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

3

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¹ Author contribution: HS, OL, HCP, PW and JDCL have at various stages been responsible for coordinating the project within their respective institutions. PW, HS, HCP and OL initiated and planned the study. HS, OL and PW were responsible for field work and data collection. JM and HCP compiled and organised the data. JM and VG formalised the analytical and statistical design. JM performed the statistical analyses except the part in figure 2 and appendix 1 which was performed and designed by GRR. JM wrote the first draft of the manuscript; All authors contributed to fruitful discussions on manuscript drafts.

16 **Abstract** Home range size in mammals is a key ecological trait and an important parameter in
17 conservation planning, and has been shown to be influenced by ecological, demographic and
18 social factors in animal populations. Information on space requirements is especially
19 important for carnivore species which range over very large areas and often come into direct
20 conflict with human interest. We used long term telemetry-location data from a recovering
21 wolf population in Scandinavia to investigate variation in home range size in relation to
22 environmental and social characteristics of the different packs. Wolves showed considerable
23 variation in home range size, from 259 km² to 1676 km². Although wolf density increased
24 fourfold during the study period, we found no evidence that intraspecific competition
25 influenced range size. Local variation in moose density, which was the main prey for most
26 packs, did not influence wolf home range size. Home ranges increased with latitude and
27 elevation and decreased with increased roe deer density. Although, prey biomass alone did not
28 influence range size, our data suggest that there is a correlation between habitat
29 characteristics, choice of prey species and possible hunting success, which currently combine
30 to shape home range size in Scandinavian wolves.

31

32 **Keywords** *territory, Canis lupus, prey density, population density*

33

34 **Introduction**

35

36 Home range size is one of the most fundamental ecological parameters that can be described
37 for any given species and can be viewed as a trade-off between resource access and energetic
38 costs. The minimum size of an animal's home range is fundamentally determined by the
39 ability to obtain enough food resources for survival and to secure successful reproduction
40 (Burt 1943) but the actual use of space is influenced by a far more complex array of factors.

41 Range use in mammals appears to be influenced by a combination of ecological and social
42 factors, including not only resource abundance and prey predictability (Loveridge et al. 2009),
43 but also environmental productivity (Herfindal et al. 2005), body mass (Harstad and Bunell
44 1979; Swihart et al. 1988, but see Nilsen and Linnell 2006), population density (Dahle and
45 Swenson 2003; Benson et al. 2006), migration of prey (Mech and Boitani 2003), social
46 organization (Peterson et al. 1984; Loveridge et al. 2009), population stage or phase of
47 colonisation (Okarma et al. 1998; Fuller et al. 2003; Mech and Boitani 2003), anthropogenic
48 influence (Rich et al. 2012) and individual variation (Jedrzejewski et al. 2007; van Beest et al.
49 2011).

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

63 The aim of this study was to determine the influence of ecological and social factors in
64 shaping home range size in a large carnivore, the wolf (*Canis lupus*). The wolf is a well-
65 studied territorial, group-living species (Harrington 1987; Vilà et al. 1994; Mech and Boitani

66 2003; Zub et al. 2003) that often uses much larger areas than expected from its body size
67 (Harestad and Bunell 1979). Wolves display a large variation in home range size both
68 between and within populations. Although there is a general understanding of large scale
69 variation in wolf home range size (see reviews in Fuller et al. 2003; Nilsen et al. 2005;
70 Jedrzejewski et al. 2007), the underlying mechanisms causing finer scale variation within
71 populations is poorly understood (Rich et al. 2012, Gurarie et al. 2011; Fritts and Mech 1981;
72 Hayes and Harestad 2000). On a global scale, wolf home range size has been shown to relate
73 negatively to prey biomass and wolf density whereas pack size, latitude, and human density
74 tend to correlate with larger home ranges (Ballard et al 1987; Wydeven et al. 1995; Okarma et
75 al. 1998; Fuller et al. 2003; Jedrzejewski 2007; Rich et al. 2012). However, the results have
76 not been consistent between studies suggesting that the mechanisms shaping home ranges are
77 complex and likely to be influenced by several interacting social and ecological factors.

78 Prey biomass, for example, is expected to have a negative influence on home range size
79 alone but the predictability and availability of prey (Rich et al. 2012), the choice of prey
80 species (Fuller et al. 2003) and landscape features correlated with hunting success (Kauffman
81 et al. 2007; Rich et al. 2012; Gervasi et al. *in press*) may play an equally important role in
82 modulating this effect. Wolves preying on small to medium sized ungulates have in general
83 smaller ranges and a stronger correlation between range size and prey density than those
84 preying on large ungulates (moose *Alces alces* or bison *Bison bison*; Wydeyen et al. 1995;
85 Fuller et al. 2003). Landscape features, such as ruggedness, may facilitate predation and
86 therefore increase the prey biomass available to wolves resulting in smaller home ranges, but
87 can also act as a refuge for the prey with the opposite result (Rich et al. 2012).

88 Although access to food resources is believed to be a key factor in determining home range
89 size, social factors can be equally important, especially in a territorial species. Within
90 populations, harvest of wolves has been shown to increase home range size by creating social

91 disturbance in the packs, (Rich et al. 2012), whereas an increase in population density reduced
92 range size as an effect of enhanced inter-territorial competition (Fritts and Mech 1981; Hayes
93 and Harestad 2000), given that at least part of the population is approaching saturation. In
94 addition, many species show high intraspecific variability in home range size, where a
95 substantial part of the variation is related to individual differences (Loveridge et al. 2009, van
96 Beest et al. 2011).

97 Using the Scandinavian wolves as the study species gave us the opportunity to analyze
98 space use in a recovering wolf population. In addition to a large telemetry-based dataset from
99 43 resident, scent-marking wolves in 1999-2011, extensive national monitoring systems in
100 Norway and Sweden have tracked the establishment of wolf packs during the process of re-
101 colonisation and generated a near complete overview of the population's density and
102 distribution (starting in 1983 with the first confirmed reproduction; Wabakken et al. 2001;
103 Vilà et al. 2003; Liberg et al. 2005). The growing wolf population on the Scandinavian
104 Peninsula (had reached ~300 wolves by 2011; Wabakken et al. 2011) not only gives us the
105 possibility to study the influence of social dynamics and increasing inter-pack competition but
106 generated an extensive variability in ecological factors within the study area. The northern
107 geographical location of the Scandinavian Peninsula displays a distinct latitudinal gradient
108 (mild coast to continental interior) even within the relatively small area used by the wolf
109 population. In addition, we examined the influence of ungulate prey density, prey choice, and
110 landscape-prey related factors on home range size using density estimates of ungulate prey in
111 a multi-ungulate prey ecosystem.

112 First, we explored the effect of prey density on wolf home range size which is expected to
113 be negatively correlated if space use is mainly shaped by resource abundance. We did this for
114 the two main prey species (moose and roe deer *Capreolus capreolus*; Sand et al. 2005, 2008)
115 combined and separately, in order to detect potential effects of the large body size differences

116 between these two prey species on shaping home ranges. Secondly, we tested for the
117 influence of environmental features on range size, and discuss them in relation to correlated
118 productivity, prey availability, and anthropogenic impact and their possible influence on wolf
119 behaviour. In addition, we included social factors (wolf density, social organisation within
120 packs) to investigate the influence and strength of social dynamics in comparison to the
121 ecological factors.

122

123 **Materials and Methods**

124

125 Study area

126

127 The study area is located across the south-central parts of Sweden and Norway on the
128 Scandinavian Peninsula (Fig. 1; 59°-62°N, 11°-19°E). The area primarily consists of
129 intensively managed boreal coniferous forest interspersed with bogs and lakes. Norway
130 spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) are the dominant tree species, mixed
131 with varying amounts of birch (*Betula pendula* and *B. pubescens*), aspen (*Populus tremula*)
132 and alder (*Alnus incana* and *A. glutinosa*). Intensive forest management has created an
133 extensive network of forest gravel roads throughout the area. The influence of infrastructure
134 and the proportion of agricultural land in the landscape increases in the south-western, eastern
135 and southern parts of the study area while elevation range increase towards the north-west
136 reaching up to 1750 m a.s.l.. Human density in Scandinavia averages 17 humans km⁻², but
137 large parts of the wolf range have less than 1 human km⁻² (Swedish National Atlas 1991;
138 Statistics Norway 2003). The climate is continental with average temperatures of -7C° in
139 January and 15C° in July. The ground is usually snow covered between December and March
140 with a general snow depth of 30 to 60 cm in mid-winter (Swedish National Atlas 1991;

141 Statistics Norway 2003). Moose and roe deer are the two most common ungulates within the
142 wolf range and are by far the main prey for the Scandinavian wolves (Sand et al. 2005, 2008).
143 All wolves had access to both species but with a spatial variation in densities and ratio
144 between the two species. Red deer (*Cervus elaphus*), wild reindeer (*Rangifer tarandus*),
145 fallow deer (*Dama dama*) and wild boar (*Sus scrofa*) occurred locally, but have not been
146 observed as important prey species among the studied packs.

147

148 Study animals and data collection

149

150 We used location data on wolves monitored within the on-going Scandinavian Wolf Research
151 Project (<http://skandulv.nina.no>) between 1999 and 2011. Wolves were immobilised from
152 helicopters following continuously updated veterinary procedures (Arnemo et al. 2011) and
153 equipped with either a VHF radio collar (Telonics Mod. 500, Mesa Arizona), a GPS remote
154 downloadable collar (GPS-Simplex, TVP Positioning AB, Lindesberg, Sweden) or a GPS-
155 GSM collar (Tellus, TVP Positioning AB; GPS-plus, Vectronic Aerospace, Berlin, Germany).
156 The capture methods were approved by the Swedish Animal Welfare Agency and the
157 Norwegian Experimental Animal Ethics committee. For more detailed description of capture
158 and handling see Sand et al. (2006). Location data from VHF-collars were collected from the
159 ground or from a fix-winged airplane at least once per week and GPS-collars were
160 programmed to take a location 2-6 times per 24-hour. Location frequency was increased up to
161 one location every half hour during intensive study periods (Sand et al. 2008). Only data from
162 adult resident, scent-marking individuals were used in the analyses and each “pack” was
163 classified according to their social organisation: solitary (one wolf), pair-living (two scent-
164 marking wolves) or pack-living (3-10 wolves). Scandinavian wolf packs are in general small,
165 consisting of an adult male and female with or without pups of the year. Offspring older than

166 one year rarely stay with the parents. Reproductive status in summer was estimated from a
167 combination of pre- and post-reproduction intensive monitoring of movement patterns by
168 adult radio collared wolves during the parturition period. Successful reproduction was later
169 confirmed by observations of pups or their signs (Alfredéen 2006) and occasionally by
170 examinations of dens or rendezvous sites. The minimum number of wolves within each pack
171 (pack size) was estimated by comprehensive and repeated snow-tracking and faecal DNA
172 monitoring during a five months period each winter as a part of national surveys of wolves
173 (see below under wolf density).

174

175 Estimations of home range size

176

177 Available location data for each pack varied greatly in duration (number of days) and
178 location frequency. Analyses of annual home range size against number of months of data
179 collection indicated that a minimum of nine months with ≥ 5 locations per month was
180 necessary to estimate an annual home range (Fig. 2). Detailed methodology for this
181 conclusion is provided in the Electronic Supplementary Materials (ESM; Appendix 1). Only
182 annual home ranges that fulfilled these requirements were used in further analyses. Sufficient
183 data was available for 43 wolf individuals belonging to 28 different packs (ESM: Table S1).

184 Wolf home ranges were estimated according to their biological cycle starting from May 1st
185 (time of birth; Alfredéen 2006) until April 30th the next year. When possible, we estimated
186 several annual ranges per pack ($n_{\text{total}} = 63$). Extreme outliers and extra-territorial forays were
187 removed before running the analyses (0.3% of all locations). No differences in space use were
188 found between the female and male wolves in a pack when both were collared
189 simultaneously (paired t-test; $t_{19} = 0.9167$, $P = 0.37$, $n = 20$), thus the data was pooled in
190 subsequent analyses. The social organisation (i.e. “solitary”, “pair” or “pack-living”) of the

191 wolves within a specific pack may have changed between years but the approximate
192 geographical placement was always the same. Partial turnover (one of the individuals
193 replaced) occurred on a few occasions between years. If there was a complete turnover the
194 new wolves were given a new pack name even if the “new” pack had approximately the same
195 geographical location

196 We used three different home range estimators: (i) Minimum Convex Polygon (MCP
197 100% of locations; Mohr and Stumpf 1966), (ii) Objective Restricted Edge Polygon (OREP
198 100%) and (iii) Fixed kernel (95%; Seaman and Powell 1996) with the smoothing multiplier
199 set to 1. All estimates of home range size were obtained using Ranges8 software (v2.7,
200 Anatrack Ltd, Wareham, UK). OREP can be described as a concave polygon and was used
201 because it better described non-linear shaped outlines of an animal’s range than MCP’s and
202 thereby excludes areas not being used by the animal (Getz et al. 2007). Ranges defined by
203 OREPs are equivalent to the local nearest neighbour Convex Hull method (Getz and Wilmers
204 2004), but with an objective choice of the edge-restriction distance, here set to a kernel-based
205 outlier exclusion distance (Ranges8). For methods (i) and (ii) the full data set with all
206 available locations was used. A reduced dataset (maximum of 2 randomly selected locations
207 per calendar day) was used for method (iii) as kernel smoothing is strongly influenced by
208 sampling frequency (Seaman et al. 1999).

209

210 Wolf density

211

212 National wolf population surveys have been conducted in both Sweden and Norway (by
213 county and national wildlife management agencies and staff from several universities and
214 research institutes) every year during this study (Wabakken et al. 2011). These annual
215 population surveys were based on intensive snow-tracking and generated a near complete

216 description of the spatial distribution of existing wolf pairs, packs and stationary solitary
217 individuals each winter, as well as an estimate of population size. We used local density of
218 packs as a proxy for analyzing effect of wolf density on home range size. Centre points
219 (north and east coordinates) were available from the surveys for all packs including both
220 marked and unmarked wolves (based on snow tracking). We used a 40 km radius (i.e. two
221 times the radius of a large home range in this study) buffer zone around the centre point of
222 each pack in the study to estimate the number of neighbouring packs (both marked and
223 unmarked), i.e. pack density.

224

225 Prey density

226

227 To estimate winter density of moose and roe deer, pellet count surveys were conducted
228 during one unique year for 15 of the packs (1 pack was surveyed in 2 years). In each home
229 range, a grid of 1x1 km squared plots was systematically distributed over the area (about 50-
230 100 plots per home range). Each square plot contained 40 circular sub-plots along its
231 perimeter, each of them covering 100 m² for moose and 10 m² for roe deer. All sample plots
232 were surveyed in spring, after snow melt. During data collection, we looked at the pellets'
233 structure, consistency, color, and their position in relation to the vegetation in order to include
234 only new pellet groups i.e., produced after leaf fall the previous autumn. Winter density of
235 moose and roe deer (individuals km⁻²) was estimated by dividing mean pellet group counts for
236 all sample plot by period of accumulation (days between leaf fall and field count: 198-231
237 days) and assumed defecation rate (roe deer: 22 day⁻¹ Cederlund and Liberg 1995; moose: 14
238 day⁻¹ Rönnegård et al. 2008). During the study period, roe deer and moose populations in
239 Scandinavia have been fluctuating due to changes in harvest policy, winter conditions,
240 forestry strategies and predation pressure (Lavsund et al. 2003, Grøtan et al. 2005). These

241 fluctuations discourage the extrapolation of density estimates from one year to another,
242 resulting in an incomplete dataset of prey density estimates. Before proceeding, we
243 investigated possible influences of winter prey densities on home range size using the limited
244 data in a set of simple linear regression models. Data on prey choice was available for each of
245 the sampled packs (Sand unpublished, c.f. Sand et al. 2005; 2008). Wolves preyed mainly on
246 moose (73-100 % of ungulate kills) except in two packs where roe deer was the main prey (71
247 and 98 %). We evaluated the importance of moose and roe deer density for the total dataset (n
248 = 16), and for a subset of the packs where moose dominated the diet of wolves ($n=14$). These
249 analyses revealed a negative correlation between roe deer density and home range size but no
250 correlation with moose density, irrespectively of the main prey species (see results). With this
251 information, we decided to include only an index of roe deer density (and not moose), based
252 on annual hunting statistics, in the proceeding multivariate analyses. Previous research has
253 indicated that hunting bag statistics are a reliable index of ungulate density under
254 Scandinavian conditions (Solberg et al. 1999; Grøtan et al. 2005). The use of hunting bag
255 statistics as an index of roe deer density was supported by a strong positive correlation with
256 density based on pellet counts (Spearman correlation = 0.83, $n = 16$). Consequently, we
257 expect hunting bag statistics to accurately reflect temporal and spatial variation in roe deer
258 density for our data.

259 Annual hunting bag statistics were available at municipality level in Norway (Statistics
260 Norway; www.ssb.no) and at hunting district level in Sweden (Liberg, unpublished). A
261 separate map was produced for each year with the number of roe deer shot km^{-2} estimated for
262 each Norwegian municipality or Swedish district excluding water bodies. An index of roe
263 deer density per annual home range was extracted using area weighted means (AWM) in
264 Hawth's tools (Beyers 2004), ArcGIS v 9.3 (ESRI, Redlands, CA, USA). We lacked data from
265 a few districts or municipalities for some of the years. If the area of missing data was < 50 %,

266 we estimated AWM on the existing data (10 home ranges with partial missing data). When
267 exceeding 50 %, we used the average value from the previous and the subsequent year of data
268 (4 home ranges).

269

270 Environmental data

271

272 As an index of increasing human influence on the landscape, the proportion of open cultivated
273 land below the altitudinal tree line (agricultural land, orchards, fields or other types of
274 cultivated land) was calculated from a vegetation map (Swedish Corine land cover map
275 Lantmäteriet, Sweden, 25^x25 m merged with Northern Research Institute's vegetation map,
276 Norway, 30^x30m into a 25^x25m raster). Based on national road maps (Road map 1:100 000,
277 Lantmäteriet, Sweden; N50 kartdata, Statens kartverk, Norway), roads were categorised into
278 main and minor roads. In Norway, main roads included public roads (European, national,
279 county and municipal roads) which are most often paved, but sometimes narrow. Minor roads
280 included forest gravel roads which are mainly private. The Swedish categories of roads differ
281 from Norway but were converted based on existing overlaps of the two maps to fit the same
282 categories. Roads were divided into two categories, main roads (all tarred) and minor roads
283 (mostly gravel forest roads). Road density (main and minor roads separately) was calculated
284 by first converting roads to points spacing 250 m, on which a kernel density was estimated
285 with bandwidth (h) set to 1000 and raster cell size to 500 m. Mean road density and mean
286 elevation (DEM 25^x25 m; Geographical Data Sweden, Lantmäteriet; Norge digital, Statens
287 kartverk, Norway) in each home range was extracted using the National Water-Quality
288 Assessment (NAWQA) Area-Characterization tool box (Price et al. 2010. Latitude (degrees
289 north) was derived at the arithmetic mean of all locations in each home range. All GIS
290 analyses were performed in ArcGIS v 9.3.

291

292 Statistical analyses

293

294 To examine variation in annual wolf home range size we used linear mixed models (LMM) in
295 the library *nlme* (Pinheiro et al. 2010) implemented in program R (R Development Core Team
296 2011). Home range size (km²) was fitted as the response variable in all models. Two extreme
297 outliers (MCP: 3 525 and 2 589 km²) were identified and removed before proceeding with the
298 analyses. These outliers included one reproducing pack composed of a father who mated with
299 his daughter, possibly explaining the extraordinary movement patterns (Koppang, ESM:
300 Table S1; Eriksen et al. 2009), and one single wolf in a transition state after losing its partner
301 (Ulriksberg, ESM: Table S1), resulting in a 50 % increase in home range size from the
302 previous year. There was no spatial correlation between home range sizes (i.e. home ranges
303 closer to each other were not more similar in size).

304 Prior to entry into models, the fixed variables (reproduction, wolf density, social
305 organisation, pack size, area of open cultivated land, elevation, road densities, roe deer
306 density and latitude; ESM: Table S2) were assessed for multicollinearity using the variance
307 inflation factor (VIF; Zuur et al. 2009) in the R library *AED* (Zuur 2010). Pack identity was
308 fitted as a random intercept in all models to account for patterns in the residuals of the fixed
309 effects occurring due to repeated observations of the same pack. We used likelihood ratio tests
310 to evaluate if the inclusion of a random effect was indeed necessary (global model with MCP:
311 $L_1 = 18.61$, $P < 0.0001$; Zuur et al. 2009). As each pack ($n = 28$) had only a few data entries (
312 $\bar{x} = 2.2$) we were not able to fit pack identity as a random slope in the model.

313 Model selection was performed based on AIC_c , (Burnham and Andersen 2002) in the R
314 package *MuMIn* (Barton 2009). All variables were centralized and standardized with 2 SD to
315 facilitate interpretation of the relative strength of parameter estimates (Gelman 2008; Grueber

316 et al. 2011). When needed, we tested if using different transformations gave a better fit. We
317 performed model averaging, based on AIC_c with conditional standard errors and confidence
318 intervals (Burnham and Anderson 2002), as it is usually more stable than only choosing the
319 best model (Grueber et al. 2011). We choose to include models with $\Delta_i \leq 2$ as a cut off in the
320 averaging process, as these are considered to have sustainable support (Burnham and
321 Anderson 2002). A cut off of $\Delta_i \leq 4$ generated far too many models, increasing the risk of
322 spurious results from parameter estimates of models with low weight (Grueber et al. 2011).
323 To assess the amount of variation explained by the fixed effects of the models used in the
324 average model (not possible to estimate directly for the average model), we calculated R^2 as
325 the square of the correlation between the predicted values of the models, without the random
326 effect, and the observed data. R^2 for the random part was estimated by calculating the intra-
327 class correlation ρ (Rodriguez and Elo, 2003; Skrondal and Rabe-Hesketh, 2004), which
328 provides the ratio of the variance of the random effect to the total variance, and thus can be
329 interpreted as the proportion of variation explained by each individual pack. Model selection
330 and model averaging was run for all three methods of estimating home ranges (MCP, OREP
331 and Kernel) to examine whether the choice of home range estimator influences the results.

332

333

334 **Results**

335

336 We observed large variation in home range size between packs, even when excluding the two
337 outliers mentioned above (259-1676 km²; Table 1). Home ranges estimated using the MCP
338 method were significant larger than the corresponding ranges estimated with OREP (paired t-
339 test: $t_{58} = 5.38$, $P < 0.0001$) or with kernel methods ($t_{58} = 13.14$, $P < 0.0001$). There was a

340 high year-to-year stability in space use (mean overlap between annual ranges; MCP: $84 \pm 8\%$
341 SD; OREP: $81 \pm 9\%$; Kernel: $76 \pm 12\%$).

342

343 Home range size and prey density

344

345 The variation in roe deer densities across wolf home ranges ($0.0-4.0$ roe deer km^{-2} ; SE = 0.30,
346 $n = 16$) was much larger than observed for moose density ($0.86-1.74$ moose km^{-2} , SE= 0.069
347 excluding one outlier at 3.4 moose km^{-2}). Wolf home range size was not correlated with
348 moose density but was negatively correlated with roe deer density (Fig. 3). The exclusion of
349 two packs where wolves mainly preyed on roe deer did not change the observed correlations
350 (Fig 3, ESM: Table S3). The method of home range estimator did not influence the result
351 (ESM: Table S3). Average winter ungulate biomass for all home ranges was 401 kg km^{-2} (\pm
352 160 SD; based on mean weight of standing population: moose = 271 kg, roe deer = 22.6 kg;
353 Zimmerman et al. unpublished) and because of the large size difference between the prey
354 species, biomass was mainly driven by moose density. Prey biomass was stable along the
355 latitude gradient within the study area (linear regression: $r^2 = -0.07$, $P = 0.87$).

356

357 Model performance - effects on home range size

358

359 Several of the fixed variables were correlated (VIF > 3; ESM: Table S4) which required
360 caution when deciding which variables to include in the same model. For the variables
361 describing social status, we chose to keep pack size rather than social organisation (single,
362 pair or pack). Scandinavian wolf packs are small (relative to other populations) resulting in
363 reproductive status being strongly correlated with pack size (i.e. non-reproducing: pack size =
364 1-3 wolves, reproducing: 3-10 wolves) thus preventing these two variables from being

365 included in the same model. Model sets including the variable “reproduction in summer”
366 (binary) indicated that this variable was uninformative across all methods of home range
367 estimates, so we therefore retained pack size in the final models. Among the environmental
368 variables, roe deer density was negatively correlated with elevation and latitude and positively
369 correlated with increasing proportion of open cultivated land. We chose to keep roe deer
370 density and latitude in the global model, as these variables were possible to combine (VIF <
371 3). A prior examination of the roe deer density index using the global model justified the use
372 of a reciprocal transformation of the variable (roe deer: untransformed [$\Delta_i = 2.44$] or log-
373 transformed [$\Delta_i = 1.9$]).

374 According to the final models, latitude and roe deer density were the most important
375 variables explaining variation in home range size (Table 2 and 3). Home ranges decreased
376 with increasing roe deer density and increased with increasing latitude. The importance of roe
377 deer density and latitude were stable across all types of home range estimates. The density of
378 minor roads was positively related to home range size estimated by OREP’s (Table 3) and
379 was almost as important as roe deer density (Table 2) but had less effect for the other types of
380 estimates. An effect of pack size on home range size was mainly observed when using kernel
381 estimates, where range size decreased with increasing number of wolves in a pack (Table 3).
382 Local wolf density did not influence range size. To evaluate whether excluded environmental
383 variables may better explain variation in home range size than the variables chosen, we used
384 the final model for each range estimator (Table 2) and first replaced the roe deer density index
385 with proportion of open cultivated land, while keeping all other variable constant. The model
386 including roe deer density better explained variation in home range size than the model with
387 proportion of open cultivated land (MCP: $\Delta_i = 5.71$; OREP: $\Delta_i = 2.26$, Kernel: $\Delta_i = 1.68$). The
388 process was repeated with latitude replaced by elevation which improved the models across
389 all estimates (MCP: $\Delta_i = -1.19$, OREP : $\Delta_i = -1.10$, Kernel: $\Delta_i = -3.36$). Altogether, these results

390 suggest that home range size is influenced by a productivity gradient in the landscape which is
391 reflected in the density of roe deer and influenced by elevation. In addition, we observed large
392 inter-pack variation in home range size (i.e. R^2 of random effects), ranging between 0.55 and
393 0.65 for MCP, 0.54-0.55 for OREP and 0.37-0.53 for Kernel.

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

401

402 **Discussion**

403

404 Scandinavian wolves display a large variation in home range size, with even the smallest ones
405 ($< 260 \text{ km}^2$) being larger than the average size in continental Europe (150-240 km^2 ; Ciucci et
406 al. 1997, Okarma et al. 1998, Jedrzejewski et al. 2001, Kusak et al. 2005), whereas the upper
407 range ($< 1680 \text{ km}^2$) approaches home range sizes of Alaskan and Yukon wolf populations
408 (Hayes and Harestad 2000; Adams et al., 2008). Large within and between population
409 variation in home range size exists among wolves wherever they occur (Adams et al. 2008;
410 Fuller et al. 2003; Jedrzejewski et al. 2007) which was further confirmed in this study.

411 A combination of correlated ecological factors, rather than social factors, explained most
412 of the intra-population variation observed in home range size among Scandinavian wolves,
413 after large individual variation was taken into account. Roe deer density, elevation and
414 latitude were all important variables predicting wolf home range size. Roe deer density was

415 negatively correlated with, elevation and latitude, and positively correlated with open
416 cultivated land. These correlations likely reflect both the sensitivity of roe deer to snow depth
417 and their preferences for agricultural areas which increase foraging opportunities (Myserud et
418 al. 1997, 1999; Gervasi et al. *in press*). In the process of understanding why we find smaller
419 ranges in areas of high roe deer densities, with consequently lower average elevation and a
420 higher proportion of open cultivated land, we need to consider the different components
421 separately as well as the interactions between them. Latitude has previously been observed to
422 influence home range size among wolf populations (Okarma et al 1998; Jedrzejewski et al.
423 2007). Resource availability is generally believed to be the driving force explaining variation
424 in animal home range size (Burt 1943) and these observations were mainly explained by
425 decreased primary productivity and prey biomass with increasing latitude. Jedrzejewski et al
426 (2007) found that range size increased with latitude, also independently from prey density on
427 a large geographical scale. In our study area, the decrease in primary productivity with
428 latitude was not reflected in a decrease in ungulate biomass but rather represented a noticeable
429 environmental gradient from a mosaic of open cultivated land and forest in the south, to a
430 more homogeneous coniferous taiga with increasing elevation range and winter snow depths
431 in the north. This suggests that a different mechanism other than pure prey biomass is likely to
432 drive variation in home range size among Scandinavian wolves.

433 Applying Scandinavian wolf home ranges on to a North American data set (Fuller et al.
434 2003) showed an interesting deviation from the general pattern. Average home range size in
435 Scandinavia was much larger than in North American areas with corresponding levels of prey
436 biomass (Fig. 4). Moose are the main prey species for a large part of the Scandinavian wolf
437 population (Sand et al 2005; 2008) except for some few packs where roe deer are their main
438 prey. Even if we excluded packs where wolves were known to primarily feed on roe deer,
439 Scandinavian home ranges remained an outlier. This shows that prey biomass is not a limiting

440 factor for Scandinavian wolves, further supported by the fact that the space restricted wolf
441 population on Isle Royale can survive within ranges one third of the size of those documented
442 in our study, although prey (moose) density is similar and pack sizes generally larger (Sand et
443 al. 2012). An alternative explanation could be that home range size reflects prey availability
444 rather than prey biomass. However, Scandinavian wolves preying on moose strongly select
445 for calves (Sand et al. 2005, 2008) and because of a highly selective hunter harvest regime,
446 the moose population contains a relatively high proportion of calves compared to North
447 American populations (Sand et al. 2012). Therefore, it is not likely that variation in prey
448 availability of moose can explain the observed deviation of mean home ranges size of wolves
449 in Scandinavia either (Fig. 4). Prey choice is more likely to be an important source of
450 variation in home range size within the Scandinavian wolf population. Even though moose
451 density was a poor predictor of home range size, an effect of prey density was apparent when
452 considering only the smaller ungulate prey species, the roe deer.

453 Wolves are flexible and opportunistic predators (Peterson & Ciucci 2003; Gurarie et al.
454 2011) and Scandinavian wolves are likely to prey on roe deer opportunistically. A switch of
455 main prey species from moose to the smaller roe deer may thus be expected with an
456 increasing roe deer density (Eklund 2012), possibly explaining the decrease in home range
457 size at lower latitudes (Fuller et al. 2003). Whereas the predation patterns on moose are
458 strongly influenced by both age of the moose and habitat characteristics (Wikenros et al.
459 2009; Sand et al. 2005, 2008; Gervasi et al. *in press*), the small size of the roe deer may not
460 require selection neither for certain individuals nor for specific habitats. If prey availability
461 rather than abundance is important (Rich et al 2012), the lack of response in home range size
462 to moose density may partly be explained by the relation between predation success and
463 habitat (Gervasi et al. *in press*).

464 Home ranges at higher elevations were larger, suggesting that elevation has some influence
465 on wolf movement pattern. Within our study area, higher elevation is correlated with rugged
466 habitat and with latitude. In the south the landscape is almost flat while further north the
467 topography becomes increasingly broken and steep. These habitat features may have an effect
468 both on wolf movement behaviour and on the behaviour of the prey and the accessibility of
469 prey for wolves. Rich et al. (2012) suggested that increased difficulties in hunting deer
470 explained the positive correlation between wolf home range size and a ruggedness index. It is
471 also possible that latitude, and elevation, reflect a gradient in the density of some smaller
472 (non-ungulate) prey species that we were not able to measure. Although there is no evidence
473 that these non-ungulate species constitute major parts of wolf diet, they may have more subtle
474 influences in some key periods or on larger scale movement patterns.

475 The Scandinavian wolf population has constantly increased during the years of the study
476 and an effect of population density on home range size was expected but not observed. The
477 lack of a density effect, in contrast to observations in several other carnivore species (Dahle
478 and Swenson 2003, Benson et al 2006) including wolves (Fritts and Mech 1981, Hayes and
479 Harestad 2000; Rich et al. 2012), suggests that the population is still in a recolonizing phase
480 and has not yet reached the threshold where density has become a limiting factor on space
481 use. This may be further supported by the low number of observed intraspecific killings
482 among Scandinavian wolves (Wabakken et al. 2009) compared to North America (Mech
483 1994, Mech and Boitani, 2003; Adams et al. 2008). Still, some packs in the centre of the
484 Scandinavian wolf range had up to five neighbouring packs which may be expected to have a
485 limiting effect on space use. The inverse effect of density may however be masked by some of
486 the smallest home ranges being isolated from the main population's distribution (Fig. 1). The
487 apparently low intra-specific competition observed between the Scandinavian wolves is likely
488 contributing to a low-cost of maintaining large home ranges for the wolves.

489 Following Powell (2000) an animal's home range should not be larger than that size at
490 which the benefits received exceeds the cost of maintaining it. Linear elements (such as gravel
491 forest roads and conventional seismic lines) have been shown to facilitate wolf movement
492 when used as low energy travel paths (Eriksen et al. 2008; Gurarie et al. 2011; Latham et al.
493 2011). High densities of these elements may reduce the cost of keeping a large home range
494 thus explaining the positive correlation between home range size and minor roads.
495 Alternatively this correlation could be a response to more human disturbance (Rich et al.
496 2012), but as most minor roads are only occasionally used by loggers, hunters, and for other
497 recreational use, this explanation is less likely.

498 Previous research has shown that Scandinavian wolves choose to settle in areas of
499 continuous conifer forest, rich in prey but with low densities of urban areas, roads and
500 cultivated land (Karlsson et al. 2007). However, the increase of the Scandinavian wolf
501 population has since resulted in increasingly more packs in close proximity to areas of high
502 anthropogenic influence. This exposure may result in a behavioural adaptation of wolves
503 towards human presence (Gurarie et al. 2011; Bateman and Fleming 2012). Our results show
504 that home ranges were in general much smaller in more developed areas (i.e. areas with high
505 roe deer density) suggesting that the resource quality in some areas is high enough to allow
506 for a rather drastic decrease ($< 85\%$) in range size but still being sufficient to support
507 successful reproduction among the wolves. Smaller home ranges in human inhabited areas
508 allow for higher wolf densities with the potential to trigger an increment in human-wolf
509 conflict in the future. There is likely to be a major debate in the near future about the desired
510 distribution of wolves given that the social conflicts with wolves are already intense (Skogen
511 et al. 2013), and that political goals call for a further increase in wolf numbers in Scandinavia.

512

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524

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716 **Table 1** Annual home range size (km²) of Scandinavian adult, scent-marking wolves monitored
 717 between 1999 -2011, estimated as Minimum Convex Polygons (MCP), Objective Restricted Edge
 718 Polygons (OREP) and Fixed Kernels (Kernel). Two outliers were removed before calculating mean
 719 (MCP: 3525 and 2589 km²)

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

Note: Mean and standard error were based on the number of unique packs (n = 27).

720

721 **Table 2** Multi-model interference based on linear mixed models on effects of latitude (Lat),
722 roe deer density index (Roe: reciprocal transformed), density of wolf packs (Dens), pack size
723 (Pack), minor roads (MiR) and major roads (MaR) on annual home range size ($n = 63$) in
724 Scandinavian wolves. Only models with $\Delta AIC_c < 2$ are shown. Pack identity was fitted as
725 random factor in all models. R^2 values show the amount of variation explained by the fixed
726 effects combined after excluding the random factor.

Method	Model	k	AIC_c	ΔAIC_c	ω_i	R^2
<i>MCP 100%</i>	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
<i>OREP 100%</i>	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
<i>Kernel 95%</i>	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

727

728 **Table 3** Summary results after model averaging the effects of each parameter on annual home
729 range size ($n = 63$) in wolves using three different methods of range estimations (Minimum
730 Convex Polygon, Outlier Restricted Edge Polygon and Fixed Kernel). Model-averaged
731 parameter estimate with unconditional SE, 95% confidence limits and the relative importance
732 of parameters (Anderson 2008) are based on the sum of Akaike's weights across models with
733 $\Delta AIC_c < 2$. Pack identity was fitted as random factor in all models.

Method	Parameter	Relative importance	Estimate ^a	Unconditional SE	Confidence interval	
					Lower	Upper
<i>MCP 100%</i>						
	(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	-124.60	422.31
	Major roads	0.08	116.3	131.85	-142.12	374.72
<i>OREP 100%</i>						
	(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	7.85
	Minor roads	0.70	226.46	126.11	-20.73	473.64
<i>Kernel 95%</i>						
	(Intercept)		718.45	53.03	614.5	822.4
	Latitude	1.00	420.57	129.00	167.8	673.4
	Roe deer index	1.00	-275.93	136.65	-543.8	-8.1
	Pack size	0.62	-145.50	80.70	-303.7	12.7
	Minor roads	0.37	121.51	104.15	-82.62	325.64

734 ^a Effect size has been standardized on two SD following Gelman (2008).

735

736 **Fig. 1** Study area with home ranges of radio collared wolves (dark polygons) in Sweden and Norway,
737 1999 to 2011. The distribution of scent marking pairs and packs in the Scandinavian wolf population,
738 all years combined, is displayed by the grey area (20 km buffer zones around centre point of each
739 home range). Black crosses shown locations of resident solitary wolves outside the main distribution.

740

741 **Fig. 2** Proportion of annual wolf home range size (MCP 100%) in relation to number of months
742 included in the range estimation when resampling 34 annual Scandinavian wolf ranges (mean = 120,
743 range 5-1264 locations month⁻¹). Mean range sizes above the dotted line decreased less than 10%
744 compared to the annual range.

745

746 **Fig. 3** Annual home range size (Outlier Restricted Edge Polygon: OREP) of Scandinavian wolves
747 in relation to **a** moose density and **b** roe deer density (logarithmic scale). Solid regression lines include
748 all sampled packs ($n = 16$), dotted regression lines exclude two packs mainly preying on roe deer (n
749 = 14).

750

751 **Fig 4.** Mean home range size (MCP) of wolf populations in relation to ungulate biomass.
752 North American data from Fuller et al. 2003 (table 6.3), with the inclusion of Scandinavia
753 (encircled; this study). Symbols indicate the main prey species for the wolf population. In
754 Fuller et al. 2003, density of each ungulate species was multiplied with a relative index
755 depending on size. Roe deer was not present, so a relative index of 0.5 was given for roe deer
756 in the Scandinavian data.