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Seasonal release from competition explains partial migration in European moose

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Abstract:	Partial migration, whereby a proportion of a population migrates between distinct seasonal ranges, is common throughout the animal kingdom. However, studies linking existing theoretical models of migration probability, with empirical data are lacking. The competitive release hypothesis for partial migration predicts that due to density-dependent habitat selection, the proportion of migrants increases as the relative quality and size of the seasonal range increases, but decreases with increasing migration cost and population density. To test this prediction, we developed a quantitative framework to predict the proportion of migrants, using empirical data from 545 individually GPS-marked moose (Alces alces) from across Fennoscandia, spanning latitudes of 56° to 68°N. Moose contracted their ranges to common and spatially limited winter areas (typically at lower elevation), but expanded them during summer due to an increase in suitable habitat (at highland ranges). As predicted from our model, a better and larger highland range relative to the lowland range corresponded to a higher proportion of migrants in an area. Quantitative predictions coupling the balance of habitat availability of seasonal ranges with the probability of migrating in a large herbivore is a necessary step towards an enhanced understanding of the mechanisms underlying migration at the population level.

1   *Introduction*

2   Migration is a behavioral adaptation to seasonal changes in the geographic distribution of

3   suitable habitat either through genotypic (Boyle and Conway 2007, Holt and Fryxell 2011) or

4   phenotypic changes in habitat selection (Van Moorter et al. 2020). Partial migration, whereby

5   a fraction of a population migrates, is widespread across the animal kingdom (Lack 1943,

6   Chapman et al. 2011a and 2011b, Berg et al. 2019). Several mechanisms have been proposed

7   for the persistence of different movement strategies within a single population. Chapman et

8   al. (2011b) reviewed eight such hypotheses to explain partial migration: arrival time,

9   competitive release, fasting endurance, predation vulnerability, sexual conflict, social fence,

10   thermal tolerance, and trophic polymorphism (see also Berg et al. 2019 for a discussion

11   focused on ungulates). Underlying all these hypotheses is either individual variation in

12   tolerance of environmental constraints or some form of inter-individual competition resulting

13   in density-dependent habitat selection. In the absence of individual variation in tolerance to

14   adverse conditions, theoretical models suggest that density-dependent habitat selection is

15   necessary to explain partial migration (e.g. Kaitala et al. 1993, Taylor and Norris 2007, Holt

16   and Fryxell 2011, Fryxell and Holt 2013, Van Moorter et al., 2020).

17   Partial migration can exist in populations where residents and migrants either share a

18   common summer ground and separate during winter (i.e. non-breeding partial migration or

19   shared breeding) or share a common wintering area and separate during summer (i.e.

20   breeding partial migration or shared non-breeding). Although, both forms of partial migration

21   have been described in a range of species (Griswold et al. 2010, Chapman et al. 2011b), it is

22   shared non-breeding that is most common among ungulates at northern latitudes (Mysterud et

23   al. 2011, Berg et al. 2019). Ungulates are often forced from areas with high snow depth

24   during winter (e.g. Mysterud, Bjørnsen and Østbye, 1997) due to reduced access to food

25   (Schwab, Pitt, and Schwab 1987) and increased cost of locomotion (Telfer and Kelsall 1979,

26   1984) into areas with less snow cover, which results in an elevational migration from

27   highland to lowland ranges often observed in ungulates at northern latitudes (Mysterud et al.

28   2011, Berg et al. 2019). Spatiotemporal variation in forage quality – as proposed by the

29   forage maturation hypothesis (FMH) – is a common explanation (Fryxell and Sinclair 1988,

30   Albon and Langvatn 1992, Hebblewhite et al. 2008) for individuals migrating away from the

31   winter area during summer. Migration, according to the FMH, is a tactic to exploit spatial

32   variation in plant phenology (or forage maturation) as the animals move along a gradient of

33   early plant growth, which provides high-quality forage, during spring green-up. Although

34   there is little doubt that ungulates move along the spring green-up wave (Bischof et al. 2012,

35   Van Moorter et al. 2013, Merkle et al. 2016, Aikens et al. 2017), it fails to explain why some

36   individuals do not follow this migration pattern in partially migratory populations.

37   The Competitive Release Hypothesis (CRH) suggests that certain individuals opt for a

38   different movement tactic to avoid intraspecific competition on the sympatric range

39   (Chapman et al 2011b, Berg et al. 2019). Van Moorter et al. (2020) presented a model for the

40   CRH based on density-dependent habitat selection. In general, density-dependent habitat

41   selection is a major mechanism resulting in an 'ideal free distribution' (IFD; Fretwell and

42   Lucas 1969, 1972). Under an IFD, individuals will experience equal fitness across patches

43   under a Nash equilibrium, i.e. moving from one patch to another will not increase individual

44   fitness. Van Moorter et al. (2020) showed that when the distribution of the most suitable

45   habitat changes across seasons, density-dependent habitat selection results in partial

46   migration. Moreover, they found that the migration rate should increase as the suitability

47   (intrinsic growth and/or carrying capacity) of the highland range increases compared to the

48   lowland range (Van Moorter et al. 2020).

49   In this study, we tested the predicted ideal free migration rates from the model

50   presented by Van Moorter et al. (2020) for migratory ungulates. These migrations are often

51   elevational from lowland ranges in winter to highland ranges in summer (e.g. Mysterud et al.

52   2011). We will use seasons (summer and winter) exclusively to indicate periods of the year

53   and adopt the geographic reference ('highland' and 'lowland' respectively) for the seasonal

54   ranges for simplicity and to avoid confusion. The model predicts that the proportion of

55   migrants increases as the relative habitat suitability of the highland range increases compared

56   to the lowland range (in agreement with the CRH; e.g. Chapman et al. 2011b, Berg et al.

57   2019). We define habitat suitability as habitat-dependent individual fitness, which is density-

58   dependent and corresponds to the intrinsic growth or carrying capacity in a habitat patch at

59   respectively low and high population densities (reviewed in Johnson 2007). In practice,

60   however, these two components are often highly correlated across habitats (Griffen and

61   Drake 2008 and references therein).

62   We tested the main prediction from the model using migration data from a large set of

63   GPS-tracked moose (*Alces alces*; $n = 545$) throughout Norway, Sweden, and Finland and

64   moose harvest statistics as an index of relative local population abundance, estimated at the

65   moose management area level. The tracking data, combined with remotely-sensed

66   environmental characteristics, allowed us to assess the suitability of highland and lowland

67   ranges for moose using resource selection functions (Manly et la. 2002, Boyce et al. 2002,

68   Boyce et al. 2016), which we validated using the harvest data. Vegetation and snow cover are

69   the most important factors determining seasonal ranges for moose (Ball, Nordengren and

70   Wallin, 2001, Allen et al. 2016). We expected a strong effect of snow (or a lack of) driving

71   seasonal habitat suitability: only the lowland range would be suitable habitat during winter,

72   whereas both the low- and highland range would be suitable during summer (baseline

73   Prediction 0). We then related local differences in the relative suitability of the highland

74   compared to the lowland range during summer to the proportion of migratory moose.

75   Following the CRH and more specifically our model predictions, we predicted that the

76   proportion of migratory moose would increase with both higher suitability of habitat

77   (Prediction 1) and overall greater availability of suitable habitat (Prediction 2) on the

78   highland range compared to the lowland range.

79

80   ***Material and Methods***

81   <u>Model for partial migration</u>

82   To investigate the relationship between seasonal variation in habitat suitability and the

83   proportion of migrants, we used the model presented by Van Moorter et al. (2020). This

84   model builds upon the two-patch population model from Fryxell and Holt (2013) and Holt

85   and Fryxell (2011), in which the dynamics of population size in each patch follow a Ricker

86   model (Ricker 1954, which is a discrete-time model); with scaled densities (*i.e. N = N'/K'*,

87   where *N'* is the unscaled population size in spring just prior to the calving period (May-June),

88   and *K'* is the carrying capacity during summer or population size at which each individual, on

89   average, replaces itself). Following Fryxell and Holt (2013), we assumed recruitment (*r*)

90   during summer to be density-dependent and mortality during winter (*μ*) to be density-

91   independent as supported by many empirical studies of ungulates (Saether 1997, Gaillard et

92   al. 2000). The two patches or seasonal ranges are linked through the movement of migratory

93   animals, which move with migration probability, *m*, and a demographic cost, *c*, after the

94   winter season from range L to H and back after summer. The range L is defined as the range

95   with the lowest winter mortality (*i.e.* $\mu_L \leq \mu_H$). See Van Moorter et al. (2020) for more details

96   (and the Supplementary Material for a summary).

97   The ideal-free migration strategy (Mariani et al., 2016; Van Moorter et al. 2020),

98   where the ideal-free migration probability ($\hat{m}$) equalizes the summer fitness for lowland

99   residents and migrants, is calculated as follows:

100
$$\hat{m} = \frac{1 - \frac{r_L}{r_H}[1 - N] - \frac{c}{r_H}}{[\frac{r_L}{r_H} + \frac{K'_L}{K'_H}]N}$$
　　　　　　　　　　　　　　　　　　　　　Eq. 1

101　This ideal-free migration probability is determined by three main components: migration cost

102　(scaled by the recruitment on the highland range), relative habitat suitability of highland

103　versus lowland range both in terms of the relative intrinsic growth ($\frac{r_H}{r_L}$) and the relative

104　carrying capacity ($\frac{K'_H}{K'_L}$), and population density or saturation with respect to the lowland range

105　(N). Consequently, increasing the cost of migration leads to a reduction in the migration

106　probability. However, as the cost of migration seems negligible for moose (Rolandsen et al.

107　2017), we will assume zero migration cost. Whereas, increasing the benefits of migration

108　from access to suitable habitat (increasing $\frac{r_H}{r_L}$ or $\frac{K'_H}{K'_L}$) increases migration probability (Figure

109　1). If the intrinsic growth rate differs between migrants and residents, then the migration rate

110　will be density-dependent (Figure 1). If the intrinsic growth rate of migrants is higher than

111　those of residents (e.g. due to higher quality forage following the forage maturation

112　hypothesis; Fryxell and Sinclair 1988, Hebblewhite et al. 2008), all individuals of the

113　population would be migrating at low densities. As the highland range becomes more

114　crowded due to increasing population density, some individuals will shift to a resident

115　strategy. The opposite will occur if the migrants experience a lower intrinsic growth on the

116　highland ranges (red line in Figure 1), and then individuals will only start migrating once the

117　population density on the lowland range is sufficiently high.

118

119　The study area

120　The study area covers nearly the whole of Fennoscandia: Norway, Sweden, and Finland (Fig.

121　2). Climate varies greatly with latitude, elevation, and distance from the ocean. We find

122　subarctic conditions in the north and more temperate conditions in the south. High elevation

5

123   areas are characterized by alpine conditions. Coastal areas are characterized by higher

124   precipitation than inland areas. The most common land cover class is coniferous forest,

125   especially in the north. Moors and heathland, and broad-leaved and mixed forests are also

126   commonly found in Fennoscandia. Even though most of the forested land is managed for

127   silviculture, human inhabited areas occupy only a small fraction of the land cover. Most areas

128   experience a snow free period of about 6 months, with longer snow cover and greater snow

129   depths in the north and at higher elevations.

130

131   Data

132   We analyzed both GPS-tracking data from adult moose (see Bunnefeld et al. 2010 for further

133   details) and harvest data from Finland, Norway, and Sweden, during 2005-2011. The GPS-

134   tracking data were collated in the Wireless Remote Animal Monitoring (Dettki et al. 2013)

135   database system for data validation and management. We screened these data using the

136   approach developed by Bjørneraas et al. (2010) and subsampled data to obtain one location

137   randomly throughout each day. We considered data from mid-January through mid-March as

138   winter data, and from July through the end of August as summer data, as moose during these

139   periods have usually finished their fall and spring migration, respectively (Rolandsen et al.

140   2010, Bunnefeld et al. 2010, Singh et al. 2012). All moose (n = 545) included in our analysis

141   had a complete summer and winter season. We used harvest statistics as a proxy for

142   abundance of moose at the moose management area level (Ueno et al 2014). Annual harvest

143   statistics (number of moose shot per year) were collected at municipality level in Norway

144   (n=356), hunting district level in Sweden (n=308), and county level in Finland (n=60).

145   We focused on two large-scale environmental variables: vegetation type or land cover

146   and snow cover. We used CORINE land cover data from 2006 (Büttner et al. 2004), which

147   has European coverage, including Finland, Norway, and Sweden. Snow cover is an important

148   environmental variable that restricts access to forage for moose during winter (except

149   conifers). Unfortunately, no common snow depth model was available for Fennoscandia, so

150   instead we used the duration of snow cover as a proxy. We followed a similar approach to

151   Dietz et al. (2015) to estimate the length of snow cover from MODIS remote-sensing

152   composites from an 8-day period (MOD10A2) with an approximately 500 m spatial

153   resolution. We linearly interpolated a maximum gap of 3 missing scenes (i.e. a gap of a

154   month). Using these data, we derived the average proportion of the year with snow cover

155   during the study period (2000-2011). The MODIS sensors require light to detect snow and

156   during the darkest period in winter no sun light is available above the arctic circle; we will

157   therefore likely underestimate the length of the snow season as we move north. However, as

158   few animals moved distances long enough to exploit latitudinal variation, we did not expect

159   this to affect our results.

160

161   <u>Analysis</u>

162   To quantify seasonal ranges (labeled 'lowland' and 'highland' to avoid confusion, see above),

163   we used seasonal resource selection probability functions (RSPF) instead of relying on the

164   actual geographic ranges occupied by moose in each season. We did this to avoid risking

165   circularity in our argument, as we relied on moose geographic space use to determine their

166   migratory status. The seasonal RSPF were based on a used and available points comparison

167   in environmental space, which comprises multiple dimensions representing different biotic

168   and abiotic environmental variables (Aarts et al. 2008). We assumed that moose in

169   Fennoscandia are generally well-adapted and select the most suitable locations for that season

170   from those available during winter and summer (i.e. those locations that give the highest

171   individual seasonal fitness with low winter mortality and high summer recruitment

172   respectively).

7

173   Testing the predictions from Equation 1 requires the quantification of habitat

174 suitability of the highland and lowland range during the summer season both in terms of

175 intrinsic growth rate and carrying capacity. These correspond to individual fitness at

176 respectively low and high population density. Griffen and Drake (2008) argue that the

177 intrinsic growth rate and carrying capacity refer to a population's response to the quality and

178 quantity of available habitat respectively. Indeed, in their experimental study on *Daphnia*

179 *magna*, Griffen and Drake (2008) found that both the quality and size of the habitat affect the

180 carrying capacity, whereas habitat quality mainly affects the intrinsic growth rate. We used

181 the selection probability of a habitat as an index of its quality or suitability (Manly 2002,

182 Boyce et al. 2002, Boyce et al. 2016), and tested this assumption using harvest statistics (see

183 below). The integrated (i.e. summed) selection probability over each range summarizes both

184 the quality and quantity of habitat available to moose, which we used as a proxy for the

185 carrying capacity. The maximum (i.e. 95 percentile) selection probability of each range

186 summarized the best available habitat, which we used as a proxy for the intrinsic growth rate.

187

188 *Habitat selection and Range prediction*

189 To identify the ranges that moose selected more during summer than during winter (i.e.

190 highland) or *vice versa* (i.e. lowland), we compared the selection probability in each

191 predicted pixel from the RSPF, which compares available and used habitat. We represented

192 the area available to each moose by the 99% Minimum Convex Polygon for the locations of

193 each individual with a 10 km buffer. For each GPS-location (i.e. used point) we sampled 10

194 points randomly from the available area to represent the habitat types available to each

195 moose. We estimated the maximum likelihood estimators of the RSPF with a logit-link

196 function from these use-available data using the combination of partial likelihood and data

197 cloning implemented in the ResourceSelection library (Lele and Keim, 2006; Lele, 2009) for

198　R (R Development Core Team, 2011). We analyzed the used locations from both seasons

199　separately to obtain a population-level summer and winter RSPF, and the locations were

200　matched with random points by individual to account for differential availability of habitat

201　among individuals. We evaluated these RSPF using cross validation (similar to Boyce et al.

202　2002) based on a leave-one-out approach. For this cross validation, we re-fitted the model to

203　all but one individual and then predicted habitat use for this individual. We divided these

204　predicted values into 10 equal sized bins, and then computed the spearman rank correlation

205　between the bin number and the proportion of used versus available locations within each bin

206　(see Boyce et al. 2002 for more details).

207　　　　Following Lele et al. (2013): "The resource selection probability function, RSPF, […]

208　is defined as the probability that a resource unit of type x is selected (or, becomes part of the

209　use set) when encountered." As our analysis is focusing on regions where moose are

210　generally present and moose have large ranging capabilities, we can assume all resource units

211　to be available to moose. We therefore interpret our seasonal predictions as the higher

212　probability of moose occurrence in a given location during winter or summer. We rescaled

213　these probabilities to conserve the probability of moose occurrence over Fennoscandia across

214　seasons.

215　　　　We defined 'lowland' ranges as those pixels (x) that are more or equally selected (s)

216　during winter than during summer (i.e. $s_s(x) \leq s_w(x)$), and the 'highland' ranges as those

217　that are more selected during summer than during winter (i.e. $s_s(x) > s_w(x)$). We

218　approximated the summer carrying capacity of these ranges using the integrated selection

219　probability during the summer. Thus, we estimated the ratio of the summer and winter

220　carrying (K) capacity as:

221　　　　$$\frac{K_H}{K_L} = \frac{\sum_{x \in A}[s_s(x) > s_w(x)]s_s(x)}{\sum_{x \in A}[s_s(x) \leq s_w(x)]s_s(x)}$$

9

222 where numerator and denominator are the sum of selection probabilities during summer (s_s)

223 for all pixels of the area available to a 'population' (A; which is defined below) that are part

224 of respectively its highland range ($s_s(x) > s_w(x)$) and its lowland range ($s_s(x) \leq s_w(x)$). The

225 summer intrinsic growth rate (r) of these ranges was approximated using the 95 percentile of

226 the selection probability during the summer:

227 $$\frac{r_H}{r_L} = \frac{perc(s_s(x)) \; for \; s_s(x) > s_w(x)}{perc(s_s(x)) \; for \; s_s(x) \leq s_w(x)}$$

228

229 *Harvest statistics and Population distribution*

230 First, to test the appropriateness of the RSPF as a proxy for habitat suitability, we

231 investigated the relationship between the average annual harvest (2005-2011) and the total

232 RSPF for each reporting unit with linear regression. We log-transformed both harvest and

233 summer and winter RSPF to reduce skew. Moose harvest in Fennoscandia takes place during

234 fall, with most individuals harvested during September - October. As the main migration of

235 moose to their winter range generally occurs later in the year (i.e. November-December; see

236 Bunnefeld et al. 2010, Allen et al. 2016), most individuals will be harvested from their

237 summer range. We therefore expected the summer RSPF to be a better predictor of harvest

238 than the winter RSPF.

239 Second, to estimate the distribution (N') of moose within Fennoscandia, we

240 distributed the mean number of harvested moose within each management unit in proportion

241 to the summer RSPF for each pixel. The population density (N) is computed as the ratio of

242 the abundance (N') and carrying capacity (K'), see the model description above. This density

243 was computed for each 'population' cluster, see below.

244

245 *Proportion of migrants*

10

246   To quantify the proportion of migrants, we need first to identify the migratory status for each

247   individual, and second to group individuals into 'population' clusters. Following Cagnacci et

248   al. (2016), we assessed the migratory status of each individual using two methods: first, by

249   the overlap between seasonal home ranges, and second, by the movement distance between

250   them. Overlap in seasonal home ranges was determined using the volume of intersection for

251   the kernel utilization distributions (Fieberg and Kochanny 2005) from winter and summer

252   locations (respectively: January 15th till March 15th and July 1st till August 31st). We

253   considered migrating animals to be those that had less than 1% overlap between their

254   seasonal home ranges. We used adehabitatHR library (Calenge 2006) for R (R Development

255   Core Team, 2011) to calculate seasonal home range overlap. We based the second migration

256   criterion on the straight-line distance between the median summer and the median winter

257   locations. We considered animals with migration distances >10 km as migratory animals,

258   whereas animals with shorter distances were considered resident (see Hjeljord 2001).

259   Second, although moose throughout Scandinavia experience different local

260   conditions, there are no distinct boundaries between different 'populations'. To analyze the

261   proportion of migrants as a function of local environmental conditions, we therefore

262   performed a clustering analysis on the median winter location of each moose. We used

263   hierarchical clustering ('hclust') with the gap-statistic to identify the optimal number of

264   clusters (Tibshirani et al., 2001) in R with the factoextra library. We do not assume these

265   clusters to correspond to separate sub-populations, they merely represent clusters of moose

266   that experience similar local conditions.

267   We then computed the proportion of migrants for each cluster using either the overlap

268   or distance criterion between seasonal home ranges. We considered the area within 300 km of

269   a cluster to be available to the moose within that cluster, with this distance combining both

270   the long-distance migrations observed in moose (up to about 200 km, see Bunnefeld et al.

271   2010) and the spatial variation in location of moose within each cluster. For this area, we

272   computed the ratio of the highland and lowland range intrinsic growth and carrying capacity

273   as explained above. The density of moose for each cluster was computed as the sum of the

274   moose distribution within the area (derived from the annual harvest, see above) divided by

275   the carrying capacity.

276

277   *Hypothesis testing*

278   Finally, to test our hypotheses, we fitted four statistical models to the data. First, a basic

279   logistic regression used the range ratios as predictors of the proportion of migrants. However,

280   as the correlation between the ratio of the intrinsic growth rate and carrying capacity was

281   very high (*r=0.97*), we did not include them in the same model:

282    $$m = \beta_0 + \beta_1 {r_H}/{r_L} + \varepsilon$$ Eq. 2a

283    $$m = \beta_0 + \beta_1 {K_H}/{K_L} + \varepsilon$$ Eq. 2b

284   Second, using nonlinear least-squares estimates ('nls' from the nlme-library [Pinheiro et al.

285   2012] in R [R Development Core Team, 2011]), we parameterized Equation 1, assuming no

286   cost to migration:

287    $$m = \frac{1 - \beta_1 {r_L}/{r_H}(1 - \beta_3 N)}{\left(\beta_1 {r_L}/{r_H} + \beta_2 {K_L}/{K_H}\right)(\beta_3 N)}$$ Eq. 3

288   here β_1 estimates the effect of the ratio of intrinsic growth rates between lowland and

289   highland range, β_2 the effect of the ratio of carrying capacity on both ranges, and β_3 the

290   effect of the density of moose in Fennoscandia on the lowland ranges during summer. We

291   expected $\beta_1 = \beta_2 = 1$ according to Equation 1, whereas β_3 represents the proportional

292   constant between our proxy for density and the actual population density.

293   Third, given the coarseness of our density proxy, we also fitted a simplified model

294   where we assumed a constant density across Fennoscandia:

295
$$m = \frac{1 - \beta_1 {}^{r_L}/_{r_H}(1 - \beta_3)}{\left(\beta_1 {}^{r_L}/_{r_H} + \beta_2 {}^{K_L}/_{K_H}\right)\beta_3}$$
Eq. 4

296   Finally, we further simplified the model by assuming both $N=1$ and ${}^{r_L}/_{r_H} = 1$ to

297   focus exclusively on the ratio between the highland and lowland range of availability of

298   suitable habitat:

299
$$m = \frac{1}{\beta_1 + \beta_2 {}^{K_L}/_{K_H}}$$
Eq. 5

300

301   ***Results***

302   *Habitat selection and Range prediction*

303   Duration of the snow cover season and the land cover classes affected moose habitat selection

304   both in summer and winter. As expected (Prediction 0), the duration of the snow-free period

305   had a stronger effect on space use during winter (slope ± SE: 12.23 ± 0.43) than during

306   summer (slope ± SE: -2.55 ± 0.14). In addition, considerable differences existed in the

307   selection of the land cover classes. Moose avoided most other land cover classes compared to

308   coniferous forests, and selected only a few land cover classes over it (Table 1). In summer,

309   moose selected for broad-leaved forests over coniferous forests, whereas broad-leaved forests

310   were avoided during winter. A similar effect, albeit much weaker, was found for mixed

311   forests, which moose selected during summer and avoided during winter compared to

312   coniferous forests. In winter, woodland-shrub tended to be strongly selected over coniferous

313   forests, a selection that was much weaker in effect during summer. The habitat selection

314   models showed high cross validation performance based on the leave-one-out approach (see

315   Supplementary Figure S2), both during summer (correlation: median, mean ± SE: 0.53, 0.45

13

± 0.02) and during winter (correlation: median, mean ± SE: 0.64, 0.56 ± 0.01). We used these

habitat selection models to predict the preferred 'highland' and 'lowland' ranges (see Figure

2), which as expected occur on average at different elevations (average elevation on the

lowland and highland range was respectively 174 m and 401 m, *p-value* < 0.001; see

Supplementary Figure S6).

Harvest and Habitat suitability

We found a positive relationship between harvest and the RSPF (see Figure 3), which

supported our interpretation of the RSPF as a metric for habitat suitability. Somewhat

surprisingly, we found a lower AIC for the RSPF from winter than from summer (Δ

$AIC = 6.6$). The relationship between the RSPF and harvest was close to unity on a

logarithmic scale (winter: $\beta \pm SE$: 1.05 ± 0.04; summer: $\beta \pm SE$: 0.95 ± 0.04), with half the

variance in harvest explained by the RSPF (for either the winter or summer RSPF). A notable

deviation from the predicted relationship between harvest and RSPF occurred in Western

Norway (see Supplementary Figure S3), where, despite the presence of suitable moose

habitat, harvest is close or equal to zero. This is probably due to a combination of historical

overharvesting, movement barriers, and competition with local red deer populations. As these

areas are not occupied by a sizable moose population, they are not part of our study area on

moose migration. Removing these areas would result in a stronger relationship between

harvest and RSPF (see Supplementary Figure S4), with the harvest better predicted by the

summer than winter RSPF ($\Delta AIC = 236.5$), as expected.

Migration probability

When clustering individuals into groups experiencing a similar environment, the gap-statistic

kept increasing up to 37 clusters, with extremely small cluster sizes. We therefore opted to

apply the 'elbow' criterion by selecting the number of clusters where the increase in gap-statistic decelerated. We clustered the moose into 19 clusters, where moose within a cluster were on average 35 km apart (and up to 165 km).

Our two migration criteria, based on the overlap versus the distance between winter and summer home ranges (see above for a detailed description), gave very similar results for each individual: there was 85% agreement between methods. The proportion of migrants in each cluster was highly correlated (*r>0.95*, see Supplementary Figure S8), giving qualitatively identical results. We therefore only report the results from the range overlap criterion.

We found a strong positive correlation between the ratio of the intrinsic population growth rate and the ratio of the carrying capacity between highland and lowland ranges (*r=0.96, p <0.001*); therefore, we did not use both variables simultaneously in the logistic regression. We found a significant positive effect of both ratios on the proportion of migrants (Table 2; ratio of intrinsic growth: $\beta_1 \pm$ SE: 0.85 ± 0.14, *p-value* < 0.001; ratio of carrying capacity: $\beta_1 \pm$ SE: 0.36 ± 0.07, *p-value* < 0.001). The AIC was lower for the model explaining the proportion of migrants based on the proxy for intrinsic growth than for the proxy for carrying capacity (ΔAIC = 6).

Estimating the parameters in Equation 1 (assuming cost *c=0*), we found that the best model was the one in which we made the additional assumptions of constant intrinsic growth rate ratios and the population density to be one across clusters (Eq. 5, Table 2). The fully parameterized model (Eq. 3) suffered from convergence issues, while after constraining the parameter range to realistic values, some estimates corresponded to those boundaries (see Table 2). Thus, the estimates for Eq. 3 are unreliable. Assuming constant density across clusters (Eq. 4) allowed the model to converge with a density of one (i.e. high population density).

366   In the best model (i.e. Eq. 5), the intrinsic growth rates on the highland and lowland

367   ranges were not significantly different (Table 2; β_1 (± SE): 1.37 (± 0.33) ≈ 1). As expected

368   from Equation 1, the effect of the ratio of the carrying capacity between the lowland and

369   highland ranges was not significantly different from one (Table 2 and Figure 3; β_2 ± SE: 0.98

370   ± 0.68).

371

372   ***Discussion***

373   Multiple explanations have been proposed for the evolution of differential migratory

374   tendencies among individuals within a population (reviewed in Chapman et al. 2011b and

375   Berg et al. 2019), but there is still lack of a quantitative framework to predict the level of

376   partial migration. Using a simple density-dependent habitat selection model from Van

377   Moorter et al. (2020), we propose (Eq. 1 and Figure 1) that the ideal-free migration

378   probability is determined by three main components: migration cost (scaled by the

379   recruitment on the highland range), relative habitat suitability of the seasonal range (i.e. $\frac{r_H}{r_L}$

380   and $\frac{K'_H}{K'_L}$), and population density or saturation (N). Given its basis in ideal-free migration, the

381   proposed model presents a formal representation of the Competitive Release Hypothesis, as

382   individuals opt for a different strategy to escape from competition on the sympatric range

383   (e.g. Berg et al. 2019). In our empirical test of this model, we found that moose ranges in

384   Fennoscandia do indeed show an expansion-contraction dynamic during summer and winter

385   (Prediction 0), and that the proportion of migrants increased with the amount of suitable

386   habitat becoming available during summer (Prediction 2). However, the proportion of

387   migrants did not increase with their access to higher quality habitat *per se* (Prediction 1).

388   *Seasonal Range Dynamics*

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389   We found seasonal changes in moose's selection of land cover classes, such as an increased

390   selection for broad-leaved forest, natural grassland, moors and heathland during the summer.

391   However, the main driver for the seasonal range expansion-contraction dynamic was the

392   difference in duration of the snow-free period due to elevational gradients. The link between

393   the almost universal seasonal range contraction of cervids in fall and snow has been known

394   for decades (e.g. Brazda 1953, LeResche 1974). Surprisingly, an underlying explanation of

395   range expansion in spring including the mechanism of density-dependent habitat selection –

396   where partial migration is a competition avoidance tactic (Kaitala et al. 1993, Taylor and

397   Norris 2007, Holt and Fryxell 2011) – has rarely been focused on. In our case, this is

398   addressed in the ratio of the suitability of the highland range relative to the lowland range.

399   In our tests of the model predictions, we found support for the expected increase in

400   migration probability as the relative high-density suitability of the highland range increased

401   compared to the lowland range ($\frac{K'_H}{K'_L}$; in support of Prediction 2). Moreover, the observed

402   increase was not significantly different from the model prediction (observed slope ≈ predicted

403   slope = 1). However, our best model did not lend support to the relative low-density

404   suitability of highland versus lowland range ($\frac{r_H}{r_L}$) as a driver for migration (not supporting

405   Prediction 1). This absence of an effect of the intrinsic growth rate could be due to (1) our

406   proxy not adequately capturing the spatial heterogeneity in intrinsic growth, or (2) the similar

407   response of intrinsic growth and carrying capacity to spatial heterogeneity, which resulted in

408   highly correlated metrics. Although different from a theoretical perspective, intrinsic growth

409   and carrying capacity respond relatively similarly to changes in habitat quality and quantity

410   (Griffen and Drake 2008). Alternatively, (3) the role of variation in intrinsic growth rate may

411   be dependent upon the level of population saturation on the lowland range during summer, as

412   predicted by the model (Figure 1). Moose densities in Fennoscandia are generally high

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413   (Lavsund et al. 2003, Jensen et al. 2020), which could lead to the intrinsic growth rate not

414   being that important for migration in Fennoscandia.

415   *Population Density and Habitat Suitability*

416   Previous studies have found conflicting roles of increasing population density on the

417   proportion of migrants in partially migratory populations. For instance, Geremia et al. (2011)

418   found an increase in the proportion of bison in Yellowstone that migrated outside the park,

419   whereas Mysterud et al. (2011) reported a decrease in the number of migratory red deer

420   (*Cervus elaphus*), with an increase in density. Part of this discrepancy could be due to using a

421   spatial contrast in density rather than temporal variation in density in the latter case, and the

422   link to competition therefore being uncertain. However, migrants' access to high quality

423   forage (following the Forage Maturation Hypothesis) would lead to migration in spring even

424   at low population density (Figure 1; Mysterud et al. 2012), which could explain a reverse

425   density-dependence with a reduced proportion of migrants until high elevation ranges fill up

426   at high density. In the model (Eq.1), whether migration rates increase or decrease with

427   population density depends upon the intrinsic quality of the lowland compared to the

428   highland range (Fig. 1). At low densities, all individuals would migrate towards an

429   intrinsically better highland range or remain resident in an intrinsically better lowland range.

430   Whereas, as densities increase, an increasing proportion of individuals would adopt the

431   opposite tactic to get released from competition. Thus, contrasting effects of density on the

432   migration rate are predicted by this model.

433   In our study, we did not find support for an effect of spatial variation in local moose

434   densities on the migration rate (as expected from Equation 1). However, the proportion of

435   migrants is most sensitive to changes in population density at low densities and when the

436   intrinsic growth rate differs between the highland and lowland ranges (Figure 1). We found

437   no support for an effect of differences in intrinsic population growth on proportion of

438   migratory moose, and moose densities in Fennoscandia are generally relatively high

439   (Lavsund et al. 2003, Jensen et al. 2020).

440   *Limitations and Further Developments*

441   As with all models, we made several simplifying assumptions (cf. Holt and Fryxell 2011;

442   Fryxell and Holt 2013; Van Moorter et al. 2020). For instance, our model does not include

443   ecological interactions other than immediate density-mediated competition during the

444   summer season (see also Fryxell and Holt, 2013). When allowing for density-dependent

445   competition during both seasons, as in the original Holt and Fryxell (2011) model, no simple

446   solution exists for the proportion of migrants and more complex dynamics may occur (Steinar

447   Engen, pers. comm.).

448   To avoid confusion with seasons as periods of the year, we referred to the winter

449   range and exclusive summer range as respectively the "lowland" and "highland" range. This

450   was a convenient terminology because the seasonal range dynamics were largely driven by

451   differences in the duration of the snow-free period linked to an elevational gradient, as is

452   often observed with ungulates at northern latitudes (Mysterud et al. 2011). Although, while

453   the "lowland" ranges on average were at lower elevation than the "highland" ranges (see also

454   Supplementary Figure S6), it should be noted that deviations from this elevational pattern

455   occur as the choice of seasonal range is not only driven by snow cover (Ball et al. 2001). We

456   found differences in land cover classes between the seasonal ranges. Previous studies have

457   also documented marked differences in forest composition between summer and winter

458   ranges linked to seasonal shifts in the diet (Histøl and Hjeljord 1993, Månsson et al. 2007,

459   Wam and Hjeljord, 2010). This may also explain why moose may choose an opposite

460   strategy where they migrate towards higher elevation winter areas (Andersen 1991). Thus, the

19

461 terms lowland and highland range in this paper refer to areas that are respectively more or

462 less preferred during winter than during summer, rather than strictly the elevation of those

463 areas.

464 For browsing herbivores, like moose, one expects a lagged decrease in forage

465 availability on the lowland range after the presence of many animals during winter (Persson,

466 Danell, and Bergström 2005; van Beest et al. 2010). Illius and O'Connor (2000) explored the

467 ecological effects of range expansion and contraction due to seasonal rainfall in semi-arid

468 grazing systems. They found that increased range contraction leads to increased pressure on

469 the contracted area and decreased pressure on the expansion area. Such lagged effects of

470 density were not implemented in our model and may reduce carrying capacity and intrinsic

471 growth rate on the lowland range during summer, and could lead to a higher migration

472 probability.

473 Our model did not include individual heterogeneity such as age, which are known to

474 influence migration probability in moose, or unequal competition between migrants and

475 residents on the lowland range (Histøl and Hjeljord 1993, Singh et al. 2012). Several

476 explanations for partial migration are based on individual heterogeneity (see Chapman et al.

477 2011b). The transition equations (e.g. Supplementary Material Eq. S2) could easily be

478 extended to include individual heterogeneity, which is an interesting avenue for future

479 research. Although, some variation in body size between resident and migrant individuals has

480 been observed in moose (Rolandsen et al. 2017), this was considered a consequence rather

481 than the cause of their different migratory behavior.

482 The assumption of habitat selection as a proxy for habitat suitability is not trivial (e.g.

483 Gaillard et al. 2010). Remotely-sensed data such as length of snow cover are relatively crude

484 proxies for ecological dynamics and so are land use – land cover maps. For instance, moose

485   are likely more affected by the conditions (wet vs. dry) and depth of the snow than by the

486   cover *per se* (Ball et al. 2001, Singh et al. 2012). In addition, the habitat selection process

487   itself may also be more complex than addressed in a simple RSPF, for instance, selection for

488   habitat features may depend upon population density (van Beest et al. 2013, Avgar et al.

489   2020). Fortunately, the strong positive relationship we found between the annual moose

490   harvest in areas with more selected habitat (Figure 2) is supportive of this assumption in our

491   study, indicating that the RSPF also represents the main dynamics affecting habitat

492   suitability.

493   Finally, we did not address the cost of migration and assumed it was zero in our

494   analysis. In our study system, the demographic cost of migration, if there is any, seems

495   extremely low (Rolandsen et al. 2017), as given by the extremely low natural mortality rate

496   of adult moose in Fennoscandia (Solberg et al. 2005). Also, the pure energetic cost associated

497   with migration is likely rather limited for moose, as their migrations seem to result more from

498   their movements becoming more directional, than by a strong increase in their movement rate

499   (Van Moorter et al. 2013).

500

501   *Conclusions*

502   Our results show that spatial variation in the proportion of migrants is partly explained by

503   spatial variation in seasonal changes in suitable habitat, which results in range expansion-

504   contraction. This can contribute to an improved management and conservation of partially

505   migratory species (Allen and Singh 2016), which is crucially needed as migratory behavior in

506   large ungulates is under pressure from human fragmentation and climate change (Berger

507   2004, Bolger et al. 2008). Migratory species can range over larger areas than administrative

508   units of management (Meisingset et al. 2018), which complicates their management

509   substantially (Thirgood et al. 2004, Skonhoft 2005). For example, Nilsen et al. (2009) showed

510   that migratory moose can cause a dissociation of costs (i.e. browsing damage and moose-

511   vehicle collisions) and benefits (i.e. harvest) associated with moose, leading to non-optimal

512   management. Therefore, areas with larger range expansion-contraction face more challenges

513   in reaching management and conservation goals for partially migratory species (Allen et al.

514   2016). Moreover, as changes in snow cover due to climate change are likely to affect the

515   benefits of migration at northern latitudes, our framework can be extended to predict

516   developments of partial migration under climate change.

517

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723   TABLES

724   Table 1

725   Parameter estimates for moose Resource Selection Functions in summer and winter. The

726   reference land cover class was coniferous forest, which is the most common land cover class

727   in Fennoscandia.

	Summer		Winter	
	$\beta \pm SE$	*p-value*	$\beta \pm SE$	*p-value*
Intercept	-1.98 ± 0.99	< 0.001	-7.87 ± 0.18	< 0.001
Length snow-free period	-2.55 ± 0.14	< 0.001	12.23 ± 0.43	< 0.001
Artificial structures	-2.81 ± 0.22	< 0.001	-3.68 ± 0.15	< 0.001
Homogeneous agriculture	-0.86 ± 0.04	< 0.001	-1.88 ± 0.07	< 0.001
Heterogeneous agriculture	-0.31 ± 0.03	< 0.001	-0.52 ± 0.05	< 0.001
Broad-leaved forest	1.23 ± 0.05	< 0.001	-1.83 ± 0.04	< 0.001
Mixed forest	0.41 ± 0.03	< 0.001	-0.10 ± 0.04	< 0.01
Natural grassland	-0.77 ± 0.12	< 0.001	-2.26 ± 0.26	< 0.001
Moors and heathland	-0.49 ± 0.03	< 0.001	-3.13 ± 0.05	< 0.001
Woodland shrub	0.35 ± 0.02	< 0.001	1.32 ± 0.04	< 0.001
Sparse vegetation	-2.00 ± 0.06	< 0.001	-2.75 ± 0.09	< 0.001
Wetlands	-0.07 ± 0.03	< 0.005	-1.16 ± 0.04	< 0.001
Water bodies	-2.63 ± 0.08	< 0.001	-4.76 ± 0.13	< 0.001
Unclassified	0.94 ± 0.08	< 0.001	-3.31 ± 0.50	< 0.001

728

729 Table 2

730 Parameter estimates from the analyses of the proportion of moose migrants (migrants had less

731 than 1% overlap between the summer and winter home ranges). We performed five analyses:

732 ordinary logistic regression using intrinsic growth rate ratio (Eq. 2a in the main text) or

733 carrying capacity ratio (Eq. 2b), and non-linear least squares parameterization of Eq. 1 in the

734 main text based on three sets of additional assumptions (corresponding to Eq. 3, 4, and 5 in

735 the main text). See the main text for further details.

		AIC:	224
Eq. 2a	$\beta_0 + \beta_1 {}^{r_H}\!/_{r_L}$	$\beta_0 \pm$ SE:	-1.60 ± 0.28
		$\beta_1 \pm$ SE:	0.85 ± 0.14
		AIC:	230
Eq. 2b	$\beta_0 + \beta_1 {}^{K_H}\!/_{K_L}$	$\beta_0 \pm$ SE:	-0.81 ± 0.18
		$\beta_1 \pm$ SE:	0.36 ± 0.07
		AIC:	15
Eq. 3	$\dfrac{1 - \beta_1 {}^{r_L}\!/_{r_H}(1 - \beta_3 N)}{\left(\beta_1 {}^{r_L}\!/_{r_H} + \beta_2 {}^{K_L}\!/_{K_H}\right)(\beta_3 N)}$	$\beta_1 \pm$ SE:	1.11 ± 1.28
		$\beta_2 \pm$ SE:	5.00[*] ± 5.51
		$\beta_3 \pm$ SE:	20.00[*] ± 19.47
		AIC:	6
Eq. 4	$\dfrac{1 - \beta_1 {}^{r_L}\!/_{r_H}(1 - \beta_3)}{\left(\beta_1 {}^{r_L}\!/_{r_H} + \beta_2 {}^{K_L}\!/_{K_H}\right)\beta_3}$	$\beta_1 \pm$ SE:	3.88 ± 1.44
		$\beta_2 \pm$ SE:	0.06 ± 2.37
		$\beta_3 \pm$ SE:	1.00[*] ± 0.28
		AIC:	-0.4
Eq. 5	$\dfrac{1}{\beta_1 + \beta_2 {}^{K_L}\!/_{K_H}}$	$\beta_1 \pm$ SE:	1.37 ± 0.33
		$\beta_2 \pm$ SE:	0.98 ± 0.68

736 [*] Note: these estimates resulted in the upper boundary set for the parameter search, without

737 these upper boundaries the model did not converge.

738

739 FIGURES

740 **Figure captions**

741 Figure 1

742 The proportion of moose migrants as a function of population density, growth rate, and

743 carrying capacity. Following Equation 1, the proportion of migrants depends on the migration

744 cost (here assumed zero), population density on the lowland range, the ratio of the lowland

745 and highland range growth rates (lines in red = 1.05, in black = 1, in light blue = 0.95, and in

746 dark blue = 0.9), and the ratio of the lowland and highland range carrying capacity (solid

747 lines = 2, dashed = 1, dot-dashed = 0.5, and dotted lines = 0.33). Note, for clarity we only

748 displayed the $r_L/r_H = 1.05$ (red line) for the low carrying capacity ratio ($K_L/K_H = 2$). See main

749 text for further discussion.

750

751 Figure 2

752 The seasonal ranges and the proportion of moose migrants (black) versus residents (grey) for

753 19 clusters in Fennoscandia. The lowland range is shown in blue and the highland range in

754 green. See Supplementary Figure S7 for an overview of the number, sex, and age of the

755 individuals in each cluster.

756

757 Figure 3

758 The relationship between moose harvest and habitat suitability in Fennoscandia. The

759 logarithm of the average annual harvest plotted against the total summer suitability for each

760 reporting unit in Fennoscandia with the fitted regression line.

761

762 Figure 4

763   The proportion of migrants versus the size of the ratio in highland and lowland range carrying

764   capacity for each cluster. The proportion of migrants is calculated using the seasonal range

765   overlap criterion. The clusters are marked with the first letter of the country (i.e. Finland,

766   Norway, and Sweden) from which most moose originated. The full grey line represents the

767   expected proportion of migrants following Eq. 1, when both ranges would not differ in

768   intrinsic growth ($r_L/r_H = 1$), are fully saturated ($N_w=1$), and migration is cost-free ($c=0$).

769   The different fitted models from Eq. 2b, 3, 4, and 5 are represented respectively by a dashed,

770   dot-dashed, dotted, and full black line. See Table 1 for the model performance and parameter

771   estimates, and the main text for further explanations.

773   **Figure 1**
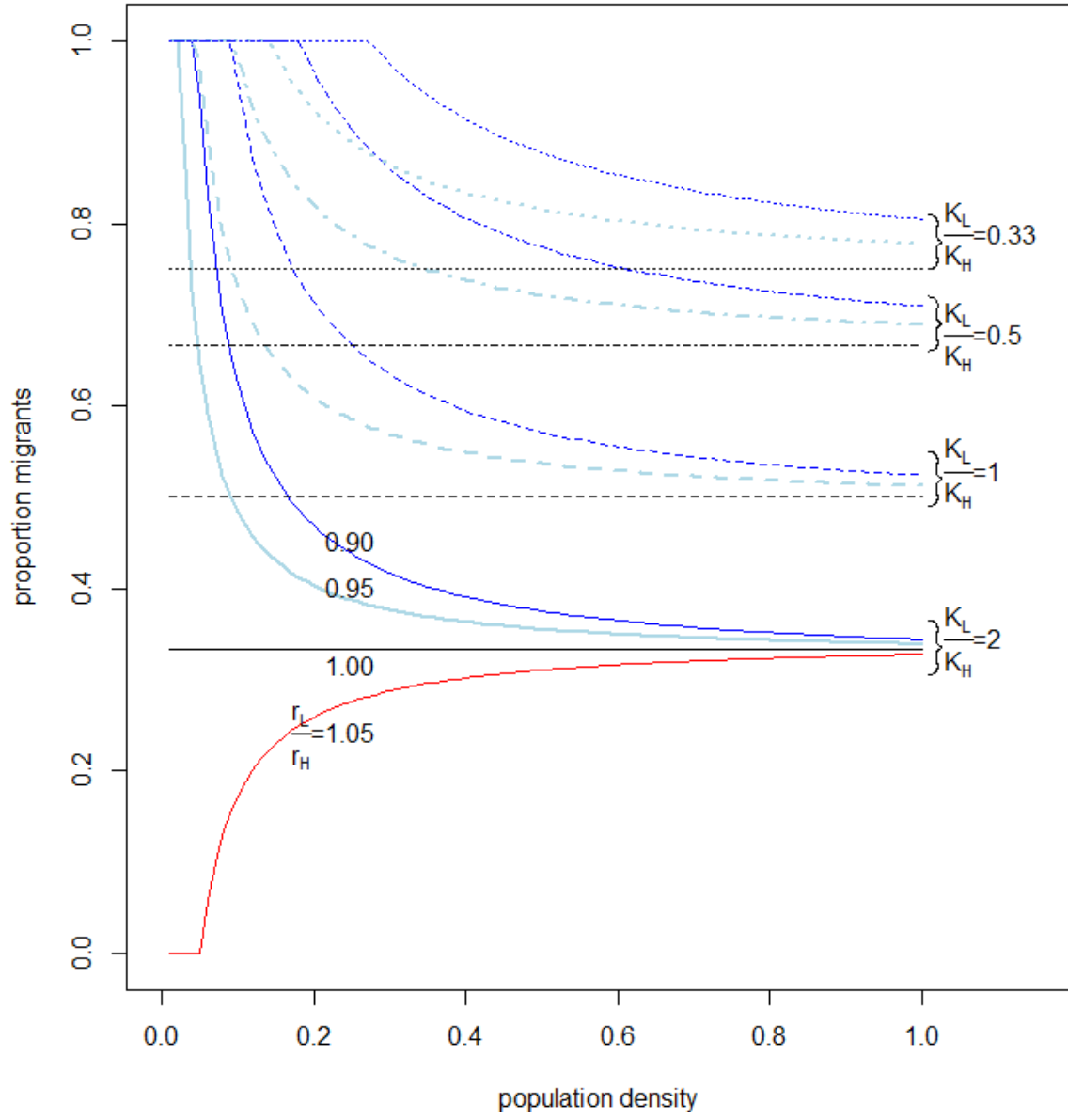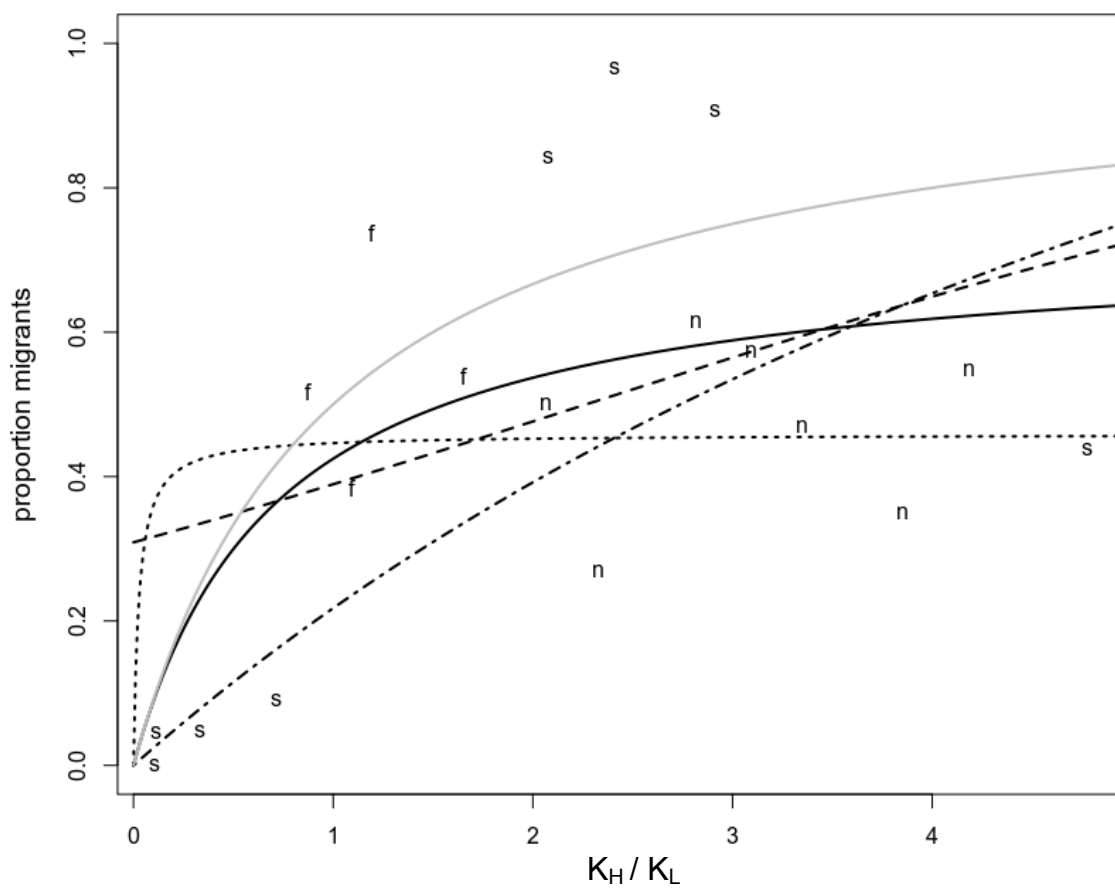
774

775 **Figure 2**

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Oikos
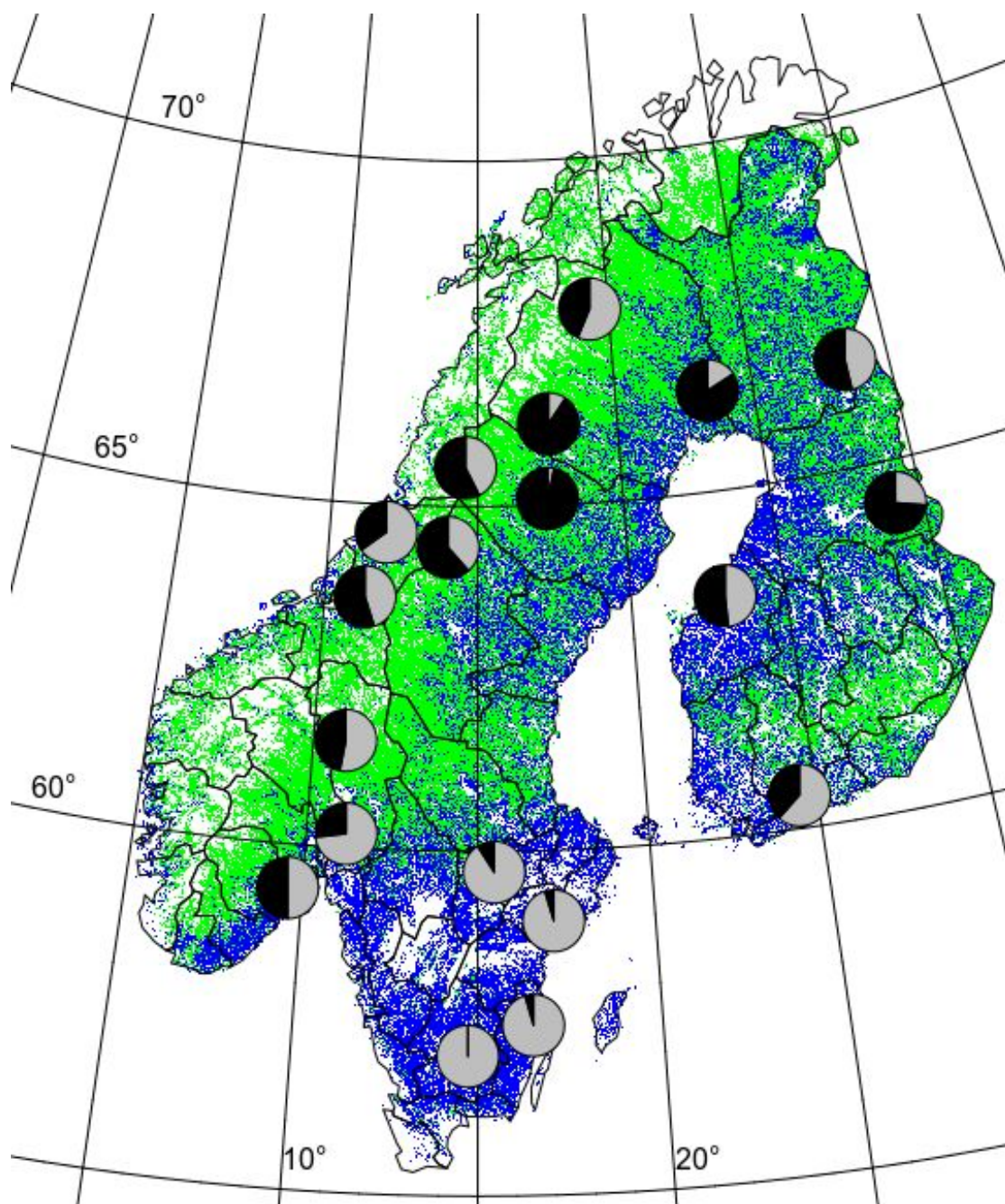
778 **Figure 3**
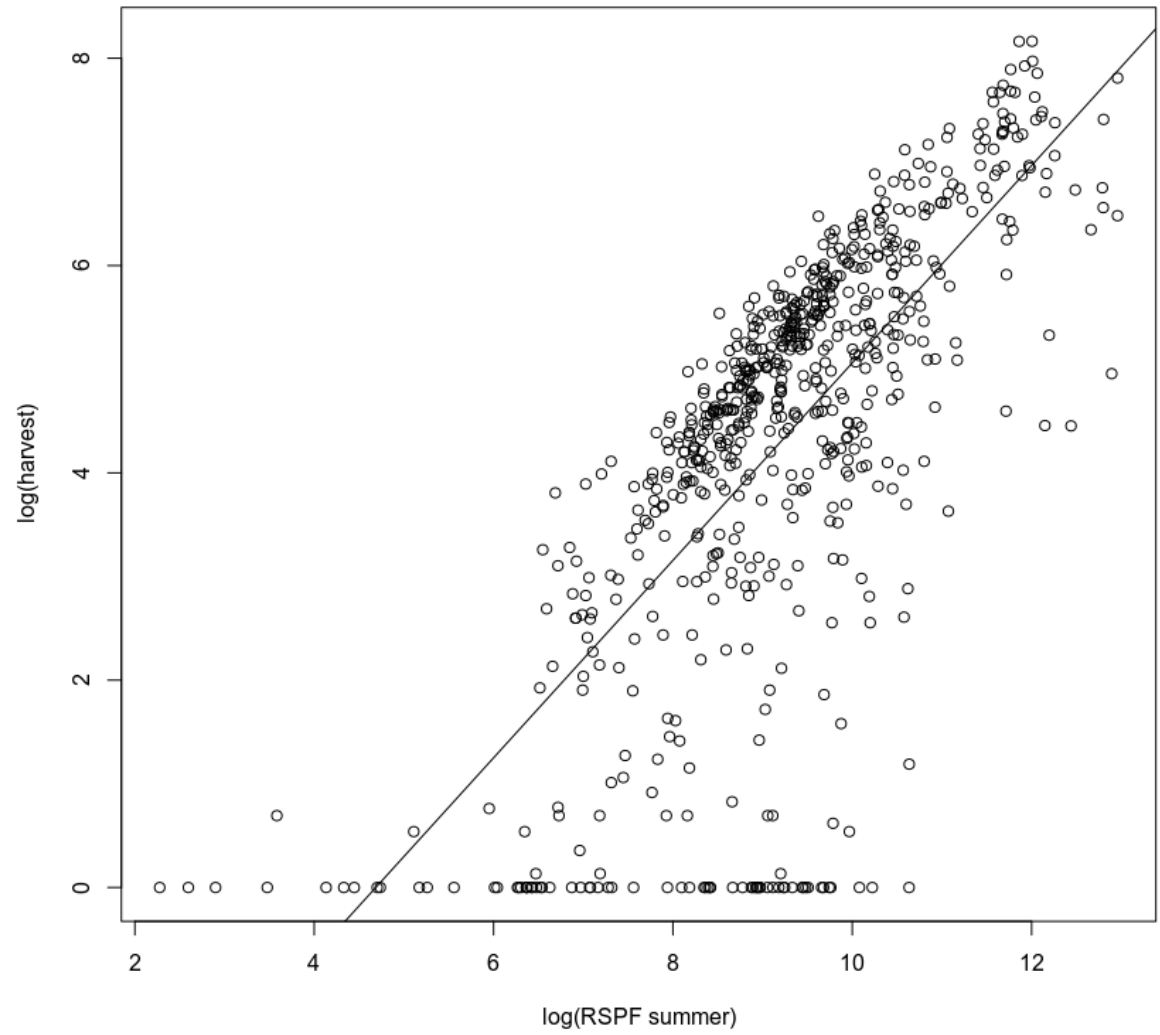
779

780   **Figure 4**

781

Supplementary Material

Model for partial migration

To investigate the relationship between seasonal variation in habitat suitability and the proportion of migrations, we used the model presented by Van Moorter et al. (2020). This model builds upon the population model from Fryxell and Holt (2013), we refer to Van Moorter et al. in which the dynamics of population size follow a Ricker model (Ricker 1954, which is a discrete-time model); with scaled densities (*i.e. N = N'/K'*, where *N'* is the unscaled population size in spring just prior to the reproduction season, and *K'* is the population size at which on average each individual replaces itself during summer). Following Fryxell and Holt (2013), we assumed recruitment (*r*) during summer to be density-dependent and mortality during winter (*μ*) to be density-independent as supported by many empirical studies of ungulates (Saether 1997, Gaillard et al. 2000).

Using the Ricker formula to represent episodes of summer reproduction, the multiplicative growth rate equals exp(*r[1-N' /K']*)=exp(*r[1-N]*), where *e^r* is the maximum per capita recruitment during summer. Assuming density-independent winter survival probability *e^{-μ}*, the number of animals after one year at the end of winter is calculated as follows:

N (t+1) = N (t) exp(r[1 - N (t)] -μ)   Eq. S1

Following Fryxell and Holt (2013), we linked two seasonal ranges through the movement of migratory animals, which move with migration probability, *m*, and cost, *c*, after the winter season from range L to H and back after summer. We define range L as the range with the lowest winter mortality (*i.e.* $\mu_L \leq \mu_H$). Therefore, we assumed only migration during spring from L to H; we did not consider individuals moving in the opposite direction, the so called `perverse' migrants (*sensu* Fryxell and Holt, 2013). Importantly, we focus our analysis on migration from the shared lowland range in winter towards a highland range used only in summer, *i.e.* the highland range can either not sustain residents year-round or highland residents are outcompeted by migrants who benefit from lower mortality on the lowland range (see for more details Van Moorter et al. 2020).

Following the population model in Equation S1, the number of animals at the end of winter in the lowland range, *N*, after 1 year is the sum of residents in L and migrants:

$$N(t + 1) = (1 - m)N(t) \exp(r_L [\, 1 - (1 - m)N(t)] - \mu_L) +$$

$$mN(t) \exp(r_H [\, 1 - \frac{K'_L}{K'_H}mN(t)] - \mu_L - c)$$ Eq. S2

where *m* is the migration probability, and *c* is the demographic cost of migration. For simplicity, we assumed that the migration cost was incurred after summer. Density-dependent recruitment (*r*) takes place during summer, which is for migrants in range H (*i.e.* r_H) and for lowland residents in range L (*i.e.* r_L), whereas the density-independent winter mortality (*μ*) occurs when migrants and lowland range residents share their common lowland range L.

As more animals migrate (*i.e.* increasing migration probability, *m*) from range L, the density of animals in L decreases and the summer fitness of residents in L increases, whereas the density of animals in H increases and the summer fitness of migrants in L decreases. We assumed an ideal-free migration strategy (Mariani et al., 2016; Van Moorter et al. 2020), where the ideal-free migration probability ($\hat{m}$) equalizes the summer fitness for lowland residents and migrants, calculated from Equation S2:

$$\exp(r_L [\, 1 - (1 - m)N(t)]) = \exp(r_H [\, 1 - \frac{K'_L}{K'_H}mN(t)] - c)$$

Since this equation is linear in m, the ideal-free migration probability ($\hat{m}$) is calculated as follows:

$$\hat{m} = \frac{1 - \frac{r_L}{r_H}[1 - N] - \frac{c}{r_H}}{[\frac{r_L}{r_H} + \frac{K'_L}{K'_H}]N}$$

Eq. S3 = Eq. 1 in main text

This ideal-free migration probability is determined by three main components: migration cost (scaled by the recruitment on the highland range), relative habitat suitability of highland versus lowland range both in terms of the relative intrinsic growth ($\frac{r_H}{r_L}$) and the relative carrying capacity ($\frac{K'_H}{K'_L}$), and population density or saturation with respect to the lowland range (N). Consequently, increasing the cost of migration leads to a reduction in the migration probability. However, as the cost of migration seems negligible for moose (Rolandsen et al. 2017), we will assume zero migration cost in this paper. Whereas, increasing the benefits of migration from access to suitable habitat (increasing $\frac{r_H}{r_L}$ or $\frac{K'_H}{K'_L}$) increases migration probability (Figure 1). If the intrinsic growth rate differs between migrants and residents, then the migration rate will be density-dependent (Figure 1). If the intrinsic growth rate of migrants is higher than those of residents (e.g. due to higher quality forage following the forage maturation hypothesis; Fryxell and Sinclair 1988, Hebblewhite et al. 2008), all individuals of the population would be migrating at low densities. As the highland range becomes more crowded due to increasing population density, some individuals will shift to a resident strategy. The opposite will occur if the migrants experience a lower intrinsic growth on the highland ranges (red line in Figure 1), then individuals will only start migrating once the population density on the lowland range is sufficiently high.

Supplementary Figures

Figure S1

Moose migration in Fennoscandia

For each moose in our study the centroid of the summer (in green) and winter (in blue) locations are connected with a red line.
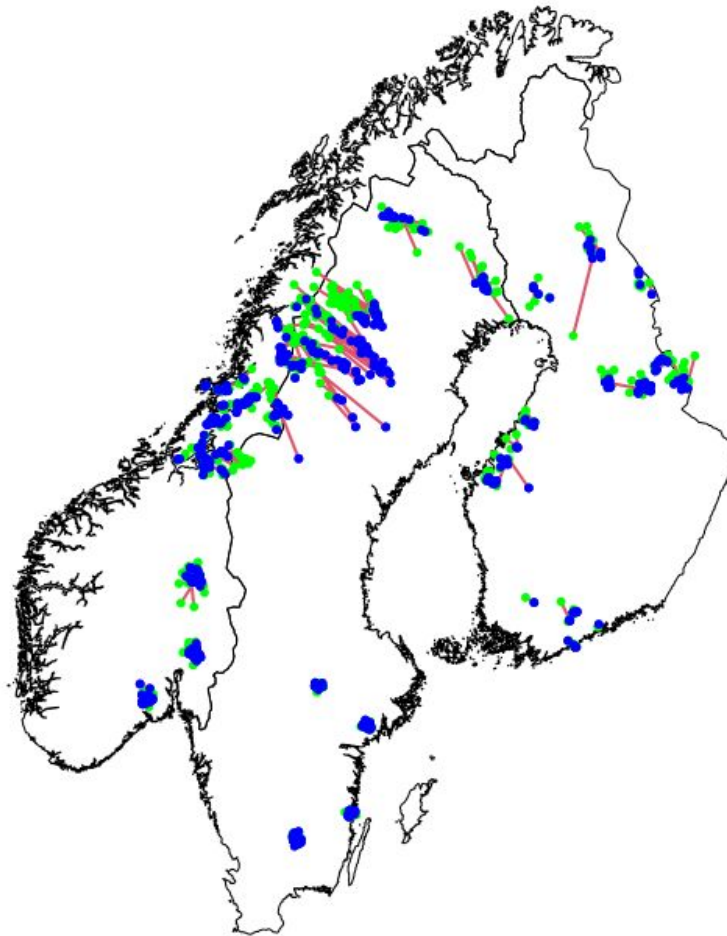

Moose migration in Fennoscandia

Figure S2

Boxplot with the "leave-one-out" cross validation

The Spearman rank correlation for each moose between the observed and predicted occupancy from a model without the focal moose (i.e. leave-one-out cross validation) for the summer and winter resource selection probability function.
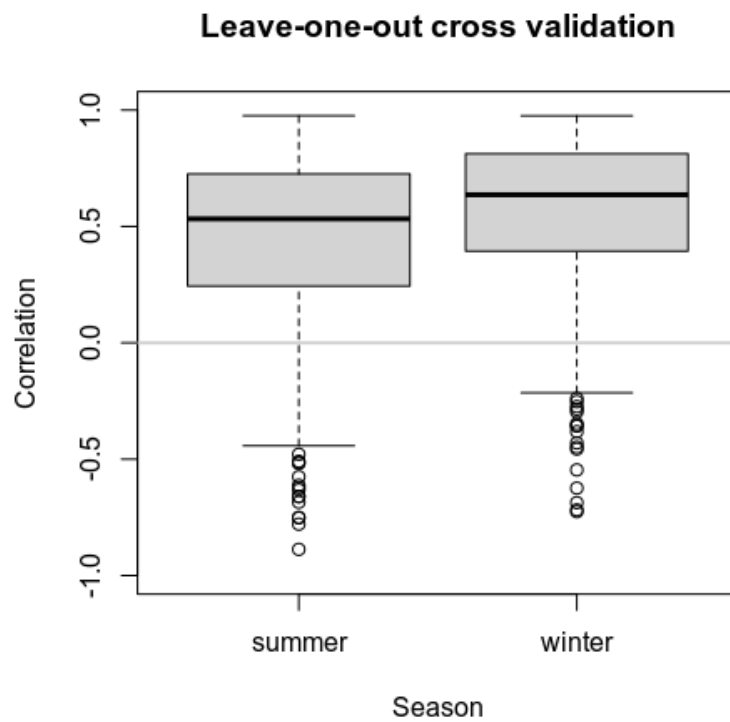

Leave-one-out cross validation

Figure S3

Residuals from the relationship between harvest and habitat suitability in Fennoscandia

The residuals from the linear regression between the average annual harvest and the total summer suitability for each mapping unit in Fennoscandia ($\log(harvest) = \beta_0 + \beta_1 \log(RSPF_{summer}) + \varepsilon$). The largest deviation from the prediction occurs in the Norwegian west coast, which has extremely low numbers of moose compared with the amount of available habitat. This area is generally not considered part of the moose range in Fennoscandia, however, the mechanisms for this are not well understood. It could be a combination of historical overharvest combined with difficulties in recolonization due to topography and local competition with red deer. If we removed those municipalities from the analysis, we obtained an even stronger relationship between the amount of suitable habitat and moose harvest (see Figure S5). Note that none of the other results, related to moose migration, are affected by the in- or exclusion of the Norwegian west coast, as for obvious reasons we studied migration only in areas where moose are present.
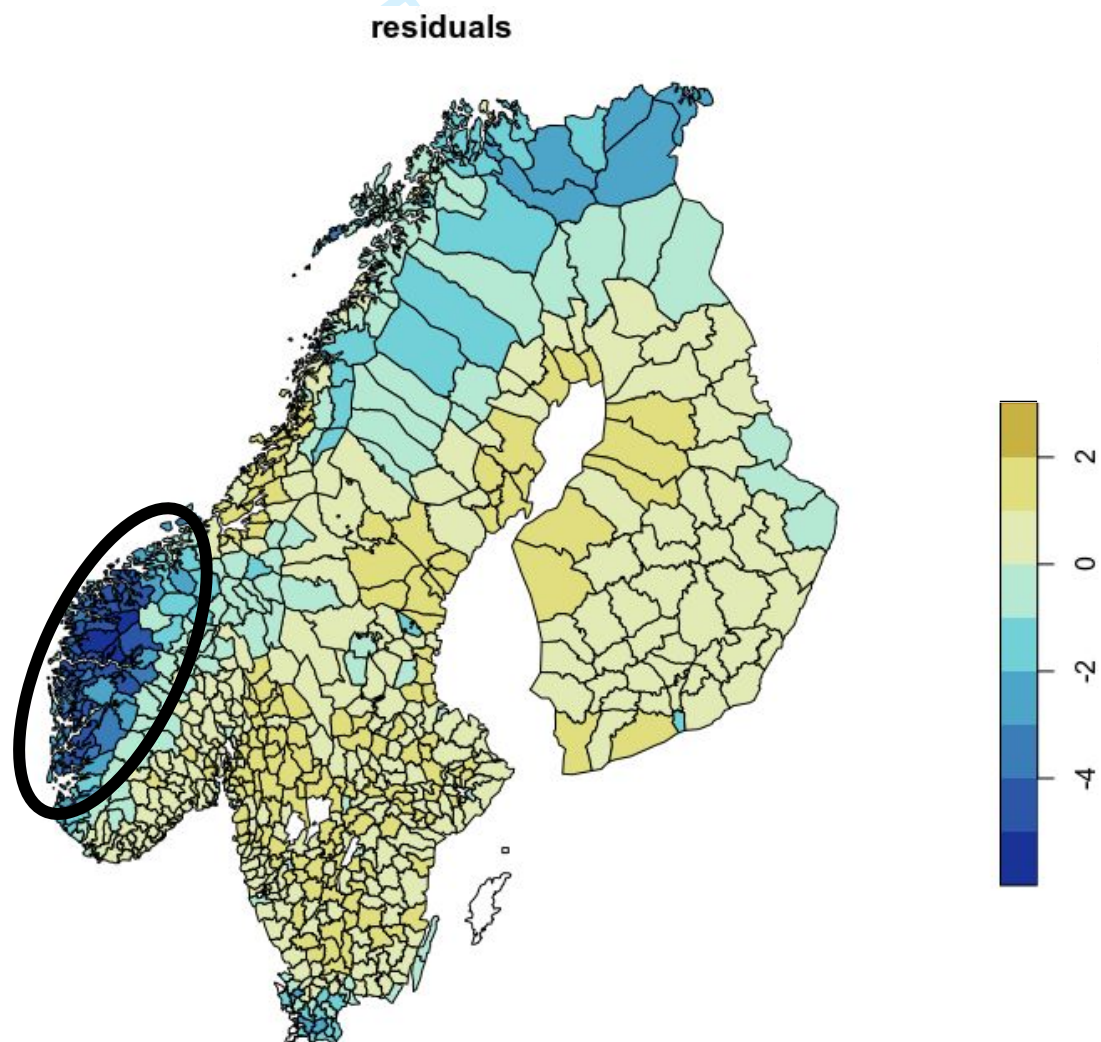

residuals

Figure S4

Relationship between harvest and habitat suitability in Fennoscandia

The logarithm of the average annual harvest plotted against the total summer suitability for each reporting unit in Fennoscandia. As noted above, an important deviation from the prediction occurs in Western Norway (see Figure S4). After removal of this area the linear regression ($\log (harvest) = \beta_0 + \beta_1 \log (RSPF_{summer}) + \varepsilon$) explains 66% of the variance in harvest (compared to a variance explained of 50% reported in the main text, and $\beta_1 = 0.86$).
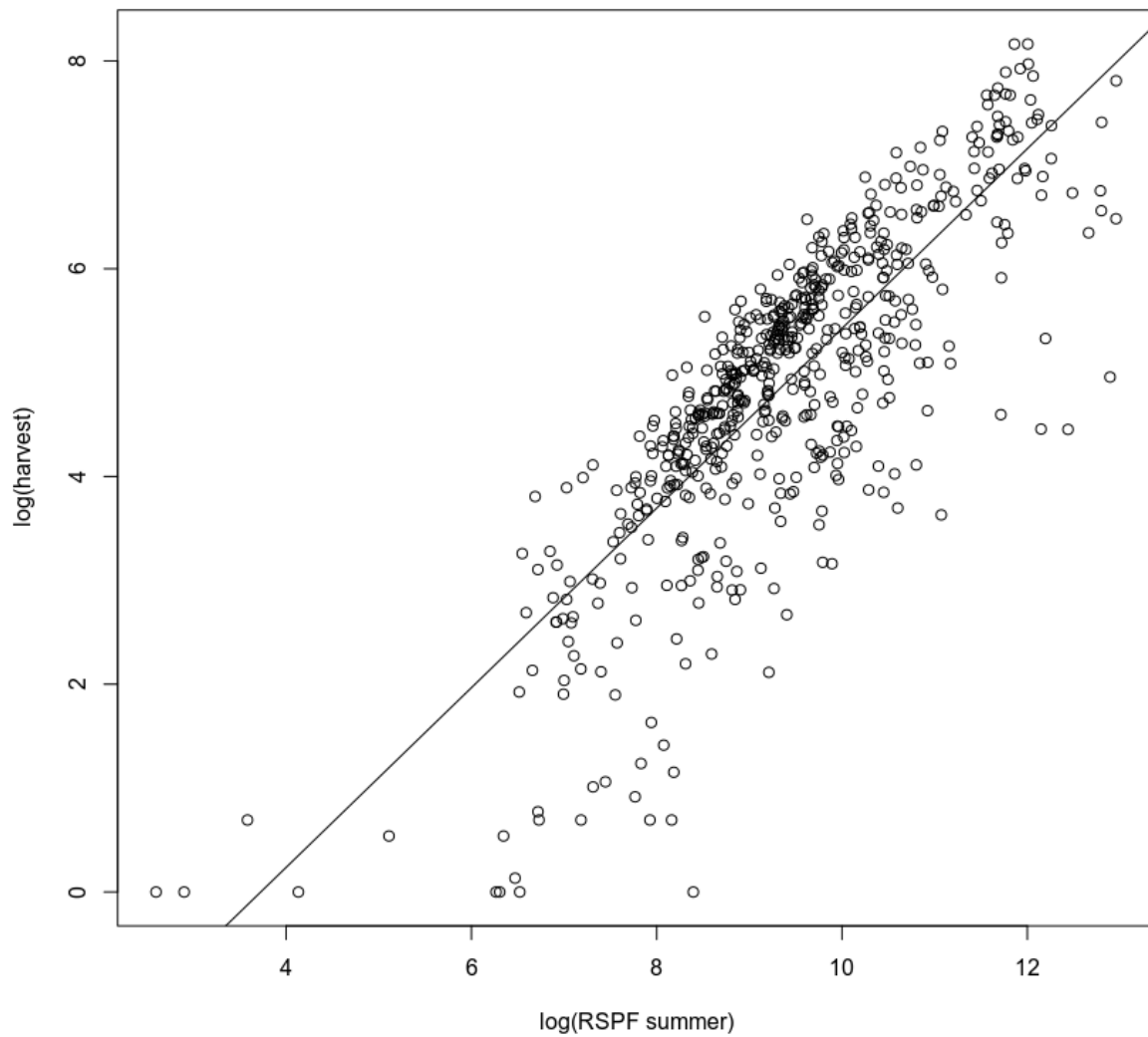
Figure S5

Moose population distribution during summer in Fennoscandia

The population distribution of moose (in harvested individuals per km^2) derived from the harvest data and the predicted summer RSPF.
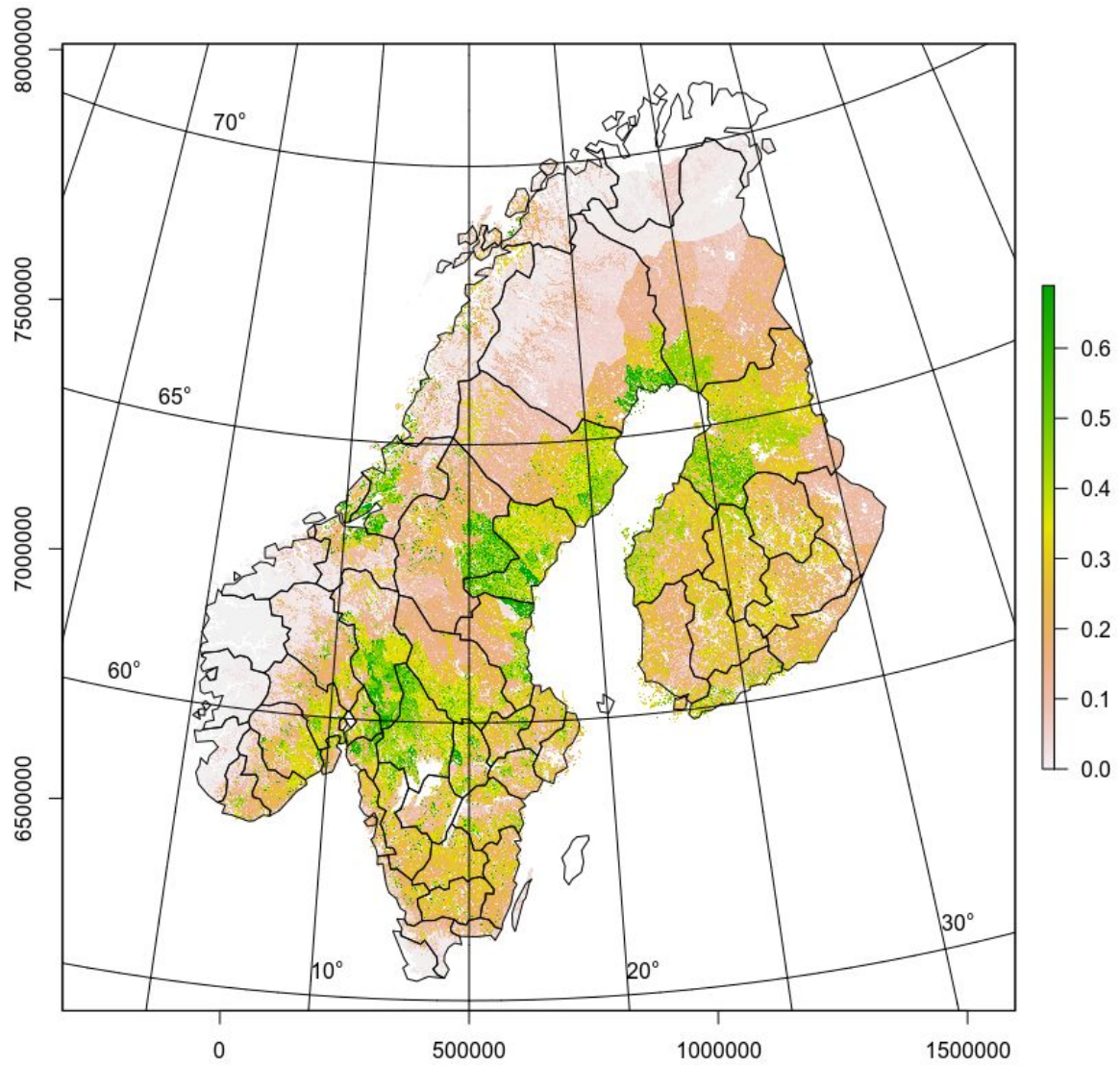
Figure S6

Boxplot with the distribution of elevation at the lowland and highland range across Fennoscandia. We labelled the geographic areas that were more selected during winter than during summer as lowland ranges and those that were more selected during summer than during winter as highland ranges. We used these geographic labels instead of summer and winter ranges to avoid confusion with summer and winter in reference to seasons. Although, altitude is unlikely to be a direct driver of migration itself, it is common to observe altitudinal migration in response to ecological variables with an altitudinal gradient. For instance, in our study snow was an important variable related to migration. Not surprising and in support of our a priori labels, we did observe lower elevations in the areas more selected during winter, and higher elevations in the areas more selected during summer.
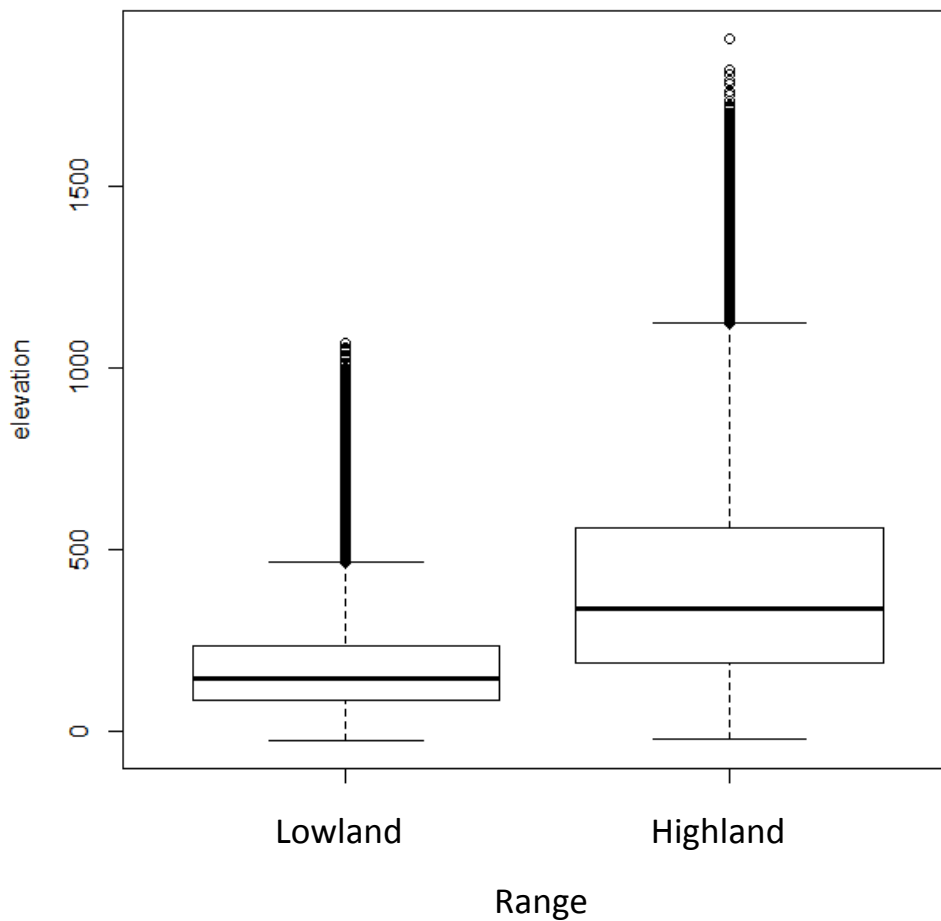
Figure S7

Descriptive details for the different clusters: number of individuals (N), number of males, number of females, number of migrants & residents (VI criterion), mean age of the moose at marking (note that age was not available for all clusters).

Name	N_{total}	N_{male}	N_{female}	$N_{migrant}$	$N_{resident}$	avg(age)
A	30	9	21	29	1	4.9
B	54	8	46	31	23	4.8
C	54	8	46	49	5	5.2
D	19	6	13	16	3	5.5
E	16	4	12	7	9	5.8
F	21	2	19	1	20	8.4
G	42	20	22	31	11	NA
H	29	7	22	15	14	NA
I	13	4	9	5	8	NA
J	13	8	5	7	6	NA
K	24	3	21	0	24	7.1
L	22	5	17	1	21	6.7
M	43	6	37	15	28	3.0
N	31	10	21	17	14	2.7
O	13	2	11	8	5	3.1
P	41	13	28	11	30	NA
Q	22	4	18	2	20	NA
R	26	0	26	13	13	7.1
S	32	0	32	15	17	8.7

Figure S8

Relationship between different migration criteria

The proportion of migrants in each cluster determined by the Volume of Intersection VI criterion on the x-axis and the distance above 10km criterion on the y-axis. Given the high agreement between both criteria results were qualitatively identical, we therefore only reported those for the VI criterion.