

Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia

ANDRÉS ORDIZ,^{1,†} CYRIL MILLERET,² JONAS KINDBERG,³ JOHAN MÅNSSON,¹ PETTER WABAKKEN,²
JON E. SWENSON,^{4,5} AND HÅKAN SAND¹

¹Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-730 91 Riddarhyttan, Sweden

²Faculty of Applied Ecology and Agricultural Sciences, Hedmark University College, Evenstad, NO-2480 Koppang, Norway

³Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden

⁴Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Postbox 5003, NO-1432 Ås, Norway

⁵Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

Citation: Ordiz, A., C. Milleret, J. Kindberg, J. Månsson, P. Wabakken, J. E. Swenson, and H. Sand. 2015. Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia. *Ecosphere* 6(12):284. <http://dx.doi.org/10.1890/ES15-00243.1>

Abstract. Interspecific competition can influence the distribution and abundance of species and the structure of ecological communities and entire ecosystems. Interactions between apex predators can have cascading effects through the entire natural community, which supports broadening the scope of conservation from single species to a much wider ecosystem perspective. However, competition between wild large carnivores can hardly be measured experimentally. In this study, we analyzed the expansion of the Scandinavian wolf (*Canis lupus*) population during its recovery from the early 1990s. We took into account wolf-, habitat-, human- and brown bear (*Ursus arctos*)-related factors, because wolf expansion occurred within an area partially sympatric with bears. Wolf pair establishment was positively related to previous wolf presence and was negatively related to road density, distance to other wolf territories, and bear density. These findings suggest that both human-related habitat modification and interspecific competition have been influential factors modulating the expansion of the wolf population. Interactions between large carnivores have the potential to affect overall biodiversity. Therefore, conservation-oriented management of such species should consider interspecific interactions, rather than focusing only on target populations of single species. Long-term monitoring data across large areas should also help quantify and predict the influence of biotic interactions on species assemblages and distributions elsewhere. This is important because interactive processes can be essential in the regulation, stability, and resilience of ecological communities.

Key words: Brown bears; *Canis lupus*; conditional-logistic regression; habitat selection; human disturbance; interspecific competition; population expansion; Scandinavia; *Ursus arctos*; wolves.

Received 23 April 2015; **revised** 10 August 2015; **accepted** 17 August 2015; **published** 21 December 2015. Corresponding Editor: D. P. C. Peters.

Copyright: © 2015 Ordiz et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. <http://creativecommons.org/licenses/by/3.0/>

† **E-mail:** andres.ordiz@gmail.com

INTRODUCTION

Interspecific competition holds a central place in ecological and evolutionary theory and has

implications for conservation and management. Competition influences the distribution and abundance of species (Wisiz et al. 2013), including carnivores (Creel et al. 2001), and it plays an

important role in the structure of ecological communities (Schoener 1983) and entire ecosystems, marine and terrestrial alike (Estes et al. 2011, Ripple et al. 2014).

Competition between carnivores can reduce the population size of one of the competitors and affect lower trophic levels (Caro and Stoner 2003). It can lead to spatial avoidance and shifts in habitat use and, in cases of exploitative competition, when predators share the same food resources, kleptoparasitism can force affected species to additional hunting (Elbroch et al. 2015), with its inherent risks and costs. Ultimately, carnivores can also kill each other, sometimes limiting population sizes (Palomares and Caro 1999, Caro and Stoner 2003, Donadio and Buskirk 2006).

Although competition may cause extirpation, it often results in resource partitioning. The outcome may change with environmental conditions and human activities, which can have an overwhelming influence on the population dynamics of the interacting species, their distribution, and the effects of competition (Apps et al. 2006). This may be the case for large carnivores inhabiting human-dominated landscapes, given the long history of human persecution of the carnivores and their avoidance of people (Ordiz et al. 2011, 2013, 2014).

Competition between wild large carnivores can hardly be measured experimentally. However, it may be evaluated by comparing the spatial distribution of each species, while controlling for landscape-related variables (Apps et al. 2006). In a gradient of spatial levels, populations range geographically in a landscape, animals establish home ranges, choose habitat patches, and, finally, select particular sites, such as dens or daybeds (Johnson 1980). Competition may be influential at each level if the presence of a competitor affects where to settle down and/or limits resource use. This is particularly interesting in situations where the recovery of a large carnivore occurs in an area already inhabited by another carnivore and both species have some common requirements of habitat or resources, which can potentially lead to spatial and/or exploitative competition.

Individual interactions have been documented between gray wolves (*Canis lupus*) and brown bears (*Ursus arctos*). Brown bears are omnivo-

rous, but both species prey on ungulates and using the same food resources can lead to exploitative competition. Bears often kleptoparasitize wolf kills in North America (Ballard et al. 2003, Smith et al. 2003) and in Scandinavia (e.g., Milleret 2011). However, wolves can prevail at carcasses and simultaneous scavenging by both species also has been reported (Smith et al. 2003, Lewis and Lafferty 2014). Wolves and bears can also kill each other (Ballard et al. 2003, Gunther and Smith 2004). Therefore, the outcome of individual interactions between these species includes all of the above-mentioned forms of interspecific competition between carnivores. Nevertheless, beyond individual interactions, we lack knowledge about the effects of wolf-bear competition at the population level for both species (Ballard et al. 2003).

Interactions are most relevant if competition reduces the chances that an area is used for breeding (Tannerfeldt et al. 2002). Some individual wolf-bear encounters have been described in this regard, including bears passing by wolf rendezvous sites and a few cases of bear cubs presumably killed by wolves (Ballard et al. 2003, Gunther and Smith 2004). However, the potential effects of interspecific, intraguild competition between bears and wolves on their population recovery and expansion process have not been studied.

In Scandinavia (Sweden and Norway), the recent and ongoing recovery of the wolf population in an area partially sympatric with brown bears and the long-term monitoring of both species offer the opportunity to analyze the spatial relation between these two apex predators, taking also into account intraspecific-, habitat-, and human-related factors. Wolves and bears once occupied most of the Northern Hemisphere, but for as many large mammals they were largely eradicated during the last two centuries due to human persecution (e.g., Morrison et al. 2007). Scandinavia was no exception. Wolves were functionally extinct in the 1960s, but wolf recovery accelerated during the 1990s (Wabakken et al. 2001), with ~11 packs in 2001 (Vilà et al. 2003), 31 packs in 2010 (Liberg et al. 2012), and 43 packs (~400 wolves) in 2014 (Svensson et al. 2014). Regarding brown bears, as few as ~130 were left in Sweden by 1930 (Swenson et al. 1995), but legislation changed

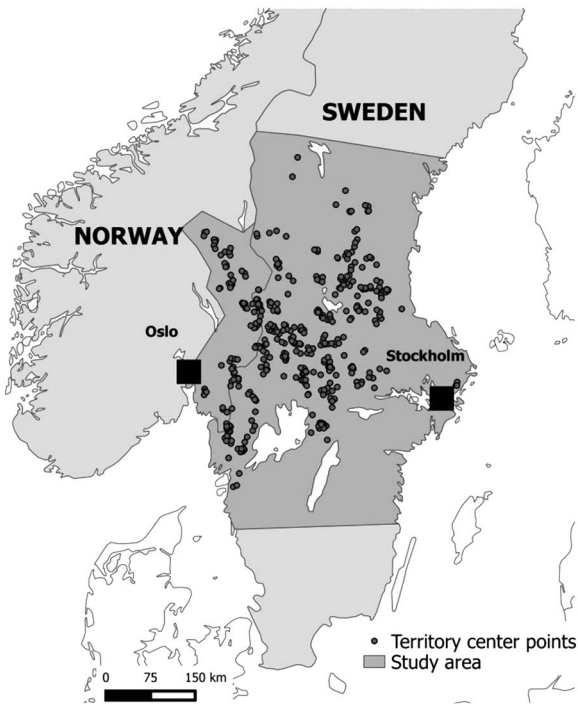


Fig. 1. Study area in south-central Scandinavia (dark gray), showing the center points of all wolf pairs detected between 1990 and 2012.

and the population increased steadily, reaching ~1000 bears in the 1990s (Zedrosser et al. 2001) and ~3,300 by 2008 (Kindberg et al. 2011). Presently most wolves and bears are in Sweden; few inhabit Norway.

We used data on the annual locations of wolf pairs to analyze the factors involved in the expansion of the wolf population in Scandinavia during 1990–2012. Wolf packs originate when a male and female wolf form a pair and reproduce (Rothman and Mech 1979). Packs are the functional, reproductive unit of wolf populations (Mech and Boitani 2003). Scent-marking pairs of wolves establish territories before they breed (Wabakken et al. 2001). Therefore, we used wolf pair establishment as a measure of survival and reproductive performance and linked it to a particular behavior, i.e., home-range establishment. This link between habitat selection and fitness is important, because it allowed us to study wolf habitat selection in terms of breeding performance (Gaillard et al. 2010), i.e., we analyzed habitat selection by wolves during the expansion of the Scandinavian wolf population.

Human factors continue to be a major limitation of large carnivore distribution and habitat use in Scandinavia (Karlsson et al. [2007] for wolves, Ordiz et al. [2011] for bears, May et al. [2008] for the whole large carnivore guild) and elsewhere (Woodroffe et al. 2005, Ripple et al. 2014). Therefore, we predicted a negative effect of human-related variables on wolf establishment. We also predicted that wolf pairs would select areas with lower density of the partially sympatric brown bear when establishing territories, and that previous wolf presence and prey abundance would be positively correlated with the functional selection of territories (Fritts and Mech 1981).

MATERIAL AND METHODS

Study area

Resident wolves currently inhabit over ~100,000 km² in south-central Scandinavia (59–62° N, 11–19° E; Liberg et al. 2012; Fig. 1). The area is mainly an intensively managed boreal coniferous forest of primarily Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. Bogs and lakes are common, and agricultural land occurs mostly in the southwestern, eastern, and southern parts. Snow covers the ground from ~December to ~March. In the area where bears occur within the wolf range (Fig. 2), independent estimates of bear density yielded similar values in the 1990s and 2000s; up to ~30 bears/1000 km² (Solberg et al. 2006). Moose (*Alces alces*) is the staple prey of wolves in Scandinavia (>95% of the biomass of wolf diet; Sand et al. 2005, 2008), where one of the world's largest and most productive moose populations thrives, with a winter population of ~500,000 moose and densities reaching 5–6 moose/km² (Lavsund et al. 2003). Human density is generally low within Scandinavian wolf range, with <1 person/km² over large areas (Wabakken et al. 2001). The density of primary roads within wolf range is $0.2 \pm 0.02/\text{km}^2$, and gravel road density is on average 4.6 times higher (Zimmermann et al. 2014).

Study period and wolf-related variables

We defined the start of our study period as 1990, when the arrival of an immigrant coincided with a sudden increase in the growth of the

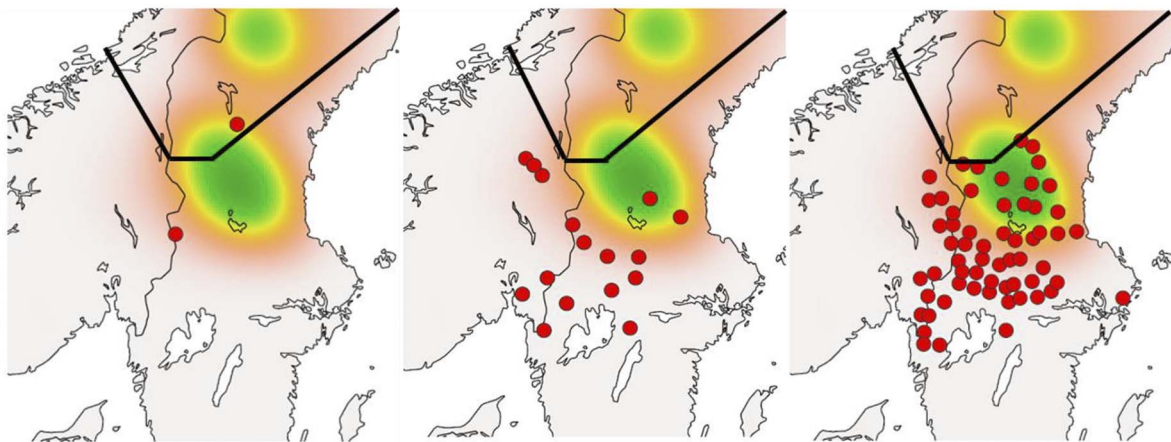


Fig. 2. Location of wolf pairs (red dots) and brown bear density (green color shows the densest bear areas) in south-central Scandinavia, at the beginning (1990, left), middle (2000, central) and towards the end of the study period (2010, right). The black line shows the southern edge of the reindeer husbandry area in Scandinavia.

Scandinavian wolf population (Vilà et al. 2003). Annual censuses were performed every winter by a combination of snow-tracking, genetic pedigrees based on DNA analyses, and radio-tracking methods (Wabakken et al. 2001, Liberg et al. 2005, Svensson et al. 2014). Identifying reproductive territories and updating the pedigree annually were major goals of the monitoring and research (Liberg et al. 2012), thus the genetic identification of new wolf territories and new established wolf pairs received special attention.

When a new territorial pair has been identified by snow-tracking, its identity was confirmed by genetic analyses of scats and estrous blood (Liberg et al. 2005, 2012, Bensch et al. 2006). Beyond mere presence-absence, genetic identification of new wolf pairs allowed us to monitor the rate at which pairs established territories. Wolf packs are territorial and usually occupy a specific area for a long time (Mech and Boitani 2003), with high interannual stability in space use (Mattisson et al. 2013). Therefore, the process of territory selection is especially interesting, because overall quality of the habitat within the territory has a great influence on individual fitness (Gaillard et al. 2010). To analyze the selection of wolf territories from this perspective, we used the first year when each new wolf pair was detected by the winter monitoring program.

Spatial locations of pairs were collected by snow-tracking and when animals were radio-collared for a variety of research and manage-

ment purposes (Sand et al. 2005, Wabakken et al. 2007, Mattisson et al. 2013; see Liberg et al. [2012] for very detailed information on the monitoring protocol in Sweden and Norway). We used the centroid of all available locations for a specific pair-winter as the center of its territory, because the accuracy of spatial locations varied among pairs. We applied a 1000 km² buffer (average wolf home range size; Mattisson et al. 2013) around the centroid to define the territory occupied by a wolf pair.

We used the number of winters that wolf territories were identified in a specific area as an estimate of wolf “historical presence” during the study period. We calculated average longitude and latitude coordinates annually for all wolf territories, and measured the distance from the centroid of new wolf pairs to previously existing wolf territories. We used the number of neighboring territories’ centroids within a 40-km radius from an existing territory centroid as a measure of local density (Mattisson et al. 2013). Table 1 summarizes all the parameters we used in the analyses.

Prey-, human- and landscape-related variables within the buffer around wolf territories

Prey density: We obtained moose harvest density (number of moose harvested/km²) at the municipality and management unit (“älgförvaltningsområde”) in Sweden and Norway. Harvest density is a robust, but slightly

Table 1. Summary of parameters used to analyze wolf pair establishment in Scandinavia in 1990–2012 (details in *Methods*).

Parameter, by group	Description	Source
Wolf		Wabakken et al. 2001, Liberg et al. 2012, Mattisson et al. 2013, Svensson et al. 2014
Territory center	Centroid location of all available locations for every specific wolf pair and winter	
Territory size	Buffer of 1000 km ² around the centroid	
Historical presence	No. winters with identified wolf territories (pairs or packs) in a given area	
Local density	No. neighboring wolf territories' centroids in a 40-km radius around a given territory	
Bear		
Bear density	Kernel density estimator based on records of shot bears	Scandinavian brown bear project, <i>unpublished data</i>
Human and landscape, with all layers converted to 200 × 200 m. grid cells		
Main road density	km of main roads per km ²	1:100 000 Lantmäteriet, Sweden; N50 kartdata, Staten-skartverk, Norway
Secondary road density	km of gravel roads per km ²	1:100 000 Lantmäteriet, Sweden; N50 kartdata, Staten-skartverk, Norway
Human density	No. inhabitants per km ²	www.scb.se, Sweden; www.ssb.no, Norway
Remoteness and accessibility	Combination of building and road densities per km ²	C. Milleret et al., <i>unpublished manuscript</i>
Altitude	Altitude in meters above sea level	DEM 25 × 25 m; Geographical Data Sweden, Lantmäteriet; Norge digital, Statens kartverk, Norway
Open land	Percentage of open land cover	Mattison et al. 2013; Swedish Corine land cover map Lantmäteriet, Sweden, 25 × 25 m merged with Northern Research Institute's vegetation map, Norway, 30 × 30 m into a 25 × 25-m raster
Prey		
Moose density	Annual harvest density at municipality/management unit	www.viltadata.se, Sweden; www.ssb.no, Norway

delayed estimate of local variation in moose density. The temporal variation in harvest density was better explained by moose density in year $t - 1$ than in year t or year $t - 2$ (Ueno et al. 2014), so we used harvest density with a one-year time lag (C. Milleret, *unpublished manuscript*). Moose harvest data was unavailable locally in some years before 1998. Thus, we used average moose harvest density in 1998–2000 as a proxy for the 1990–1998 period, which was justified, because moose density was fairly stable within the Scandinavian wolf range during the 1990s (e.g., see Fig. 3 in Lavsund et al. 2003).

Human activities and landscape-related variables: We used the density of both main and gravel roads (km/km²) as proxies of human disturbance (Ordiz et al. 2014, Zimmermann et

al. 2014); human density (inhabitants/km²) at the municipality level, and also an index of remoteness and accessibility of the landscape, based on combined building and road densities (C. Milleret, *unpublished manuscript*). We also considered altitude (m above sea level), and amount of open, agricultural land cover, which is strongly avoided by wolves (Karlsson et al. 2007).

Brown bear density within the wolf distribution range

Confirmed bear mortality has been shown to be a good proxy of bear distribution and density (Swenson et al. 1998, Kindberg et al. 2009). We used brown bear mortality records in Scandinavia in 1990–2012 ($n = 3,083$ bears), with legal hunting accounting for 88% of them, to construct

a kernel density estimator (Worton 1989) with the “href” procedure in the R package *adehabitatHR* (Calenge 2006). This estimator yielded a relative probability of finding a dead bear in a given pixel. We created an index of bear density between 0 and 1 by rescaling the values from the kernel estimator across the study area, dividing each obtained value by the maximum observed.

Case-control design

One of the main assumptions of habitat selection studies is that the area defined as available should be entirely available to all animals (Manly et al. 2002). Wolves are a highly mobile species, with a documented strong capacity for long-distance dispersion (Wabakken et al. 2007). However, population management limits the geographical range of the Scandinavian wolf population, i.e., its first-order habitat selection (Johnson 1980), to south-central Scandinavia (Liberg et al. 2012). Therefore, our definition of available space did not include areas where this management prevented wolf establishment. Wolves were killed when they settled within the reindeer husbandry area that covers roughly the northern half of Sweden and Norway, and in Norway wolves establishing outside a specified area along the Swedish border were also killed (Fig. 1). In addition, the area available for spatial expansion of the wolf distribution changed annually, because an area occupied by a wolf pair is, by definition, not available for a new pair. Therefore, we used a longitudinal matched case-control design (Craiu et al. 2004, Fortin et al. 2005). We matched available, random sites at winter t to the actually selected area of newly formed pairs at winter $t + 1$, with a 10:1 ratio for paired randomly selected sites (Thurfjell et al. 2014, Zimmermann et al. 2014).

Definition of random sites

Preliminary analyses showed that the establishment of wolf territories within our study area did not occur randomly, but in close vicinity of existing territories. Due to this “quasi-philopatric” pair establishment pattern, we constrained the creation of available and random territories to the observed distribution of distances from a newly established pair to the closest existing wolf territory. Because a new pair cannot establish within the same area of an existing one, we

prevented random sites from occurring within 15 km (distance from center territory points), which corresponded to a 47% overlap. In fact, wolf territories often overlap, with variable buffer zones among study areas (Mech 1994, Mech et al. 1998, Mech and Boitani 2003). It is also unlikely that the center point of a new wolf pair is in a heavily human-dominated area, thus we hindered random sites from falling in human-dominated areas larger than 10 km² (~0.01% of a wolf territory home-range size).

Statistical analyses

We used conditional logistic regression to analyze wolf pair establishment in 1990–2012, contrasting the actual sites where wolves established (1) with random territories (0). We followed a step-selection function procedure with the observed location of a pair as the actual step and 10 random locations as a set of random steps (Fortin et al. 2005, Thurfjell et al. 2014). The 10 random locations and the observed pair location are a “stratum” (Fortin et al. 2005). We used a generalized estimating equation (GEE), including year (winter) as a cluster term of the *coxph*-command (R package *survival*; Therneau 2014) to obtain robust standard errors among different years (Fortin et al. 2005).

We performed model selection based on corrected Akaike’s information criterion (AIC_c) (Burnham and Anderson 2002). We first inspected correlations between variables, with a threshold set at 0.6 (Pearson r coefficient) to avoid inclusion of correlated parameters. Thus, we excluded human density, the index of remoteness and accessibility, elevation, and agricultural land cover from the model selection, due to high correlation with main and/or secondary road densities (r scores > 0.6). We built simple models, including single variables and their quadratic forms, which would reflect a nonlinear relation with the response variable. If the model with the quadratic form had a lower AIC_c (Δ AIC_c ≤ 2), we retained the quadratic form of the variable in the model selection; otherwise we retained the linear form of the variable. We standardized all continuous covariates to 1 SD to facilitate the interpretation and comparison of the relative strength of parameter estimates (Schielzeth 2010, Grueber et al. 2011). All combinations of variables were biologically plausible. There-

Table 2. Multimodel inference based on conditional logistic regression of wolf pair establishment in Scandinavia, 1990–2012. Best models ($\Delta AIC_c < 2$) of all combinations of possible models are ranked in terms of AIC_c and AIC_c weight. The null model is also presented for comparison. Spearman ranks correlation coefficients (r_s) of actually used sites by wolf pairs and random available sites are presented as an index of model robustness; $r_s > 0.6$ indicates robust models.

Variables	df	logLik	AIC_c	ΔAIC_c	AIC_weight	r_s controlled [95%CI]	r_s observed [95%CI]
1/3/4/5/6/7/8	7	-302.27	618.61	0	0.26	0.06 [-0.58;0.69]	0.67 [0.37;0.91]
1/3/4/5/6/7/8/9/10/11	10	-299.32	618.78	0.17	0.24	0.04 [-0.70;0.69]	0.71 [0.47;0.92]
1/3/4/5/6/7/8/9	8	-301.60	619.30	0.69	0.19	0.05 [-0.62;0.65]	0.68 [0.38;0.91]
3/4/5/6/7/8	6	-303.64	619.33	0.72	0.18	0.05 [-0.65;0.64]	0.69 [0.38;0.89]
1/3/4/5/6/7/8/10/11	9	-300.94	620.00	1.39	0.13	0.04 [-0.73;0.76]	0.70 [0.39;0.93]
Null	1	-338.10	676.20	57.6

Note: Variables: Brown bear density = 1; density of wolves = 3, wolf historical presence 1990–2012 = 4; quadratic effect of wolf historical presence = 5; distance to other wolf territory = 6; main road density = 7; quadratic effect of main road density = 8; moose density = 9; secondary road density = 10; quadratic effect of secondary road density = 11.

fore, we computed all combinations of possible models, without interaction terms, and performed model averaging with shrinkage of parameters of the models that had $\Delta AIC_c \leq 2$ (Burnham and Anderson 2002), using the MuMin R package (Barton 2009).

We used 10-fold cross-validation to evaluate the robustness of best models (Boyce et al. 2002). We built a conditional logistic regression using 90% of randomly selected strata. We then used this conditional logistic regression to predict scores for the actually used and random sites of the 10% remaining strata. First, the observed site of each stratum was ranked against its associate random sites from 1 to 11 (i.e., given that a stratum included one observed and 10 random sites, there were 11 potential ranks). Second, we randomly selected one control site and ranked it against the controls only. We used Spearman rank correlation (r_s) to estimate the degree of

correlation between the rank of the observed and random sites and their relative frequency. We repeated this process 100 times for each final model and the average r_s , and reported the associated 95% confidence intervals (CI). We rejected all models with $r_s < 0.6$ (Zimmermann et al. 2014). All analyses were conducted in R 3.0.3 (R Core Team 2014).

RESULTS

We detected the establishment of 142 different wolf pairs in 1990–2012. Wolf pair establishment in a given site was positively related to previous wolf presence in the area ($\beta = 0.52$, $SE = 0.16$), and was negatively related to main road density ($\beta = -0.54$, $SE = 0.19$), distance to other wolf territories ($\beta = -0.35$, $SE = 0.08$), and bear density ($\beta = -0.21$, $SE = 0.15$; Tables 2 and 3). The 95% CI around the effect sizes (β) of these covariates did

Table 3. Effect size (β) and robust standard error (SE) of explanatory parameters of wolf pair site selection in Scandinavia, 1990–2012, estimated from the conditional logistic regression. We performed model averaging (with shrinkage) of best models to estimate the effect size of each parameter. Covariates were all scaled to 1 SD to facilitate comparison and interpretation of effect sizes.

Variable	β	SE	95% CI
Historical wolf presence	0.52	0.16	[0.21; 0.84]
Main road density	-0.54	0.19	[-0.92; -0.17]
Distance to other wolf territory	-0.35	0.08	[-0.51; -0.18]
Wolf density	-0.32	0.16	[-0.63; 0.02]
Brown bear density	-0.21	0.15	[-0.49; -0.03]
Main road density _quadratic	-0.17	0.13	[-0.42; 0.08]
Historical wolf presence _quadratic	-0.07	0.03	[-0.14; 0.00]
Secondary road density _quadratic	-0.08	0.15	[-0.55; 0.12]
Moose density	-0.07	0.11	[-0.40; 0.09]
Secondary road density	-0.06	0.13	[-0.49; 0.15]

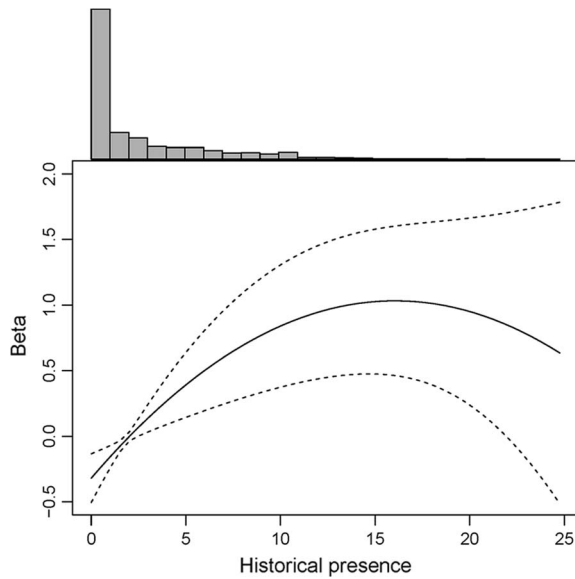


Fig. 3. Beta coefficient of the quadratic effect of wolf pair establishment in Scandinavia, 1990–2012, in relation to the index of wolf historical presence computed from model averaging (Table 3). Dashed line shows 95% confidence interval and bar plots show relative availability of both actually used and random sites.

not include 0 (Table 3), i.e., the sign of their effect on the probability of wolf pair establishment was clear. Wolf density ($\beta = -0.32$, $SE = 0.16$), moose density ($\beta = -0.07$, $SE = 0.11$), secondary road density ($\beta = -0.06$, $SE = 0.13$), and the quadratic form of the variables wolf previous presence ($\beta = -0.07$, $SE = 0.03$), main road density ($\beta = -0.17$, $SE = 0.13$), and secondary road density ($\beta = -0.08$, $SE = 0.15$) also had negative influence on the probability of wolf pair establishment. However, their 95% CI overlapped 0 (Table 3), suggesting a weaker, less conclusive effect than those mentioned previously. Indeed, the effect of the quadratic forms of previous wolf presence and main and secondary road density might just have reflected a lack of data in the tails of their respective distributions (Figs. 3 and 4).

The negative effect of bear density on the probability of wolf pair establishment (Fig. 5) was retained in four of five best models ($\Delta AIC_c = 1.39$ between the top and the fifth model), and the effect of density of wolves, wolf historical presence, distance to other wolf territory, and main road density was retained in all of them

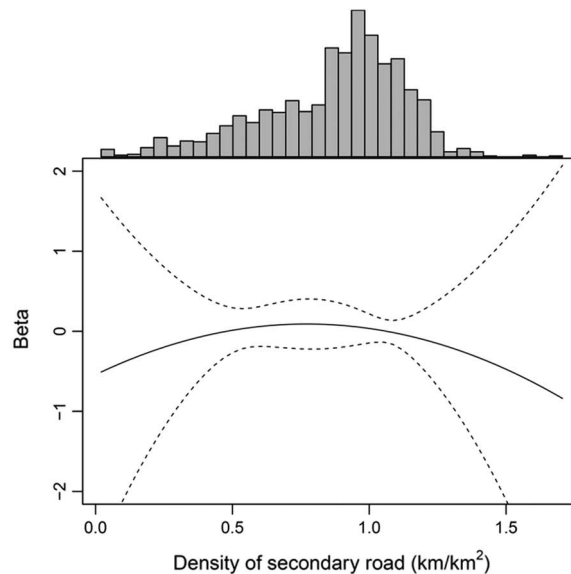
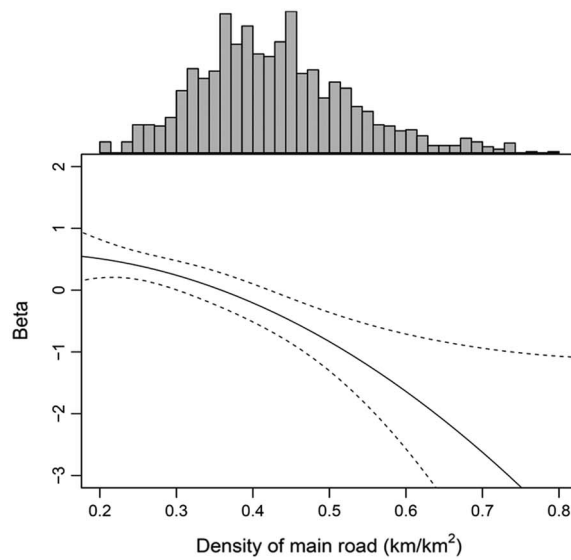


Fig. 4. Beta coefficient of the quadratic effect of wolf pair establishment in Scandinavia, 1990–2012, in relation to the density of main road (top panel) and secondary road (bottom panel) densities, computed from model averaging (Table 3). Dashed lines show 95% confidence intervals and bar plots show the relative availability of both actually used and random sites.

(Table 2). Selected models were robust, as shown by the distribution of r_S (averaged $r_S \geq 0.67$), which was higher than the expected by chance alone (averaged $r_S \leq 0.06$; Table 2).

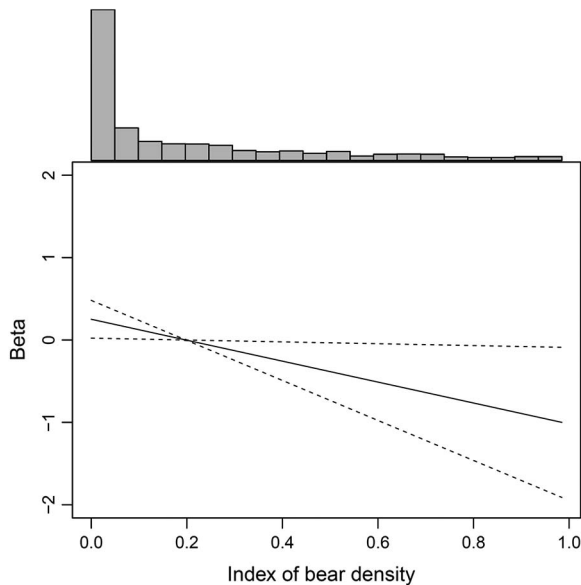


Fig. 5. Beta coefficient of wolf pair establishment in Scandinavia, 1990–2012, in relation with the index of bear density from model averaging (Table 3). Dashed line shows the 95% confidence interval and bar plots show the relative availability of both actually used and random sites.

DISCUSSION

Human-related factors (negative effect of road density), intraspecific factors (positive effect of previous wolf presence and negative effect of increasing distance to other wolf territories), and presence of a competitor species (negative effect of brown bear density) were the most influential factors affecting territory selection by wolf pairs in Scandinavia in 1990–2012, a period of demographic recovery and expansion of the wolf population. Wolf establishment started outside the area with the highest density of bears, which seemed to be progressively occupied by wolves as the population expanded (Fig. 2). The negative effect of bear density on the probability of wolf pair establishment confirmed that pattern (Tables 2 and 3, Fig. 5) and this is the most novel result of our study. Interspecific interactions can affect the species' distributions, but it is rarely possible to incorporate this concept into species distribution models (Godsoe and Harmon 2012). The results suggest that interspecific competition has been one of the influential factors modulating the

expansion of the Scandinavian wolf population, reinforcing the role of interspecific competition in shaping ecological communities.

A positive effect of previous wolf presence and negative effect of increasing distance to other wolf territories on the probability of wolf pair establishment has previously been documented. In Minnesota, for instance, edges of parental territories appeared to be preferred sites for wolf establishment, maybe to maximize parental fitness by tolerating the colonization of edges by offspring (Fritts and Mech 1981). The negative effect of main roads on wolf establishment was not surprising. Roads are a good proxy of human disturbance, often even better than human density per se (Ordiz et al. 2014). Main roads are used less by wolves for traveling than gravel roads (Zimmermann et al. 2014), which fits well with our result of a larger negative effect of main road density on wolf establishment, compared to the (also negative) effect of secondary roads (Tables 2 and 3). Regarding prey, wolf pair establishment occurred in areas with varying moose density, even when there was available space in the highest moose density areas, which would explain the negative, yet weak effect (95% CI of the β overlapping 0) of moose density in our study (Table 3). This result reinforces previous findings that wolves in Scandinavia are generally not constrained by moose density, which neither predicted the occurrence of wolf packs (Karlsson et al. 2007) nor influenced wolf home range size (Mattisson et al. 2013). However, it is possible that moose density plays a role at finer scales. In all Scandinavian studies, including ours, moose density estimates have been based on moose data from larger areas than the actual wolf territories.

Scavenging, including kleptoparasitism between carnivores as one of its major forms, is a key ecological process involved in energy flow in ecosystems (DeVault et al. 2003). Brown bears are a primary scavenger in the Northern Hemisphere (Krofel et al. 2012), and the generalized occurrence of bear kleptoparasitism in areas with high bear density (up to ~ 30 bears/1000 km² during the whole study period) might lie behind the negative effect of bear density on wolf establishment. Both wolves and bears feed on moose (Sand et al. 2005, Swenson et al. 2007), and bears are a very efficient predator on newborn moose

calves (Barber-Meyer et al. 2008). However, bear predatory efficiency is limited in time, only until the calves are 4 weeks old (Rauset et al. 2012), and bears mainly access larger moose by scavenging other predators' kills (Swenson et al. 2007).

In temperate latitudes with higher densities of predators, brown bears kleptoparasitize up to 50% of Eurasian lynx (*Lynx lynx*) kills during the lynx breeding season, which may ultimately affect lynx fitness (Krofel et al. 2012), and American black bears (*Ursus americanus*) used > 50% of mountain lion (*Puma concolor*) kills (Elbroch et al. 2015). Conversely, additional protein obtained from scavenging kills may increase bear fitness, and wolf kills are particularly important for bears in late winter and early spring (Ballard et al. 2003). Most of the documented individual interactions between wolves and brown bears in North America and Eurasia have occurred near ungulate kills of both predators (Ballard et al. 2003), and it is possible that bears affect wolves and lynx in a similar way. Bears also kleptoparasitize > 50% of the wolf kills in our study area and can displace wolves from their kills (Milleret 2011; A. Ordiz et al., *unpublished data*), i.e., frequency of kleptoparasitism is high also in spring and early summer, when bears also kill moose calves themselves.

In North America 14% of 108 interactions between wolves and bears has been documented to occur near wolf dens (Ballard et al. 2003). As in the lynx case, bear kleptoparasitism could be quite costly during the wolf pup nursing period, when a continuous food supply is needed and fewer members of the wolf pack are available for hunting. Such an effect might be larger for small wolf packs and it has been shown that the effects of kleptoparasitism differ in relation to group size of the affected species (Carbone et al. 2005). Loss of food to scavengers is indeed important for wolf foraging ecology. For instance, wolf pack size increases with increasing scavenging rates by ravens (*Corvus corax*) (Vucetich et al. 2004). In Scandinavia, wolf packs often consist of just an adult pair with or without pups, and wolves >1 year old rarely stay with the pack (Mattisson et al. 2013). Even if prey density is not a limiting factor for Scandinavian wolves, losing food to scavengers may lead to additional hunting effort, which is costly and particularly risky when

moose are the target prey (Peterson and Ciucci 2003). This may illustrate the dynamics of intra-guild interactions in resource-pulse environments (Greenville et al. 2014), which, in our case, involves wolves as obligate carnivores, bears as facultative predators and scavengers, and moose as their common prey (Moleón et al. [2014] and Pereira et al. [2014] for reviews on the functional complexity of predation and scavenging strategies).

Wolf pairs generate packs, the reproductive, functional units of wolf populations, making habitat selection by wolf pairs especially interesting, because of its relation with breeding performance or fitness (see Gaillard et al. 2010). Genotyped and geo-localized data on both wolf pairs and bears during the entire process of wolf recovery in an area with a gradient of bear density provided the opportunity for this study. Yet quite unique, our approach was necessarily coarse, because the study area was very large (~100,000 km²) and the study period very long (22 years). Before a scent-marking pair of wolves can be detected by the monitoring program, both animals must survive during the process of dispersion, meet each other, and settle down. Poaching is a major driver of large carnivore population dynamics in human-dominated landscapes, including wolves in Scandinavia (Liberg et al. 2011). Bears and wolves show preference for forested areas (May et al. 2008), which may facilitate poaching compared to lower altitudes with less persistent snow cover and thus less detectable carnivores. Poaching may be a cryptic factor involved in wolf establishment and therefore may affect our results. Nevertheless, one would expect bears also to be affected by poaching in the same area, but the highest bear density in Scandinavia actually overlaps with the wolf range (Fig. 2). Given these circumstances (large study area, long study period, and potential cryptic factors that may be considered as potentially confounding factors), we suggest that the documented negative effect of bear density on wolf pair establishment is especially remarkable.

Interactions between apex predators can have cascading effects through the entire natural community, which supports broadening the scope of conservation from single species to a much wider ecosystem perspective (Linnell and

Strand 2000). The relative role of top-down and bottom-up processes in ecosystems is a long-lasting ecological debate (e.g., Sinclair and Krebs 2002), but the effects that apex predators have on each other in a broad ecosystem context has gained increasing recognition recently (Estes et al. 2011, Ripple et al. 2013, 2014). Interactions between carnivores have the potential to affect overall biodiversity, e.g., by influencing the structure and composition of the vertebrate scavenger community (Allen et al. 2014). Therefore, the management of large carnivores should consider interspecific interactions (Ordiz et al. 2013), rather than focusing only on target populations of single species. This applies both to marine ecosystems, e.g., for fisheries management (Belgrano and Fowler 2011), and terrestrial ecosystems, e.g., to adjust harvest quotas of game species to account for the return of large, sympatric predators (Jonzén et al. 2013, Wikenros et al. 2015).

Predator kill rates increase as a result of kleptoparasitism by other carnivores and scavengers (e.g., Krofel et al. 2012). Therefore, the effects of predation can be better understood within a whole-community context that takes interactions into account (Elmhagen et al. 2010, Letnic et al. 2011, Elbroch et al. 2015). For instance, wolves provide biomass to scavengers throughout the year (Wilmers et al. 2003, Wikenros et al. 2013), and they also drive changes in the density, distribution, and diet of other predators (Berger and Gese 2007, Kortello et al. 2007). Such interactive processes can be essential in the regulation, stability, and resilience of ecological communities (Ripple et al. 2014). This emphasizes the need of further research at finer scales, i.e., within home-ranges, to disentangle the mechanisms driving interactions and the particular ecological functions of different predators, scavengers, and prey species.

Long-term monitoring data across large areas with environmental gradients, like our case with wolves and bears in Scandinavia, will help quantify and predict the influence of biotic interactions on species assemblages and distributions (Wisz et al. 2013). The current recovery of some large carnivores in Europe and North America (e.g., Chapron et al. 2014), along with the expanded use of GPS-based telemetry, should provide opportunities to study interspecific

competition among sympatric apex predators at large, population levels in other ecosystems.

ACKNOWLEDGMENTS

A. Ordiz and C. Milleret contributed equally to this work. We are indebted to all the people monitoring wolves and bears in Scandinavia for decades and to J.M. Arnemo, P. Ahlqvist, T. Strømseth and S. Brunberg, who captured and handled the animals. The Scandinavian wolf and bear projects (SKANDULV and SBBRP, respectively) have been funded by the Norwegian Environment Agency, the Swedish Environmental Protection Agency, the Norwegian Research Council, the Norwegian Institute for Nature Research, Hedmark University College, the Office of Environmental Affairs in Hedmark County, the Swedish Association for Hunting and Wildlife Management, the Worldwide Fund for Nature (Sweden), and the Swedish University of Agricultural Sciences. A. Ordiz was funded by Marie-Claire Cronstedts Stiftelse. C. Wikenros provided comments on a preliminary manuscript. This is scientific paper No. 191 from the SBBRP.

LITERATURE CITED

- Allen, M. L., L. M. Elbroch, C. C. Wilmers, and H. U. Wittmer. 2014. Trophic facilitation or limitation? Comparative effects of pumas and black bears on the scavenger community. *PLoS ONE* 9(7):e102257.
- Apps, C. D., B. N. McLellan, and J. G. Woods. 2006. Landscape partitioning and spatial inferences of competition between black and grizzly bears. *Ecography* 29:561572.
- Ballard, W. B., L. N. Carbyn, and D. W. Smith. 2003. Wolf interactions with non-prey. Pages 259–271 in D. L. Mech and L. Boitani, editors. *Wolves. Behavior, ecology and conservation*. University of Chicago Press, Chicago, Illinois, USA.
- Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs* 169:1–30.
- Barton, K. 2009. MuMIn: multi-model inference. R package version 0.12.2/r18. <http://R-Forge.R-project.org/projects/mumin/>
- Belgrano, A., and C. W. Fowler. 2011. *Ecosystem-based management for marine fisheries: an evolving perspective*. Cambridge University Press, New York, New York, USA.
- Bensch, S., H. Andrén, B. Hansson, H. C. Pedersen, H. Sand, D. Sejberg, P. Wabakken, M. Akesson, and O. Liberg. 2006. Selection for heterozygosity gives hope to a wild population of inbred wolves. *PLoS ONE* 1:e72.
- Berger, K. M., and E. M. Gese. 2007. Does interference

- competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology* 76:1075–1085.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. Second edition. Springer, New York, New York, USA.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.
- Carbone, C., L. Frame, G. Frame, J. Malcolm, J. Fanshawe, C. Fitz, G. Schaller, I. J. Gordon, J. M. Rowcliffe, and J. T. Du Toit. 2005. Feeding success of African wild dogs (*Lycaon pictus*) in the Serengeti: the effects of group size and kleptoparasitism. *Journal of Zoology* 266:153–161.
- Caro, T. M., and C. J. Stoner. 2003. The potential for interspecific competition among African carnivores. *Biological Conservation* 110:67–75.
- Chapron, G., et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346:1517–1519.
- Craiu, R., T. Duchesne, and D. Fortin. 2004. Inference methods for the conditional logistic regression model with longitudinal data. *Biometrical Journal* 50:97–109.
- Creel, S., G. Spong, and N. M. Creel. 2001. Interspecific competition and the population biology of extinction-prone carnivores. Pages 35–59 in D. Macdonald, J. Gittleman, R. Wayne, and S. Funk, editors. *Conservation of carnivores*. Cambridge University Press, Cambridge, UK.
- DeVault, T. L., O. E. Rhodes, and J. A. Shivik. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102:225–234.
- Donadio, E., and S. W. Buskirk. 2006. Diet, morphology, and interspecific killing in Carnivora. *American Naturalist* 167:524–536.
- Elbroch, L. M., P. E. Lendrum, M. L. Allen, and H. U. Wittmer. 2015. Nowhere to hide: pumas, black bears, and competition refuges. *Behavioral Ecology* 26:247–254.
- Elmhagen, B., G. Ludwig, S. P. Rushton, P. Helle, and H. Lindén. 2010. Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. *Journal of Animal Ecology* 79:785–794.
- Estes, J. A., et al. 2011. Trophic downgrading of planet Earth. *Science* 333:301–306.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic Cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Fritts, S. H., and L. D. Mech. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildlife Monographs* 80.
- Gaillard, J. M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat–performance relationships: finding the right metric at a given spatial scale. *Proceedings of the Royal Society B* 365:2255–2265.
- Godsoe, W., and L. Harmon. 2012. How do species interactions affect species distribution models? *Ecography* 35:811–820.
- Greenville, A. C., G. M. Wardle, B. Tamayo, and C. R. Dickman. 2014. Bottom-up and top-down processes interact to modify intra-guild interactions in resource-pulse environments. *Oecologia* 175:1349–1358.
- Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* 24:699–711.
- Gunther, K. A., and D. W. Smith. 2004. Interactions between wolves and female grizzly bears with cubs in Yellowstone National Park. *Ursus* 15:232–238.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Jonzén, N., H. Sand, P. Wabakken, J. E. Swenson, J. Kindberg, O. Liberg, and G. Chapron. 2013. Sharing the bounty—adjusting harvest to predator return in the Scandinavian human–wolf–bear–moose system. *Ecological Modelling* 265:140–148.
- Karlsson, J., H. Brøseth, H. Sand, and H. Andréén. 2007. Predicting occurrence of wolf territories in Scandinavia. *Journal of Zoology* 272:276–283.
- Kindberg, J., G. Ericsson, and J. E. Swenson. 2009. Monitoring rare or elusive large mammals using effort-corrected voluntary observers. *Biological Conservation* 142:159–165.
- Kindberg, J., J. E. Swenson, G. Ericsson, E. Bellemain, C. Miquel, and P. Taberlet. 2011. Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildlife Biology* 17:114–123.
- Kortello, A. D., T. E. Hurd, and D. L. Murray. 2007. Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta. *Ecoscience* 14:214–222.
- Krofel, M., I. Kos, and K. Jerina. 2012. The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators. *Behavioral Ecology and Sociobiology* 66:1297–1304.
- Lavsund, S., T. Nygren, and E. J. Solberg. 2003. Status of moose populations and challenges to moose management in Fennoscandia. *Alces* 39:109–130.

- Letnic, M., A. Greenville, E. Denny, C. R. Dickman, M. Tischler, C. Gordon, and F. Koch. 2011. Does a top predator suppress the abundance of an invasive mesopredator at a continental scale? *Global Ecology and Biogeography* 20:343–353.
- Lewis, T. M., and D. J. Lafferty. 2014. Brown bears and wolves scavenge humpback whale carcass in Alaska. *Ursus* 25:8–13.
- Liberg, O., H. Andrén, H. C. Pedersen, H. Sand, D. Sejberg, P. Wabakken, M. Åkesson, and S. Bensch. 2005. Severe inbreeding depression in a wild wolf (*Canis lupus*) population. *Biology Letters* 1:17–20.
- Liberg, O., Å. Aronson, H. Sand, P. Wabakken, E. Maartman, L. Svensson, and M. Åkesson. 2012. Monitoring of wolves in Scandinavia. *Hystrix, the Italian Journal of Mammalogy* 23(1):29–34.
- Liberg, O., G. Chapron, P. Wabakken, H. C. Pedersen, N. T. Hobbs, and H. Sand. 2011. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society B* 279:910–915.
- Linnell, J. D.C., and O. Strand. 2000. Conservation implications of aggressive intra-guild interactions among mammalian carnivores. *Diversity and Distributions* 6:169–176.
- Manly, B. F. J., L. L. McDonald, D. A. Thomas, T. L. McDonald, and W. E. Erickson. 2002. *Resource selection by animals, statistical design and analysis for field studies*. Second edition. Kluwer Academic, Dordrecht, The Netherlands.
- Mattisson, J., H. Sand, P. Wabakken, V. Gervasi, O. Liberg, J. D. Linnell, G. R. Rauset, and H. C. Pedersen. 2013. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. *Oecologia* 173:813–825.
- May, R., J. van Dijk, P. Wabakken, J. E. Swenson, J. D. C. Linnell, B. Zimmermann, J. Odden, H. C. Pedersen, R. Andersen, and A. Landa. 2008. Habitat differentiation within the large-carnivore community of Norway's multiple-use landscapes. *Journal of Applied Ecology* 45:1382–1391.
- Mech, L. D. 1994. Buffer zones of territories of gray wolves as regions of intraspecific strife. *Journal of Mammalogy* 75:199–202.
- Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. *The wolves of Denali*. University of Minnesota, Minneapolis, Minnesota, USA.
- Mech, L. D., and L. Boitani. 2003. Wolf social ecology. Pages 1–34 in D. L. Mech and L. Boitani, editors. *Wolves: behavior, ecology and conservation*. University of Chicago Press, Chicago, Illinois, USA.
- Milleret, C. 2011. Estimating wolves (*Canis lupus*) and brown Bear (*Ursus arctos*) interactions in Central Sweden. Does the emergence of brown bears affect wolf predation patterns? Thesis. Grimsö Wildlife Research Station, Department of Ecology, SLU, Sweden.
- Moleón, M., J. A. Sánchez-Zapata, N. Selva, J. A. Donàzar, and N. Owen-Smith. 2014. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews* 89:1042–1054.
- Morrison, J. C., W. Sechrest, E. Dinerstein, D. S. Wilcove, and J. F. Lamoreux. 2007. Persistence of large mammal faunas as indicators of global human impacts. *Journal of Mammalogy* 88:1363–1380.
- Ordiz, A., R. Bischof, and J. E. Swenson. 2013. Saving large carnivores, but losing the apex predator? *Biological Conservation* 168:128–133.
- Ordiz, A., J. Kindberg, S. Sæbø, J. E. Swenson, and O.-G. Støen. 2014. Brown bear circadian behavior reveals human environmental encroachment. *Biological Conservation* 173:1–9.
- Ordiz, A., O.-G. Støen, M. Delibes, and J. E. Swenson. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia* 166:59–67.
- Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. *American Naturalist* 153:492–508.
- Pereira, L. M., N. Owen-Smith, and M. Moleón. 2014. Facultative predation and scavenging by mammalian carnivores. *Mammal Review* 44:44–55.
- Peterson, R. O., and P. Ciucci. 2003. The wolf as a carnivore. Pages 104–130 in D. L. Mech and L. Boitani, editors. *Wolves: behavior, ecology and conservation*. University of Chicago Press, Chicago, Illinois, USA.
- Rauset, G. R., J. Kindberg, and J. E. Swenson. 2012. Modeling female brown bear kill rates on moose calves using Global Positioning Satellite data. *Journal of Wildlife Management* 76:1597–1606.
- R Core Team. 2014. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ripple, W. J., R. L. Beschta, J. K. Fortin, and C. T. Robbins. 2013. Trophic cascades from wolves to grizzly bears in Yellowstone. *Journal of Animal Ecology* 83:223–233.
- Ripple, W. J. et al. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343:1241484.
- Rothman, R. J., and L. D. Mech. 1979. Scent-marking in lone wolves and newly formed pairs. *Animal Behaviour* 27:750–760.
- Sand, H., P. Wabakken, B. Zimmermann, Ö. Johansson, H. C. Pedersen, and O. Liberg. 2008. Summer kill rates and predation pattern in a wolf-moose system: Can we rely on winter estimates? *Oecologia* 156:53–64.
- Sand, H., B. Zimmermann, P. Wabakken, H. Andrén, and H. C. Pedersen. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in

- wolf-ungulate ecosystems. *Wildlife Society Bulletin* 33:914–925.
- Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1:103–113.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* 122:240–285.
- Sinclair, A. R. E., and C. J. Krebs. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Proceedings of the Royal Society B* 357:1221–1231.
- Smith, D. W., R. O. Peterson, and D. B. Houston. 2003. Yellowstone after wolves. *BioScience* 53:330–340.
- Solberg, K. H., E. Bellemain, and O. M. Drageset. 2006. An evaluation of field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population size. *Biological Conservation* 128:158–168.
- Svensson, L., P. Wabakken, I. Kojola, E. Maartmann, T. H. Strømseth, M. Åkesson, and Ø. Flagstad. 2014. The wolf in Scandinavia and Finland: final report from wolf monitoring in the 2013-2014 winter. Hedmark University College and Viltskadecenter, Swedish University of Agricultural Sciences.
- Swenson, J. E., B. Dahle, H. Busk, O. Opseth, T. Johansen, A. Söderberg, K. Wallin, and G. Cederlund. 2007. Predation on moose calves by European brown bears. *Journal of Wildlife Management* 71:1993–1997.
- Swenson, J. E., F. Sandegren, and A. Söderberg. 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *Journal of Animal Ecology* 67:819–826.
- Swenson, J. E., P. Wabakken, F. Sandegren, A. Bjärvall, R. Franzén, and A. Söderberg. 1995. The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildlife Biology* 1:11–25.
- Tannerfeldt, M., B. Elmhagen, and A. Angerbjörn. 2002. Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia* 132:213–220.
- Therneau, T. M. 2014. A package for survival analysis in S. <http://cran.r-project.org/web/packages/survival/survival.pdf>
- Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. *Movement Ecology* 2:4.
- Ueno, M., E. J. Solberg, H. Iijima, C. M. Rolandsen, and L. E. Gangsei. 2014. Performance of hunting statistics as spatiotemporal density indices of moose (*Alces alces*) in Norway. *Ecosphere* 5:13.
- Vilà, C., A.-K. Sundqvist, Ø. Flagstad, J. Seddon, S. Blörnerfeldt, I. Kojola, A. Casulli, H. Sand, P. Wabakken, and H. Ellegren. 2003. Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. *Proceedings of the Royal Society B* 270:91–97.
- Vucetich, J., R. O. Peterson, and T. A. Waite. 2004. Raven scavenging favours group foraging in wolves. *Animal Behaviour* 67:1117–1126.
- Wabakken, P., H. Sand, I. Kojola, B. Zimmermann, J. M. Arnemo, H. C. Pedersen, and O. Liberg. 2007. Multistage, long-range natal dispersal by a Global Positioning System-collared Scandinavian wolf. *Journal of Wildlife Management* 71:1631–1634.
- Wabakken, P., H. Sand, O. Liberg, and A. Bjärvall. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978–1998. *Canadian Journal of Zoology* 79:710–725.
- Wikenros, C., H. Sand, P. Ahlqvist, and O. Liberg. 2013. Biomass flow and scavengers use of carcasses after re-colonization of an apex predator. *PLoS ONE* 8(10):e77373.
- Wikenros, C., H. Sand, R. Bergström, O. Liberg, and G. Chapron. 2015. Response of moose hunters to predation following wolf return in Sweden. *PLoS ONE* 10(4):e0119957.
- Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology* 72:909–916.
- Wisz, M. S., et al. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* 88:15–30.
- Woodroffe, R., S. Thirgood, and A. Rabinowitz. 2005. *People and wildlife, conflict or coexistence?* Cambridge University Press, Cambridge, UK.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.
- Zedrosser, A., B. Dahle, J. E. Swenson, and N. Gerstl. 2001. Status and management of the brown bear in Europe. *Ursus* 12:9–20.
- Zimmermann, B., L. Nelson, P. Wabakken, H. Sand, and O. Liberg. 2014. Behavioral responses of wolves to roads: scale-dependent ambivalence. *Behavioral Ecology* 25:1353–1364.