were tested as random effects to address the potential impact of unequal sample sizes of parental pairs or years on recruitment success, as offspring from the same year and or same parental pair may share genetic or environmental characteristics that could introduce non-independence among observations. In addition, we included, as a fixed factor in all models, the number of days between the theoretical birth date (set as 1 May of the birth year) and the first detection date as a nuisance variable that accounts for variations in detection throughout the monitoring season. For collared wolves, we used the collaring date instead, to account for the potential selection bias towards juveniles that survived until the time of collaring which can occur later in the monitoring season. This nuisance variable was set as a fixed parameter, included in all models.

The correlation between the explanatory factors was assessed by a correlation test (*cor.test* function in R) and by calculating the variance inflation factor (*check_collinearity* function from the R package 'performance' ver. 0.11.0 (Fox et al. 2023)). None of the explanatory factors were excluded due to collinearity (all pairwise Pearson $r < 0.39$) and the highest variance inflation factor was 2.77 for birth country. No deviation from the model assumptions were detected in the full model using the *simulateResidua*ls function from the 'DHARMa' package in R ver. 0.4.6 (Hartig and Lohse 2022). As we included a large number of factors, we used a model selection procedure to determine the combination of factors that best fit the data. First the best structure for random effects was tested using a likelihood ratio test with the R function *anova* by fitting the full (with birth year and parental pair ID) and reduced models (with only parental pair ID as random and without any random effects). As the inclusion of the random effects did not provide a significant improvement in explaining the variability in the data (p-value = 1 for the addition of parental pair id and p-value = 0.98 for birth year) the model without random effects was retained for parsimony. Model selection was thereafter performed to test the fixed effects using the dredge function from the 'MuMIn' package ver. 1.47.5 (Bartoń 2024), based on the Akaike information criterion corrected for small sample sizes (AICc). To ensure robustness, only models with a $\Delta\text{AICc} \leq 2$ were retained for model averaging with the function *model.avg* of the 'MuMIn' package. A factor was considered significant if its p-value in the full model average was below 0.05.

To further explore the effect of collaring on recruitment probability and its potential link to poaching, we performed a post hoc analysis. This analysis incorporated two additional factors in the full model that are correlated with poaching in Scandinavia, as identified by Liberg et al. (2020): the wolf population size and the number of wolves legally culled. The annual wolf population size was estimated based on monitoring data, adjusted by subsequent monitoring years (Svensson et al. 2021) while the number of wolves culled per year was extracted from the database Rovbase (www.rovbase.no). These two factors were included for the birth year of each individual. The post hoc analysis was performed on the main dataset (excluding legally killed individuals), using the same modelling procedure as above.

Results

Among the 456 individuals detected as pups or juveniles in their birth territory, 108 (0.24) reproduced with at least one pup confirmed alive during the following monitoring season. When including also wolves that were legally killed before five years of age, the recruitment probability was reduced to 0.21 (Table 2).

In our analysis, 10 models had $\Delta\text{AICc} \leq 2$ and were included in the model averaging. In the full averaged model, collaring was significant (p = 0.01), and was retained in all top-ranked models (Table 3, Fig. 2). Among the 19 wolves collared during their first year of life, reproduction was recorded for 9 individuals, resulting in a recruitment probability of 0.50 [CI = 0.25–0.74] compared to 0.22 [CI = 0.15–0.28] (Fig. 3) for non-collared individuals. Collared wolves had more than three times the odds (odds ratio = 3.57) of recruiting than non-collared wolves (Table 3).

Table 3. Model selection and model-averaged parameter estimates (β), standard errors (SE) and p-values (p) for conditional and full averaged models on the recruitment probability for wolves in Scandinavia during 2003–2021. The models were ranked based on AICc and only the top models (ΔAICc ≤ 2) were kept and used for model averaging. The best model has an AICc of 495.05. The reference in the analyses is 'No' for the predictor Collared, 'Norway' for Country and 'Male' for Sex. The number of days before the first detection was set up as a fixed parameter during the dredging. *** < 0.001 < ** < 0.01 < * < 0.05.

		Int.	Collared	Human density	Inbreeding	Gravel road density	Birth country	Wolf density	Sex	Snow depth	Days before detection (fixed)	df	ΔAICc	Weight
		X	X	X	X						X	5	0	0.20
		X	X	X							X	4	0.85	0.13
		X	X	X	X		X				X	6	1.54	0.09
		X	X	X	X	X					X	6	1.56	0.09
		X	X	X	X				X		X	6	1.70	0.09
		X	X			X	X				X	5	1.85	0.08
		X	X	X	X			X			X	6	1.92	0.08
		X	X	X	X					X	X	6	1.95	0.08
		X	X	X		X					X	5	1.96	0.08
		X	X			X					X	4	1.97	0.08
Full model averaged	β	−1.30***	1.27*	0.21	−0.12	0.05	0.05	3×10^{-3}	0.01	4×10^{-3}	−0.04			
	SE	0.18	0.50	0.14	0.13	0.11	0.17	0.03	0.08	0.04	0.11			
	p	$<2 \times 10^{-16}$	0.01	0.15	0.35	0.63	0.76	0.92	0.88	0.93	0.75			
Conditional model averaged	β	−1.30***	1.27*	0.25*	−0.19	0.16	0.31	0.04	0.13	0.05	−0.04			
	SE	0.18	0.50	0.12	0.11	0.14	0.31	0.11	0.23	0.14	0.11			
	p	$<2 \times 10^{-16}$	0.01	0.04	0.09	0.24	0.33	0.71	0.56	0.74	0.75			

The human density in the natal territory showed weak but non-significant evidence for a positive association with a higher recruitment probability as it was retained in eight of the 10 best models with a p-value of 0.15 (Table 3, Fig. 3). Inbreeding was retained in six of the 10 best models but its negative effect was not statistically significant ($p = 0.33$) (Table 3). The other explanatory factors (gravel road density, birth country, wolf density, sex and snow depth) were retained in only a few of the top-rated models whereas moose density and distance to non-breeding zones were not included in any top-ranked models (Table 3).

The post hoc analysis, which further explored the role of collaring and its relationship with poaching risk, showed that the positive effect of collaring on recruitment probability remained unchanged when accounting for population size and birth year (Table 4). Indeed, in the post hoc analysis collaring had a p-value of 0.01. Moreover, the positive relationship between human density and the recruitment probability was stronger compared to the main analysis, being here retained in all top-ranked models and with a p-value of 0.04 (Table 4).

The two additional analyses, one with the inclusion of legally killed individuals (Supporting information) or the removal of collared wolves (Supporting information) gave similar results and did not change the main outcomes of our analysis. In our data, 55% of the individuals were killed legally within the area where wolves are allowed to reproduce, and 64% of these events took place in Sweden, which also accounts for 78% of the individuals in our study.

Discussion

Wolf recruitment probability in Scandinavia was not associated with any early-life biologically related predictor, but was positively correlated with two human-related factors: being collared during the first year of life and the human population density experienced in the natal territory. In addition, we could not find support for inbreeding depression hypothesis. Although inbreeding was included in several of the top-ranked models, the variable was uninformative.

The observed relation of recruitment probability with collaring within the first year of life and with the human density in the natal territory may reflect complex direct and indirect interactions between wolves and human activities, involving human disturbance and the risk of being poached. In this respect, the observed higher recruitment probability among collared wolves, both when excluding and including from our analysis the wolves legally killed before 5 years of age, aligns with findings by Milleret et al. (2021b). Indeed, that study reported an apparent positive effect of GPS-collars on survival of wolverines in Scandinavia, with comparable risk of dying from legal culling for collared and uncollared individuals, but with collared individuals experiencing a lower risk of dying for causes other than legal culling (Milleret et al. 2021b). This was attributed to the collars acting as a deterrent and potentially favouring fitness by shielding animals

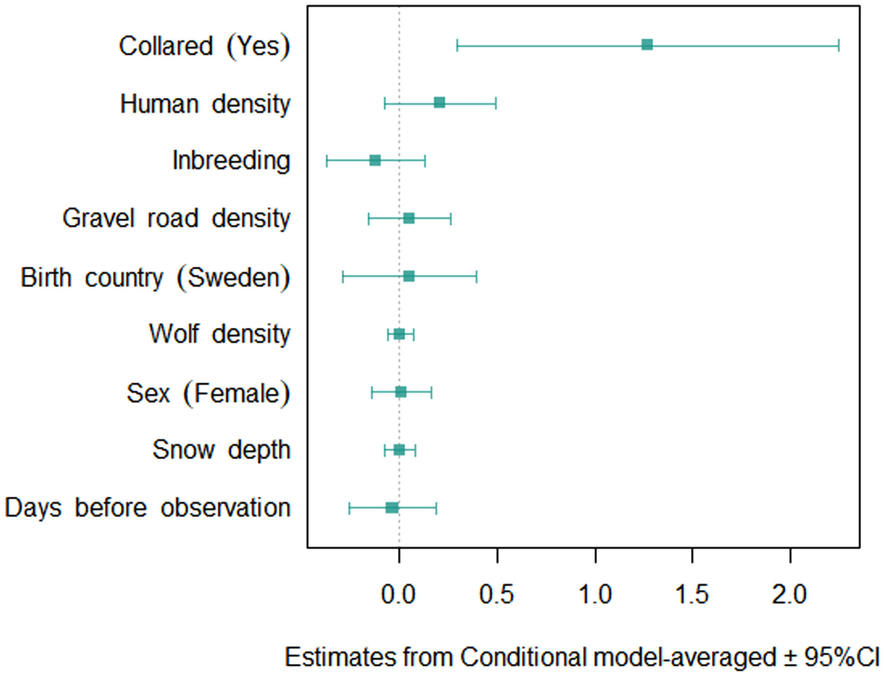

Figure 2. Coefficient plot of the averaged model of factors impacting recruitment probability for wolves in Scandinavia. The bars represent the 95% confidence interval of the coefficients estimated by the averaged model (Table 3). Coefficients come from the full-model averaged, while see Table 3 for both full-model and conditional averaged results.

from poaching (Milleret et al. 2021b). In our post hoc analysis, wolf population size and the number of legally culled wolves were included as poaching-related factors, based on the findings of Liberg et al. (2020), and were not informative while the positive effect of collaring persisted. Although we expected a weaker collaring effect when including poaching-related factors, the post hoc results do not rule out a relationship between collaring and reduced poaching risk. As done for all factors in this study, we included population size and the number of legally culled wolves measured during the first year of life. However, if the collar acts as a deterrent against poaching, its effect extends beyond the first year of life (collars with a drop-off function are programmed to drop off after 900 days, i.e. when wolves are on their fourth year). This overlaps with the dispersal and establishing phases, and in most cases also with the time of first reproduction (2-3 years of age), which likely explains the higher recruitment probability for collared wolves. A hypothetical alternative explanation is that collaring may directly influence wolves' behaviour toward humans. Learning from past capture experiences, wolves may develop an avoidance behaviour towards humans, by perceiving these capturing events as traumatic. If this avoidance behaviour is realized, it could make wolves less exposed and vulnerable to human presence and activities, including poaching. This interpretation would question the validity of utilizing collared individuals to estimate poaching rates, a common approach used for many studies (Liberg et al. 2012, 2020, Suutarinen and Kojola 2017, 2018, Treves et al. 2017b, Santiago-Ávila and Treves 2022). Therefore, the estimation of mortality rate in general and poaching rate in particular and its consequences in the Scandinavian population based on collared individuals (Liberg et al. 2012, 2020) might have been underestimated.

We cannot completely exclude sampling bias as an explanation for the higher recruitment of wolves collared during their first year. However, the risk of higher detection of reproductions from collared individuals is most likely absent in this monitored wolf population. Specifically, the rate of detection of wolf reproduction events is 97% during the monitoring period and the rest is identified subsequently from kinship analyses (Åkesson et al. 2022). In addition, in our analysis we tested the collaring effect restricted to those individuals collared during the first year of life, reflecting a condition experienced during the early-life stage. Considering only the collaring during the juvenile stage entails that there is less bias toward individuals that survived until later stages and were collared as adults. Such individuals would indeed have a higher recruitment probability compared to non-collared individuals, regardless of the collaring effect. Moreover, to account for the potential bias of collared wolves within the first monitoring season, we added a nuisance variable in our modelling. This variable controlled for the fact that juvenile wolves must survive until the time of collaring, which often occurs later in the season, whereas non-invasive DNA sampling is conducted throughout the entire monitoring period. Our results have been obtained from a limited number of collared individuals (5% of the analysed dataset). Future research should examine the fitness consequences of fitting

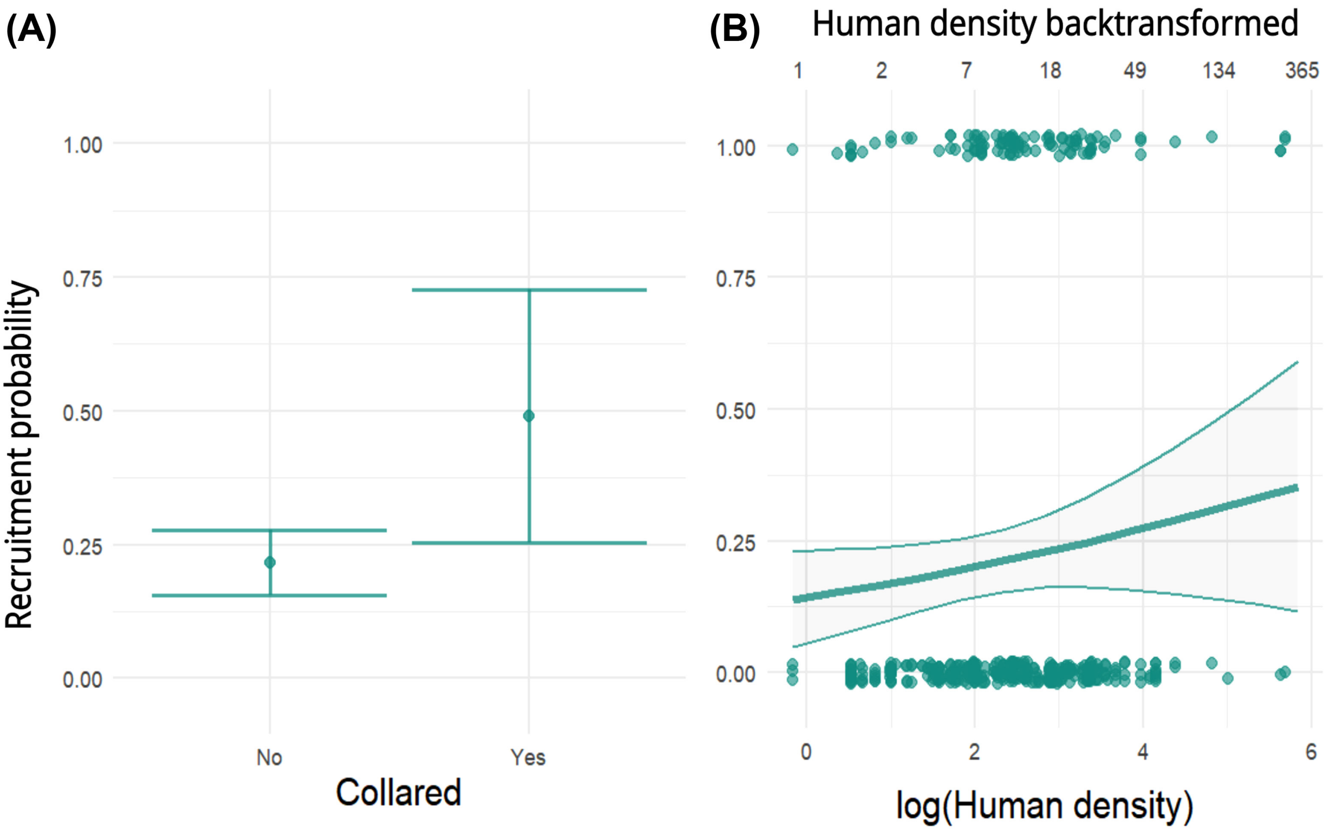

Figure 3. Recruitment probability in relation to (A) collaring in the first year of life and (B) the human density in the natal territory (inhabitants km^{-2}). The lines indicate the fitted values, with associated 95% confidence interval from the model-averaged estimates (Table 3). For (B), sex was held constant at 'Male', birth country at 'Norway', collared at 'No', and the other continuous factors coefficients (inbreeding, human density, gravel road density, snow depth, moose density, distance to non-breeding zones for wolves, and wolf density) were kept at their mean. The dots in the (B) correspond to the observed data points, where their position on the y-axis represents the actual binary outcome of reaching reproduction (0 or 1). The x-axis of the probability obtained from standardized factors of (B) was back transformed into the original units.

wolves with collars during the early-life stage as well as later in life, by conducting a targeted analysis comparing the proportion of collared individuals with the uncollared segment of the population.

Despite the varying strength of significance across our different analyses, the human density in the natal territory was overall an informative factor related to the recruitment probability. Although many studies suggest that large carnivores, such as wolves, are more conflict-prone in areas of high human density (Mladenoff et al. 1995, Theuerkauf et al. 2003a, Kaartinen et al. 2005, Oakleaf et al. 2006), several studies have also suggested that wolves are highly capable of persisting in human-altered landscapes (Bateman and Fleming 2012, Llaneza et al. 2012, Lesmerises et al. 2012). A higher abundance of ungulate prey in agricultural areas (Dellinger et al. 2013) has been suggested as a potential reason for the selection of human-altered habitats over natural ones by red wolves *Canis rufus*. In our study, the observed positive relation between recruitment probability and human density in the natal territory could be functionally linked to easier access to prey in more inhabited and agricultural areas. Another potential explanation is that higher human densities may discourage poaching due to an increased risk of being discovered and caught by legal enforcement (Suutarinen and Kojola 2018). Relatedly, the acceptance of large carnivores, including wolves, tends to be higher in more urbanized areas, whereas inhabitants in rural areas generally express a more negative attitude (Skogen and Krange 2003, Gangaas et al. 2013).

Although inbreeding seemed to explain some of the observed variation in the recruitment probability, the direction of the effect was unclear. Previous studies of the Scandinavian wolf population have found negative impacts of inbreeding on various fitness traits (Liberg et al. 2005, Åkesson et al. 2016, Wikenros et al. 2021). A reason for the lack of clear evidence in our study might be due to the interplay between inbreeding and environmental variation. Inbreeding often interacts with the environment leading to a stronger disadvantage of inbred individuals in stressful environments (Fox and Reed 2011). Indeed, the high density of moose or alternative ungulate prey across the distribution range of wolves in Scandinavia (Sand et al. 2012, 2016,

Table 4. Model selection and model-averaged parameter estimates (β), standard error (SE) and p-values (p) for conditional and full averaged model on the post hoc analysis for the recruitment probability for wolves in Scandinavia during 2003–2021. The models were ranked based on AICc and only the top models (ΔAICc ≤ 2) were kept and used for model averaging. The best model has an AICc of 496.39. The reference in the analyses is 'No' for the predictor Collared, 'Norway' for Country and 'Male' for Sex. The number of days before the first detection was set up as a fixed parameter during the dredging. *** < 0.001 < ** < 0.01 < * < 0.05.

		Int.	Collared	Human density	Inbreeding	Gravel road density	Country	Wolf density	Sex	Moose density	Population size	Legal culling	Days before detection (fixed)	df	ΔAICc	Weight
		X	X	X	X						X	X	X	7	0	0.16
		X	X	X	X								X	5	0.40	0.13
		X	X	X	X						X		X	6	1.23	0.09
		X	X	X									X	4	1.24	0.09
		X	X	X	X		X				X	X	X	8	1.31	0.08
		X	X	X	X			X			X	X	X	8	1.39	0.08
		X	X	X	X				X		X	X	X	8	1.54	0.07
		X	X	X	X	X					X	X	X	8	1.82	0.06
		X	X	X	X					X	X	X	X	8	1.87	0.06
		X	X	X	X		X						X	6	1.93	0.06
		X	X	X							X	X	X	6	1.95	0.06
		X	X	X	X	X						X	X	6	1.96	0.06
Full model averaged	β	−1.30***	1.27*	0.25*	−0.18	0.01	0.03	8×10^{-3}	0.01	-3×10^{-3}	−0.21	0.17	−0.03			
	SE	0.16	0.51	0.12	0.13	0.05	0.14	0.04	0.08	0.03	0.21	0.19	0.11			
	p	$<2 \times 10^{-16}$	0.01	0.04	0.16	0.86	0.81	0.86	0.87	0.92	0.31	0.37	0.79			
Conditional model averaged	β	−1.30***	1.27*	0.25*	−0.21	0.08	0.23	0.10	0.17	−0.05	−0.32	0.30	−0.03			
	SE	0.16	0.51	0.12	0.12	0.13	0.29	0.12	0.23	0.12	0.18	0.16	0.11			
	p	$<2 \times 10^{-16}$	0.01	0.04	0.06	0.56	0.43	0.41	0.47	0.66	0.08	0.07	0.79			

Mattisson et al. 2013) may not represent stressful conditions. Moreover, our estimates of inbreeding at the level of individual wolves are based on a pedigree and may not reflect true levels of homozygosity and what proportion of the genome that are identical by descent (Kardos et al. 2015, 2018, Shafer and Kardos 2025). Therefore, given that the Scandinavian wolf population is not saturated and is strongly impacted by human activities and management (Liberg et al. 2012, 2020, Recio et al. 2018, 2020), conducting the same analysis on wholly or partially naturally regulated populations may yield different results. This may be particularly true for environmental conditions, such as wolf density, moose density, and snow depth, which may exert a stronger influence on fitness in contexts where higher wolf densities can lead to increased competition for space and resources.

To conclude, human activity is recognized to exert various influences on wolf populations in Europe, by impacting their behaviour (Theuerkauf et al. 2003a, Zimmermann et al. 2014), population dynamics (Liberg et al. 2020) and distribution (Ripple et al. 2014, Recio et al. 2020). In Scandinavia, the conservation conflict poses significant challenges for the wolf management as poaching has been estimated to account for up to half of the total wolf mortality and severely limits population growth (Liberg et al. 2012). While our results suggest that collaring and human density in the early-life stage have a positive relationship with recruitment probability, further research is warranted to disentangle the mechanisms driving such indirect associations. This should possibly include the environment experienced in later life-stages preceding first reproduction, i.e. dispersal and territory establishment. Overall, with a focus on the juvenile early-life stage, our findings contribute to our understanding on the biological and human-related factors related to the conditions in the natal territory and their relationship to the wolves' recruitment probability, highlighting the management and conservation challenges of wolves coexisting with humans in increasingly anthropogenic landscapes.

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Permits – All procedures including capture, handling and GPS-collaring of wolves fulfilled ethical requirements and have been approved by the Swedish Animal Experiment Ethics Board (permit no. C 281/6) and the Norwegian Experimental Animal Ethics Committee (permit no. 2014/284738-1). The GPS-data were collected into the Wireless Remote Animal Monitoring database system for data validation and management (Dettki et al. 2013).

Author contributions

Léa Auclair and **Cecilia Di Bernardi** share first authorship. **Léa Auclair**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Writing – original draft (equal); Writing – review and editing (equal); **Cecilia Di Bernardi**: Conceptualization (equal); Data curation (equal); Writing – original draft (equal); Writing – review and editing (equal); **Håkan Sand**: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Writing – review and editing (equal); **Mikael Åkesson**: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Writing – review and editing (equal); **Barbara Zimmermann**: Writing – review and editing (equal); **Øystein Flagstad**: Data curation (equal); Writing – review and editing (equal); **Petter Wabakken**: Writing – review and editing (equal); **Camilla Wikenros**: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.xksn02vs8 (Auclair et al. 2025).

Supporting information

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

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