



Environmental variability across space and time drives the recolonization pattern of a historically persecuted large carnivore

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Wildlife populations are not static. Intrinsic and extrinsic factors affect individuals, which lead to spatiotemporal variation in population density and range. Yet, dynamics in density and their drivers are rarely documented, due in part to the inherent difficulty of studying long-term population-level phenomena at ecologically meaningful scales. We studied the spatiotemporal density dynamics in a recolonizing large carnivore population, the wolverine *Gulo gulo*, across the Scandinavian Peninsula over nine years. We fitted open-population spatial capture-recapture models to noninvasive genetic sampling data collected across Norway and Sweden to estimate annual density surfaces and their drivers. This approach allowed us to model sex-specific changes in wolverine density and the effect of landscape-level environmental determinants over time. Our results revealed that, as wolverines successfully recolonized many parts of their historical range in Scandinavia, the relationship with spatial determinants of density has changed over time. We also found support for sex-specific responses of the Scandinavian wolverine to the environmental determinants of density and differences in the temporal dynamics of their relationships, indicating disproportionate recolonization ability and anthropogenic pressures. We observed significant changes in the relationship of female wolverine density with several determinants during the study period, suggesting still ongoing expansion of female wolverines whereas males might have already reached the range limits. These findings show that the Scandinavian wolverine population is still recovering from centuries of persecution and severe range contraction. Our study sheds light on the dynamics and challenges of recolonizing large carnivores in human-dominated landscapes across time and space.

density | spatial capture-recapture | population dynamics | transboundary wildlife populations | wolverine

Many wildlife populations have historically been persecuted by humans. Despite the widespread loss of wilderness, effective management and conservation measures have reversed the extinction trajectory for several wild species (1–3). Such successes have even been achieved in altered ecosystems, where natural habitats were transformed to meet human interests (4–6). However, this means that recovering wildlife populations need to cope with drastically altered environments within their historical ranges. In the Anthropocene, land use history and management interests are dominant forces that are transforming ecosystems and altering fundamental patterns of landscape heterogeneity (7–9). Understanding how environmental factors determine the distribution and density of wildlife is a primary goal of ecology and crucial for the adaptive management of recovering wildlife populations in today's human-dominated landscapes.

Different factors contribute to the successful recovery and expansion of wildlife into currently unoccupied habitats. For some species, recovery starts from a relict range where the species survived persecution. Relict ranges can be original core areas of highly suitable habitat, or suboptimal habitat with comparatively low human pressure that the last remnant population was pushed into—i.e., habitat refuge (10, 11). Recovery can also follow successful restoration attempts, where a viable population is established after reintroduction in suitable habitats (12, 13). Nevertheless, recovery is often poorly documented for many wildlife populations. This is in part because of a long history of human-induced changes to populations and their habitats, constantly shifting baselines of population status (14, 15). In addition, different methodologies are used to reconstruct historical reference points for species persisting in human-altered landscapes. The resulting uncertainty in wildlife population trajectory and distribution dynamics makes impact assessments of threats difficult and inhibits reliable inferences of population status, a prerequisite to detect changes.

Significance

Across Europe and North America, some large carnivore species are recovering their former ranges. The spatial and temporal dynamics of this recovery are still poorly understood. We used nine years of transnational noninvasive genetic sampling to quantify temporal changes in the drivers of density of a recovering wolverine *Gulo gulo* population across the Scandinavian Peninsula. We provide pervasive evidence for successful expansion of the wolverine population from the refuge-like alpine range into boreal forest, which was previously considered suboptimal habitat for wolverines in Scandinavia. The ongoing recovery of the Scandinavian wolverine demonstrates that coexistence of apex predators with humans on multiuse landscapes is possible.

The authors declare no competing interest.

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Recently developed analytical methods to estimate population density have significantly boosted our ability to quantify and study spatial distribution of species and, thus, range limits and recovery processes (16–18). However, estimates of density are often of limited use to study the process of population recovery. First, these estimates are usually derived from a portion of the population only and may not represent the status of the entire population and its responses to different environmental factors. Second, density estimates are often limited to a sporadic snapshot of the population, making it difficult to quantify temporal dynamics in density and important changes in habitat–density relationships. The current distribution and density of a given wildlife population are the result of both historical and present-day factors that are constantly shaping that population (11, 19, 20). Biotic and abiotic environmental characteristics vary spatially and temporally and this variability influences species and ecological processes. Specifically, past and current management regimes, primarily harvest, can have a strong influence on the density dynamics and even obscure ecological mechanisms (21, 22). In addition, the relationship between environmental variables and density can change over time as a result of demographic shifts during recovery, modulated by increasing density, or simply because a wider range of conditions are encountered by the expanding population. Identifying such changes can help better understand species–environment interactions, track recovery more closely, and more reliably forecast population responses to future changes in the environment and human interventions. This, in turn, requires long-term monitoring data at the population level and a spatially explicit analytical framework that can handle the associated large computation demands (17, 23–25).

The Scandinavian wolverine *Gulo gulo* population has recolonized many parts of its historical range in Norway and Sweden after a long period of intense persecution (5, 26–29). Once almost functionally extinct, a combination of protective measures, higher tolerance of wolverines by humans, and a surviving relict population along the alpine border between Norway and Sweden has contributed to the recovery of the wolverine in Scandinavia (20, 26, 30, 31). The wolverine is a red-listed species in both countries, classified as Endangered in Norway and Vulnerable in Sweden. Nonetheless, and like other members of the Scandinavian large carnivore guild, the wolverine is still intensely harvested in many areas, especially in Norway, to control population size and expansion and to mitigate conflicts (28, 31–34). Management goals, laws, and regulations vary not only between Norway and Sweden but also at the regional level within each country (20, 28, 35, 36). On a national level, both countries aim for viable wolverine populations, but management differs substantially due to different livestock husbandry practices, conflict levels, and regulatory contexts (26, 37, 38). In Norway, which is not a member of the European Union (EU), increasing conflicts with the domestic sheep *Ovis aries* farming industry and semidomesticated reindeer *Rangifer tarandus* husbandry have resulted in the abolishment of core conservation areas and introduction of large annual hunting quota (27, 32–34, 36, 39, 40). In contrast, EU member Sweden strictly protects wolverines throughout the country (41); a conservation performance payment system is the main tool to mitigate conflicts in reindeer husbandry areas, while lethal control has until recently only been permitted in areas with high levels of predation on semidomesticated reindeer (28, 30, 33, 42). Successful management of this conflict-prone large carnivore requires up-to-date information on the spatiotemporal impact of the factors shaping the spatial configuration of the transboundary population and its trajectory.

As the spatial manifestation of wildlife populations changes over time, we ask: How does this process affect the relationship between density and its spatial determinants? To approach this question, we used a comprehensive dataset of genetically identified wolverine individuals collected across their entire range in Norway and Sweden over nine consecutive years (*SI Appendix, Fig. S1 and Tables S1 and S2*). We fitted open-population spatial capture-recapture (OPSCR) models (43–46) to detect and quantify potential changes in the relationship between wolverine population density and landscape-level environmental conditions, while controlling for spatially and temporally variable imperfect detectability (*SI Appendix, Tables S3 and S4*). There is evidence that wolverine density today reflects the location of the relict range along the Norwegian–Swedish border (*SI Appendix, Fig. S2*), where the population survived human persecution until the 1970s and presumably started to recolonize its historical range (20, 27, 31, 47). Although the Scandinavian wolverine has long been restricted to alpine areas, the species has recently expanded into the boreal forest (i.e., taiga) and is now occupying areas that were not considered prime habitat during the last century (26–29, 48, 49). Therefore, we hypothesized that a combination of historical and present-day environmental factors has driven the wolverine density in the Scandinavian Peninsula over the past decade and that the relative effects of these determinants have changed through time. Specifically, we expected that proximity to the relict range, characterized by distance to alpine habitat along the Norwegian–Swedish border, would become less important over time as the wolverine population expanded. We also expected that, by successfully establishing themselves in the neighboring boreal forest, the importance of forest and forest-associated determinants for wolverine density would become more pronounced over time.

Results

Noninvasive Genetic Monitoring. Management authorities conducted between 197,673 and 316,839 km of structured searches for wolverine DNA annually between winters 2013/2014 and 2021/2022 within our study area. Structured and unstructured sampling efforts and genetic analyses led to a total of 8,418 and 10,327 successfully genotyped female and male wolverine samples, respectively, belonging to 1,360 female (median = 481, range = 337 to 529 individuals detected annually) and 1,190 male wolverines (median = 425, range = 274 to 471; *SI Appendix, Tables S1 and S2*). The annual number of detections per identified individual ranged from 1 to 11 for females and 1 to 12 for males. On average, 58.9% (range = 54 to 65.3%) of females and 56.3% (range = 51.1 to 62.3%) of males detected in a given year were detected during structured sampling and the remainder during unstructured sampling (*SI Appendix, Fig. S1*).

Density Determinants. A key driver of the wolverine density dynamics in the Scandinavian Peninsula appeared to be the distance from the relict range along the alpine border between Norway and Sweden (Fig. 1 and *SI Appendix, Figs. S2 and S3*). Over the nine years of the study, wolverine density consistently declined with increasing distance from the relict range for both sexes (*SI Appendix, Table S5*). This association diminished over time for female wolverines (median and 90% Bayesian Credible Interval [BCI] $\hat{\beta}_{1\text{Relict}_F} = 0.04$ [0.01 to 0.08]) but not for males ($\hat{\beta}_{1\text{Relict}_M} = 0.003$ [−0.04 to 0.04]).

Forest percentage was positively associated with wolverine densities, and this association significantly strengthened over time

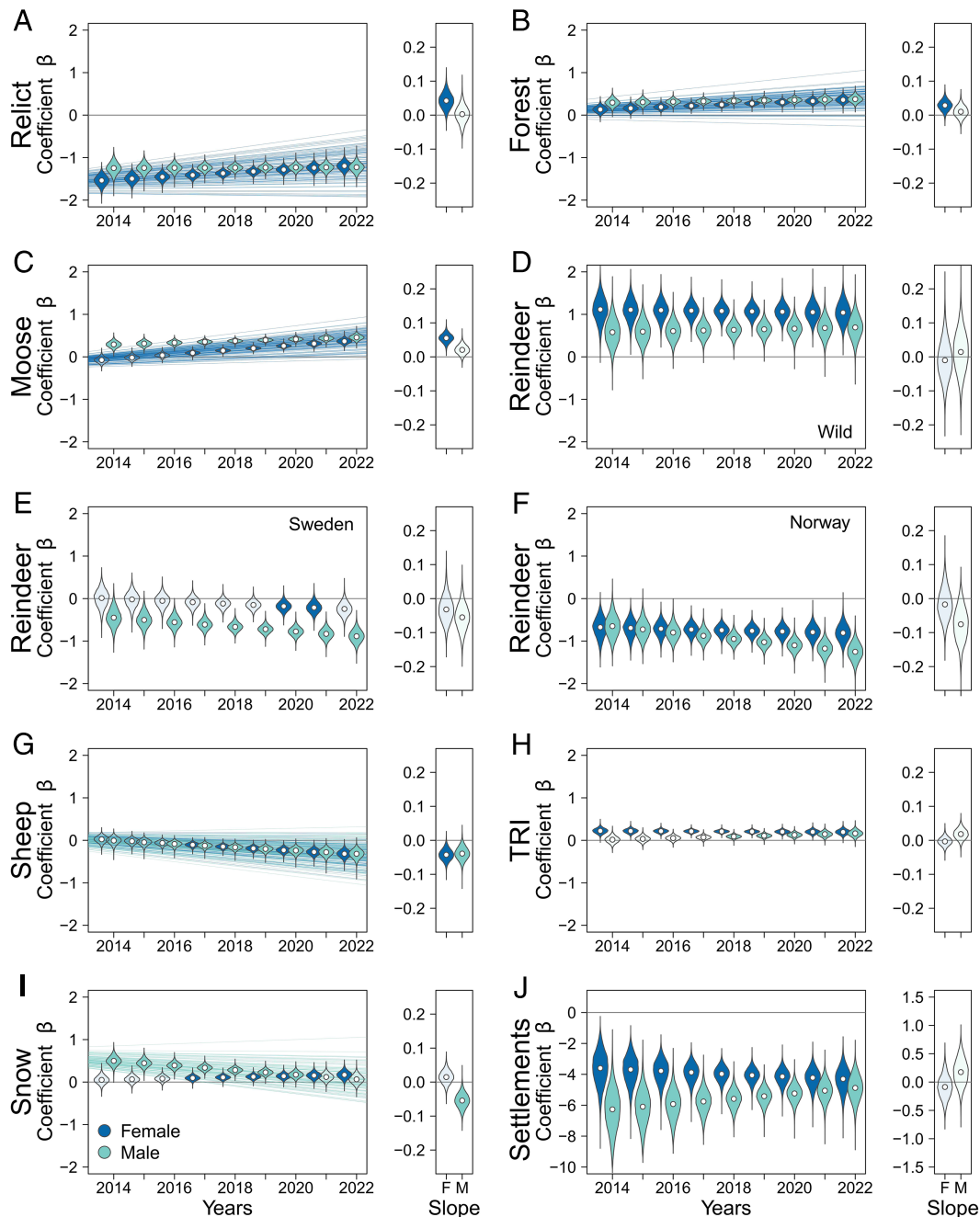


Fig. 1. Relationships between 10 spatial covariates (A–J) and female (dark blue) and male (light blue) wolverine *Gulo gulo* densities across the study landscape on the Scandinavian Peninsula during nine monitoring seasons between 2013/2014 and 2021/2022. The violin plots show the estimated median (white dots) and posterior distribution of 1) large boxes: annual regression coefficients β —i.e., association between each covariate and wolverine density in a given year; and 2) small boxes: temporal change in the coefficients—i.e., trend (slope) of the association over the nine-year of the study for female (F) and male (M) wolverines. Effect sizes are on the exponential scale. Violins representing parameters whose 90% Bayesian credible interval overlapped zero are shown in semitransparent colors. A hundred random samples from the posterior of the temporal trend in the effects are provided in the time series plots as semitransparent lines when the temporal change in effect size was strong. The spatial covariates (A–J) are described in [SI Appendix, Table S4](#).

for female wolverines ($\hat{\beta}_{1\text{Forest}_F} = 0.03$ [0.001 to 0.05]) but not for males ($\hat{\beta}_{1\text{Forest}_M} = 0.01$ [−0.02 to 0.04]; Fig. 1).

Among the food-related covariates, the moose *Alces alces* density proxy appeared to be one of the main drivers of wolverine density for both sexes (Figs. 1 and 2 and [SI Appendix, Figs. S4 and S5](#)). This covariate was strongly and positively associated with male wolverine density across the monitoring seasons without a clear temporal trend ($\hat{\beta}_{1\text{Moose}_M} = 0.02$ [−0.001 to 0.04]). In contrast, we observed an increasingly positive association of

the moose covariate for female wolverines, starting from slightly negative association in the first monitoring season to positive during the last years ($\hat{\beta}_{1\text{Moose}_F} = 0.06$ [0.03 to 0.08]).

The wild reindeer covariate had a consistently positive relationship with both female and male wolverine densities, with no noticeable change over time ($\hat{\beta}_{1\text{Reindeer}_F} = -0.01$ [−0.1 to 0.09] for females and $\hat{\beta}_{1\text{Reindeer}_M} = 0.01$ [−0.09 to 0.11] for males; Figs. 1 and 2). By contrast, the presence of semidomesticated reindeer areas in Sweden was negatively

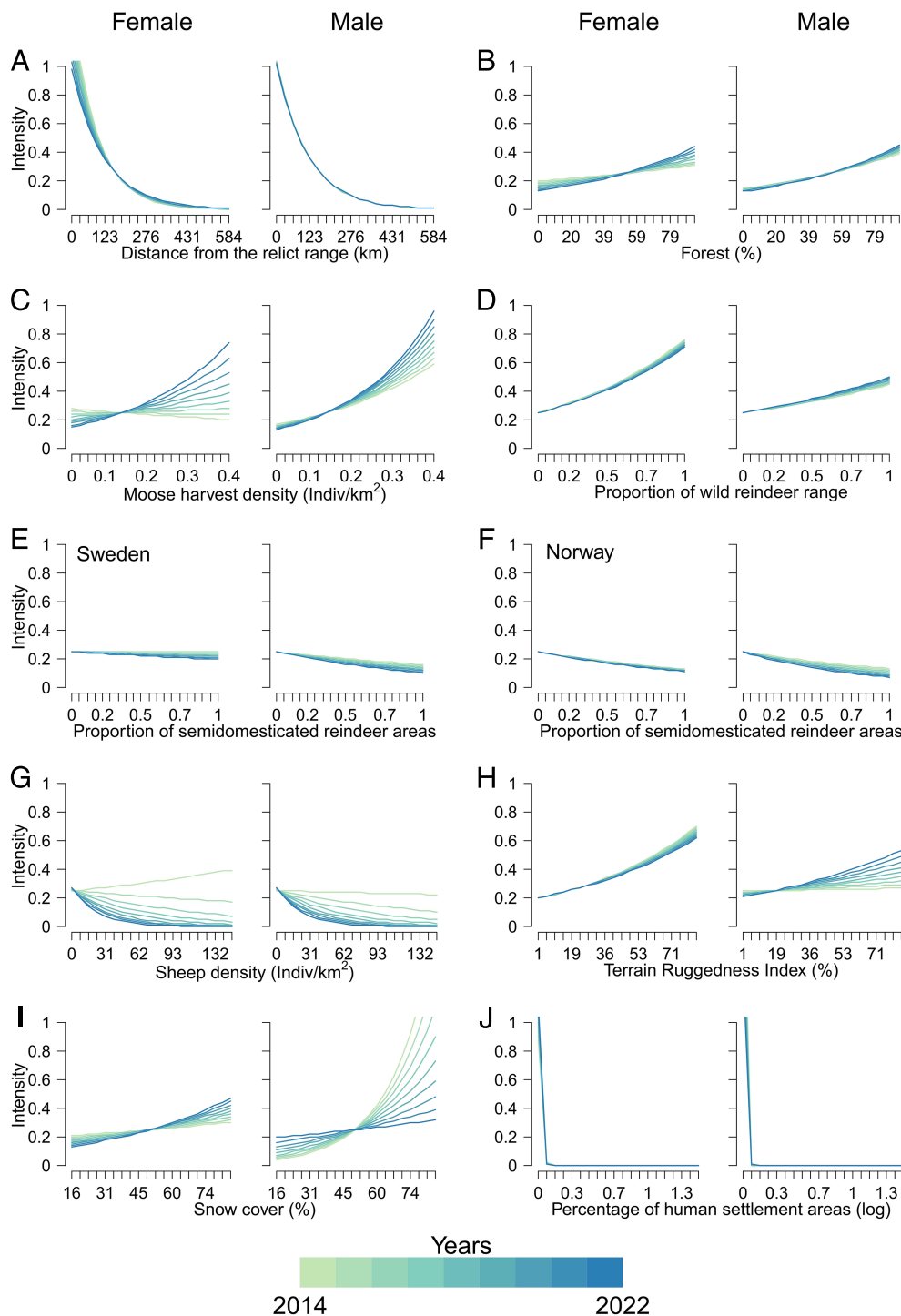


Fig. 2. Intensity of the density point process for female and male wolverines *Gulo gulo* in the Scandinavian Peninsula during nine monitoring seasons between 2013/2014 and 2021/2022 as a function of 10 environmental covariates (A–J). Median predicted responses in each sampling year are represented by lines, color coded by year. The intensity of the point process reflects the relative distribution of individual activity centers, so that, for example, twice as many individuals are expected to have their activity center located in a habitat cell with an intensity of 1 compared to 0.5. To depict uncertainty, the lower and upper limits of the 95% Bayesian credible interval of the posterior predicted responses are also presented in *SI Appendix, Figs. S4 and S5*.

associated with male wolverine density, while we detected no strong association with female wolverine density (Fig. 1). We evidenced no strong temporal trend in these associations for either of the sexes ($\hat{\beta}_{1\text{ReindeerS}_F} = -0.03 [-0.09 \text{ to } 0.03]$ and $\hat{\beta}_{1\text{ReindeerS}_M} = -0.06 [-0.12 \text{ to } 0.01]$). The pattern was overall similar for the presence of semidomesticated reindeer areas in Norway, with the notable difference that female wolverine density was also

negatively associated with this covariate (Fig. 1). Here too, no strong trend over the nine-year monitoring period was evidenced for both females ($\hat{\beta}_{1\text{ReindeerN}_F} = -0.02 [-0.09 \text{ to } 0.06]$) and males ($\hat{\beta}_{1\text{ReindeerN}_M} = -0.08 [-0.16 \text{ to } 0.01]$).

The relationship between free-ranging domestic sheep density and wolverine densities was similar for both sexes, with a slight to moderate negative association across years (Fig. 1). Despite

the relatively small effect size, our analysis revealed a negative temporal trend for both sexes, indicating an increasingly negative association between the sheep covariate and wolverine density for both sexes during the study period ($\hat{\beta}_{1\text{Sheep}_F}$ and $\hat{\beta}_{1\text{Sheep}_M} = -0.04$ [-0.07 to -0.01]; Fig. 2).

Terrain ruggedness was overall positively associated with wolverine densities, particularly for females (Fig. 1). We observed no strong trend over time for the association of either of the sexes with ruggedness ($\hat{\beta}_{1\text{TRI}_F} = -0.003$ [-0.02 to 0.02] and $\hat{\beta}_{1\text{TRI}_M} = 0.02$ [-0.01 to 0.04]; Fig. 2).

The relationship between average year-round snow cover and wolverine density differed between the two sexes (Figs. 1 and 2). The positive association of female wolverine density with snow cover was less marked and only became strong toward the end of the study period ($\hat{\beta}_{1\text{Snow}_F} = 0.01$ [-0.02 to 0.05]). In contrast, male wolverine density had strong positive association with snow cover, but this relationship diminished considerably over time and became weak toward the end of the nine-year study period ($\hat{\beta}_{1\text{Snow}_M} = -0.05$ [-0.09 to -0.02]; Fig. 2).

The human settlement areas index had a strong negative association with both female and male wolverine densities throughout the monitoring years (Fig. 1), without pronounced temporal trends ($\hat{\beta}_{1\text{Settlements}_F} = -0.09$ [-0.42 to 0.25] and $\hat{\beta}_{1\text{Settlements}_M} = 0.18$ [-0.20 to 0.56]). Despite the weak trend, we observed indications of contrasting associations between this covariate and female and male wolverine densities (Fig. 1).

Results concerning model runs with a Bayesian variable selection approach to quantify the relative importance of temporal changes in the association between each spatial covariate and time are presented in *SI Appendix, Tables S6–S8*. The temporal trend in the effects of both the moose density proxy and forest percentage on female wolverine density received the most support (inclusion probability = 30.3%), followed by distance from the relict range and domestic sheep density (*SI Appendix, Tables S6–S8*). For male wolverines, temporal change in the association of density with year-round snow cover was most supported (75.5%), followed by the moose density proxy and the human settlement areas index (*SI Appendix, Tables S6–S8*). We observed no changes in the direction of the regression coefficient β estimates when comparing the estimates from OPSCR models with and without indicator variables, and the quantitative results were comparable (*SI Appendix, Tables S5–S8*).

Abundance Estimates and Density Surfaces. Our estimates of female and male wolverine abundance suggested an increasing trend over the nine-year monitoring period (*SI Appendix, Figs. S6–S11*). Estimated total abundance in the entire study area changed from 673 females (95% BCI $N_{F2014} = 605 - 748$) and 416 males (95% BCI $N_{M2014} = 365 - 472$) in the first monitoring season between December 2013 and June 2014 to 807 females (95% BCI $N_{F2022} = 741 - 877$) and 457 males (95% BCI $N_{M2022} = 424 - 494$) during the last monitoring season in December 2021–June 2022. The Scandinavian wolverine population was also estimated to be skewed toward females (F:M = 1.5 to 1.8 during the nine monitoring seasons; *SI Appendix, Fig. S10*). Comparison of the annual expected density surfaces suggested an increase in both female and male wolverine densities in the boreal forest outside the transboundary relict range between the first and last monitoring seasons (Fig. 3 and *SI Appendix, Figs. S8 and S9*).

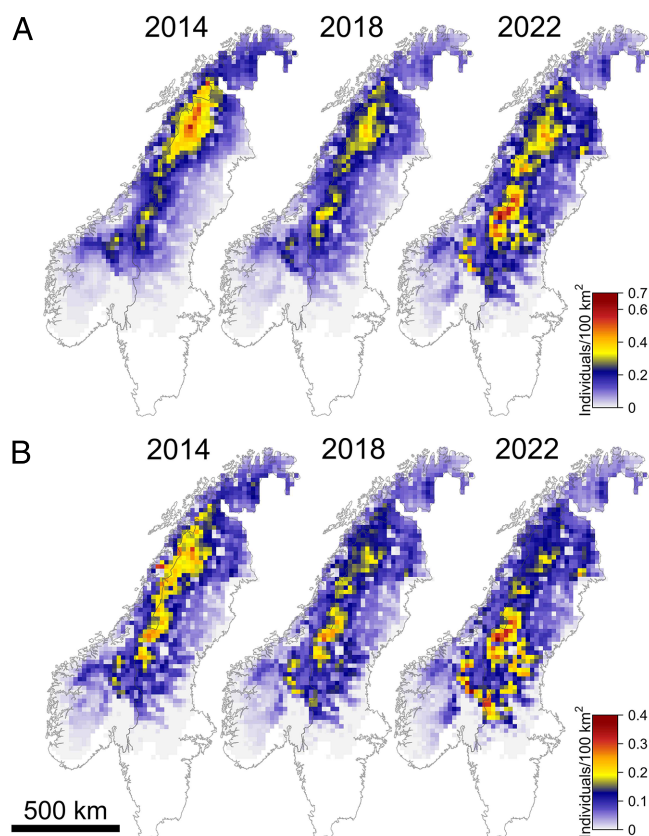


Fig. 3. The expected average density (individuals per 100 km²) of female (A) and male (B) wolverines *Gulo gulo* in the Scandinavian Peninsula for three selected monitoring seasons during our study, as a function of 10 environmental covariates. The white areas in each map represent regions that were excluded from the analysis. Annual surfaces for the entire nine-year monitoring period are presented in *SI Appendix, Fig. S8*.

Other Parameters. Sex-specific estimates of annual baseline detection probabilities during the structured p_{01} and unstructured sampling p_{02} and the associations with the detection determinants, the spatial scale parameter of the detection function σ , recruitment probability γ , and survival probability ϕ , as well as alternative scenarios of data inclusion, are presented in *SI Appendix, Figs. S10–S18*.

Discussion

A Population in Flux. Our study provides strong evidence that the spatial configuration of the Scandinavian wolverine population, as well as the relationship with several spatial determinants, have changed during the nine-year study period. We found clear evidence that the wolverine population has successfully expanded from the relict alpine range into the boreal forest. Population-level determinants of density and temporal changes in their effects have rarely been quantified at such a large spatial extent (18). We were able to detect pronounced changes despite the comparatively short monitoring period relative to the generation time, dispersal potential, and fecundity of large carnivores (50, 51). This is indicative of how rapidly the spatial configuration of the Scandinavian wolverine population has changed, but also reveals that recolonization continues today. We showed that although the shrinkage of the Scandinavian wolverine population possibly ended half a century ago (5, 26, 27), the population is still in flux and a combination of natural and anthropogenic factors

keeps shaping population density. We also found indication that sex-specific differences in wolverine ecology, such as space use and dispersal (51, 52), as well as variation in human pressure (30, 42, 53–55), have resulted in different responses of female and male wolverines to some of the environmental determinants of density and the dynamics of these effects over time.

Recovery from the Relict Range. The Scandinavian wolverine population started expanding from the relict range along the Norwegian–Swedish border (*SI Appendix, Fig. S2*) after management switched from legal persecution to protection in 1969 in Sweden and gradually during 1973–1982 in Norway (5, 26, 27, 47). Currently, wolverines have successfully recolonized many areas across their historical range, pushing the expansion front far beyond the relict range (20, 31, 46). The fact that distance from the relict range still plays an important but diminishing role in driving the density of female wolverines reflects this ongoing population expansion. Wolverines are still managed in many areas by legal harvest to control their population size and expansion (20, 31, 32, 40). On the extreme is the large carnivore management region of southwest Norway with a policy and practice of zero tolerance for wolverine reproductions in this region (34, 36, 56). As long as the wolverine is not tolerated in some areas, proximity to the relict range—as the long-term core area of reproduction—will continue playing an important role in shaping the population density and dynamics.

Moving into the Forest. The Scandinavian wolverine has long been restricted to sparsely forested alpine areas (26, 27, 48, 49), although the species inhabits the taiga further east in Russia and in North America (51, 57). In recent decades, the wolverines appeared to have begun reoccupying boreal forests in Scandinavia as well (20, 28, 29, 31, 46), and our results confirm this. Historical range maps in Scandinavia suggest that the wolverine was once present in both the alpine areas above the treeline and in the boreal forest, before the peak of their persecution in the mid-nineteenth to early twentieth centuries (26, 27, 47, 58). The relict range along the Norwegian–Swedish border consists mostly of rugged alpine areas with very low human density, often with the boreal forest nearby (48, 49, 59). Our understanding of the wolverine’s habitat selection and preference in the last half-century is therefore influenced by the relict range being the starting point of their modern expansion. However, human-caused mortality is not necessarily correlated with terrain ruggedness or human population density, and in some areas of the Scandinavian Peninsula wolverine removal (legal and illegal) occurs more commonly within or close to the relict range (32, 34, 42, 55). Such complex and confounded relationships make it difficult to determine whether Scandinavian wolverines prefer rugged alpine areas or low-elevation boreal forests.

Large-Scale Impact of Food Resources and Management. We observed contrasting responses of wolverine densities to large-scale distributions of food and prey. The positive association of the moose density proxy with wolverine density was expected, because moose carrion is an important food source for the Scandinavian wolverine in many areas, especially during winter (60–64). These are either carcasses left by sympatric large carnivores (i.e., wolves *Canis lupus* and, to a lesser extent, bears *Ursus arctos*), or are the result of natural and human-induced mortality (e.g., roadkill, hunting baits, and slaughter remains).

Nonetheless, the increasing importance of this covariate over the nine-year study period is presumably in part due to the wolverine population’s expansion into the boreal forest; wolverines rarely prey on the moose (60, 62, 65, 66) and the covariate roughly reflects forest productivity in the Scandinavia Peninsula (cell-based Pearson’s correlation coefficient r between the moose density proxy and percentage of forest was 0.64; *SI Appendix, Fig. S3*). In our OPSCR model using reversible jump Markov chain Monte Carlo (MCMC) with indicator variables, we observed that a temporal trend in the association of either of these covariates with female wolverine density was supported when the temporal trend in the effect of the other covariate was not included (*SI Appendix, Tables S6–S8*). Thus, it is possible that moose and forest covariates masked some of each other’s effects.

Free-ranging domestic sheep and their lambs are only available to wolverine in summer in Norway, with higher numbers in southwestern Norway (*SI Appendix, Fig. S2*). In this region authorities conduct intense wolverine removal operations, especially targeting females with cubs, to reduce wolverine predation on unattended domestic sheep (27, 34, 36, 40, 67, 68). Thus, the domestic sheep proxy not only represents seasonal sheep availability but also reflects the risk of human-induced mortality for wolverines (32). This could explain the increasingly negative association of this covariate with wolverine density over the years as the wolverines are pushing to establish themselves into new areas with high density of domestic sheep (Figs. 1–3).

Although we observed positive associations between the wolverine density and wild reindeer distribution range, we detected slight differences in the relationship between semidomesticated reindeer areas and wolverine density between Norway and Sweden (Fig. 1). Negative association of both female and male wolverine densities with semidomesticated reindeer areas in Norway compared to Sweden can be related to more intense lethal control of the wolverine in Norway. Wild reindeer are an important part of the wolverine’s diet in southern Norway only (60, 66), whereas semidomesticated reindeer are the most important food for the Scandinavian wolverine within reindeer herding areas (33, 39, 62, 66), which cover the majority of our study landscape in both Norway and Sweden (*SI Appendix, Fig. S2*). Thus, similar to the effect of wild reindeer availability, one would expect semidomesticated reindeer availability to be positively associated with wolverine density. However, we were not able to obtain a reliable Scandinavian-wide dataset for semidomesticated reindeer density with comparable resolution between Norway and Sweden. Instead, we used areas where semidomesticated reindeer are allowed to graze in each country throughout the year, as well as the geographic range of the wild reindeer, as proxies of reindeer availability (*SI Appendix, Fig. S2 and Table S4*). Therefore, neither of the reindeer covariates reflect the spatial and temporal variation in reindeer density or availability across the study landscape (39, 69, 70). Such information would be key for a better understanding of the drivers of wolverine recovery.

The semidomesticated reindeer covariate probably interacts with other environmental factors included in the analysis, particularly distance from the relict range, as well as with the current zonal management that aims at controlling wolverine density through harvest in high conflict areas (20, 36). Semidomesticated reindeer areas included in this study virtually match northern large carnivore management regions defined in Norway and Sweden where higher numbers of wolverine reproductions are allowed by authorities, but the level of conflict with reindeer herders is also higher (30, 33, 36, 56). Attempts have been made to quantify the role of zoning management in our

study system (20). However, modeling interactions involving multiple covariates requires analytical solutions to overcome data sparsity, especially for management zones in the south of the Scandinavian Peninsula where there have been few or no genetic detections of wolverines (*SI Appendix, Figs. S1 and S17*).

Sex-Specific Responses to Density Determinants. Our findings suggest slight differences between male and female wolverines regarding the relationships of the environmental covariates with density, as well as changes in these associations during the nine-year monitoring period (Figs. 1 and 2). Behavioral differences between female and male wolverines with respect to their environment have been documented (48, 71–74), which may also reflect their responses to landscape-level determinants of density. For example, wolverines, like many solitary large carnivores, show intrasexual territoriality and adult males maintain substantially larger home ranges that can overlap with several female home ranges (71, 75–77). Male wolverines are also more likely than females to make long-distance dispersal, while female wolverines tend to settle closer to their natal area (71, 72, 75, 78–80). In accordance, we detected five times more male wolverines making long-distance movements than females in our dataset (*SI Appendix, Table S2*). Sex-specific space use strategies and differences in recolonization ability can also help explain the diverging relationships we observed between female and male wolverine densities and year-round snow cover (Figs. 1 and 2); by moving faster into the boreal forest, male wolverine density is becoming less and less dependent on year-round snow cover. Although it has been suggested that snow is an important factor for wolverine population dynamics and distribution (74, 81–83), the importance of snow might not be as crucial as believed earlier (29).

We observed a substantial negative relationship between the human settlement areas index and both female and male wolverine densities. Several studies have shown that wolverines avoid human settlements even in areas with low risk of human-caused mortality (48, 84–86). Nevertheless, the pattern we detected could at least partially be explained by the fact that most human-dominated areas in Norway and Sweden are located along the coastline and in the south of our study landscape (*SI Appendix, Fig. S2*). In Sweden, the current management plan allows the wolverine to recolonize these areas but population expansion is restricted in Norway by intense legal harvest of the wolverine to protect free-ranging domestic sheep (27, 36, 40, 67). The southern part of the Scandinavian Peninsula is also the area the farthest from the relict range (Fig. 3) and the likely wolverine expansion front (20). Consequently, we could expect that male wolverines occur more commonly at the expansion frontline, which, in turn, may result in disproportionate anthropogenic pressures on female and male wolverines. Although the relationship between wolverine density and human settlement areas remained relatively unchanged during the study period, we observed contrasting weak trends between female and male wolverines (Fig. 1 and *SI Appendix, Table S5*). We suspect that at the beginning of the nine-year study period, more males than females had already expanded from the relict range into the boreal forest and beyond. As the population expansion continued further through the boreal forest where the covariate does not change considerably (*SI Appendix, Fig. S2*), the negative relationship between male wolverine density and human settlement areas is becoming less pronounced (Fig. 1). In contrast, because of slower recolonization, at the beginning of the study a larger part of the female population was still in

the alpine relict range initiating their expansion into the boreal forest, resulting in less pronounced negative relationships with the human settlement areas. Then, during the study period, the range expansion of females crossed the area outside of the relict range where forest changes substantially and reached the area already recolonized by males, resulting in comparable associations of distance from the relict range, forest-related covariates, and human settlement areas with female and male wolverine densities (Figs. 1 and 2).

By expanding faster across the reindeer husbandry areas and recolonizing faster than female wolverines, the sex-biased dispersal might make males more vulnerable to both legal removal and retaliatory killing compared to females (30, 33, 42, 55). We found that female survival was higher than that of males and that the population was strongly skewed toward females (*SI Appendix, Figs. S10 and S11*). There is evidence that male wolverines are more exposed to poaching than females in this population (30). Yet, the removal of female wolverines with cubs in conflict-rich areas, such as in the no-wolverine zone in southwestern Norway, is also intensive (34, 36). This was supported by the comparable negative trends in the association of female and male wolverine densities and sheep density in our results (Figs. 1 and 2). Thus, although the total mortality rate does not seem to be significantly different between sexes (46, 87), it is likely that there are differences in cause-specific mortality of wolverines between the two countries (54, 88), which might have contributed to our findings. We expect these country-level differences in the management of the wolverine in the south to result in important human-caused regional variation in wolverine densities across the Scandinavian Peninsula in the coming decades.

Future Directions. We attempted to untangle the changing impacts of historical and present-day environmental covariates on the density of the recovering Scandinavian wolverine population during the past decade. We acknowledge that the spatiotemporal trends in the association between density and environmental factors is likely to be more intricate. The already complex OPSCR model and computational challenges arising from a large spatiotemporal extent of our study precluded substantial increases in complexity in this study. Methodological advancements in hierarchical models and computational improvements could allow for a more nuanced evaluation of the nonlinearity and context dependence of the factors impacting density in space and time. Furthermore, future adjustments could more comprehensively account for fully and partially latent spatiotemporal variation in search effort associated with wolverine DNA sampling (56, 89, 90).

Reliable estimates of current population density and its determinants can help establish baselines for forecasting the population status under different scenarios. We stress that human killing (legal and illegal) is probably the main driving force shaping our study system (22, 42, 54, 55, 91, 92), which can obscure ecological processes and wolverine responses to the changing environment. However, it is challenging to quantify to which extent removals affect wolverine density. First, there is insufficient spatiotemporal information concerning illegal events that are by nature cryptic (42, 55, 91, 93). Second, quantifying legal mortality risk does not only require knowing mortality events and their location but also the density of individuals at risk. Density itself being the response variable of our analysis, it was not possible to include such a covariate in this study. A comprehensive understanding of the effect of legal removal on

wolverine density would require the explicit estimation of its effect on vital rates (88) and the movement of individuals (54). Instead, we focused on capturing large-scale effect of differential management between Norway and Sweden using domestic livestock and other human-related covariates (*SI Appendix, Table S4*), because we were interested in the spatiotemporal outcome of population dynamics without attempting to disentangle the dynamics of the constituent vital rates. Further insight into how interannual movements and vital rates interact with population density to shape the Scandinavian wolverine population can help inform management and advance our understanding of the determinants and dynamics of wolverine density. Future research on spatiotemporal determinants of wolverine population density would also benefit from incorporating better spatial and temporal information on food availability throughout the population extent, and considering intra- and interspecific interactions in addition to the abiotic and biotic covariates we considered. Particularly, interactions with co-occurring large carnivores (i.e., wolves, lynx *Lynx lynx*, and bears) over resources are known drivers of wolverine resource partitioning in Scandinavia (59–62, 94) and is therefore an important area of research in the future.

Conclusions

Large carnivores have been long associated with pristine wilderness, which is juxtaposed with the near absence of impact-free areas in most modern-day landscapes (5, 95, 96). The recovery of the Scandinavian wolverine population demonstrates that even such an elusive and quintessential symbol of wilderness can live and recover in an increasingly human-altered environment (5, 6, 97, 98). Although the Scandinavian Peninsula remains less impacted by human activities than other parts of Europe, the wolverine population expansion poses challenges for society and managers. The wolverine population has recolonized areas with free-ranging domestic sheep and semidomesticated reindeer husbandry where wolverines have been absent for decades (20, 27, 29, 36). Yet, by expanding into areas with lower potential for conflict, such as regions south of the reindeer herding areas in Sweden and into the management zone in southeastern Norway where there is little sheep husbandry (*SI Appendix, Fig. S2*), continued recolonization of the Scandinavian wolverine range may not be accompanied by a proportional increase in conflict. Although we quantified changes in the relationship between wolverine density and large-scale environmental determinants at the population level, we do not see the full picture while the recolonization is still ongoing. Because wolverine recovery has occurred in a heterogeneous landscape shared by two countries with different national and regional management goals, legislation, and obligations (20, 26, 37, 46), a diverse set of management strategies to increase tolerance toward the wolverine is essential for human-wolverine coexistence. Our study underlines the importance of the collection of long-term and coordinated monitoring data and adaptive management of recovering transboundary wildlife populations.

Materials and Methods

Noninvasive Genetic Monitoring. We used noninvasive genetic sampling (NGS) data of the wolverine collected between the winters 2013/2014 and 2021/2022 in Norway and Sweden from the Scandinavian large carnivore

monitoring database Rovbase 3.0 (www.rovbase.no and www.rovbase.se). This is a comprehensive multinational database containing data collected in a structured fashion by authorities, but also opportunistically collected records of large carnivores by different means over the past two decades, such as noninvasive DNA samples, dead recoveries, public observations, and livestock predation (35, 46, 56, 99). We used wolverine NGS data with unambiguous coordinates, collection date, and individual and sex identification (i.e., genotypes; *SI Appendix, Fig. S1*) to construct spatially referenced individual detection histories for nine consecutive monitoring seasons (16, 17, 25).

Collection of noninvasive DNA samples and protocols to process the samples in DNA labs are described in detail elsewhere (27, 35, 56, 99–102). In brief, field staff of management authorities in Norway (The Norwegian Nature Inspectorate) and Sweden (County Administrative Boards) annually conduct extensive searches for carnivore signs and DNA samples across both countries at the level of carnivore management regions in Norway and counties in Sweden. Investigators search for putative wolverine DNA material (e.g., scat, hair, secretion) on snow and record their search effort with either handheld Global Positioning System (GPS) or, more recently, smartphones using a custom mobile application. These data contain detailed records of the spatial configuration and intensity of effort during the structured NGS. In addition to these structured searches, authorities and volunteer hunters and other members of the public also provide opportunistically collected DNA samples for analysis, but no direct measure of their search effort exists. Collected samples are sent to specialized labs for DNA extraction and genotyping to identify species, individuals, and sex using multiple nuclear DNA markers (101, 102). The protocol has evolved through the sampling years and was increasingly automated to ensure high-quality DNA data by using as many wolverine-specific markers as possible, including both single nucleotide polymorphism and microsatellite markers, and controlling for genotyping errors using standard procedures (27, 100–102). The genotypes from each sample are then used to identify wolverine individuals and their sex, which can be regarded as a genetic detection of that individual.

In this study, we used the NGS data collected between December 1 and June 30 each year (i.e., December 2013–June 2014 to December 2021–June 2022; *SI Appendix, Table S1*). We discarded samples that were suspected to be from wolverine cubs (i.e., individuals born during the sampling season) based on the matching genotypes from scat samples collected during the monitoring of natal dens in spring, and the fact that the cub-of-the-year litters were mostly in their dens during the NGS (34, 35, 99, 103). However, we cannot exclude the possibility of inclusion of subadult wolverines in our dataset. Therefore, all individuals in our dataset were at least 10 mo old—i.e., born in February and detected the earliest in December. We further discarded a total of 67 female and 394 male genetic detections belonging to 54 female and 241 male individuals from the nine-year dataset, which made long-distance movements of more than 60 km during each monitoring season (*SI Appendix, Table S2*). We assumed these incidents were unlikely to be movements within the home range but rather dispersal events (71, 75, 78); thus, their inclusion could induce an unmodeled source of individual heterogeneity in our study (20, 104, 105). This step led to a slight reduction in the number of detections, but not in the number of detected individuals.

We defined the surveyed area as the entire contiguous land area in Norway and Sweden extending 100 km beyond the outermost wolverine genetic detections during the nine-year sampling period for both sexes combined (58° 22' to 70° 46' N, 7° 18' to 31° 55' E; *SI Appendix, Fig. S1*). One exception was Norrbotten County in northern Sweden, which was only comprehensively searched for wolverine DNA during three out of nine sampling years (2016/2017–2018/2019). Therefore, we treated Norrbotten differently across the sampling years (*SI Appendix, Figs. S1 and S12–S15*). We repeated the analysis by considering alternative scenarios of data inclusion to test whether our results were affected by this step, which was not supported (*SI Appendix, Figs. S17 and S18*). We then defined the detector grid for the OPSCR analysis by superimposing 10 × 10 km grid cells over the surveyed area each year. To allow detection of individuals with home range or activity centers located outside the detector grid (106), we placed a 60-km buffer around the 606,156-km² surveyed area to define the habitat, which included parts of the neighboring Finland and Russia in the north (*SI Appendix, Fig. S1*). We chose

this buffer based on the average home-range radius of adult Scandinavian wolverines (76, 107). This amounts to a buffer width more than five times the average estimated spatial scale parameter (σ , which accommodates individual variation in detection; *SI Appendix, Table S3*) for male wolverines in this population (20, 46, 87).

Open-Population Spatial Capture-Recapture Analysis. Spatial capture-recapture (SCR) is an extension of capture-recapture models (16–18, 108, 109). Conventional capture-recapture models use the information contained in a detection history of individuals from the target population (i.e., detections and nondetections) to estimate abundance and other ecological parameters, while accounting for imperfect detection—i.e., the fact that not all individuals from the target population are detected during sampling (16, 110). SCR models include an additional spatial component, which exploits the spatial information contained in the detections. From the spatial pattern of individual detections and nondetections, SCR models estimate the relationship between individual detection probability and the distance from the center of their home range (16, 109). SCR models estimate the latent activity centers of all individuals potentially available for detection, including those alive individuals that were never detected during sampling. Thus, SCR provides a spatially explicit estimate of abundance in the study area—i.e., density.

SCR models can be used to estimate density, the effect of spatial and individual covariates on detection probability, and the effect of spatial covariates on density for a given point in time, with the assumption that the target population is demographically closed during sampling—i.e., no births, mortality, immigration, or emigration (16). When data are collected over multiple years and the interest lies in understanding population changes, OPSCR models can be used to simultaneously estimate density and vital rates, such as recruitment and survival (43–45, 111). Thus, OPSCR models provide not only estimates of annual density and its determinants but also estimates of the demographic parameters needed to predict changes in population dynamics and forecast the impact of management actions (46). OPSCR models can also quantify temporal changes in the effect of spatial determinants of density, although such models are not widely used yet (18). In this study, we developed an OPSCR model for estimating temporal patterns in large-scale determinants of wolverine density in the Scandinavian Peninsula. We fitted separate OPSCR models to the nine-year wolverine data time series for each sex, because of female–male differences in morphology, physiology, behavior, and ecology (51, 52).

Our OPSCR model was composed of three submodels for density, demography, and detection (*SI Appendix, Table S3*). Details about each of the submodels are provided in *SI Appendix*. Considering the body of literature about the determinants of wolverine distribution, habitat selection, and density in Scandinavia and globally (20, 51), we selected 10 spatial covariates that may have influenced population-level density of wolverines in the Scandinavian Peninsula (*SI Appendix, Fig. S2 and Table S4*): 1) Distance from the relict range as a measure of recolonization history; 2) Forest percentage to describe land use, habitat productivity, food availability, and shelter; 3) Moose harvest density as a proxy of forest productivity and ungulate carrion availability to describe food availability; 4) Proportion of wild reindeer geographic distribution range as a measure of prey availability; Proportion of semidomesticated reindeer herding areas and districts in 5) Sweden and 6) Norway as proxies of ungulate prey availability, risk of human-caused mortality, and large-scale management practices in each country; 7) Density of free-ranging domestic sheep and their lambs as a proxy for alternative prey source, management pressure, and risk of human-caused mortality; 8) Terrain ruggedness as a measure of topographic heterogeneity, human disturbances, and refuge availability; 9) Year-round snow cover to describe climate suitability and a proxy of vulnerability of prey to wolverine predation; and 10) Human settlement areas, an index defined as the percentage of ground surface covered by human settlements, to represent human residential areas and associated disturbances. Details on how the spatial covariates were obtained and prepared for the OPSCR analysis are provided in *SI Appendix, Table S4*. A single layer of each covariate was created to model the association with wolverine density over the nine years (*SI Appendix, Fig. S2*). We transformed all covariate raster layers from their original projections to

the Universal Transverse Mercator (zone 33N) and locally interpolated the raster values using the “bilinear” method of the `resample` function of the R package `terra` (112) to match the 20×20 km habitat grid used in the OPSCR analysis (*SI Appendix, Fig. S2*). The ecological process involved in the density submodel can be compared to the second-order of habitat selection—i.e., placement of home range (113). We standardized all continuous covariates prior to their inclusion in the analysis to have a mean of zero and one unit SD.

Model Fitting. We used a Bayesian framework to fit our OPSCR models to the data (25, 46, 114). All parameters were given noninformative priors in the form of Uniform distributions (*SI Appendix, Table S3*). We fitted separate OPSCR models for female and male wolverines using MCMC with NIMBLE version 1.0.1 (115, 116) and nimbleSCR version 0.2.1 (117) in R 4.3.1 (118). We performed model fitting on the Norwegian University of Life Sciences’ high performance computing grid. We ran five chains of (a) females: 144,500 MCMC iterations with a burn-in period of 44,500 iterations; and (b) males: 150,000 MCMC iterations with a burn-in period of 50,000 iterations. We thinned the chains keeping every fifth sample, resulting in a total of 100,000 MCMC samples from the posterior distribution for each sex, from which all estimates were derived. For creating density surfaces (see below), we retained every tenth iteration only for estimates of activity center locations to reduce memory usage, resulting in a total of 50,000 MCMC iterations. We considered MCMC chains from each model run as converged when the Gelman–Rubin diagnostics was less than or equal to 1.1 for all parameters (119) and by visually inspecting the mixing of MCMC chains using trace plots. We considered a minimum effective sample size of 100 to ensure high posterior autocorrelation and stable parameter estimates. We used the mean and associated 95% BCI to summarize posterior distributions of abundance for each sex. For the rest of the parameters, we report median and 90% BCI, because they have more stable posterior distributions than 95% BCI. We considered covariate effects to have a strong support if the 90% BCI did not overlap zero.

In addition, we explored the relative importance of temporal effect of each determinant of wolverine density (i.e., changes in regression coefficients over time) by incorporating a Bayesian variable selection approach in NIMBLE using reversible jump MCMC with indicator variables (20, 120–122). More information about this step is provided in *SI Appendix, Table S3*. We ran six chains of (a) 425,000 MCMC iterations for females; and (b) 500,000 MCMC iterations for males. We included a burn-in period of 300,000 iterations for each sex. Because of computation challenges during the post processing of data, we further thinned chains by a factor of 10, resulting in a total of 150,000 and 240,000 MCMC samples from the posterior distribution for females and males, respectively. Unless specified otherwise, we report all results based on the OPSCR model without reversible jump MCMC and refer the reader to *SI Appendix* for results concerning additional model runs with indicator variables, description of the OPSCR models, list of priors, data, and R code (*SI Appendix, Tables S3–S8*).

To obtain an estimate of abundance for a given habitat cell, we summed the number of predicted individual activity center locations of live individuals that fell within that cell for each iteration of the MCMC chains and generated a posterior distribution of abundance for that cell (i.e., realized density). We constructed two types of annual sex-specific density surfaces (*SI Appendix, Figs. S6–S9*): (a) maps of realized density based on the estimated locations of activity centers each year; and (b) maps of expected density based on the estimated intensity of the density point process and the estimated wolverine abundance each year. In other words, realized density surfaces show density based on the average model estimated activity center locations of individuals, while expected density surfaces are density predicted based on the regression model underlying the intensity surface. Annual realized density surfaces were constructed by summing the number of alive individuals with their activity center in each habitat cell s at time t for each iteration of the MCMC, before calculating the mean and SD across iterations in each cell. The expected density in habitat cell s and time t was calculated as $N_t \lambda_{s,t} / \sum_{s=1}^S \lambda_{s,t}$ for each iteration of the MCMC, where λ is the intensity function at a given habitat cell, and N size (*SI Appendix*). We then derived the mean and SD of the expected density surface across iterations in each cell. Data and model code for performing the OPSCR analysis described here are available in ref. 123.

Data, Materials, and Software Availability. The .RData files with input data for OPSCR model fitting have been deposited in Github: <https://github.com/eMoqanaki/WolverineDensityOPSCR> (123).

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