Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors

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Abstract Home range size in mammals is a key ecological trait and an important parameter in conservation planning, and has been shown to be influenced by ecological, demographic and social factors in animal populations. Information on space requirements is especially important for carnivore species which range over very large areas and often come into direct conflict with human interest. We used long-term telemetry-location data from a recovering wolf population in Scandinavia to investigate variation in home range size in relation to environmental and social characteristics of the different packs. Wolves showed considerable variation in home range size, which ranged from 259 to 1,676 km^2. Although wolf density increased fourfold during the study period, we found no evidence that intraspecific competition influenced range size. Local variation in moose density, which was the main prey for most packs, did not influence wolf home range size. Home ranges increased with latitude and elevation and decreased with increased roe deer density. Although prey biomass alone did not influence range size, our data suggest that there is a correlation between habitat characteristics, choice of prey species and possible hunting success, which currently combine to shape home range size in Scandinavian wolves.

Introduction

Home range size is one of the most fundamental ecological parameters that can be described for any given species and can be viewed as a trade-off between resource access and energetic costs. The minimum size of an animal's home range is fundamentally determined by the ability to obtain enough food resources for survival and to secure successful reproduction (Burt 1943) but the actual use of space is influenced by a far more complex array of factors. Range use in mammals appears to be influenced by a combination of ecological and social factors, including not only resource abundance and prey predictability (Loveridge et al. 2009), but also environmental productivity (Herfindal et al. 2005), body mass (Harstad and Bunnell 1979; Swihart et al. 1988, but see Nilsen and Linnell 2006), population density (Dahle and Swenson 2003; Benson et al. 2006), migration of prey (Mech and Boitani 2003), social organization (Peterson et al. 1984; Loveridge et al. 2009), population stage or phase of colonisation (Okarma et al. 1998; Fuller et al. 2003; Mech and Boitani 2003), anthropogenic influence (Rich et al. 2012) and individual variation (Jedrzejewski et al. 2007; van Beest et al. 2011).

Apart from its interest as an ecological parameter, the identification of factors shaping home range size is

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important in both management and conservation planning of species and populations. Home range size is often used for designing management units or protected areas (Woodroffe and Ginsberg 2000) and can be used as a tool for obtaining estimates of population size (Gros et al. 1996), in which accurate estimates of home range size and their variation are vital. Territoriality, a common behaviour in many large carnivores, results in limited spatial overlap among individuals or social groups, thus home range size can act as a good proxy for their local density in a given area. Understanding the process behind variation in home range size can facilitate extrapolation and aid in creating qualified predictions of a species' space use or local density in new areas (Herfindal et al. 2005). This can be particularly important for large carnivores that roam extensive areas and whose presence often causes conflicts with human interest (Woodroffe et al. 2005), including through their potential impact on prey populations.

The aim of this study was to determine the influence of ecological and social factors in shaping home range size in a large carnivore, the wolf (*Canis lupus*). The wolf is a well-studied territorial, group-living species (Harrington 1987; Vila et al. 1994; Mech and Boitani 2003; Zub et al. 2003) that often uses much larger areas than expected from its body size (Harstad and Bunnell 1979). Wolves display a large variation in home range size both between and within populations. Although there is a general understanding of large-scale variation in wolf home range size (see reviews in Fuller et al. 2003; Nilsen et al. 2005; Jedrzejewski et al. 2007), the underlying mechanisms causing finer scale variation within populations is poorly understood (Rich et al. 2012; Gurarie et al. 2011; Fritts and Mech 1981; Hayes and Harestad 2000). On a global scale, wolf home range size has been shown to relate negatively to prey biomass and wolf density whereas pack size, latitude, and human density tend to correlate with larger home ranges (Ballard et al. 1987; Wydeven et al. 1995; Okarma et al. 1998; Fuller et al. 2003; Jedrzejewski et al. 2007; Rich et al. 2012). However, the results have not been consistent between studies suggesting that the mechanisms shaping home ranges are complex and likely to be influenced by several interacting social and ecological factors.

Prey biomass, for example, is expected to have a negative influence on home range size alone but the predictability and availability of prey (Rich et al. 2012), the choice of prey species (Fuller et al. 2003) and landscape features correlated with hunting success (Kauffman et al. 2007; Rich et al. 2012; Gervasi et al. 2013) may play an equally important role in modulating this effect. Wolves preying on small to medium-sized ungulates have in general smaller ranges and a stronger correlation between range size and prey density than those preying on large ungulates (moose *Alces alces* or bison *Bison bison*;

Wydeyen et al. 1995; Fuller et al. 2003). Landscape features, such as ruggedness, may facilitate predation and therefore increase the prey biomass available to wolves resulting in smaller home ranges, but can also act as a refuge for the prey with the opposite result (Rich et al. 2012).

Although access to food resources is believed to be a key factor in determining home range size, social factors can be equally important, especially in a territorial species. Within populations, harvest of wolves has been shown to increase home range size by creating social disturbance in the packs (Rich et al. 2012), whereas an increase in population density reduced range size as an effect of enhanced inter-territorial competition (Fritts and Mech 1981; Hayes and Harestad 2000), given that at least part of the population was approaching saturation. In addition, many species show high intraspecific variability in home range size, where a substantial part of the variation is related to individual differences (Loveridge et al. 2009; van Beest et al. 2011).

Using the Scandinavian wolves as the study species gave us the opportunity to analyse space use in a recovering wolf population. In addition to a large telemetry-based dataset from 43 resident, scent-marking wolves in 1999–2011, extensive national monitoring systems in Norway and Sweden have tracked the establishment of wolf packs during the process of re-colonisation and generated a near complete overview of the population's density and distribution (starting in 1983 with the first confirmed reproduction; Wabakken et al. 2001; Vila et al. 2003; Liberg et al. 2005). The growing wolf population on the Scandinavian Peninsula (it had reached ∼300 wolves by 2011; Wabakken et al. 2011) not only gives us the possibility to study the influence of social dynamics and increasing inter-pack competition, but generated an extensive variability in ecological factors within the study area. The northern geographical location of the Scandinavian Peninsula displays a distinct latitudinal gradient (mild coast to continental interior) even within the relatively small area used by the wolf population. In addition, we examined the influence of ungulate prey density, prey choice, and landscape-prey-related factors on home range size using density estimates of ungulate prey in a multi-ungulate prey ecosystem.

First, we explored the effect of prey density on wolf home range size, which is expected to be negatively correlated if space use is mainly shaped by resource abundance. We did this for the two main prey species (moose and roe deer *Capreolus capreolus*; Sand et al. 2005, 2008), in order to detect potential effects of the large body size differences between these two prey species on shaping home ranges. Secondly, we tested for the influence of environmental features on range size, and discuss them in

relation to correlated productivity, prey availability, and anthropogenic impact and their possible influence on wolf behaviour. In addition, we included social factors (wolf density, social organisation within packs) to investigate the influence and strength of social dynamics in comparison to the ecological factors.

Materials and methods

Study area

The study area is located across the south-central parts of Sweden and Norway on the Scandinavian Peninsula (Fig. 1; 59°–62°N, 11°–19°E). The area primarily consists of intensively managed boreal coniferous forest interspersed with bogs and lakes. Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) are the dominant tree species, mixed with varying amounts of birch (*Betula pendula* and *Betula pubescens*), aspen (*Populous tremula*) and alder (*Alnus incana* and *Alnus glutinosa*). Intensive forest management has created an extensive network of forest gravel roads throughout the area. The influence of infrastructure and the proportion of agricultural land in the landscape increases in the south-western, eastern and southern parts of the study area, while elevation range increases towards the north-west reaching up to 1,750 m a.s.l.. Human density in Scandinavia averages 17 humans km^{-2}, but large parts of the wolf range have less than 1 human km^{-2} (Swedish National Atlas 1991; Statistics Norway 2003). The climate is continental with average temperatures of −7 °C in January and 15 °C in July. The ground is usually snow covered between December and March with a general snow depth of 30–60 cm in midwinter (Swedish National Atlas 1991; Statistics Norway 2003). Moose and roe deer are the two most common ungulates within the wolf range and are by far the main prey for the Scandinavian wolves (Sand et al. 2005, 2008). All wolves had access to both species but with a spatial variation in densities and ratio between the two species. Red deer (*Cervus elaphus*), wild reindeer (*Rangifer tarandus*), fallow deer (*Dama dama*) and wild boar (*Sus scrofa*) occurred locally, but have not been observed as important prey species among the studied packs.

Study animals and data collection

We used location data on wolves monitored within the ongoing Scandinavian Wolf Research Project (http://skandulv.nina.no) between 1999 and 2011. Wolves were immobilised from helicopters following continuously updated veterinary procedures (Arnemo et al. 2011) and equipped with either a very high frequency (VHF) radio
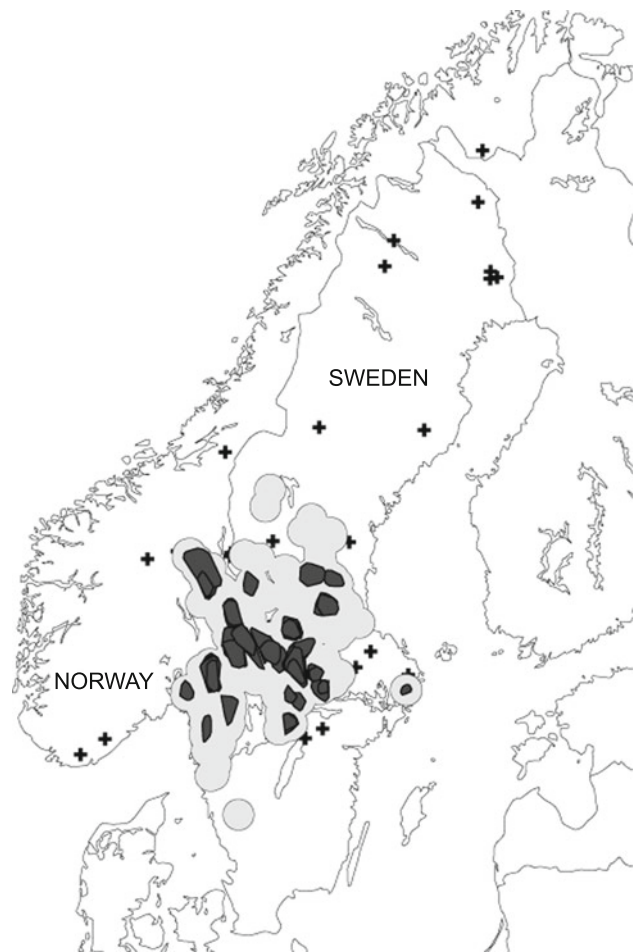

Fig. 1 Study area with home ranges of radio-collared wolves (*dark polygons*) in Sweden and Norway, 1999–2011. The distribution of scent-marking pairs and packs in the Scandinavian wolf population, all years combined, is displayed by the *grey area* (20-km buffer zones around centre point of each home range). *Black crosses* shown locations of resident solitary wolves outside the main distribution

collar (Telonics model 500, Mesa, AZ), a global positioning system (GPS) remote downloadable collar (GPS-Simplex, TVP Positioning, Lindesberg, Sweden) or a GPS-global system for mobile communications collar (Tellus, TVP Positioning; GPS-plus, Vectronic Aerospace, Berlin). The capture methods were approved by the Swedish Animal Welfare Agency and the Norwegian Experimental Animal Ethics committee. For a more detailed description of capture and handling, see Sand et al. (2006). Location data from VHF collars were collected from the ground or from a fix-winged airplane at least once per week and GPS collars were programmed to take a location two to six times per 24 h. Location frequency was increased up to one location every half hour during intensive study periods (Sand et al. 2008). Only data from adult resident, scent-marking individuals were used in the analyses and each "pack" was classified according to their social organisation: solitary (one wolf), pair-living (two scent-marking

wolves) or pack-living (from three to ten wolves). Scandinavian wolf packs are in general small, consisting of an adult male and female with or without pups of the year. Offspring older than 1 year rarely stay with the parents. Reproductive status in summer was estimated from a combination of pre- and post-reproduction intensive monitoring of movement patterns by adult radio-collared wolves during the parturition period. Successful reproduction was later confirmed by observations of pups or their signs (Alfredéen 2006), and occasionally by examinations of dens or rendezvous sites. The minimum number of wolves within each pack (pack size) was estimated by comprehensive and repeated snow-tracking and faecal DNA monitoring during a 5-month period each winter as a part of national surveys of wolves (see Wolf density below).

Estimations of home range size

Available location data for each pack varied greatly in duration (number of days) and location frequency. Analyses of annual home range size against number of months of data collection indicated that a minimum of 9 months with five or more locations per month was necessary to estimate an annual home range (Fig. 2). Detailed methodology for this conclusion is provided in the Electronic Supplementary Materials (ESM; Appendix 1). Only annual home ranges that fulfilled these requirements were used in further analyses. Sufficient data were available for 43 wolf individuals belonging to 28 different packs (ESM, Table S1).

Wolf home ranges were estimated according to their biological cycle starting from 1 May (time of birth; Alfredéen 2006) until 30 April the following year. When possible, we estimated several annual ranges per pack ($n_{total} = 63$). Extreme outliers and extra-territorial forays were removed before running the analyses (0.3 % of all locations). No differences in space use were found between the female and male wolves in a pack when both were fitted with collars simultaneously (paired t-test; $t_{19} = 0.9167$, $P = 0.37$, $n = 20$), thus the data were pooled in subsequent analyses. The social organisation (i.e. solitary, pair or pack-living) of the wolves within a specific pack may have changed between years but the approximate geographical placement was always the same. Partial turnover (one of the individuals replaced) occurred on a few occasions between years. If there was a complete turnover the new wolves were given a new pack name even if the "new" pack had approximately the same geographical location.

We used three different home range estimators: (a) minimum convex polygon (MCP 100 % of locations; Mohr and Stumpf 1966), (b) objective restricted edge polygon (OREP 100 %), and (c) fixed kernel (95 %;
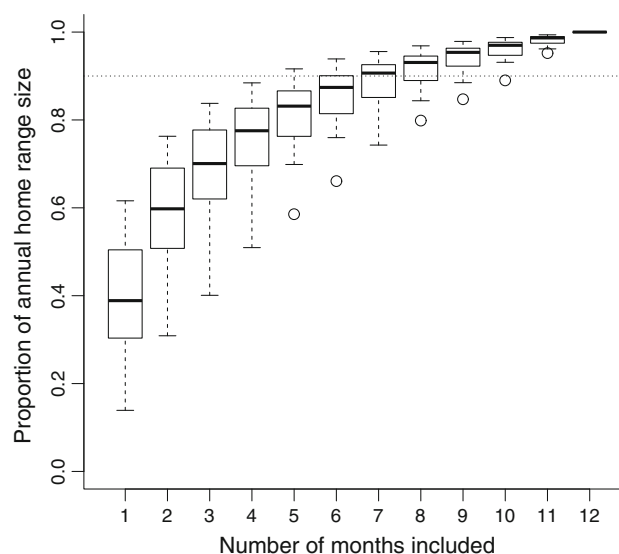

Fig. 2 Proportion of annual wolf home range size [minimum convex polygon (MCP) 100 %] in relation to number of months included in the range estimation when resampling 34 annual Scandinavian wolf ranges (mean = 120, range 5–1,264 locations month^{-1}). Mean range sizes above the *dotted line* decreased less than 10 % compared to the annual range

Seaman and Powell 1996) with the smoothing multiplier set to 1. All estimates of home range size were obtained using Ranges8 software (v2.7, Anatrack, Wareham, UK). OREP can be described as a concave polygon and was used because it better described non-linear-shape outlines of an animal's range than MCPs and thereby excludes areas not being used by the animal (Getz et al. 2007). Ranges defined by OREPs are equivalent to the local nearest neighbour convex hull method (Getz and Wilmers 2004), but with an objective choice of the edge-restriction distance, here set to a kernel-based outlier exclusion distance (Ranges8). For methods a and b the full data set with all available locations was used. A reduced dataset (maximum of two randomly selected locations per calendar day) was used for method c as kernel smoothing is strongly influenced by sampling frequency (Seaman et al. 1999).

Wolf density

National wolf population surveys have been conducted in both Sweden and Norway (by county and national wildlife management agencies and staff from several universities and research institutes) every year during this study (Wabakken et al. 2011). These annual population surveys were based on intensive snow tracking and generated a near complete description of the spatial distribution of existing wolf pairs, packs and stationary solitary individuals each winter, as well as an estimate of population size. We used local density of packs as a proxy for analysing

effect of wolf density on home range size. Centre points (north and east coordinates) were available from the surveys for all packs including both marked and unmarked wolves (based on snow tracking). We used a 40-km-radius (i.e. two times the radius of a large home range in this study) buffer zone around the centre point of each pack in the study to estimate the number of neighbouring packs (both marked and unmarked), i.e. pack density.

Prey density

To estimate winter density of moose and roe deer, pellet count surveys were conducted during 1 unique year for 15 of the packs (one pack was surveyed in 2 years). In each home range, a grid of 1×1-km square plots was systematically distributed over the area (about 50–100 plots per home range). Each square plot contained 40 circular sub-plots along its perimeter, each of them covering 100 m^2 for moose and 10 m^2 for roe deer. All sample plots were surveyed in spring, after snow melt. During data collection, we looked at the pellets' structure, consistency, colour, and their position in relation to the vegetation in order to include only new pellet groups, i.e. those produced after leaf fall the previous autumn. Winter density of moose and roe deer (individuals km^{-2}) was estimated by dividing mean pellet group counts for all sample plot by period of accumulation (days between leaf fall and field count, 198–231 days) and assumed defecation rate (roe deer, 22 day^{-1} Cederlund and Liberg 1995; moose, 14 day^{-1} Rönnegård et al. 2008). During the study period, roe deer and moose populations in Scandinavia have been fluctuating due to changes in harvest policy, winter conditions, forestry strategies and predation pressure (Lavsund and Solberg 2003; Grøtan et al. 2005). These fluctuations discourage the extrapolation of density estimates from one year to another, resulting in an incomplete dataset of prey density estimates. Before proceeding, we investigated possible influences of winter prey densities on home range size using the limited data ($n = 16$) in a set of simple linear regression models. Data on prey choice were available for each of the sampled packs (H. Sand, unpublished data; cf. Sand et al. 2005, 2008). Wolves preyed mainly on moose (73–100 % of ungulate kills) except in two packs where roe deer was the main prey (71 and 98 %). We evaluated the importance of moose and roe deer density for the total dataset ($n = 16$), and for a subset of the packs where moose dominated the diet of wolves ($n = 14$). These analyses revealed a negative correlation between roe deer density and home range size but no correlation with moose density, irrespective of the main prey species (see Results). With this information, we decided to include only an index of roe deer density (and not moose), based on annual hunting statistics, in the proceeding multivariate analyses.

Previous research has indicated that hunting bag statistics are a reliable index of ungulate density under Scandinavian conditions (Solberg et al. 1999; Grøtan et al. 2005). The use of hunting bag statistics as an index of roe deer density was supported by a strong positive correlation with density based on pellet counts (Spearman correlation = 0.83, $n = 16$). Consequently, we expect hunting bag statistics to accurately reflect temporal and spatial variation in roe deer density for our data.

Annual hunting bag statistics were available at municipality level in Norway (Statistics Norway; www.ssb.no) and at hunting district level in Sweden (O. Liberg, unpublished data). A separate map was produced for each year with the number of roe deer shot per squared kilometre estimated for each Norwegian municipality or Swedish district excluding water bodies. An index of roe deer density per annual home range was extracted using area weighted means (AWM) in Hawths tools (Beyers 2004), ArcGIS v. 9.3 (ESRI, Redlands, CA). We lacked data from a few districts or municipalities for some of the years. If the area of missing data was <50 %, we estimated AWM on the basis of the existing data (ten home ranges with partial missing data). When exceeding 50 %, we used the average value from the previous and the subsequent year of data (four home ranges).

Environmental data

As an index of increasing human influence on the landscape, the proportion of open cultivated land below the altitudinal tree line (agricultural land, orchards, fields or other types of cultivated land) was calculated from a vegetation map (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). Based on national road maps (road map 1:100 000, Lantmäteriet, Sweden; N50 kartdata, Statens kartverk, Norway), roads were categorised into main and minor roads. In Norway, main roads included public roads (European, national, county and municipal roads) which are most often paved, but sometimes narrow. Minor roads included forest gravel roads which are mainly private. The Swedish categories of roads differ from Norway but were converted based on existing overlaps of the two maps to fit the same categories. Roads were divided into two categories: main roads (all tarred), and minor roads (mostly gravel forest roads). Road density (main and minor roads separately) was calculated by first converting roads to points spaced at 250 m, on which a kernel density was estimated with bandwidth set to 1,000 and raster cell size to 500 m. Mean road density and mean elevation (DEM 25×25 m; Geographical Data Sweden, Lantmäteriet; Norge digital, Statens kartverk, Norway) in each home

range was extracted using the National Water-Quality Assessment area-characterization tool box (Price et al. 2010). Latitude (degrees north) was derived at the arithmetic mean of all locations in each home range. All geographic information system (GIS) analyses were performed in ArcGIS v. 9.3.

Statistical analyses

To examine variation in annual wolf home range size we used linear mixed models in the library nlme (Pinheiro et al. 2010) implemented in program R (R Development Core Team 2011). Home range size (km^2) was fitted as the response variable in all models. Two extreme outliers (MCP: 3,525 and 2,589 km^2) were identified and removed before proceeding with the analyses. These outliers included one reproducing pack composed of a father who mated with his daughter, possibly explaining the extraordinary movement patterns (Koppang, ESM, Table S1; Eriksen et al. 2009), and one single wolf in a transition state after losing its partner (Ulriksberg, ESM: Table S1), resulting in a 50 % increase in home range size from the previous year. There was no spatial correlation between home range sizes (i.e. home ranges closer to each other were not more similar in size).

Prior to entry into models, the fixed variables (reproduction, wolf density, social organisation, pack size, area of open cultivated land, elevation, road densities, roe deer density and latitude; ESM, Table S2) were assessed for multicollinearity using the variance inflation factor (VIF; Zuur et al. 2009) in the R library AED (Zuur 2010). Pack identity was fitted as a random intercept in all models to account for patterns in the residuals of the fixed effects occurring due to repeated observations of the same pack. We used likelihood ratio tests to evaluate if the inclusion of a random effect was indeed necessary (global model with MCP, $L_1 = 18.61$, $P < 0.0001$; Zuur et al. 2009). As each pack ($n = 28$) had only a few data entries ($\bar{x} = 2.2$) we were not able to fit pack identity as a random slope in the model.

Model selection was performed based on corrected Akaike's information criterion (AIC_c) (Burnham and Anderson 2002) in the R package MuMIn (Barton 2009). All variables were centralized and standardized with 2 SD to facilitate interpretation of the relative strength of parameter estimates (Gelman 2008; Grueber et al. 2011). When needed, we tested if using different transformations gave a better fit. We performed model averaging, based on AIC_c with conditional SEs and confidence intervals (Burnham and Anderson 2002), as it is usually more stable than only choosing the best model (Grueber et al. 2011). We choose to include models with $\Delta_i \leq 2$ as a cut off in the averaging process, as these are considered to have

sustainable support (Burnham and Anderson 2002). A cut off of $\Delta_i \leq 4$ generated far too many models, increasing the risk of spurious results from parameter estimates of models with low weight (Grueber et al. 2011). To assess the amount of variation explained by the fixed effects of the models used in the average model (it was not possible to estimate directly for the average model), we calculated R^2 as the square of the correlation between the predicted values of the models, without the random effect, and the observed data. R^2 for the random part was estimated by calculating the intra-class correlation ρ (Rodriguez and Elo 2003; Skrondal and Rabe-Hesketh 2004), which provides the ratio of the variance of the random effect to the total variance, and thus can be interpreted as the proportion of variation explained by each individual pack. Model selection and model averaging was run for all three methods of estimating home ranges (MCP, OREP and kernel) to examine whether the choice of home range estimator influences the results.

Results

We observed large variation in home range size between packs, even when excluding the two outliers mentioned above (259–1,676 km^2; Table 1). Home ranges estimated using the MCP method were significant larger than the corresponding ranges estimated with OREP (paired t-test, $t_{58} = 5.38$, $P < 0.0001$) or with kernel methods ($t_{58} = 13.14$, $P < 0.0001$). There was a high year-to-year stability in space use (mean overlap between annual ranges: MCP, 84 ± 8 % SD; OREP, 81 ± 9 %; kernel, 76 ± 12 %).

Home range size and prey density

The variation in roe deer densities across wolf home ranges (0.0–4.0 roe deer km^{-2}; SE = 0.30, $n = 16$) was much larger than observed for moose density (0.86–1.74 moose km^{-2}, SE = 0.069 excluding one outlier at 3.4 moose km^{-2}). Wolf home range size was not correlated with

Table 1 Annual home range size (km^2) of Scandinavian adult, scent-marking wolves monitored between 1999 and 2011, estimated as minimum convex polygons (*MCP*), objective restricted edge polygons (*OREP*) and fixed kernels (*Kernel*)

Home range	Mean	SE	Minimum	Maximum
MCP (100 %)	1,017	73	259	1,676
OREP (100 %)	916	74	259	1,676
Kernel (95 %)	708	57	141	1,089

Mean and SE were based on the number of unique packs ($n = 27$). Two outliers were removed before calculating the mean (MCP, 3,525 and 2,589 km^2)

moose density but was negatively correlated with roe deer density (Fig. 3). The exclusion of two packs where wolves mainly preyed on roe deer did not change the observed correlations (Fig. 3; ESM, Table S3). The method of home range estimation did not influence the result (ESM, Table S3). Average winter ungulate biomass for all home ranges was 401 kg km^{-2} ($\pm$160 SD; based on mean weight of standing population, moose = 271 kg, roe deer = 22.6 kg; B. Zimmerman et al., unpublished data) and because of the

large size difference between the prey species, biomass was mainly driven by moose density. Prey biomass was stable along the latitude gradient within the study area (linear regression, $r^2 = -0.07$, $P = 0.87$).

Model performance-effects on home range size

Several of the fixed variables were correlated (VIF > 3; ESM: Table S4), thus caution was required when deciding which variables to include in the same model. For the variables describing social status, we chose to keep pack size rather than social organisation (single, pair or pack). Scandinavian wolf packs are small (relative to other populations) resulting in reproductive status being strongly correlated with pack size (i.e. non-reproducing, pack size = 1–3 wolves; reproducing, 3–10 wolves) thus preventing these two variables from being included in the same model. Model sets including the variable reproduction in summer (binary) indicated that this variable was uninformative across all methods of home range estimates, so we therefore retained pack size in the final models. Among the environmental variables, roe deer density was negatively correlated with elevation and latitude and positively correlated with increasing proportion of open cultivated land. We chose to keep roe deer density and latitude in the global model, as it was possible to combine these variables (VIF < 3). A prior examination of the roe deer density index using the global model justified the use of a reciprocal transformation of the variable [roe deer, untransformed ($\Delta_i = 2.44$) or log-transformed ($\Delta_i = 1.9$)].

According to the final models, latitude and roe deer density were the most important variables explaining variation in home range size (Tables 2, 3). Home ranges decreased with increasing roe deer density and increased with increasing latitude. The importance of roe deer density and latitude were stable across all types of home range estimates. The density of minor roads was positively related to home range size estimated by OREPs (Table 3) and was almost as important as roe deer density (Table 2) but had less effect for the other types of estimates. An effect of pack size on home range size was mainly observed when using kernel estimates, where range size decreased with increasing number of wolves in a pack (Table 3). Local wolf density did not influence range size. To evaluate whether excluded environmental variables may better explain variation in home range size than the variables chosen, we used the final model for each range estimator (Table 2) and first replaced the roe deer density index with proportion of open cultivated land, while keeping all other variable constant. The model including roe deer density better explained variation in home range size than the model with proportion of open cultivated land (MCP, $\Delta_i = 5.71$; OREP, $\Delta_i = 2.26$; kernel, $\Delta_i = 1.68$).
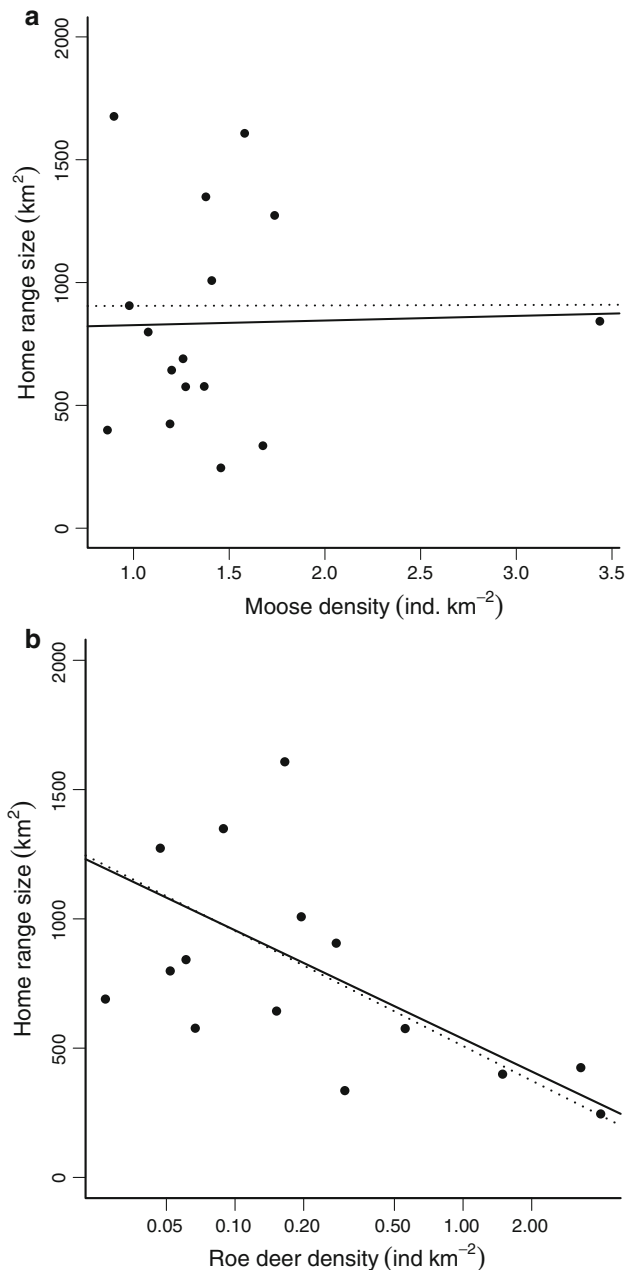

Fig. 3 Annual home range size (outlier restricted edge polygon) of Scandinavian wolves in relation to **a** moose density and **b** roe deer density (logarithmic scale). *Solid regression lines* include all sampled packs ($n = 16$), *dotted regression lines* exclude two packs mainly preying on roe deer ($n = 14$)

The process was repeated with latitude replaced by elevation which improved the models across all estimates (MCP, $\Delta_i = -1.19$; OREP, $\Delta_i = -1.10$; kernel, $\Delta_i = -3.36$). Altogether, these results suggest that home range size is influenced by a productivity gradient in the landscape which is reflected in the density of roe deer and influenced by elevation. In addition, we observed large inter-pack variation in home range size (i.e. R^2 of random effects), ranging between 0.55 and 0.65 for MCP, 0.54–0.55 for OREP and 0.37–0.53 for kernel.

The choice of home range estimator did not strongly influence the main result of the models. However, the model selection using concave polygons (OREP) included less models ($\Delta AIC_c < 2$) than for the more commonly used convex polygons (MCP) method. The inclusion of areas in MCP, which are not actually used by the wolves, may to some extent confound the results. For example, the positive effect of major roads on home range size when using MCP, but not for OREP, is likely an effect of these roads functioning as a "natural" barrier for wolf home movements which is not used but is still included in MCP ranges.

Discussion

Scandinavian wolves display a large variation in the size of their home range, with even the smallest ones (<260 km^2) being larger than the average size in continental Europe (150–240 km^2; Ciucci et al. 1997; Okarma et al. 1998; Jedrzejewski et al. 2007; Kusak et al. 2005), whereas the upper range ($<1,680$ km^2) approaches home range sizes of Alaskan and Yukon wolf populations (Hayes and Harestad 2000; Adams et al. 2008). Large within- and between-population variation in home range size exists among wolves wherever they occur (Adams et al. 2008; Fuller et al. 2003; Jedrzejewski et al. 2007) which was further confirmed in this study.

A combination of correlated ecological factors, rather than social factors, explained most of the intra-population variation observed in home range size among Scandinavian wolves, after large individual variation was taken into account. Roe deer density, elevation and latitude were all important variables predicting wolf home range size. Roe deer density was negatively correlated with elevation and latitude and positively correlated with open cultivated land. These correlations likely reflect both the sensitivity of roe deer to snow depth and their preferences for agricultural areas which increase foraging opportunities (Mysterud et al. 1997, 1999; Gervasi et al. 2013). In the process of understanding why we find smaller ranges in areas of high roe deer densities, with consequently lower average elevation and a higher proportion of open cultivated land, we need to consider the different components separately as well as the interactions between them. Latitude has previously been observed to influence home range size among wolf populations (Okarma et al. 1998; Jedrzejewski et al.

Table 2 Multi-model interference based on linear mixed models on effects of latitude (*Lat.*), roe deer density index (*Roe*; reciprocal transformed), density of wolf packs (*Dens.*), pack size (*Pack*), minor roads (*MiR*) and major roads (*MaR*) on annual home range size ($n = 63$) in Scandinavian wolves

Method	Model	k	AIC_c	ΔAIC_c	ω_i	R^2
MCP 100 %	Lat. + Roe	5	863.2	0.0	0.18	0.24
	Lat. + Roe + Dens.	6	863.5	0.2	0.16	0.25
	Lat. + Roe + Dens. + Pack	7	863.5	0.2	0.16	0.26
	Lat. + Roe + Pack	6	863.7	0.4	0.15	0.25
	Lat. + Roe + MiR	6	864.1	0.9	0.12	0.27
	Lat. + Roe + MaR	6	865.0	1.7	0.08	0.25
	Lat. + Roe + Pack + MiR	7	865.0	1.7	0.08	0.27
	Lat. + Roe + Dens. + MiR	7	865.0	1.8	0.08	0.27
OREP 100 %	Lat. + Roe + MiR	6	856.0	0.0	0.47	0.31
	Lat. + Roe	5	856.9	0.9	0.30	0.26
	Lat. + MiR	5	857.3	1.4	0.24	0.25
Kernel 95 %	Lat. + Roe + Pack	6	845.4	0.0	0.40	0.27
	Lat. + Roe	5	846.6	1.2	0.23	0.24
	Lat. + Roe + Pack + MiR	7	846.7	1.2	0.22	0.29
	Lat. + Roe + MiR	6	847.3	1.8	0.16	0.26

Only models with Δ corrected Akaike's information criterion (AIC_c) < 2 are shown. Pack identity was fitted as random factor in all models. R^2-values show the amount of variation explained by the fixed effects combined after excluding the random factor. For other abbreviations, see Table 1

Table 3 Summary results after model averaging the effects of each parameter on annual home range size ($n = 63$) in wolves using three different methods of range estimation (MCP, OREP and kernel)

Method	Parameter	Relative importance	Estimate[a]	Unconditional SE	Confidence interval	
					Lower	Upper
MCP 100 %						
	(Intercept)		1,025.6	70.01	888.4	1,162.9
	Latitude	1.00	641.5	166.96	314.3	968.8
	Roe deer index	1.00	−399.4	171.88	−736.3	−62.5
	Wolf density	0.40	−157.2	104.11	−361.3	46.9
	Pack size	0.39	−128.0	91.02	−306.3	50.4
	Minor roads	0.27	148.9	139.51	−124.6	422.3
	Major roads	0.08	116.3	131.85	142.1	374.72
OREP 100 %						
	(Intercept)		991.7	64.55	793.7	1,053.2
	Latitude	1.00	587.5	161.69	270.6	904.4
	Roe deer index	0.76	−311.4	162.90	−630.7	7.9
	Minor roads	0.70	226.5	126.11	−20.7	473.6
Kernel 95 %						
	(Intercept)		718.5	53.03	614.5	822.4
	Latitude	1.00	420.6	129.00	167.8	673.4
	Roe deer index	1.00	−275.9	136.65	−543.8	−8.1
	Pack size	0.62	−145.5	80.70	−303.7	12.7
	Minor roads	0.37	121.5	104.15	−82.6	325.6

Model-averaged parameter estimate with unconditional SE, 95 % confidence limits and the relative importance of parameters (Anderson 2008) are based on the sum of Akaike's weights across models with $\Delta AIC_c < 2$. Pack identity was fitted as random factor in all models. For abbreviations, see Tables 1 and 2

[a] Effect size has been standardized on 2 SD following Gelman (2008)

2007). Resource availability is generally believed to be the driving force explaining variation in animal home range size (Burt 1943) and these observations were mainly explained by decreased primary productivity and prey biomass with increasing latitude. Jedrzejewski et al. (2007) found that range size increased with latitude, also independently from prey density on a large geographical scale. In our study area, the decrease in primary productivity with latitude was not reflected in a decrease in ungulate biomass but rather represented a noticeable environmental gradient from a mosaic of open cultivated land and forest in the south, to a more homogeneous coniferous taiga with increasing elevation range and winter snow depths in the north. This suggests that a different mechanism other than pure prey biomass is likely to drive variation in home range size among Scandinavian wolves.

Applying Scandinavian wolf home ranges on to a North American data set (Fuller et al. 2003) showed an interesting deviation from the general pattern. Average home range size in Scandinavia was much larger than in North American areas with corresponding levels of prey biomass (Fig. 4). Moose are the main prey species for a large part of the Scandinavian wolf population (Sand et al. 2005, 2008)

except for some few packs where roe deer are their main prey. Even if we excluded packs where wolves were known to primarily feed on roe deer, Scandinavian home ranges remained an outlier. This shows that prey biomass is not a limiting factor for Scandinavian wolves, further supported by the fact that the space-restricted wolf population on Isle Royale can survive within ranges one third of the size of those documented in our study, although prey (moose) density is similar and pack sizes generally larger (Sand et al. 2012). An alternative explanation could be that home range size reflects prey availability rather than prey biomass. However, Scandinavian wolves preying on moose strongly select for calves (Sand et al. 2005, 2008) and because of a highly selective hunter harvest regime, the moose population contains a relatively high proportion of calves compared to North American populations (Sand et al. 2012). Therefore, it is not likely that variation in prey availability of moose can explain the observed deviation of mean home ranges size of wolves in Scandinavia either (Fig. 4). Prey choice is more likely to be an important source of variation in home range size within the Scandinavian wolf population. Even though moose density was a poor predictor of home range size, an effect of prey density
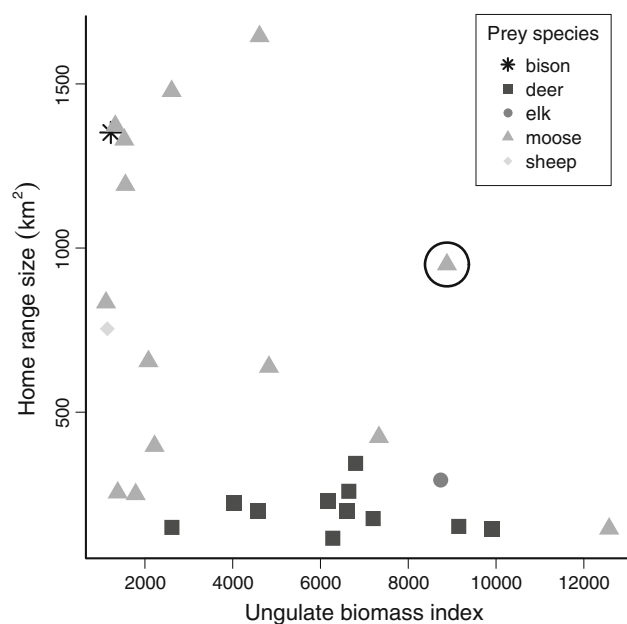
Fig. 4 Mean home range size (MCP) of wolf populations in relation to ungulate biomass. North American data from Fuller et al. (2003 Table 6.3), with the inclusion of Scandinavia (*encircled*; this study). *Symbols* indicate the main prey species for the wolf population. In Fuller et al. (2003), density of each ungulate species was multiplied by a relative index depending on size. Roe deer were not present, so a relative index of 0.5 was given for roe deer in the Scandinavian data

was apparent when considering only the smaller ungulate prey species, the roe deer.

Wolves are flexible and opportunistic predators (Peterson and Ciucci 2003; Gurarie et al. 2011) and Scandinavian wolves are likely to prey on roe deer opportunistically. A switch of main prey species from moose to the smaller roe deer may thus be expected with an increasing roe deer density (Eklund 2012), possibly explaining the decrease in home range size at lower latitudes (Fuller et al. 2003). Whereas the predation patterns on moose are strongly influenced by both age of the moose and habitat characteristics (Wikenros et al. 2009; Sand et al. 2005, 2008; Gervasi et al. 2013), the small size of the roe deer may not require selection either for certain individuals or for specific habitats. If prey availability rather than abundance is important (Rich et al. 2012), the lack of response in home range size to moose density may partly be explained by the relation between predation success and habitat (Gervasi et al. 2013).

Home ranges at higher elevations were larger, suggesting that elevation has some influence on wolf movement pattern. Within our study area, higher elevation is correlated with rugged habitat and with latitude. In the south the landscape is almost flat while further north the topography becomes increasingly broken and steep. These habitat features may have an effect both on wolf movement behaviour and on the behaviour of the prey and the

accessibility of prey for wolves. Rich et al. (2012) suggested that increased difficulties in hunting deer explained the positive correlation between wolf home range size and a ruggedness index. It is also possible that latitude, and elevation, reflect a gradient in the density of some smaller (non-ungulate) prey species that we were not able to measure. Although there is no evidence that these non-ungulate species constitute major parts of the wolf's diet, they may have more subtle influences in some key periods or on larger scale movement patterns.

The Scandinavian wolf population has constantly increased during the years of the study and an effect of population density on home range size was expected but not observed. The lack of a density effect, in contrast to observations in several other carnivore species (Dahle and Swenson 2003; Benson et al. 2006) including wolves (Fritts and Mech 1981; Hayes and Harestad 2000; Rich et al. 2012), suggests that the population is still in a re-colonizing phase and has not yet reached the threshold where density has become a limiting factor on space use. This may be further supported by the low number of observed intraspecific killings among Scandinavian wolves (Wabakken et al. 2009) compared to North America (Mech 1994; Mech and Boitani; 2003; Adams et al. 2008). Still, some packs in the centre of the Scandinavian wolf range had up to five neighbouring packs, which may be expected to have a limiting effect on space use. The inverse effect of density may, however, be masked by some of the smallest home ranges being isolated from the main population's distribution (Fig. 1). The apparently low intra-specific competition observed between the Scandinavian wolves is likely contributing to a low cost of maintaining large home ranges for the wolves.

Following Powell (2000) an animal's home range should not be larger than the size at which the benefits received exceed the cost of maintaining it. Linear elements (such as gravel forest roads and conventional seismic lines) have been shown to facilitate wolf movement when used as low-energy travel paths (Eriksen et al. 2009; Gurarie et al. 2011; Latham et al. 2011). High densities of these elements may reduce the cost of keeping a large home range, thus explaining the positive correlation between home range size and minor roads. Alternatively, this correlation could be a response to more human disturbance (Rich et al. 2012), but as most minor roads are only occasionally used by loggers, hunters, and for other recreational use, this explanation is less likely.

Previous research has shown that Scandinavian wolves choose to settle in areas of continuous conifer forest, rich in prey but with low densities of urban areas, roads and cultivated land (Karlsson et al. 2007). However, the increase of the Scandinavian wolf population has since resulted in increasingly more packs in close proximity to areas of high

anthropogenic influence. This exposure may result in a behavioural adaptation of wolves to human presence (Gurarie et al. 2011; Bateman and Fleming 2012). Our results show that home ranges were, in general, much smaller in more developed areas (i.e. areas with high roe deer density) suggesting that the resource quality in some areas is high enough to allow for a rather drastic decrease (<85 %) in range size but is still sufficient to support successful reproduction among the wolves. Smaller home ranges in human-inhabited areas allow for higher wolf densities with the potential to trigger an increment in human-wolf conflict in the future. There is likely to be a major debate in the near future about the desired distribution of wolves given that the social conflicts with wolves are already intense (Skogen et al. 2013), and that political goals call for a further increase in wolf numbers in Scandinavia.

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Supplementary tables

Table S1. Raw data showing annual home range size, social organisation and monitoring details of wolves analysed in this paper. Only annual home ranges including ≥ 9 months of monitoring were included. All collared wolves were adult resident individuals. Annual ranges in italic were removed as outliers.

Territory	Year	Home range (km²)[1]			Social org. [2]			Monitoring details[3]		
		MCP	OREP	Kernel	Status	Rep.	No.	Ind.	Collar	Loc.
Aamäck	2008-09	1145	1145	944	Pack	Y	5	Fe	GPS	989
Amungen	2005-06	1475	1475	1309	Pack	Y	7	Fe	GPS	818
	2006-07	1243	1243	833	Pack	Y	4	Fe	GPS	459
Bograngen	2000-01	423	374	358	Pack	N	3	Fe/M	VHF	284
	2001-02	720	433	516	Pair	N	2	Fe/M	VHF	210
	2002-03	1211	842	682	Pack	N	3	Fe/M	GPS	3100
Dals Ed-Halden	2002-03	674	559	507	Pack	Y	5	M	VHF	403
Djurskog	2003-04	336	336	221	Pack	Y	5	Fe	GPS	1580
	2004-05	385	385	260	Pack	Y	8-9	Fe/M	GPS	1974
Fulufjället	2009-10	904	690	411	Pack	Y	9-10	Fe/M	GPS	2961
Glaskogen	2002-03	1109	675	734	Pack	N	2	Fe	VHF	147
Grangärde	1999-00	1220	1008	999	Pair	N	2	M	VHF	1849
	2000-01	888	643	567	Pack	Y	5	Fe/M	VHF	759
Gräsmark	2006-07	1607	1607	1088	Pack	Y	5-6	Fe/M	GPS	4615
	2007-08	1638	1638	1089	Pack	Y	5	M	GPS	1517
Gråfjell	2001-02	1476	1273	951	Pack	Y	3	Fe/M	GPS	6470
	2002-03	1310	1116	765	Pack	Y	6	Fe/M	GPS	3651
	2003-04	1268	1268	689	Pack	Y	7	Fe/M	GPS	4538
	2004-05	811	811	481	Pack	Y	6-7	M	GPS	1572
Halgån	2003-04	738	738	466	Pair	N	2	Fe	GPS	1756
	2004-05	784	784	541	Pack	Y	6	Fe	GPS	652
	2006-07	927	927	766	Pack	Y	4-5	Fe	GPS	708
	2007-08	1199	1199	894	Pack	Y	4-5	Fe	GPS	795
Hasselfors	2001-02	793	793	413	Pack	Y	7-8	M	VHF	2156
	2002-03	597	425	313	Pack	Y	4-5	M	VHF	2555
Hedbyn	2010-11	1036	951	830	Pair	N	2	Fe	GPS	1511
Juvberget	2005-06	1341	1115	1083	Pair	N	2	Fe	GPS	863
	2006-07	1276	1113	898	Pair	N	2	Fe	GPS	1101
	2007-08	1211	1043	942	Pair	N	2	M	GPS	950
Kilsbergen	2005-06	750	750	658	Pack	Y	8	M	GPS	616
Kloten	2008-09	576	576	387	Pack	Y	6	Fe	GPS	1150
	2009-10	719	719	452	Pack	Y	6	Fe/M	GPS	3377
Koppang	*2004-05*	*3525*	*3525*	*2164*	*Pair*	*Y*	*2*	*Fe/M*	*GPS*	*7119*

Table S1 continues:

Territory	Year	Home range (km^2)[1]			Social org. [2]			Monitoring details[3]		
		MCP	OREP	Kernel	Status	Rep.	No.	Ind.	Collar	Loc.
Leksand	1999-00	953	799	843	Pack	N	3	Fe	VHF	236
	2000-01	1294	1073	1246	Solitary	N	1	Fe	VHF	185
	2001-02	768	652	684	Pair	N	2	Fe	VHF	138
	2002-03	948	948	712	Solitary	N	1	M	VHF	134
Mangen	2002-03	1394	640	729	Pair	N	2	M	VHF	168
	2003-04	892	754	560	Pair	N	2	Fe	GPS	2163
	2004-05	789	644	626	Solitary	N	1	Fe	GPS	1150
Moss	2000-01	684	684	294	Pack	Y	5	M	VHF	2679
Nyskoga	2000-01	855	577	519	Pack	Y	4	Fe/M	VHF	506
	2001-02	1561	1561	1180	Pack	Y	8	Fe/M	VHF	367
	2002-03	1666	1666	1465	Pack	Y	6	M	GPS	179
Riala	2009-10	246	246	120	Pair	N	2	M	GPS	892
	2010-11	271	271	162	Pack	Y	5	Fe	GPS	1946
Rotna	2004-05	1274	1274	784	Pair	N	2	M	GPS	3896
Tenskog	2010-11	1676	1676	1037	Pair	N	2	Fe	GPS	1611
Tyngjsö	2001-02	1349	1349	971	Pack	Y	6	Fe/M	GPS	3212
Ulriksberg	2001-02	1783	1425	1562	Pair	N	2	M	VHF	214
	2002-03	1743	1245	1396	Pair	N	2	Fe/M	VHF	344
	2004-05	*2589*	*1905*	*1677*	*Solitary*	*N*	*1*	*M*	*VHF*	*577*
	2006-07	906	906	670	Pack	Y	7	Fe/M	GPS	2040
	2007-08	904	904	654	Pack	Y	5-6	Fe	GPS	800
Uttersberg	2005-06	399	399	284	Pack	Y	9	M	GPS	3373
	2006-07	329	292	300	Pack	Y	5	Fe	GPS	1251
	2007-08	399	328	307	Pair	N	2	Fe/M	GPS	1480
	2008-09	406	406	304	Pack	Y	4-5	M	GPS	767
Årjäng	2000-01	1882	1882	1080	Pack	Y	6	Fe/M	VHF	1087
	2001-02	1153	901	684	Pack	Y	8-9	Fe/M	VHF	415
	2002-03	1704	1219	1349	Solitary	N	1	Fe	VHF	142

[1] Estimated as Minimum Convex Polygons 100% (MCP), Objective Restricted Edge Polygon 100% (OREP: concave polygons), Fixed Kernel 95 % (Kernel)

[2] Occurrence of reproduction in summer of that year (Rep.: Yes or No), Mean number of wolves snow tracked during winter (No.)

[3] Indicates which individual that was collared within the pack (Ind.), what type of collar that were used (Collar); and total number of GPS/VHF locations (Loc.)

Table S2 Mean and range of the variables used in analyses of annual home range size (OREP, $n = 63$) in Scandinavian wolves in 2002-2011.

Variable	Mean	SD	Min	Max
Roe deer density (roe deer harvest km^{-2})	0.2	0.2	0.01	1.0
Main roads (km road km^2)	0.23	0.08	0.09	0.64
Main roads (density index)	1.5	0.7	0.7	5.4
Minor roads (km road km^2)	0.93	0.17	0.5	1.2
Minor roads (density index)	2.3	0.4	1.2	3.1
Pack size	4.3	2.3	1	10
Latitude (°N)	60.3	0.7	58.9	61.7
Wolf density (No. of neighboring packs)	1.3	1.1	0	5
Elevation (mean in home range [m])	298	133	42	677
Open cultivated land (%)	2.6	4.2	0.1	23

Table S3 Correlation between home range size ($n = 16$) in Scandinavian wolves and prey density (individuals km^{-2}). Values in brackets exclude two packs mainly feeding on roe deer, thus 14 packs mainly feeding on moose remain.

Range	Roe deer[*]		Moose	
	r^2	P	r^2	P
MCP	0.53 (0.42)	< 0.001 (0.007)	-0.04 (-0.05)	0.5 (0.5)
OREP	0.41 (0.26)	0.005 (0.04)	-0.07 (-0.08)	0.9 (1.0)
Kernel	0.41 (0.21)	0.004 (0.06)	-0.07 (-0.08)	0.8 (0.9)

[*]Log transformed

Table S4 Correlation index (Pearson's) between fixed variables used to explain variation in wolf annual home range size (HR).

	HR	Roe	MR	MiR	PS	Lat	WD	Ele
Roe deer (Roe)	-0.5							
Main roads (MR)	-	0.4						
Minor roads (MiR)	-0.2	0.6	0.6					
Pack size (PS)	-0.2	0.1	.	.				
Latitude (Lat)	0.4	-0.7	-0.4	-0.6	-0.1			
Wolf density (WD)	-	-0.4	-0.3	-0.3	-	0.2		
Elevation (Ele)	0.4	-0.8	-0.5	-0.7	-	0.9	0.2	
Open land	-0.4	0.8	0.5	0.9	-	-0.6	-0.3	-0.7

Electronic Supplementary Materials
J. Mattisson*, H. Sand, P. Wabakken, V. Gervasi, O. Liberg, J.D.C. Linnell, G. R. Rauset, H. C. Pedersen. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. *Corresponding author: jenny.mattisson@nina.no

Appendix 1

Analyses of annual range estimates

The number of locations required to accurately determine home range size has been frequently discussed but with inconsistent results (see Laver and Kelly 2008). Sampling frequency can severely influence estimates of space use patterns (Mills et al. 2006; Girard et al. 2002) and to accurately determine home range size it is important to consider both the number of locations and the sampling duration. For species with very large home ranges that typically takes many days or weeks to traverse and an increased duration of the study period can counteract a lower frequency of locations but a high frequency of locations may not counteract a minimum duration. Börger et al. (2006) suggest that following a greater number of individuals over a longer time span is preferable to increasing sampling frequency.

In order to determine how many months of data collections that was required to accurately estimating an annual wolf home ranges in our study area we used R (R Development Core Team 2011) and the R package *adehabitatHR* (Calenge 2006). We created individual ranges using 100% Minimum convex polygon starting with all data (i.e. 12 months) and then subsequently resampled the data by removing 1 random month at a time. We created up to 200 ranges per individual and number of months (1-11 months) using different combinations of monthly location data.

We used a subset of the data which included 34 individual wolf years, all with 12 months of data and a least 5 locations per month (minimum required for *adehabitat* to create a home range) after extreme outliers were removed. The number of locations ranged from 5 to 1264 per month and from 138 to 6470 for the whole year. The results were plotted for each individual using box plots (Fig. A1). We calculated mean home range size per set of months (1-11) separately for each individual wolf year. Based on these mean values we estimated the mean proportion of the complete annual range (12 months) by the number of months included in the range estimation. We decided that a cut-off of a 10 % maximum loss in range size for the majority of individuals (>25th quartile) was acceptable for estimating an annual home range. After plotting the proportion of decrease in range size from an annual range (see Fig. 2 in main paper), we estimated that a minimum of 9 months of data was required to adequately represent an annual range. Because the analyses were done on a dataset with a wide range in sampling frequency, expected variation dependent on the number of locations used were automatically included. We conclude that the duration of sampling is more important than sampling frequency for a reliable estimate of an annual home range (see also Börger et al. 2006).

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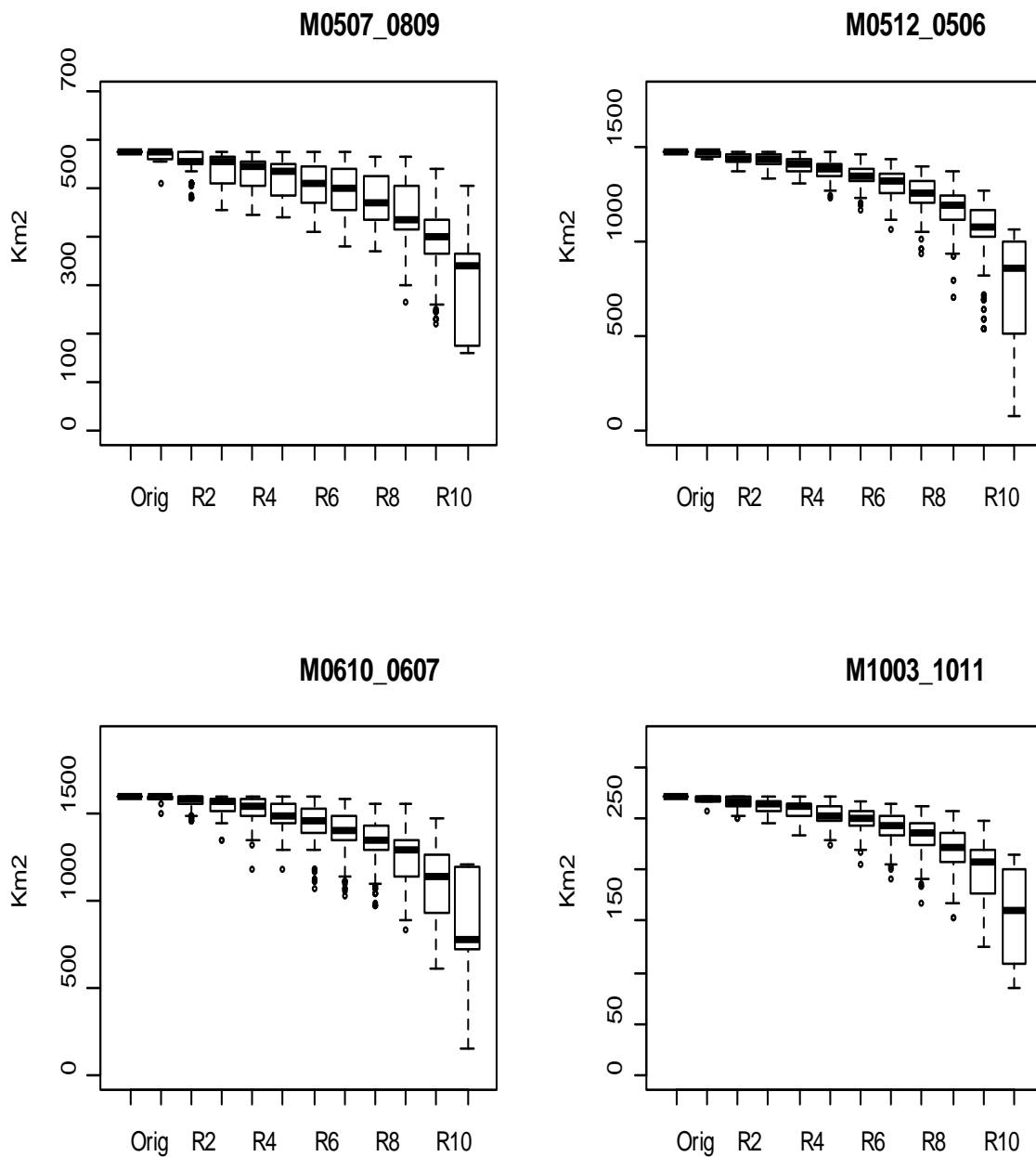
Fig. S1 Four examples, with different annual home range size, showing the decrease in range size when number of sampling month was reduced (Orig =12 months of data). (The x-axis represent the number of months removed (1-11) i.e. R2= 2 months removed = 10 months of data. The values represent ≤200 simulations of randomly selected ranges for different combinations of monthly location data. Note: The scales on the Y axis are not similar among the graphs.

The script is available on request (geir.rauset@slu.se).