

1 Running head: Future range of a migratory ungulate

2 **Future suitability of habitat in a migratory ungulate under climate change**

3 Inger Maren Rivrud^{1*}, Erling L. Meisingset², Leif Egil Loe³, and Atle Mysterud¹

4 ¹ Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences,
5 University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway

6 ² Department of Forestry and Forestry resources, Norwegian Institute of Bioeconomy Research,
7 Tingvoll gard, NO-6630 Tingvoll, Norway

8 ³ Faculty of Environmental Sciences and Natural Resource Management, Norwegian University
9 of Life Sciences, P.O. Box 5003, NO-1432 Aas, Norway

10 * Corresponding author; Phone: +47-22857294; e-mail: i.m.rivrud@ibv.uio.no

11

12

13 **Abstract**

14 With climate change, the effect of global warming on snow cover is expected to cause range
15 expansion and enhance habitat suitability for species at their northern distribution limits.

16 However, how this depend on landscape topography and sex in size-dimorphic species remains
17 uncertain, and is further complicated for migratory animals following climate-driven seasonal
18 resource fluctuations across vast landscapes. Using 11 years of data from a partially migratory
19 ungulate at their northern distribution ranges, the red deer (*Cervus elaphus*), we predicted sex-
20 specific summer and winter habitat suitability in diverse landscapes under medium and severe
21 global warming. We found large increases in future winter habitat suitability, resulting in
22 expansion of winter ranges as currently unsuitable habitat became suitable. Even moderate
23 warming decreased snow cover substantially, with no suitability difference between warming
24 scenarios. Winter ranges will hence not expand linearly with warming, even for species at their
25 northern distribution limits. Although less pronounced than in winter, summer ranges also
26 expanded and more so under severe warming. Summer habitat suitability was positively
27 correlated with landscape topography and ranges expanded more for females than males. Our
28 study highlights the complexity of predicting future habitat suitability for conservation and
29 management of size-dimorphic, migratory species under global warming.

30 *Keywords:* Climate change, IPCC, home range, landscape composition, migration, species
31 distribution models

32 **Introduction**

33 Climate change is a substantial threat to biodiversity and ecosystems worldwide [1]. Increasing
34 temperatures are affecting a wide range of taxa, leading to phenological mismatch across trophic
35 levels [2], and shifting, contracting or expanding distribution ranges [3-5]. Climate change is
36 particularly topical for migratory species [6, 7], who follow seasonal resource fluctuations in
37 time and space [8]. These resources are highly affected by climate, making management and
38 conservation of migratory species increasingly challenging [6]. In seasonal environments,
39 animals migrate between separate seasonal ranges, e.g. summer and winter ranges or wet and dry
40 season ranges, and these ranges are typically situated at different latitudes and/or elevations.
41 With the predicted increasing temperatures and lack of snow cover in the decades to come [9], it
42 is of particular interest to derive predictions of how migratory species will respond to changes in
43 their seasonal ranges.

44 A widespread method to make predictions about future habitat availability for different
45 species under climate change is species distribution models (SDMs) and estimation of habitat
46 suitability maps [10]. SDMs have been used to predict future ranges of a variety of organisms
47 such as plants, amphibians, reptiles, birds and mammals [e.g. 11, 12], including non-migratory
48 ungulates such as Svalbard reindeer [*Rangifer tarandus platyrhynchus*; 13] and mountain goat
49 [*Oreamnos americanus*; 14]. However, this becomes more complicated for migratory animals
50 with two disparate seasonal ranges, as climatic factors interact with topography and determine
51 the weather ultimately affecting migratory animals and their food resources [15]. The migration
52 patterns of ungulates in temperate environments are largely driven by snow levels during fall,
53 forcing them to stay at low elevation/low latitude during winter. In spring they expand their
54 ranges and increase access to early forage maturation in summer ranges at higher elevation or

55 latitude [8]. Thus, habitat suitability varies for migratory species depending on season, i.e. with
56 snow levels determining the available habitat in winter, and temperature influencing the quality
57 of summer habitats.

58 We aim to investigate how the current available habitat for a migratory species depends
59 on season, sex and landscape topography, and to predict how winter and summer ranges will
60 change under two alternative future emission scenarios (medium and severe), both in terms of
61 size and habitat suitability. We use 11 years of data (2005-2015) from a total of 192 GPS marked
62 red deer (*Cervus elaphus*) in Norway, a partially migratory species [16]. This study system is
63 particularly useful, as it spans over a long south-north and coast-inland gradient, and an
64 extensive ~800 meter elevation gradient including a range of different landscapes [8, 15]. Snow
65 levels is the limiting factor for winter range availability [17, 18]. Global warming predicts
66 increased temperatures, less precipitation falling as snow and a prolonged growing season, but
67 the magnitude depends on landscape topography [9]. We therefore predict an overall range
68 expansion and increase in red deer habitat suitability for both seasons and emission scenarios,
69 with a more pronounced response in the severe scenario. We expect a larger range expansion and
70 increase in habitat suitability with increasing elevation, as snow levels and temperature are
71 limiting factors for current use of high elevation areas. Finally, polygynous species such as the
72 red deer show sex-specific use of the elevation gradient, with males using higher elevation areas
73 to a larger extent since they have no dependent offspring requiring protective forest habitat [19].
74 We therefore explore differences between the sexes in future habitat suitability and range size.

75 **Materials and methods**

76 **Study area**

77 The study area comprises 4 counties (Sør-Trøndelag, Møre og Romsdal, Sogn og Fjordane and
78 Hordaland) situated in the core area for red deer on the western part of Southern Norway, where
79 ~90% of red deer in Norway are harvested yearly (<http://www.ssb.no>; Fig.1). The vegetation is
80 mostly in the boreonemoral zone dominated by Scots pine (*Pinus sylvestris*) and deciduous
81 forests, with increasing domination of birch (*Betula* sp.) northwards. Norway spruce (*Picea abies*)
82 has been planted on a large scale. Temperature and precipitation generally decrease from coast to
83 inland and from south to north, while snow depth and number of days with snow increases along
84 the same gradients. The topography is characterized by diverse elevation gradients, with
85 generally steeper terrain and higher elevations inland.

86 **Red deer GPS data**

87 Adult red deer (females \geq 1.5 and males \geq 2.5 years old) were fitted with GPS collars (Followit,
88 Sweden and Vectronic, Germany) between 2005-2015 [16, 17]. The individuals were darted on
89 winter feeding grounds in winter [January-March; 20], following a standard procedure approved
90 by the Norwegian Animal Research Authority. The GPS collars were preprogrammed to record a
91 position every 1-2 hours, and the individuals were followed between 1-3 years, depending on the
92 GPS collar battery life, technical difficulties, mortalities and recaptures. GPS locations from the
93 first 24 hours after marking were removed, and the remaining raw location data were screened
94 for outliers following Bjørneraas et al. [21; <0.01%]. The rate of successful GPS locations
95 obtained by the collars and the magnitude of the GPS location error vary with canopy cover of
96 habitat and topography [e.g. lower success rate in areas with steep mountains; 22]. In our study
97 area these sources of errors were quantified in using the same collar types as the in red deer [23].
98 Variable success rate may influence the models, and to avoid bias we simulated missing GPS
99 locations using a map of the study area with an associated probability of obtaining a GPS

100 location in each pixel, based on the models built by Godvik et al. [23] and according to Frair et al.
101 [22]. For details on the simulation of missing locations see Godvik et al. [23] and Loe et al. [24].

102 We used the model-fitting approach developed by Bunnefeld et al. [25], and sophisticated
103 by Bischof et al. [8] and Rivrud et al. [17], to determine red deer migration patterns. We retained
104 individuals with clear migratory movement patterns. Migration is rapid and merely a transit
105 between the separate summer- and winter areas [8, 17], and we therefore removed locations
106 between migration onset and -end for each individual. See Supporting Information Table S1 and
107 Fig. S1 for a summary of migration characteristics. Due to the marking/drop-off schedule, many
108 individuals were missing data for parts of the winter season. Individuals usually use the same
109 ranges every year (unpublished data), and partial winter ranges were retained if overlapping with
110 past or subsequent complete winter ranges. Seasonal ranges where individuals spent less than
111 two weeks were removed ($N_{\text{obs}}=38$ ranges).

112 A total of 62 male and 130 female individual red deer covering 89 and 167 seasons
113 respectively, were available for summer analyses ($N_{\text{obs}}=670328$), and 53 male and 117 female
114 red deer covering 119 and 261 seasons respectively were available for winter analyses
115 ($N_{\text{obs}}=842238$).

116 **Environmental variables**

117 We derived all environmental variables from maps prepared and rasterized using ArcGIS 10.3
118 (ESRI, USA), with a resolution of 100x100 m. Elevation (m a.s.l.), slope (degrees) and aspect
119 (radians) were derived from a digital elevation model. Aspect was cosine transformed to
120 northness, a continuous variable ranging from 1 (north) to -1 (south). Layers with roads and
121 coastline (scale 1:50000) were used to calculate the shortest linear distance (meters) to roads and

122 the coast for each pixel in the study area. Digital land resource maps (scale 1:5000) were
123 obtained from Norwegian Institute of Bioeconomy Research, with information on 4 functional
124 habitat types relevant for our study species (agricultural areas, forests, mountains and marshland),
125 in addition to non-relevant habitats (inhabited areas, glaciers, water bodies and uncharted areas).
126 All locations sampled as used and available in non-relevant categories were removed before
127 running models, to assure balanced data. As the use of pastures depends on the availability in our
128 study area [23], we calculated the proportion of available pasture pixels to relevant habitat types
129 within a circle for each location with a season-specific radius corresponding to the median sizes
130 of 95% seasonal adaptive Local Convex Hull (*a*-LoCoH) home ranges (summer; 799 m, winter;
131 732 m).

132 Daily 1x1 km grids of snow water equivalent (SWE; used as proxy of snow depth) and
133 temperature covering the study area and -period were provided by the Norwegian Water
134 Resources and Energy Directorate and the Norwegian Meteorological Institute's (NMI),
135 respectively. These grids were made using statistical downscaling predicting SWE and
136 temperature based on observed values of temperature and precipitation recorded by NMI weather
137 stations in the area. Tests have shown close correlation with observed data, but some
138 overestimation of SWE occurred during snow melt in spring [26]. The Norwegian Centre for
139 Climate Services provided daily 1x1 km grids with future predictions of SWE and temperature
140 covering Norway [27]. The 1x1 km predictions were based on regional 12x12 km HIRHAM
141 simulations provided by the Danish Meteorological Institute and EURO-CORDEX [COordinated
142 Regional climate Downscaling EXperiment; 28], which again were based on global predictions
143 from the Earth system model [EC-EARTH; 29]. Future predictions of red deer habitat suitability
144 were made for two alternative emission pathways, based on IPCC's Representative

145 Concentration Pathway (RCP) 4.5 and 8.5 [9, 30]. A medium emission scenario is represented by
146 RCP4.5, where emission increases until ~2040, before a reduction and stabilization from ~2080.
147 This scenario results in about 2.5°C increase in global temperature around year 2100, compared
148 to 1850-1900. RCP8.5 represents a severe emission scenario, with emissions following the same
149 trajectory as during the last decade. Global temperatures are expected to increase about 4°C in
150 year 2100 relative to 1850-1900 in this scenario. Maps of monthly means for summer and winter
151 used in the analyses can be seen in the Supplementary Material, Fig. S2.

152 All extraction of environmental variables and coupling to the red deer locations was done
153 in R.

154 **Estimation of use and availability**

155 Use and availability were estimated on the home range and landscape scale respectively,
156 corresponding to second-order selection [31].

157 *Availability:* We divided all red deer GPS locations into three regions defined by natural barriers
158 in the landscape such as great fiords ($N_{\text{obs}}=899153, 321343$ and 446578 from north to south; Fig.
159 1). As the study area is on the western coast of Norway, locations were bounded by open sea in
160 the west and high elevation areas in the east, which resulted in the total GPS locations taking a
161 banana-shape. Thus, regular kernel- or minimum convex polygon methods did not perform well.
162 The available area in each region was therefore estimated by calculating the α -convex polygons,
163 which is more flexible in shape, using the “alphahull” package in R [32]. A range of α -values
164 were tested searching for a value of α encompassing all locations, but minimizing large areas of
165 inaccessible habitats at high elevations. A radius $\alpha=70000$ m yielded the best estimate for all
166 regions. Larger values included obvious inaccessible areas, while smaller values resulted in

167 fragmented areas and excluded locations from the polygon. Available locations were sampled
168 randomly within the regional polygons. We sampled an excess of locations to be able to remove
169 locations located in non-habitat (e.g. water), and still keep a 1:1 relationship between used and
170 available locations. After removal of these locations, we retained the same amount of available
171 and used locations (N=1000 per individual/year). We also sampled 1000 random dates for each
172 individual within their individual monitoring period for extraction of SWE and temperature,
173 which were coupled with the sampled GPS locations representing availability.

174 *Use*: Used areas were estimated by calculating the 95% *a*-LoCoH home ranges for each animal
175 each season using the package “adehabitatHR” in R [33]. This method also performs very well
176 when dealing with linear home ranges or home ranges bounded by elements such as shorelines or
177 steep mountains. An *a*-value larger than the two longest distances between individual locations
178 should always give the 100% isopleth, but also keep a small radius of LoCoH elements in areas
179 of high use [34]. We therefore used this *a*-value when possible, and increased to the sum of the
180 three, four or five longest distances if the *a*-LoCoH did not converge. The mean number of
181 locations used for estimation of individual summer home ranges was 2618 (sd=1098) and 2211
182 (sd=1686) for winter ranges. Used locations were sampled within the individual 95% home range
183 polygons, and the number of locations sampled for each individual corresponded to the number
184 of available locations sampled to ensure a balanced data set. The individual dates sampled above
185 were coupled to the GPS locations representing use for extraction of SWE and temperature.

186 **Statistical analyses**

187 Resource selection functions were estimated using generalized linear mixed effects models
188 (GLMMs) with a use-availability design, and random intercept for year to account for yearly

189 sampling variation. The response is binomial, where used locations are coded 1 and available
190 locations are coded 0. We ran 4 separate models, split by season (summer and winter) and sex
191 (Supplementary Material, Table S2). The landscape variables elevation, slope, northness,
192 distance to coast, distance to roads, proportion of pasture (arcsine-square root transformed),
193 SWE (mm; winter models) and temperature ($^{\circ}\text{C}$; summer models), were all checked for
194 correlations before initial model building. Distance to roads and elevation were correlated with $r >$
195 $|0.6|$, and thus only elevation was retained as this was more relevant. We did not include the
196 categorical variable habitat type, as mountainous habitat was highly correlated with elevation.
197 All variables except proportion of pasture and northness were rescaled by centering on their
198 mean and dividing by their standard deviation to avoid convergence issues. Generalized additive
199 models were used to check for non-linearity. Temperature/SWE were included in interaction
200 with elevation, and we included the interaction between pasture availability and pasture use
201 following Godvik et al. [23] and Loe et al. [24] to account for trade-offs in pasture use. GLMMs
202 including all covariates and interactions listed above were estimated with the “glmer” function in
203 the “lme4” package [35] in R. The candidate GLMMs were subjected to backwards fixed-effect
204 model selection using likelihood ratio tests [36].

205 The most parsimonious models were extrapolated into habitat suitability maps by
206 stacking the individual environmental maps into a multi-layered raster map, and predicting from
207 the GLMMs the relative probability of detecting individual red deer in each pixel. Changes in
208 future range size and habitat suitability were then quantified separately for each of the three
209 regions. Three habitat suitability maps were estimated for each model; current (average
210 temperature (July) and SWE (February) from 2005-2014), RCP4.5 and RCP8.5 year 2100 (both
211 with average temperature (July) and SWE (February) from 2100). February and July averages

212 were chosen as these months represent the most snow rich (February) and warmest (July) months
213 in Norway. All habitat suitability maps were made in R using the “raster” package [37]. Finally,
214 we calculated the niche overlap between present and future habitat suitability maps using
215 Schoener’s D [38].

216 **Effects of sample size and measures of model quality**

217 To ensure that the sample sizes were appropriate, we investigated how sample size (number of
218 individuals) affected model quality. For each of the four models we divided the data into a
219 training set and a test set as follows: Individuals were sampled randomly (range 2-70) with
220 replacement and the data set was subset based on these individuals, representing the training data.
221 We sampled with replacement as these individuals could represent other unsampled individuals
222 with identical habitat selection strategies [24]. The rest of the data set represented the test data.
223 The models were then fitted with the training data, and model predictions were made based on
224 the test data, from which we calculated the area under the ROC curve (AUC) and Cohen’s Kappa
225 to assess prediction accuracy [39]. The process was repeated 100 times for each sample size.
226 Model quality of the 4 final models was assessed using *k*-fold cross validation [40]. The data set
227 was randomly split into 5 folds, of which 80% were assigned as training data and 20% as test
228 data. The model was fitted with the training data, and then evaluated on the test data by
229 estimating the overall prediction accuracy using the “caret” package in R [41]. The process was
230 repeated 20 times, yielding 100 model runs for each of the 4 models.

231

232 **Results**

233 *Effects of sample size and measures of model quality*

234 The mean prediction accuracy stabilized at a sample size of 15 individuals for winter models
235 (both AUC and Cohen's Kappa), and for 25-30 individuals for summer models depending on the
236 quality measure used (see Supporting Information, Fig. S3). Overall prediction accuracy for the
237 final models based on k -fold cross validation was high, and winter models
238 (mean \pm SD=0.79 \pm 0.001 and 0.80 \pm 0.0003 for males and females respectively) performed better
239 than summer models (mean \pm SD=0.71 \pm 0.003 and 0.72 \pm 0.002 for males and females respectively).

240 *Seasonal patterns of current habitat selection*

241 The final summer models for both sexes included elevation, slope, distance to coast (squared),
242 northness (squared), temperature and the interaction between elevation and temperature, and
243 pasture trade-off term were included in female summer models only (Table 1a). The final winter
244 model for both sexes included elevation, slope (squared), distance to coast, northness, pasture
245 trade-off, snow water equivalent (SWE) and the interaction between elevation and SWE (Table
246 1b).

247 Summer

248 During summer, habitat selection in the elevation gradient depended on temperature for both
249 sexes, with increased selection of high elevation areas when temperatures increased (Table 1a).
250 In general, high temperatures resulted in females showing stronger selection of high elevation
251 than males (Table 1a). Selection for distance to coast and northness were both non-linear (Table
252 1a). Both sexes selected for intermediate distances from coast, with females utilizing a larger
253 range of distances than males, and both avoided areas close to or very far from the coastline.
254 There was strong selection for southfacing aspect for both sexes, with decreasing selection

255 towards northfacing aspects. Females showed stronger avoidance of northfacing aspects than
256 males. Males and females both selected for steeper slopes and avoided flat terrain (Table 1a).

257 Winter

258 Selection in the elevation gradient during winter depended on snow levels for both sexes. In
259 general, red deer avoided high elevation areas, and avoidance increased with increasing snow
260 depths (Table 1b). The relationship was stronger for females than for males. Males and females
261 both selected for areas closer to the coast and for southfacing aspects (Table 1b). Selection of
262 slopes was non-linear for both sexes with selection for intermediate slopes and higher selection
263 for steeper slopes for males than females (Table 1b). Finally, females showed stronger selection
264 for pastures than males (Table 1b).

265 *Current habitat suitability*

266 Habitat suitability maps during the study period showed larger sex differences in winter than in
267 summer (Fig. 2). During winter the most suitable habitat was constricted to coastal areas, and
268 more so for females than males (Fig. 2). The differences also varied across the south-north
269 gradient (Fig. 3). Males had consistently larger suitable ranges than females, and the range size
270 difference varied as a function of topography and distance to coast (Figs 2-3). Range size
271 differed less between the sexes in flatter regions with higher summer temperatures and less snow
272 (Sør-Trøndelag) than in steeper regions with lower summer temperatures (Sogn og Fjordane; Fig.
273 3; Supplementary Material, Table S3).

274 *Predictions of future ranges and habitat suitability*

275 Habitat suitability increased strongly in winter under both scenarios, in particular in inland areas
276 (Fig. 4). The predicted effect of summer warming was less pronounced but differed more
277 between scenarios. In coastal areas, summer habitat suitability decreased for both sexes under
278 severe emission (Fig. 4). The future increase in habitat suitability was mainly due to poor or
279 unsuitable habitat becoming suitable during both seasons (Supplementary Material, Fig. S4).
280 Present high quality winter habitat improved further, while present high quality summer habitat
281 was unchanged or became less suitable (Supplementary Material, Fig. S4). In order to investigate
282 how changes in habitat suitability values affected range expansion, we need to set a threshold for
283 suitable habitat. With a threshold value of 0.2, the future ranges expanded in both seasons and
284 sexes, and the ranges expanded more for females than males (Fig. 3, Supplementary material,
285 Table S4). While females showed range expansion for all tested thresholds for habitat suitability
286 (0.1-0.5), male summer ranges were predicted to contract at suitability thresholds higher than 0.5,
287 implying that the currently best male summer habitat will deteriorate most (Supplementary
288 material, Table S4).

289 As predicted, future habitat suitability and range size was dependent on topography.
290 Ranges expanded substantially during winter for both sexes in all counties, but more in the
291 higher elevation counties (Hordaland and Sogn og Fjordane; Figs 3-4). Contrary to our
292 predictions, there were no differences in range size between the alternative emission scenarios
293 medium and severe (Fig. 3), suggesting that even with medium emission snow cover will be
294 limited. Summer range size was more variable both with elevation, emission scenarios and sexes.
295 There was a general future range expansion, with stronger increase under severe emission and in
296 higher elevation counties, as predicted, and the range expansion was larger for females than
297 males (Figs 3-4). The niche overlap between present and future habitat suitability, assessed by

298 Schoener's D, ranged from 0.887 – 0.994, and was higher in summer than in winter, and higher
299 for males than females (see Supporting Information, Table S5).

300 **Discussion**

301 Northern latitudes are expected to experience the greatest climate change impacts [9], with
302 potentially large consequences for migratory species following fluctuating resources across
303 broad scales [6]. Studies showing range shifts, contractions or expansions under climate change
304 are numerous, and represent many taxa [reviewed in 1]. However, few have done detailed
305 investigations of how the response varies within species over different seasons and landscapes,
306 and under alternative emission scenarios. We found three particularly important results in this
307 context. First, there was no difference in range expansion or habitat suitability between emission
308 scenarios during the winter season. This is likely due to the snow cover, which limit the winter
309 distribution ranges, disappearing already with medium emissions. Second, the magnitude of
310 range expansion and change in habitat suitability depended on landscape topography. Range
311 expansion was smaller in areas with overall lower elevation, and habitat suitability in coastal
312 areas even decreased in summer indicating possible range shifts. Finally, warmer summers
313 resulted in larger range expansion and higher habitat suitability for females than males. Males
314 remained less responsive to climate change, and even showed a marginal future range
315 contraction of highly suitable habitat. The seasonal effects interacting with sex and landscape
316 topography in response to climate change highlights the complexity of estimating future ranges
317 for migratory species.

318 Species at their northern distribution limits are expected to expand their ranges
319 northwards and to higher elevations with increasing global warming due to decrease of snow

320 cover, but this expansion will naturally reach a plateau when all snow cover is lost. In the Alps,
321 predictions show that an increase of 4°C in mean temperature will reduce the duration of snow
322 cover by 50% and 95% at 2000 and 1000 m a.s.l. respectively [42]. In our case, the predicted
323 decrease in snow cover is reflected in the large expansion of future winter ranges, but without
324 large range size differences between emission scenarios, indicating nonlinear effects of global
325 warming on snow cover and in turn habitat suitability. Range expansions reaching a plateau, or
326 range contraction, is a commonly documented pattern in species dependent on high elevation
327 habitat [1]. The magnitude of future winter range expansion differed with landscape composition,
328 where the northernmost county (Sør-Trøndelag), showed a lower increase than the remaining
329 counties. The future available red deer habitat under climate change is probably limited in this
330 region, as there is less high elevation area to expand into as snow levels decrease. Hence, the
331 global warming effects on habitat suitability are not necessarily stronger further north as
332 responses depend more on topography.

333 Increasing summer temperatures can affect migratory ungulates both directly and
334 indirectly. Large-bodied herbivores inhabiting northern environments have been shown to shift
335 to higher elevations, select habitats with more cover but lower forage quality, and reduce
336 foraging rates when temperatures increase to avoid heat stress [43]. Higher temperatures causes
337 increased lignification of plant cell walls due to rapid growth, reducing forage quality and
338 digestibility [44], and affecting the animals indirectly. Faster snow melt may cause more rapid
339 green-up, thus reducing time with high quality forage at early phenological stages [45]. Although
340 these are all predicted negative effects of a warming climate, increased temperatures can also be
341 positive, i.e. by making high elevation areas earlier covered by snow accessible. We found that
342 changes in future summer ranges and habitat suitability were less consistent than during winter,

343 and depended on sex, landscape topography and emission scenario. Female summer ranges
344 expanded more with increasing emission, and more than male ranges. Habitat suitability
345 depended on topography for both sexes, with an increase in inland areas and a decrease in coastal
346 areas. The red deer is a sexually size-dimorphic species, and the sexes also spend most of the
347 year segregated [19]. Males already use more high elevation habitat during summer than females
348 as they are not limited by offspring at heel [19]. Consequently, males will have less new
349 available habitat to expand into. Studies in birds found that male great bustards (*Otis tarda*), the
350 most sexually size-dimorphic bird species, selected areas with more shade than females during
351 the warmest periods of the day, and males also migrated further north at high summer
352 temperatures [46, 47]. Hence, both direct and indirect sex-specific responses to climate may be
353 common for dimorphic species in many taxa and should be considered when predicting future
354 suitable ranges.

355 A limitation of SDM approaches [13, 14], is that habitat changes likely to occur over long
356 time scales are not taken into account. Warming temperatures and lack of snow are expected to
357 move the tree line and vegetation upwards [48, 49], and create new suitable habitats with a time
358 lag. The tree line ecotone is a major effect causing a non-linear impact of habitat use along the
359 elevation gradient. The alpine tree line ecotone determines whether the ecosystem carbon stocks
360 will be mainly above ground (forests) or in ground (soil). Strict forest living species such as roe
361 deer (*Capreolus capreolus*) showed no change in elevation distribution over the last decades in
362 the Alps, while species more tolerant to open habitat, such as red deer and ibex (*Capra ibex*), are
363 now found at higher elevations [50]. Complicating this, large herbivores may influence the
364 advance of the tree line through grazing [49], and possibly affect their own future habitat
365 negatively. Although many species have already shifted to higher elevation or latitudes in

366 response to global warming [3], the movement in elevation even for species using open habitat
367 will eventually be limited by soil depth and quality. The soil in high alpine zone is of poor
368 quality or absent [51] and developing soil of sufficient depth takes more time than the projected
369 upwards movement of vegetation caused by rapid climate change [52]. Other consequences of
370 future climate change, such as more unpredictable and extreme weather events [53] and indirect
371 effects on habitat suitability caused by humans through i.e. changes in infrastructure and habitat
372 fragmentation are also expected to influence the future habitat suitability of species. In addition,
373 different species can be affected differently by climate change, which may alter the competitive
374 interactions between species, and in turn affect species distribution [54]. These complex
375 interactions are hard to incorporate precisely, but are also likely to play a relatively minor role
376 compared to the overall effect of climate change.

377 **Conclusion**

378 Our models predict range expansion and increase in habitat suitability for migratory deer
379 populations at their northern distribution limits, with interesting interactions with season, sex and
380 landscape topography. Annual habitat suitability predictions are therefore not sufficiently
381 detailed to foresee consequences of climate change for future conservation and management of
382 migratory species. With males and females displaying different tolerance levels to snow and
383 temperature in sexually size-dimorphic species [47, 55] and global warming affecting the
384 weather differently during summer and winter [9], incorporating these factors in species
385 distribution models is clearly necessary to improve future range predictions for these species. In
386 addition, landscape topography is crucial both for determining the speed of climate change
387 effects, and to buffer effects of global warming, thus creating possible refugia where species can
388 persist [56].

389 **Ethics**

390 All capture and handling of red deer have been approved by the Norwegian Animal Research
391 Authority.

392 **Competing interests**

393 The authors declare no competing interests.

394 **Authors' contributions**

395 A.M. and I.M.R. designed the study, and E.L.M. and A.M. organized the data collection. I.M.R.
396 analyzed the data with input from L.E.L., and I.M.R. wrote the first draft of the manuscript. All
397 authors contributed substantially to the final version.

398 **Acknowledgements**

399 We greatly acknowledge the support of The Research Council of Norway and the Norwegian
400 Environment Agency to the DeerUnit-project (Pr. No. 230275). Øystein Brekkum has been
401 valuable for handling the red deer database, and Jess Anderson at the Norwegian Water
402 Resources and Energy Directorate has kindly provided snow depth grids.

403 **Data accessibility**

404 The datasets supporting this article can be accessed at <https://doi.org/10.5061/dryad.8p003sg>.

405 **Funding**

406 The study was founded by The Research Council of Norway, Grant/Award Number: DeerUnit,
407 Pr. No. 230275.

408 **References**

- 409 [1] Parmesan, C. 2006 Ecological and evolutionary responses to recent climate change. *Annual*
410 *Review of Ecology Evolution and Systematics* **37**, 637-669.
- 411 [2] Kudo, G. & Ida, T.Y. 2013 Early onset of spring increases the phenological mismatch
412 between plants and pollinators. *Ecology* **94**, 2311-2320.
- 413 [3] Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. 2011 Rapid range shifts of
414 species associated with high levels of climate warming. *Science* **333**, 1024-1026.
- 415 [4] Zhu, K., Woodall, C.W. & Clark, J.S. 2012 Failure to migrate: lack of tree range expansion in
416 response to climate change. *Global Change Biology* **18**, 1042-1052.
- 417 [5] Thomas, C.D., Bodsworth, E., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. &
418 Conradt, L. 2001 Ecological and evolutionary processes at expanding range margins. *Nature* **411**,
419 577.
- 420 [6] Robinson, R.A., Crick, H.Q., Learmonth, J.A., Maclean, I.M., Thomas, C.D., Bairlein, F.,
421 Forchhammer, M.C., Francis, C.M., Gill, J.A. & Godley, B.J. 2009 Travelling through a
422 warming world: climate change and migratory species. *Endangered species research* **7**, 87-99.
- 423 [7] Middleton, A.D., Kauffman, M.J., McWhirter, D.E., Cook, J.G., Cook, R.C., Nelson, A.A.,
424 Jimenez, M.D. & Klaver, R.W. 2013 Animal migration amid shifting patterns of phenology and
425 predation: lessons from a Yellowstone elk herd. *Ecology* **94**, 1245-1256.
- 426 [8] Bischof, R., Loe, L.E., Meisingset, E.L., Zimmermann, B., Van Moorter, B. & Mysterud, A.
427 2012 A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave?
428 *American Naturalist* **180**, 407-424.
- 429 [9] IPCC. 2013 Climate Change 2013: The Physical Science Basis. Contribution of Working
430 Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (eds.

431 T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V.
432 Bex & P.M. Midgley), p. 1535 pp. Cambridge, United Kingdom and New York, NY, USA.

433 [10] Elith, J. & Leathwick, J.R. 2009 Species distribution models: ecological explanation and
434 prediction across space and time. *Annual review of ecology, evolution, and systematics* **40**, 677-
435 697.

436 [11] Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C.,
437 Erasmus, B.F., De Siqueira, M.F., Grainger, A. & Hannah, L. 2004 Extinction risk from climate
438 change. *Nature* **427**, 145.

439 [12] McClean, C.J., Lovett, J.C., Küper, W., Hannah, L., Sommer, J.H., Barthlott, W.,
440 Termansen, M., Smith, G.F., Tokumine, S. & Taplin, J.R. 2005 African plant diversity and
441 climate change. *Annals of the Missouri Botanical Garden*, 139-152.

442 [13] Hansen, B.B., Aanes, R., Herfindal, I., Kohler, J. & Saether, B.-E. 2011 Climate, icing, and
443 wild arctic reindeer: past relationships and future prospects. *Ecology* **92**, 1917-1923.

444 [14] White, K.S., Gregovich, D.P. & Levi, T. 2018 Projecting the future of an alpine ungulate
445 under climate change scenarios. *Global change biology* **24**, 1136-1149.

446 [15] Pettorelli, N., Mysterud, A., Yoccoz, N.G., Langvatn, R. & Stenseth, N.C. 2005 Importance
447 of climatological downscaling and plant phenology for red deer in heterogeneous landscapes.
448 *Proceedings of the Royal Society B-Biological Sciences* **272**, 2357-2364.

449 [16] Mysterud, A., Loe, L.E., Zimmermann, B., Bischof, R., Veiberg, V. & Meisingset, E. 2011
450 Partial migration in expanding red deer populations at northern latitudes - a role for density
451 dependence? *Oikos* **120**, 1817-1825.

- 452 [17] Rivrud, I.M., Bischof, R., Meisingset, E.L., Zimmermann, B., Loe, L.E. & Mysterud, A.
453 2016 Leave before it's too late: Anthropogenic and environmental triggers of autumn migration
454 in a hunted ungulate population. *Ecology* **97**, 1058-1068.
- 455 [18] Nelson, M.E. 1995 Winter range arrival and departure of white-tailed deer in northeastern
456 Minnesota. *Canadian Journal of Zoology* **73**, 1069-1076.
- 457 [19] Bonenfant, C., Loe, L.E., Mysterud, A., Langvatn, R., Stenseth, N.C., Gaillard, J.M. &
458 Klein, F. 2004 Multiple causes of sexual segregation in European red deer: enlightenments from
459 varying breeding phenology at high and low latitude. *Proceedings of the Royal Society of*
460 *London Series B-Biological Sciences* **271**, 883-892.
- 461 [20] Sente, C., Meisingset, E.L., Evans, A.L., Wedul, S.J., Zimmermann, B. & Arnemo, J.M.
462 2014 Reversible immobilization of free-ranging red deer (*Cervus elaphus*) with xylazine-
463 tiletamine-zolazepam and atipamezole. *Journal of wildlife diseases* **50**, 359-363.
- 464 [21] Bjørneraas, K., Van Moorter, B., Rolandsen, C.M. & Herfindal, I. 2010 Screening global
465 positioning system location data for errors using animal movement characteristics. *Journal of*
466 *Wildlife Management* **74**, 1361-1366.
- 467 [22] Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H.M., Stenhouse,
468 G.B. & Beyer, H.L. 2004 Removing GPS collar bias in habitat selection studies. *Journal of*
469 *Applied Ecology* **41**, 201-212.
- 470 [23] Godvik, I.M.R., Loe, L.E., Vik, J.O., Veiberg, V., Langvatn, R. & Mysterud, A. 2009
471 Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology* **90**,
472 699-710.

- 473 [24] Loe, L.E., Bonenfant, C., Meisingset, E.L. & Mysterud, A. 2012 Effects of spatial scale and
474 sample size in GPS-based species distribution models: are the best models trivial for red deer
475 management? *European Journal of Wildlife Research* **58**, 195-203.
- 476 [25] Bunnefeld, N., Boerger, L., van Moorter, B., Rolandsen, C.M., Dettki, H., Solberg, E.J. &
477 Ericsson, G. 2011 A model-driven approach to quantify migration patterns: individual, regional
478 and yearly differences. *Journal of Animal Ecology* **80**, 466-476.
- 479 [26] Saloranta, T. 2012 Simulating snow maps for Norway: description and statistical evaluation
480 of the seNorge snow model. *The Cryosphere* **6**, 1323-1337.
- 481 [27] Wong, W.K., Haddeland, I., Lawrence, D. & Beldring, S. 2016 Gridded 1 x 1 km climate
482 and hydrological projections for Norway.
- 483 [28] Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O.B., Bouwer, L.M., Braun, A.,
484 Colette, A., Déqué, M. & Georgievski, G. 2014 EURO-CORDEX: new high-resolution climate
485 change projections for European impact research. *Regional Environmental Change* **14**, 563-578.
- 486 [29] Hazeleger, W., Wang, X., Severijns, C., Ștefănescu, S., Bintanja, R., Sterl, A., Wyser, K.,
487 Semmler, T., Yang, S. & Van den Hurk, B. 2012 EC-Earth V2. 2: description and validation of a
488 new seamless earth system prediction model. *Climate dynamics* **39**, 2611-2629.
- 489 [30] Van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt,
490 G.C., Kram, T., Krey, V. & Lamarque, J.-F. 2011 The representative concentration pathways: an
491 overview. *Climatic change* **109**, 5.
- 492 [31] Johnson, D.H. 1980 The comparison of usage and availability measurements for evaluating
493 resource preference. *Ecology* **61**, 65-71.
- 494 [32] Pateiro-Lopez, B. & Rodriguez-Casal, A. 2015 *alphahull: Generalization of the Convex*
495 *Hull of a Sample of Points in the Plane*, R package version 2.0.

- 496 [33] Calenge, C. 2006 The package "adehabitat" for the R software: A tool for the analysis of
497 space and habitat use by animals. *Ecological Modelling* **197**, 516-519.
- 498 [34] Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J. & Wilmers, C.C. 2007
499 LoCoH: Nonparameteric kernel methods for constructing home ranges and utilization
500 distributions. *PLoS ONE* **2**, e207.
- 501 [35] Bates, D., Maechler, M., Bolker, B. & Walker, S. 2014 *lme4: Linear mixed-effects models*
502 *using Eigen and S4*, R package version 1.1-6.
- 503 [36] Murtaugh, P.A. 2009 Performance of several variable-selection methods applied to real
504 ecological data. *Ecology Letters* **12**, 1061-1068.
- 505 [37] Hijmans, R.J. 2018 raster: Geographic data analysis and modeling. (R package version 2.8-
506 4 ed.
- 507 [38] Warren, D.L., Glor, R.E. & Turelli, M. 2008 Environmental niche equivalency versus
508 conservatism: quantitative approaches to niche evolution. *Evolution* **62**, 2868-2883.
- 509 [39] Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. 2002 Evaluating resource
510 selection functions. *Ecological Modelling* **157**, 281-300.
- 511 [40] Stone, M. 1974 Cross-validatory choice and assessment of statistical predictions. *Journal of*
512 *the royal statistical society. Series B (Methodological)*, 111-147.
- 513 [41] Kuhn, M. 2008 Building predictive models in R using the caret package. *Journal of*
514 *statistical software* **28**, 1-26.
- 515 [42] Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli,
516 R.K., Kwon, W.-T., Laprise, R., et al. 2007 Regional climate projections. In *Climate change*
517 *2007: The physical science basis. Contributions of working group I to the Forth Assessment*

518 *Report of the Intergovernmental Panel on Climate Change* (ed. S.S.e. al.), pp. 847-940.
519 Cambridge, U.K., Cambridge University Press

520 [43] Aublet, J.F., Festa-Bianchet, M., Bergero, D. & Bassano, B. 2009 Temperature constraints
521 on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer. *Oecologia* **159**, 237-247.

522 [44] Lenart, E.A., Bowyer, R.T., Hoef, J.V. & Ruess, R.W. 2002 Climate change and caribou:
523 effects of summer weather on forage. *Canadian Journal of Zoology* **80**, 664-678.

524 [45] Pettorelli, N., Pelletier, F., von Hardenberg, A., Festa-Bianchet, M. & Cote, S.D. 2007 Early
525 onset of vegetation growth vs. rapid green-up: Impacts on juvenile mountain ungulates. *Ecology*
526 **88**, 381-390.

527 [46] Alonso, J.C., Palacín, C., Alonso, J.A. & Martín, C.A. 2009 Post-breeding migration in
528 male great bustards: low tolerance of the heaviest Palaearctic bird to summer heat. *Behavioral*
529 *Ecology and Sociobiology* **63**, 1705-1715.

530 [47] Alonso, J.C., Salgado, I. & Palacín, C. 2015 Thermal tolerance may cause sexual
531 segregation in sexually dimorphic species living in hot environments. *Behavioral Ecology* **27**,
532 717-724.

533 [48] Parmesan, C. & Yohe, G. 2003 A globally coherent fingerprint of climate change impacts
534 across natural systems. *Nature* **421**, 37.

535 [49] Speed, J.D., Martinsen, V., Mysterud, A., Mulder, J., Holand, Ø. & Austrheim, G. 2014
536 Long-term increase in aboveground carbon stocks following exclusion of grazers and forest
537 establishment in an alpine ecosystem. *Ecosystems* **17**, 1138-1150.

538 [50] Büntgen, U., Greuter, L., Bollmann, K., Jenny, H., Liebhold, A., Galván, J.D., Stenseth,
539 N.C., Andrew, C. & Mysterud, A. 2017 Elevational range shifts in four mountain ungulate
540 species from the Swiss Alps. *Ecosphere* **8**, e01761.

541 [51] Jobbágy, E.G. & Jackson, R.B. 2000 The vertical distribution of soil organic carbon and its
542 relation to climate and vegetation. *Ecological applications* **10**, 423-436.

543 [52] Jumpponen, A., Brown, S.P., Trappe, J.M., Cázares, E. & Strömmer, R. 2012 Twenty years
544 of research on fungal–plant interactions on Lyman Glacier forefront–lessons learned and
545 questions yet unanswered. *Fungal Ecology* **5**, 430-442.

546 [53] Field, C.B., Barros, V., Stocker, T.F. & Dahe, Q. 2012 *Managing the risks of extreme events*
547 *and disasters to advance climate change adaptation: special report of the intergovernmental*
548 *panel on climate change*, Cambridge University Press.

549 [54] Araújo, M.B. & Luoto, M. 2007 The importance of biotic interactions for modelling species
550 distributions under climate change. *Global Ecology and Biogeography* **16**, 743-753.

551 [55] Conradt, L., Clutton-Brock, T.H. & Guinness, F.E. 2000 Sex differences in weather
552 sensitivity can cause habitat segregation: red deer as an example. *Animal Behaviour* **59**, 1049-
553 1060.

554 [56] Ashcroft, M.B. 2010 Identifying refugia from climate change. *Journal of Biogeography* **37**,
555 1407-1413.

556

557

558 **Figures and tables**

559 **Table 1.** Parameter estimates from the final resource selection functions for both sexes during a.
 560 summer and b. winter, with year as random intercept. SE=standard error. Standard deviation for
 561 the random effects for summer was 0.088 (females) and 0.127 (males) and for winter 0.136
 562 (females) and 0.072 (males).

1a.	Summer							
	Females				Males			
	Estimate	SE	z	P value	Estimate	SE	z	P value
Variable								
Intercept	-0.079	0.029	-2.72	0.006	-0.008	0.044	-0.19	0.853
Elevation	-1.309	0.007	-194.80	<0.001	-1.297	0.009	-143.12	<0.001
Slope	0.603	0.005	128.14	<0.001	0.541	0.006	85.16	<0.001
Distance to coast	0.378	0.009	41.13	<0.001	0.666	0.012	55.58	<0.001
Northness	-0.247	0.006	-42.49	<0.001	-0.158	0.008	-20.94	<0.001
Temperature	0.152	0.005	31.78	<0.001	-0.021	0.006	-3.55	<0.001
Distance to coast ²	-0.085	0.003	-30.92	<0.001	-0.240	0.005	-48.04	<0.001
Northness ²	0.231	0.012	19.85	<0.001	0.328	0.016	21.07	<0.001
Pasture availability × pasture use	-0.904	0.028	-32.45	<0.001				
Elevation × temperature	0.275	0.006	47.20	<0.001	0.142	0.007	20.85	<0.001

1b.	Winter							
	Females				Males			
	Estimate	SE	z	P value	Estimate	SE	z	P value
Variable								
Intercept	-0.382	0.041	-9.21	<0.001	-0.401	0.026	-15.31	<0.001
Elevation	-2.089	0.010	-213.51	<0.001	-1.814	0.013	-143.97	<0.001
Slope	0.596	0.005	112.14	<0.001	0.530	0.008	69.16	<0.001
Distance to coast	-0.766	0.010	-80.62	<0.001	-0.934	0.014	-65.72	<0.001
Northness	-0.273	0.005	-49.62	<0.001	-0.259	0.008	-33.06	<0.001
Snow water equivalent	-0.467	0.009	-54.29	<0.001	-0.269	0.010	-26.63	<0.001
Slope ²	-0.172	0.003	-55.94	<0.001	-0.132	0.004	-30.87	<0.001
Pasture availability × pasture use	0.452	0.020	22.72	<0.001	0.282	0.028	10.15	<0.001
Elevation × snow water equivalent	-0.712	0.018	-40.36	<0.001	-0.315	0.017	-18.23	<0.001

564 **Figure legends**

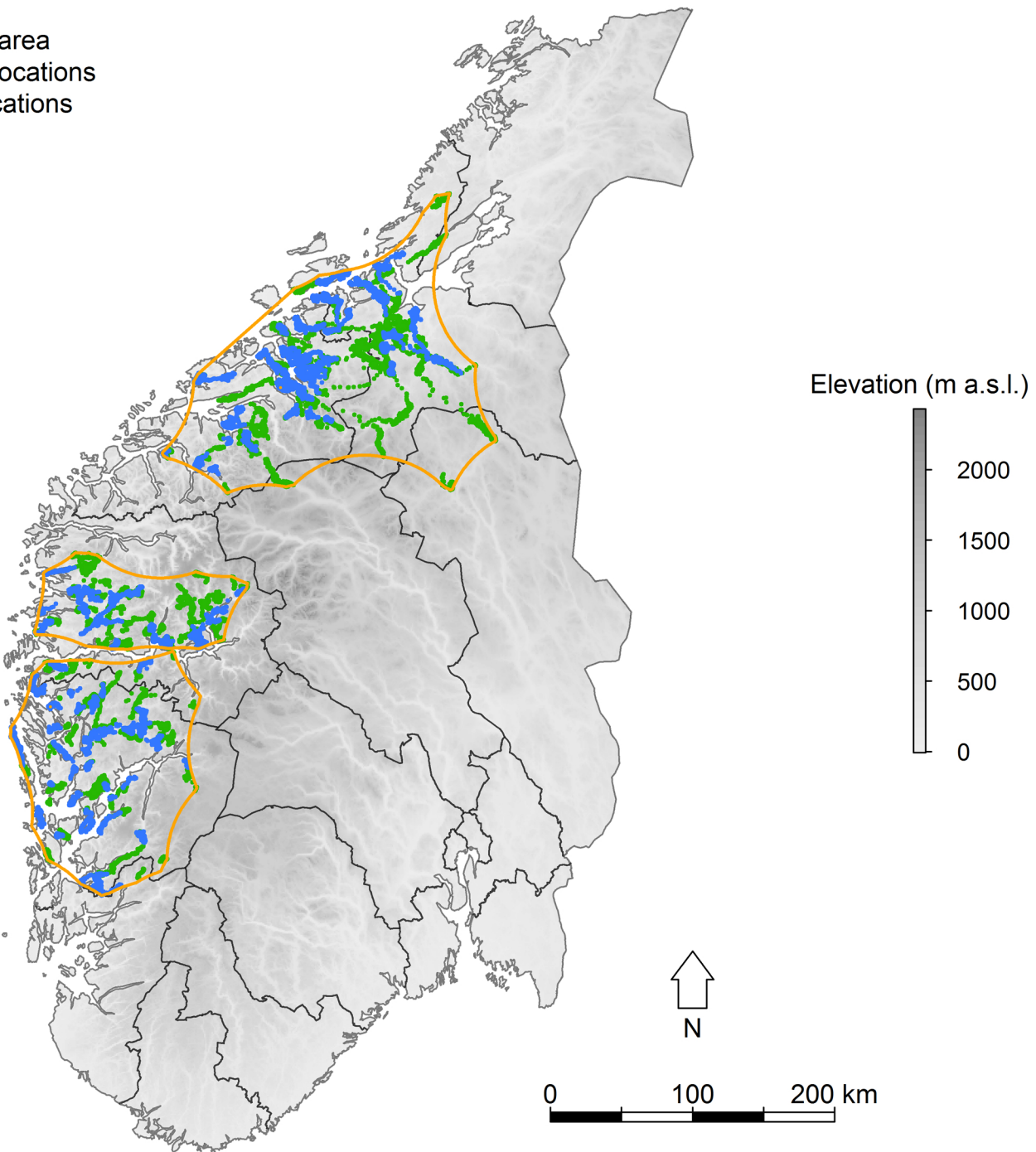
565 **Figure 1.** Map of Southern Norway showing the study area with available polygons (orange), red
566 deer winter (blue) and summer (green) locations.

567 **Figure 2.** Predicted habitat suitability for red deer in Western Norway during 2005-2014 for
568 females (top row) and males (bottom row) in summer (left) and winter (right).

569 **Figure 3.** Percentage of area consisting of suitable red deer habitat (habitat suitability threshold
570 0.2) in each county per season and sex based on resource selection functions. Predictions are
571 made for the study period (current), and for year 2100 under alternative future emission
572 scenarios medium (RCP4.5) and severe (RCP8.5). Maps on the x-axis show the elevation
573 gradient in each county with elevation mean.

574 **Figure 4.** Predicted change in habitat suitability from 2005-2014 to 2100 in Western Norway for
575 both sexes during summer (July) and winter (February). Predictions are made under the
576 alternative future emission scenarios medium (RCP4.5) and severe (RCP8.5).

- Available area
- Summer locations
- Winter locations



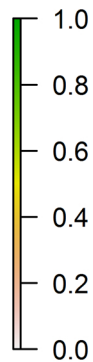
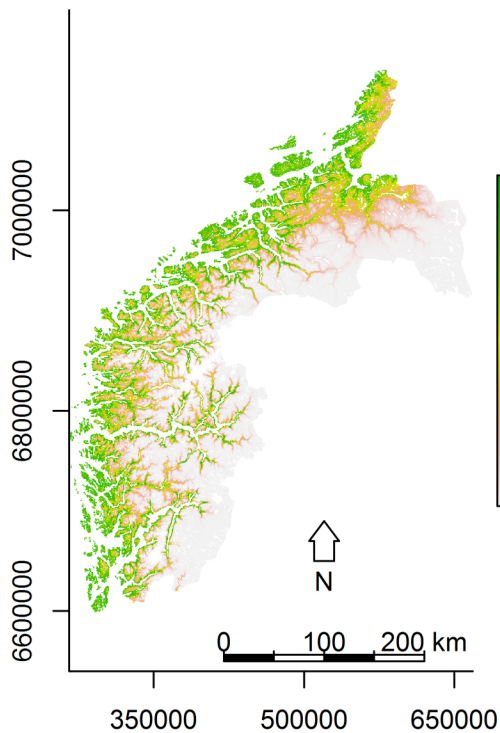
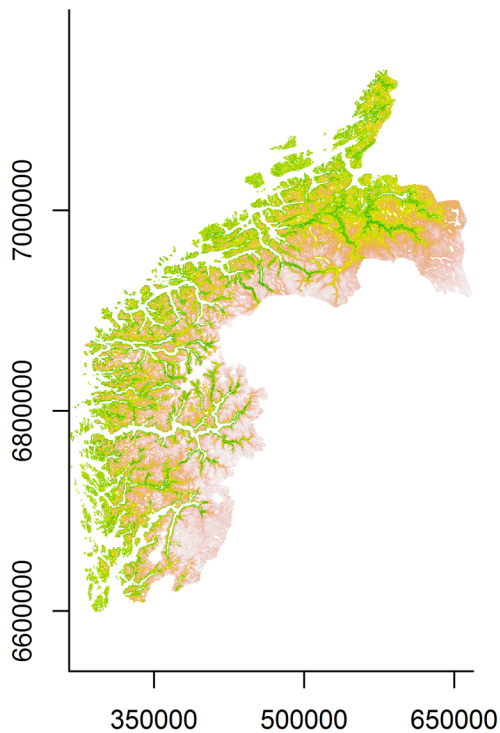
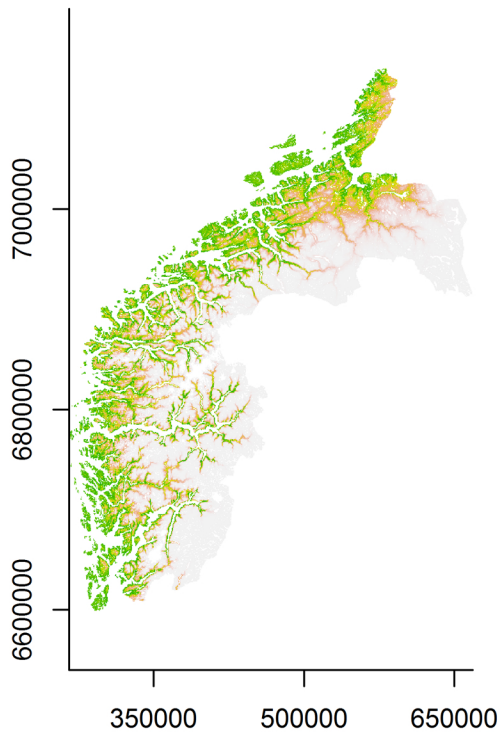
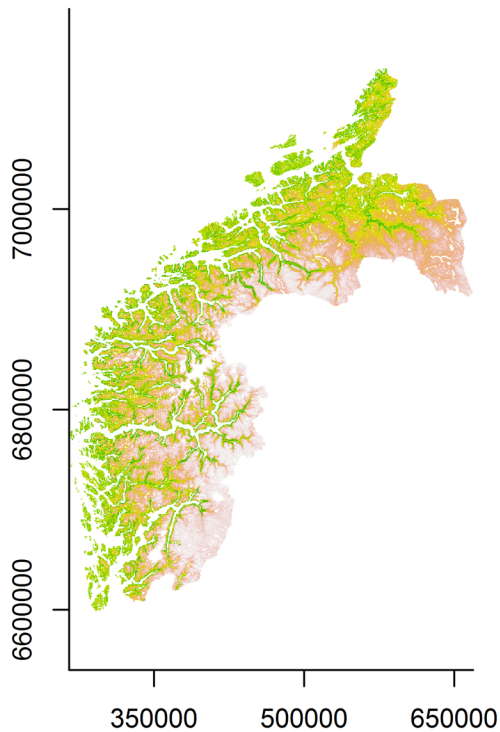
Summer

Winter

Females

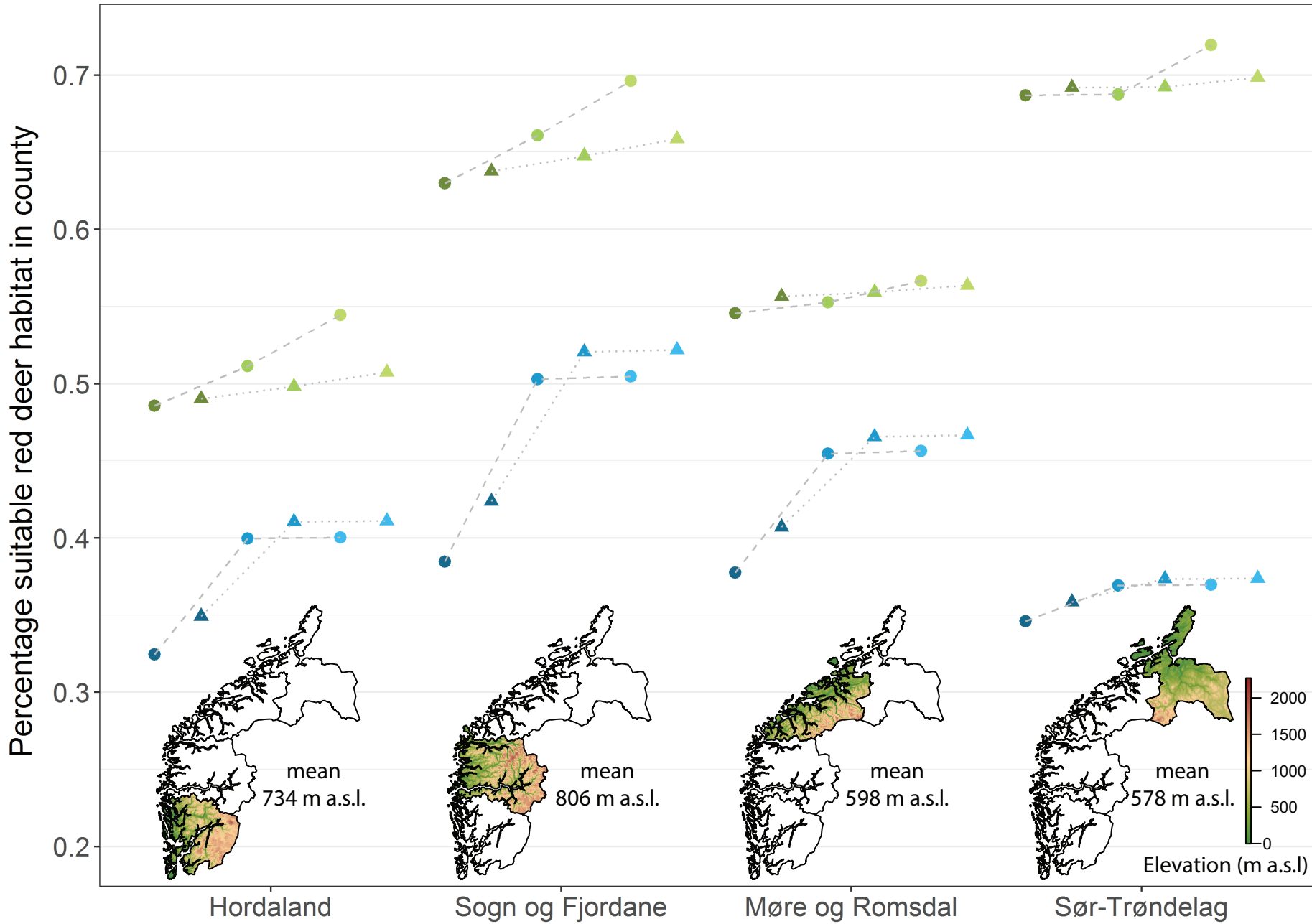
Males

North



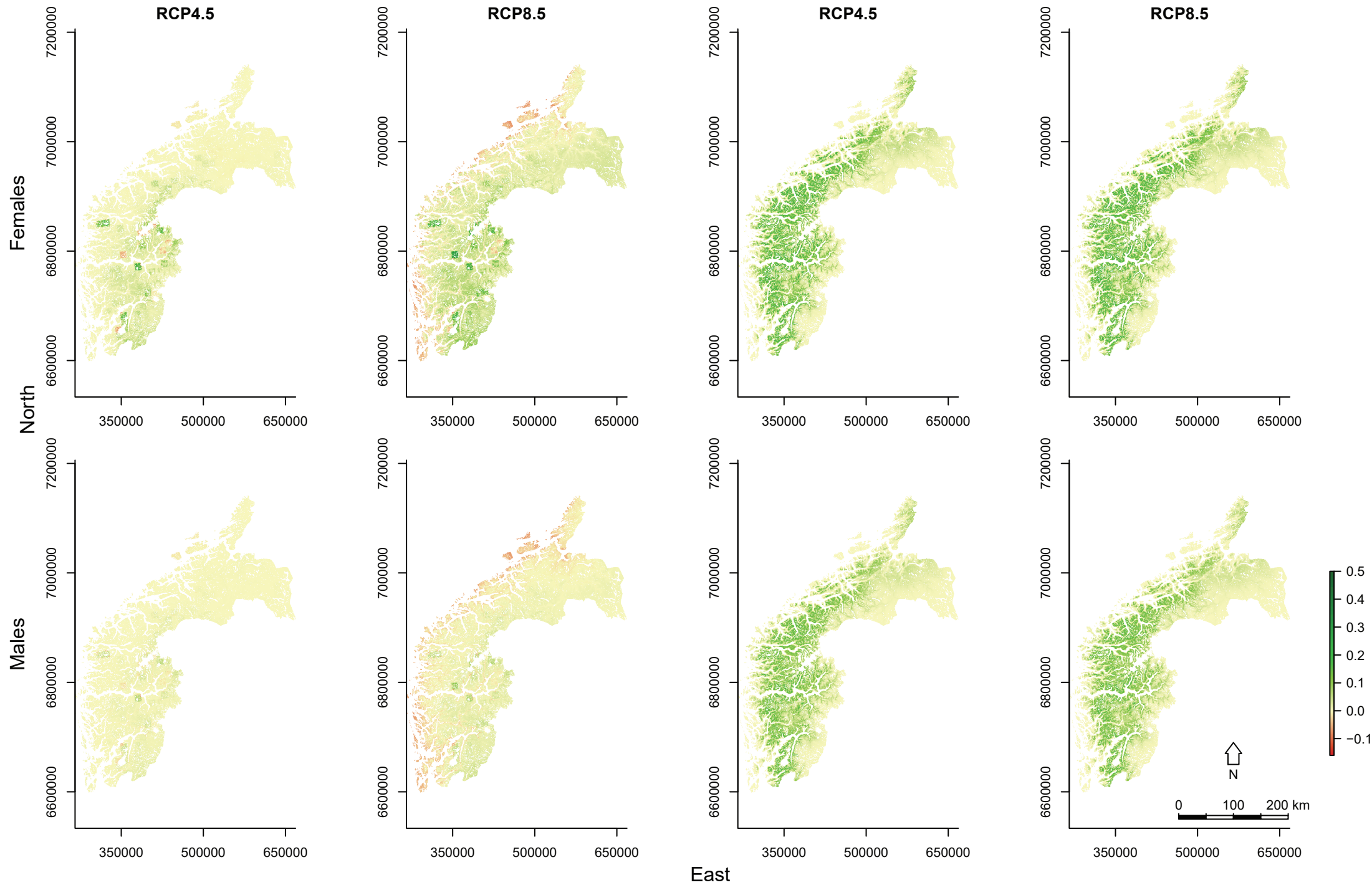
East

Current habitat suitability (2005-2014)



Summer

Winter



Change in habitat suitability from 2005–2014 to 2100

Supplementary material for:

Future suitability of habitat in a migratory ungulate under climate change

Inger Maren Rivrud, Erling L. Meisingset, Leif Egil Loe, and Atle Mysterud

Proceedings of the Royal Society B, <https://doi.org/10.1098/rspb.2019.0442>

Table S1. Mean and median of sex-specific migration characteristics for red deer in Norway used in the resource selection functions.

	Females		Males	
	<i>Mean</i>	<i>Median</i>	<i>Mean</i>	<i>Median</i>
Distance (km)	17.8	14.2	25.7	20.2
Duration spring migration (days)	5.4	2	10.5	7
Duration fall migration (days)	4.3	2	8.1	4
Direction winter to summer range (degrees)	131	107	133	120

Table S2. Number of locations (obs), years, individuals (id) and individual ranges used in the resource selection functions for the two seasons (summer and winter) and sexes.

	Summer		Winter	
	<i>Females</i>	<i>Males</i>	<i>Females</i>	<i>Males</i>
N _{obs}	326000	178000	488000	238000
N _{years}	10	9	11	9
N _{id}	127	62	110	53
N _{range}	163	89	244	119

Table S3. Key statistics on selected topography and climate variables in the four counties in Norway comprising the study area.

County	Hordaland	Møre og Romsdal	Sør-Trøndelag	Sogn og Fjordane
Area (km ²)	15 437	15 100	18 848	18 619
Elevation mean (m a.s.l.)	734	598	578	806
Elevation median (m a.s.l.)	761	517	561	788
Elevation range (m a.s.l., 5-95%)	22-1425	14-1405	42-1235	51-1568
Slope mean (degrees)	13.43	16.83	7.92	17.69
Northness mean (cos(degrees))	0.004	0.044	0.041	-0.003
Distance to coast mean (km)	101.6	84.6	403.1	94.2
Temperature mean (July; °C)	11.97	12.05	12.62	11.25
SWE ¹ mean (February; mm)	366.26	238.18	153.25	355.18
Pasture availability mean (prop)	0.029	0.036	0.037	0.024

¹SWE = Snow water equivalent

Table S4. Percent change in available red deer habitat in Western Norway from 2005-2014 to year 2100 for 5 different thresholds of habitat suitability (0.1-0.5). Predictions are made for males and females during summer and winter, and under two emission scenarios (medium, RCP4.5 and severe, RCP8.5).

	Summer				Winter			
	<i>Females</i>		<i>Males</i>		<i>Females</i>		<i>Males</i>	
Threshold	RCP4.5	RCP8.5	RCP4.5	RCP8.5	RCP4.5	RCP8.5	RCP4.5	RCP8.5
0.1	3.01	7.30	1.28	2.86	24.15	24.83	17.69	18.12
0.2	2.52	7.27	0.80	2.06	19.81	20.14	14.48	14.69
0.3	2.00	6.76	0.49	1.41	17.07	17.29	12.65	12.79
0.4	1.57	5.62	0.25	0.32	14.25	14.40	10.92	11.02
0.5	1.32	3.74	0.00	-2.64	11.17	11.26	8.96	9.02

Table S5. Niche overlap between present and future habitat suitability, assessed by Schoener's D, for red deer in Western Norway. Current habitat suitability is estimated for the study period 2005-2014, and future habitat suitability for the year 2100 under moderate (RCP4.5) and severe (RCP8.5) emission.

	Summer		Winter	
	<i>Current - RCP4.5</i>	<i>Current - RCP8.5</i>	<i>Current - RCP4.5</i>	<i>Current - RCP8.5</i>
Females	0.981	0.958	0.889	0.887
Males	0.994	0.983	0.919	0.917

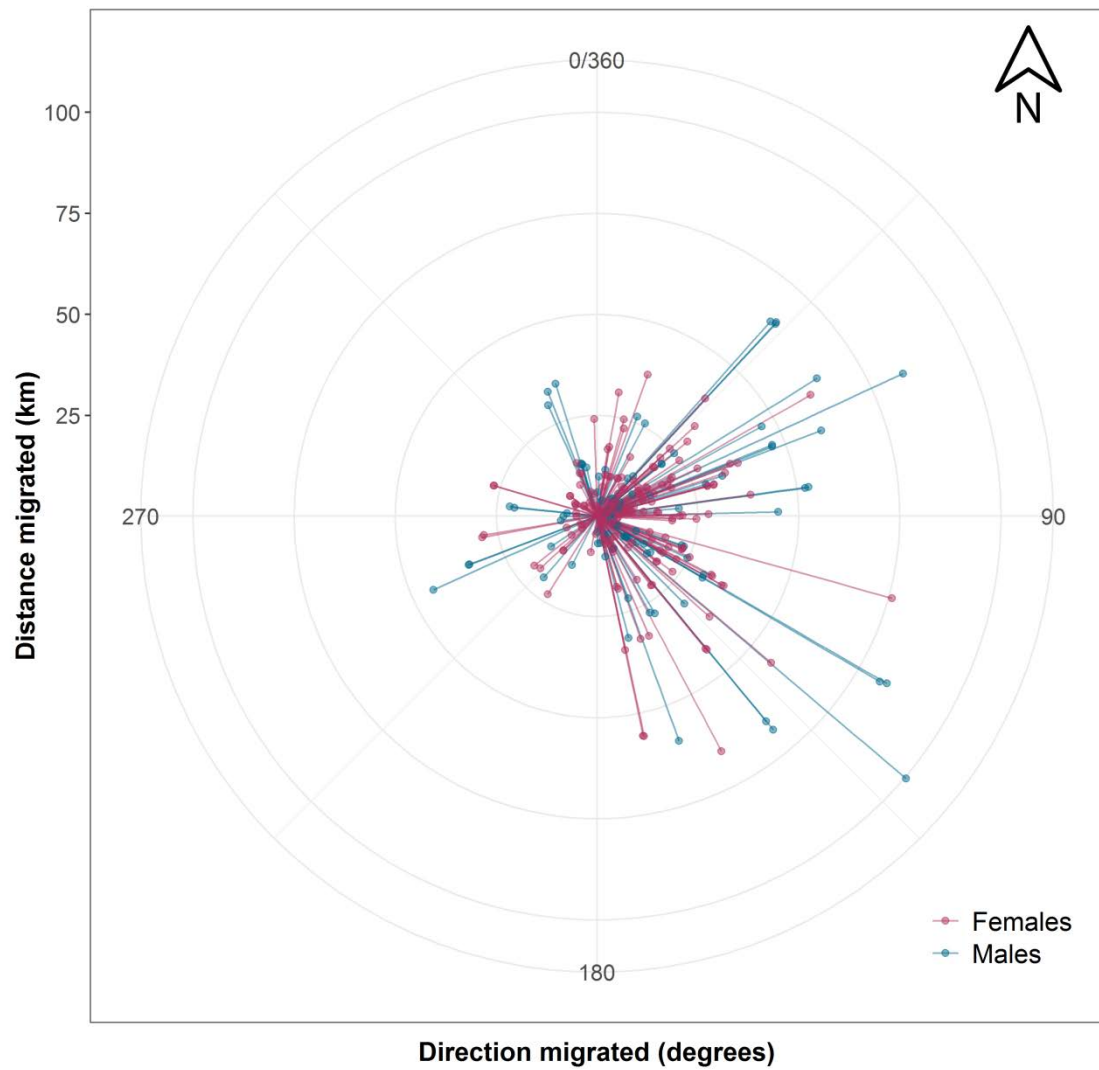


Figure S1. The distance (km; length of lines) and direction (degrees) migrated between winter and summer ranges for female (red) and male (blue) red deer in Norway from 2005-2015.

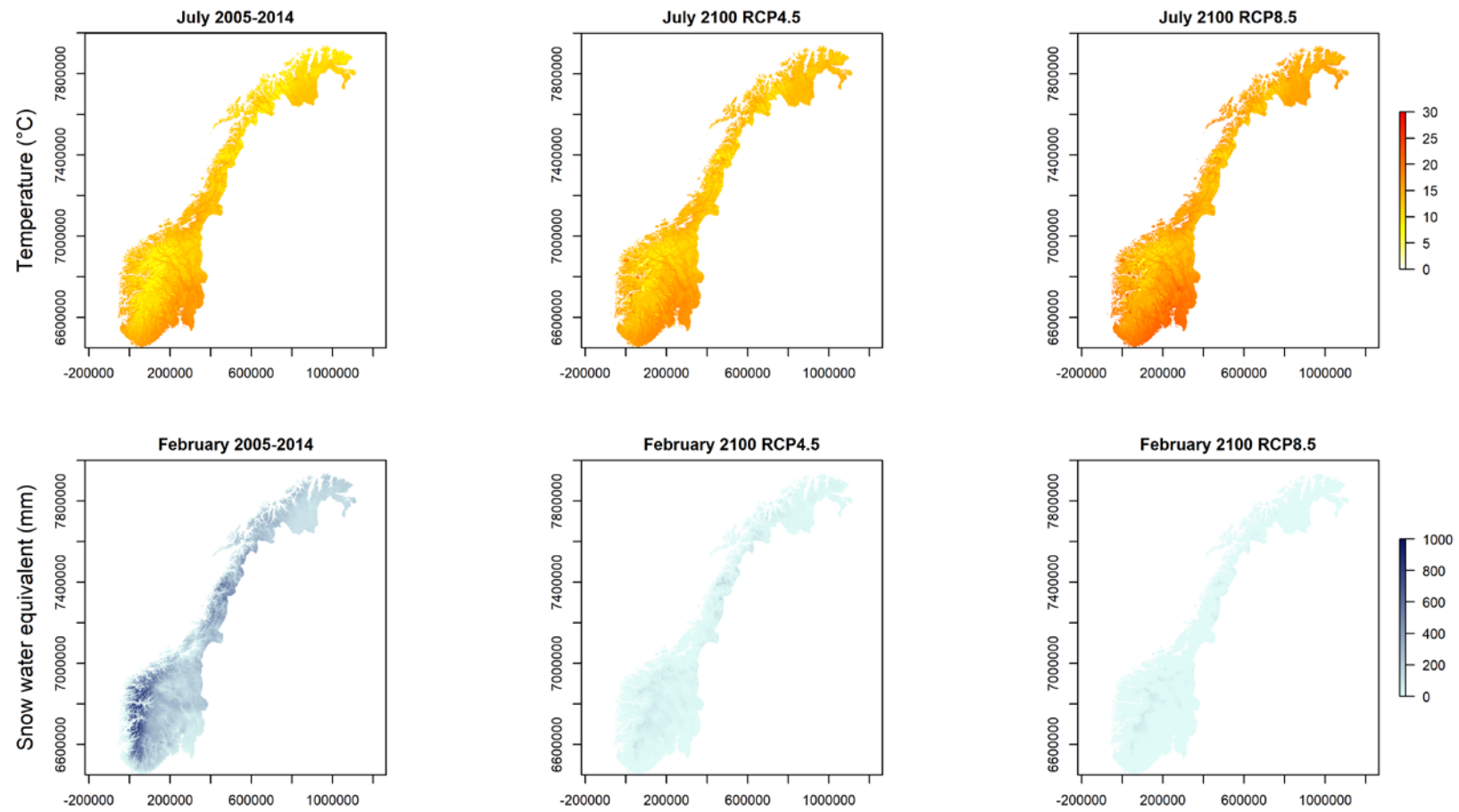


Figure S2. Monthly temperature (July; top row) and snow water equivalent (February; bottom row) means for Norway during the study period (2005-2014) and in year 2100 under two alternative emission scenarios (medium, RCP4.5 and severe, RCP8.5).

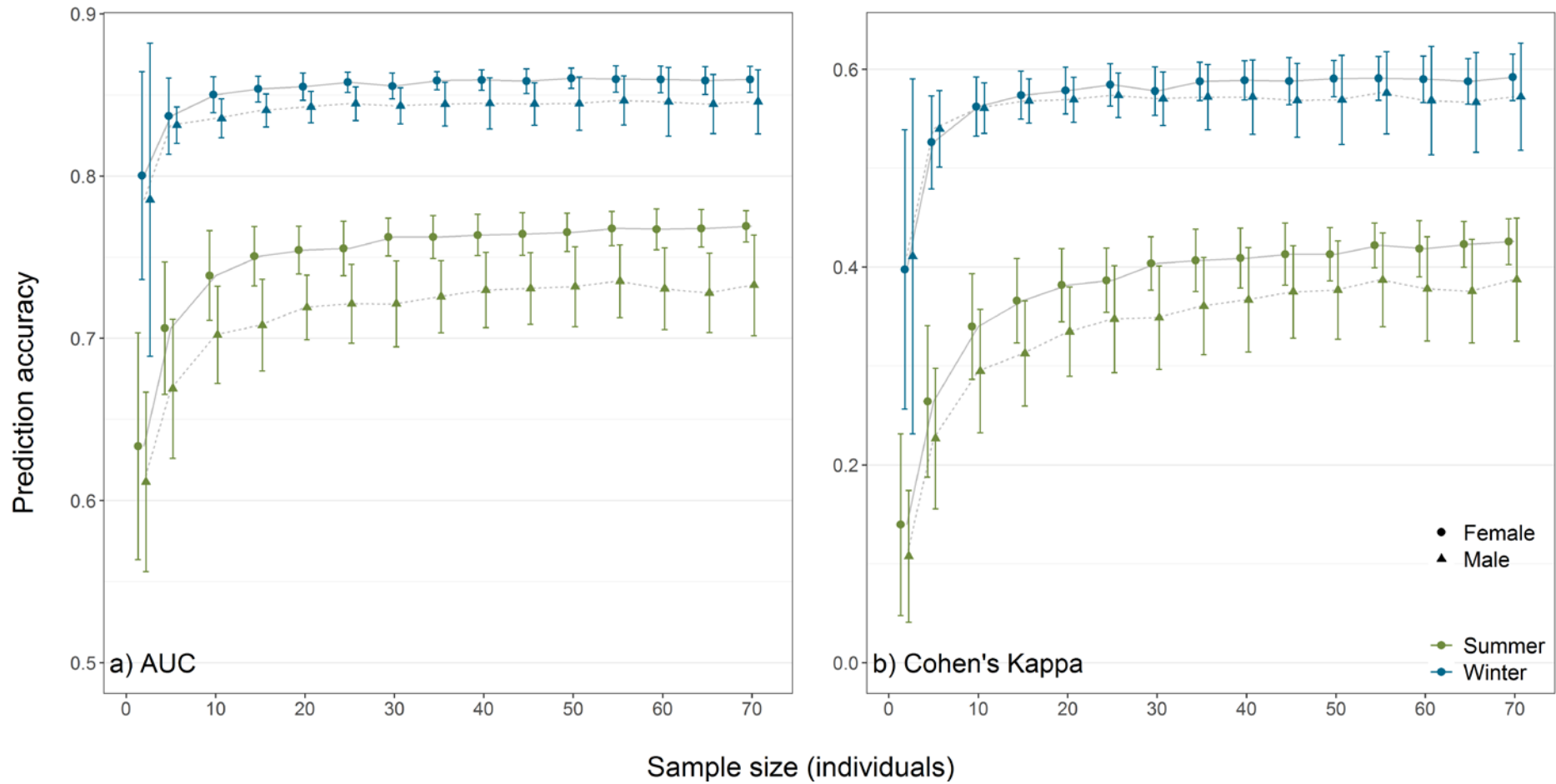


Figure S3. Effects of sample size on prediction accuracy estimated as a) AUC and b) Cohen's Kappa on resource selection functions for red deer in Norway during summer (green) and winter (blue) and for females (circles) and males (triangles). Points show the mean and error bars show the standard deviation.

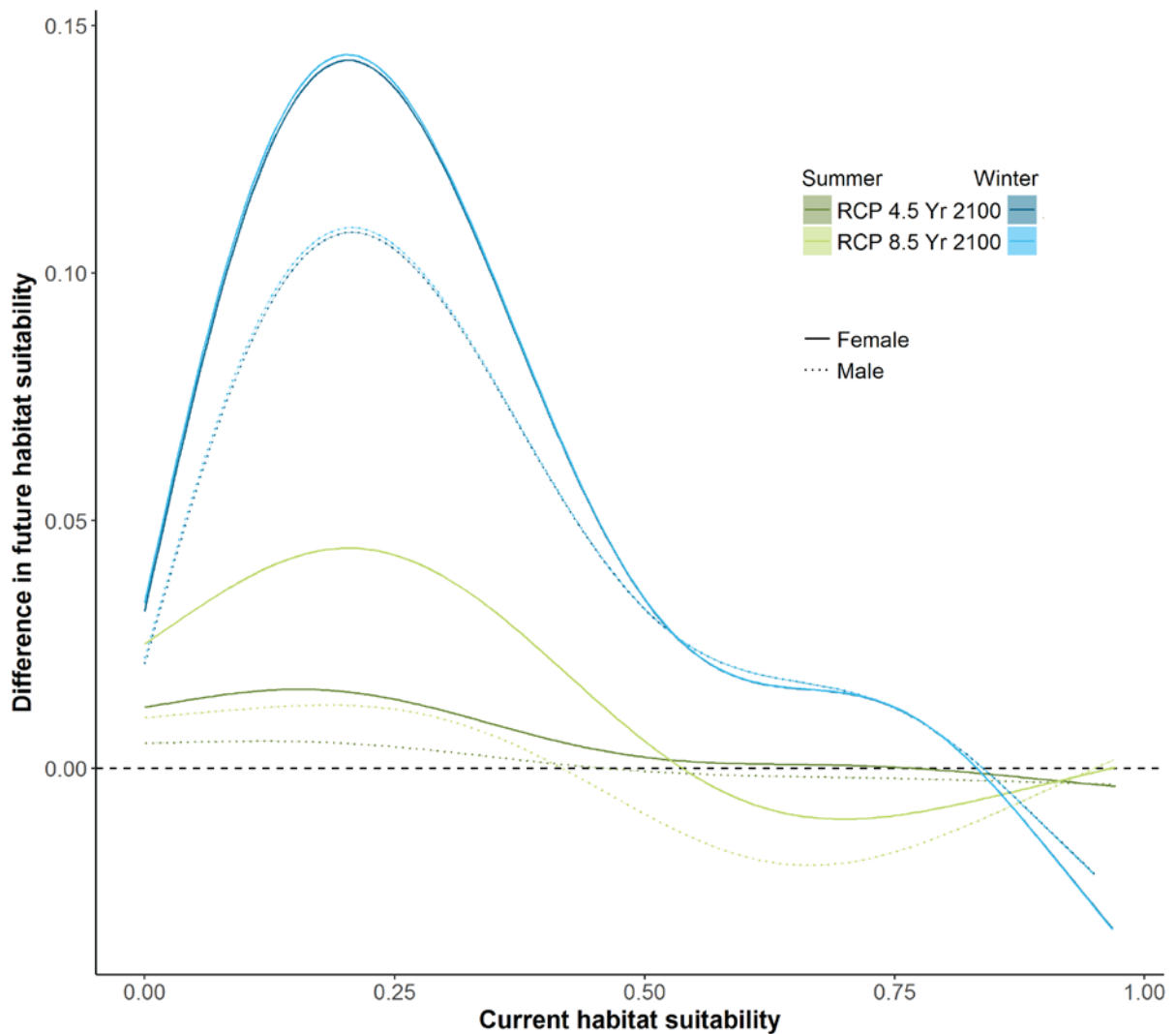


Figure S4. Relative change per pixel in habitat suitability from 2004-2014 to year 2100 for male (dashed lines) and female (solid lines) red deer during winter (blue) and summer (green) under medium (RCP4.5; darker) and severe (RCP8.5; lighter) emission. The smoothed lines are based on generalized additive models with future habitat suitability as response and current habitat suitability as predictor. The horizontal line indicates no change in habitat suitability.