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1 **Home range size variation in a recovering wolf population: evaluating the**

2 **effect of environmental, demographic, and social factors**

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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.

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, from 259 km^2 to 1676 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.

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

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.

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

5

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 (*Populous 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;

6

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 on-going 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 VHF radio collar (Telonics Mod. 500, Mesa Arizona), a GPS remote downloadable collar (GPS-Simplex, TVP Positioning AB, Lindesberg, Sweden) or a GPS-GSM collar (Tellus, TVP Positioning AB; GPS-plus, Vectronic Aerospace, Berlin, Germany). The capture methods were approved by the Swedish Animal Welfare Agency and the Norwegian Experimental Animal Ethics committee. For 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 2-6 times per 24-hour. 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 (3-10 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

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 ($n_{total} = 63$). 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 where 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 m^2 for moose and 10 m^2 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   Hawths 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 (km^2) was fitted as the response variable in all models. Two extreme

297 outliers (MCP: 3 525 and 2 589 km^2) 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 km^2; 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 ± 8%

341   SD; OREP: 81 ± 9%; Kernel: 76 ± 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} (±

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 (ΔAIC_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 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 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 (Mysterud 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

18

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

513   **Acknowledgement**

524

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716 **Table 1** Annual home range size (km^2) 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 km^2)

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
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

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
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	-124.60	422.31
	Major roads	0.08	116.3	131.85	-142.12	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	7.85
	Minor roads	0.70	226.46	126.11	-20.73	473.64
Kernel 95%						
	(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 to2011. 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.