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2 # Rock Ptarmigan *(Lagopus muta)* breeding habitat use in northern

3 # Sweden

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11 # Abstract

12 Alpine and arctic tundra regions are likely to retract as a result of climate warming and

13 concerns have been raised over the status of the Rock Ptarmigan (*Lagopus muta).* In

14 Fennoscandia, the Rock Ptarmigan has low population abundance and predictions based on

15 harvest statistics show population declines throughout the range. In this study, we used a

16 long-term opportunistic data set of Rock Ptarmigan observations, environmental predictors

17 derived from a digital vegetation map and a digital elevation model to describe the breeding

18 distribution at three different ecological scales. Patterns of spatial distribution were similar

19 across all the three study scales. The presence of permanent snow-fields positively

20 influenced the occurrence of Rock Ptarmigan at the territory and landscape scale. Open

21 vegetation, rock-dominated areas and in particular dry heath influenced the ptarmigan

22 presence positively at all scales. Altitude and terrain heterogeneity were important variables

23 at all scales, with higher probabilities of Rock Ptarmigan being present at intermediate

24 altitude ranges, with a high degree of terrain heterogeneity. This is the first study to describe

25 Rock Ptarmigan breeding distribution in Fennoscandia and our findings yield new insights

26 into the environmental variables that are important for the spatial distribution of Rock

27 Ptarmigan during the breeding season. When planning conservation efforts, this information

28 should be used to inform management regarding the protection of core areas and buffer

29 zones related to the conservation and harvest management of the Rock Ptarmigan.

30 **Key words:** Conservation, habitat model, multiple scales, management, spatial distribution

Introduction

32 The Rock Ptarmigan (*Lagopus muta)* is a circumpolar herbivorous bird characteristic of

33 alpine and arctic tundra regions (Storch 2007, Watson and Moss 2008). Concerns have been

34 raised over the status of this species (Storch 2007) and the ecosystems that it inhabits

35 because alpine and arctic tundra regions are likely to retract as a result of climate warming

36 (Post et al. 2009) and the associated shrub encroachment (Myers-Smith et al. 2011) and tree

37 line expansion (Hofgaard et al. 2012). Therefore, many species associated with tundra

38 regions, including the Rock Ptarmigan, are expected to experience shifts and contractions in

39 their distributional ranges (Huntley et al. 2008, Virkkala et al. 2008). Although the Rock

40 Ptarmigan is listed as a species of conservation concern in international and national Red

41 Lists (Storch 2007), the bird is also a popular small game species used both for recreational

42 and Sámi subsistence hunting in Fennoscandia (Eriksson et al. 2006). Its population size and

43 status are unknown throughout most of its distributional range (Storch 2007). In

44 Fennoscandia, population numbers follow approximately 10-year dynamic cycles (Hörnell-

45 Willebrand unpublished data, www.lansstyrelsen.se), with generally low abundances (0.4-1.8

46 pairs per km^{-2}; Ottosson et. al. 2012) observed between peak years of maximum 5.7 pairs

47 per km^{-2} (Hörnell-Willebrand unpublished data, www.lansstyrelsen.se) compared to North

48 America (up to 15 territories km^{-2} in peak years; Sinclair et. al. 2003) and Iceland (from 5.9

49 males per km^{-2} in low years up to 21.7 males per km^{-2} in peak years; Nielsen 1999). Harvest

50 statistics from the Nordic countries show population declines of Rock Ptarmigan over the

51 past two decades (e.g. Storch 2007; for national harvest statistics see www.ssb.no,

52 www.rktl.fi, www.smavilt.se, www.ust.is). However, Willebrand et al. (2011) showed that

53 harvest data are often too unreliable as a proxy for population abundance, and might give

54 biased estimates. Elusive species, such as the Rock Ptarmigan, inhabiting remote areas, are

55 challenging to monitor and manage, especially if they exhibit cyclical population dynamics.

56 Despite the increasing number of large-scale monitoring schemes in Europe (e.g. Gregory et

57 al. 2005), long-term monitoring of the Rock Ptarmigan is still scarce (Storch 2007; but see

58 Watson 1998, Nopp-Mayr and Zohmann 2008, Zohmann and Wöss 2008, Nielsen 2011,

59 Marty and Mossoll-Torres 2012; Pedersen et al. 2012). Longer time series (i.e. covering

60 more than one population cycle) are only available from studies in Iceland (Nielsen 2011)

61 where population are declining. Monitoring data from Sweden span from 1994 till today with

62 the last high year in 2000 with 5.7 adults per km^{-2} (Hörnell-Willebrand unpublished data,

63 www.lansstyrelsen.se). Compared with other ptarmigan species, relatively few studies have

64 focused on the population ecology of the Rock Ptarmigan (e.g., Watson et al. 1998; Nilsen

65 1999; Favaron et al. 2006; Wilson et al. 2008; Moss et al. 2010; Sawa et al. 2011; Wilson

66 and Martin 2011; Wilson and Martin 2012) and there is an urgent need in Fennoscandia to

67 develop robust management tools to ensure protection of the core habitats and sustainable

68 harvest of this species.

69   The distribution range of Rock Ptarmigan in Fennoscandia is primarily restricted to

70 mountainous regions above the tree line (Watson and Moss 2008), but information on

71 detailed habitat use is sparse. In the European Alps as well as high-arctic regions in

72 Svalbard, mid-altitude open, barren areas with rocks constitute an important breeding habitat

73 of the Rock Ptarmigan (Favaron et al. 2006; Pedersen et al. 2007; Zohmann and Wöss 2008;

74 Revermann et al. 2012; Schweiger et al. 2012). Individual male Rock Ptarmigan occupy a

75 territory during May and stay with the female until the beginning of incubation (Brodsky

76 1988). Chick hatching occurs during late June and July (Cotter 1999), and females with

77 brood forage and rear chicks in the vicinity of the nest site (Hannon and Martin 2006). During

78 the breeding season, both sexes are stationary (Unander and Steen 1985; Hörnell-

79 Willebrand unpublished 2012). Males often gather in large flocks post hatching and in

80 autumn and winter Rock Ptarmigan appear in mixed age and sex groups. In parts of the

81 distribution range the Rock Ptarmigan is able to cover distances of up to 1000 km during

82 seasonal migrations, for instance between Greenland and Iceland and throughout the

83 Russian tundra (Gudmundsson 1972; Del Hoyo et al. 1994; Storch 2007). Juvenile dispersal

84 away from the natal areas has been studied in the European Alps (Bech et al. 2009),

85 Svalbard (Unander and Steen 1985), Iceland (Gardarsson 1988; Nielsen and Bjornsson

86 1997) and Scotland (Watson 1998), but the range and frequency of such movements in

87 Fennoscandia are unknown (Pedersen and Karlsen 2007).

88   Habitat conservation and management require long-term baseline studies targeting

89 the distribution–habitat relations of Rock Ptarmigan (Revermann et al. 2012). Nilsen et al.

90 (2012) emphasized the need for such studies for predicting the potential responses of

91 ptarmigan to climate driven changes in habitat distribution. In this study we take advantage of

92 a long-term opportunistic data series of Rock Ptarmigan observations collected by

93 ornithologists and submitted to a national species data base in Sweden

94 (www.artportalen.se). Using data from the past two decades, we identified key environmental

95 variables determining the distribution of Rock Ptarmigan during the breeding season. Based

96 on current ecological literature from other parts of the distribution range of this species (e.g.

97 Favaron et al. 2006; Pedersen et al. 2007; Wilson and Martin 2008; Zohmann and Wöss

98 2008; Fedy and Martin 2011; Martin and Wilson 2011; Sawa et al. 2011; Revermann et al.

99 2012; Schweiger et al. 2012), we expected both vegetation (i.e. forage, moisture and shelter)

100 and terrain (i.e. shelter and features important for territoriality and mate guarding)

101 characteristics to affect habitat use by Rock Ptarmigan. We also investigated whether the

102 presence of permanent snowfields in the landscape (i.e. edges and associated habitat that

103 might provide shelter, moisture and foraging opportunities) was a determinant of ptarmigan

104 distribution. Selection of appropriate spatial scales is important in habitat-use studies

105 because species–habitat relations (i.e. forage sites, resting sites, nest sites, territory,

106 dispersal, home-range etc.) can vary across space and time (e.g. Graf et al. 2005; Boyce

107 2006; Mayor et al. 2009; Revermann et al. 2012). Therefore, we investigated habitat use of

108 Rock Ptarmigan at three ecologically relevant spatial scales: (i) an observation scale

109 representing the habitat in the immediate vicinity of the bird; (ii) breeding territory scale; and

110 (iii) landscape scale. Results are discussed in relation to the management and conservation

111 of low-abundance Rock Ptarmigan populations in Fennoscandia.

Materials and methods

113 *Study area*

114 The study area was located in the northwestern part of the Swedish mountain region, in four

115 municipalities in Norrbotten county situated above the Arctic Circle (66°50´N, 17°50´E) (Fig.

116 1). Norrbotten is the largest county in Sweden (98 911 km^2) and represents a quarter of the

117 total land area of the country. The county includes boreal forests bordering the Baltic Sea in

118 the east, with elevations below 300 m, and large mountain areas bordering Norway and

119 Finland in west and north with elevations above 2000 m. The mountain range covers 20% of

120 the land area and approximately 25% of the county is protected as national parks or nature

121 reserves. Boreal coniferous forest dominates the lowlands, and mountain birch forest the

122 mid–high altitude sections from approximately 600 m to the tree line (500–700 m depending

123 on latitude and distance from the coast) (Kullman 1979; Väre 2001; Kullman 2005).

124 In the Norrbotten county two sympatric ptarmigan species, the rock and the Willow

125 Ptarmigan (*Lagopus lagopus*), are harvested between 25 August and 15 March. Only

126 members of the Sami-villages are allowed to hunt in the national parks and reserves. The

127 current management system is based on a threshold for the maximum harvest rate (Aanes et

128 al. 2002; Hörnell-Willebrand 2005). Since 2004, more than 90% of all ptarmigan harvested

129 on state-owned land have been reported, and on average 10000-20000 Willow and Rock

130 Ptarmigan are harvested in Norrbotten each year (www.smavilt.se).

131 *Ptarmigan data*

132 The Rock Ptarmigan data were collected opportunistically by volunteer ornithologists without

133 dogs in four municipalities in the mountain regions located in the western part of Norrbotten

134 county (Fig. 1). We extracted Rock Ptarmigan observations (N = 1057) from 1990 to 2012

135 from a data base held by the Swedish Species Information Centre (www.artportalen.se).

136 Each of the Rock Ptarmigan observations contained a geographic position and for most of

137   them information on the number of birds, sex and age (juvenile versus adult) of the observed

138   individuals was included. To minimize the risk of including birds not correctly identified, we

139   used only ptarmigan observations gathered during the breeding season in June and July,

140   when there is less overlap between the two sympatric species (Hannon et al. 1998;

141   Pedersen and Karlsen 2007). Additionally, we excluded observations of adult birds in large

142   groups (more than ten) without juveniles, which were likely to comprise non-breeders using

143   different habitats (Watson 1956; Weeden 1964). From this dataset, we removed Rock

144   Ptarmigan observations in mountain birch forest (N = 108) because the annual ptarmigan

145   monitoring program (Länsstyrelsen 2012) documented almost all Rock ptarmigan

146   observations (98%) outside the birch forest in summer. We excluded a few observations

147   occurring in willow shrub (N=3) because this fragmented habitat type is not captured well in

148   the relatively coarse resolution of the available vegetation map. In addition, observations

149   located in habitats that we considered non-habitats (i.e. open water, cultivated land,

150   coniferous forest and on permanent snowfields; Table 1) were removed, since these could

151   be a product of erroneous coordinates in the database. The final dataset for habitat

152   modelling contained 491 Rock Ptarmigan observations (sex structure: 30 % male, 20 %

153   female, 50 % unknown birds; age structure: 51 % adults, 5 % juveniles, 44 % unknown birds)

154   (see Fig. 2 for details on sample size).

155   Because of the opportunistic approach to data collection, there was no information

156   about where observers had been present without observing ptarmigan. Therefore, we

157   generated a baseline random sample of pseudo-absence sites (N = 10 000) to represent the

158   landscape potentially available to Rock Ptarmigan (Johnson et al. 2006; Elith and Leathwick

159   2007). The method used to select pseudo-absence sites is important for modeling results

160   (Stokland et al. 2011; Barbet-Massin et al. 2012). Stokland et al. (2011) attributed this to the

161   relationship between the environmental range of the pseudo-absences (i.e. the extent of the

162   environmental space being considered) and the environmental range of the presence

163   observations (i.e. under which environmental conditions the species occurs). To approximate

164   a more realistic design (i.e. to represent areas that were likely to have been walked by an

165   observer), we constrained the area for selection of such sites within the minimum convex

166   polygon derived from the ptarmigan observations and within the altitude and slope range of

167   the actual observations. Within this area, we further restricted the pseudo-absences sites to

168   habitats assumed suitable for Rock Ptarmigan according to Table 1. From this set, we

169   randomly selected twice as many pseudo-absence sites (N = 982) as the number of

170   ptarmigan observations (N = 491) for the statistical modeling of habitat use. This selection

171   was based on a statistical exploratory procedure checking the ratio of observations

172   (presence) to pseudo-absences for model parameter estimates to vary little as a result of

173   pseudo-absences being randomly selected.

174   ***Digital spatial information***

175   All spatial data were handled in ArcGIS® version 9.3 (Environmental Systems Research

176   Institute, Inc.) with the Spatial Analyst and 3D Analyst extensions. The digital maps were

177   obtained from the Swedish University of Agricultural Sciences, which licenses maps for

178   scientific purposes from the 'Swedish mapping, cadastral and land registration authority'

179   (http://lantmateriet.se). Vegetation- and permanent snowfield data were obtained from the

180   Swedish mountain vegetation map based on interpretation of false near-infrared aerial

181   photographs with a spatial resolution of 25 × 25 m (Anderson 2008). The vegetation types

182   were originally divided into 33 classes of which 12 classes were not relevant to ptarmigan

183   breeding habitat use. The remaining classes were reclassified into 5 vegetation types based

184   on vegetation structure according to Table 1 for the purpose of this study

185   (www.lantmateriet.se; Andersson 2008). Terrain data were obtained from a digital elevation

186   model (DEM) of Sweden with a spatial resolution of 50 m; the uncertainty estimate for

187   elevations in the DEM was 2.5 m. The DEM was resampled to a 25 × 25 m spatial resolution

188   to match the resolution of the vegetation map because vegetation type was assumed to be

189   important for ptarmigan breeding habitat use at a fine scale.

190   *Environmental variables*

191   We modelled Rock Ptarmigan summer habitat use over three biologically relevant spatial

192   scales: (i) an observation scale representing the habitat in the immediate vicinity of the bird

193   (25 × 25 m and 75 × 75 m neighborhoods; 1 × 1 and 3 × 3 pixels in the digital maps with the

194   bird observation in the center); (ii) a breeding territory scale (525 × 525 m neighborhood; 21

195   × 25 pixels); and (iii) landscape scale (1025 × 1025 m neighborhood; 41 × 41 pixels). At each

196   scale the observations were placed in the middle and values were extracted as mean values

197   across this surface. The size of the territory scale was based on reported territory sizes of

198   Rock Ptarmigan from some parts of their distribution range (e.g. Unander and Steen 1985;

199   Holder and Montgomerie 1993; Favaron et al. 2006), although being aware that much

200   smaller territories are reported from other parts (e.g. Bossert 1995). All environmental

201   variables were extracted at all three spatial scales. Vegetation type was extracted as the

202   dominant type within the relevant neighborhood and treated as a categorical variable based

203   on the re-classification in Table 1. Ideally, the vegetation variable might have been modelled

204   as a continuous variable (e.g. proportion of the respective type at the selected spatial scale;

205   for examples see Pedersen et al. 2007; Zohmann and Wöss 2008; Revermann et al. 2012),

206   but treating the vegetation variable as continuous would not allow habitat models to converge

207   properly. Altitude, slope, 'vector ruggedness measure' (hereafter 'VRM' or 'terrain

208   heterogeneity'; Sappington et al. 2007) and aspect were extracted from the DEM and

209   calculated as the mean of all values within the neighbourhood with odd pixels at all scales.

210   The VRM is an integrative measure of terrain heterogeneity based on slope and aspect

211   values and was calculated in neighborhoods of 3 pixels at the observation scale. Index

212   values are low in flatter areas and are higher in steeper and more rugged areas (Sappington

213   et al. 2007). Given that aspect is a circular variable (0-360°), it was converted to sine and

214   cosine values, decomposing them into a north–south and an east–west component ('north

215   exposure' = [cos(aspect in radians)] and 'east exposure' = [sin(aspect in radians)]). Sine

216   values ranged from −1 (due west) to 1 (due east), whereas cosine values ranged from −1

217   (due south) to 1 (due north).To facilitate interpretation, the estimated parameter values for

218   the sine and cosine components of aspect were back-transformed and presented in degrees.

219   We also extracted the presence or absence of permanent snowfields (derived from the

220   vegetation map) at each spatial scale. At the observation scale we extracted presence or

221   absence at the scale of 3 pixels (75x75 m) since we assumed snow field in themselves to not

222   be ptarmigan breeding habitat (i.e. N = 18 observations of ptarmigan at the snow fields were

223   not included).

224   ***Statistical analysis***

225   The probability of presence of Rock Ptarmigan was analyzed using logistic Generalized

226   Linear Models (GLMs). Models were fitted in R (The R foundation for statistical computing

227   2012, version 2.15.1) using the library MuMIn and the dredge function to test all possible

228   model combinations at the three spatial scales. We developed candidate model sets at each

229   spatial scale where the response variable was presence versus pseudo-absence (use versus

230   availability; Johnson et al. 2006) of Rock Ptarmigan. Six environmental variables were

231   included as candidate predictor variables: vegetation (as a factor with three levels;

232   dominance of 'dry', 'open' and 'rock'; Table 1 for content of classes), altitude, aspect (sine

233   and cosine components), slope, VRM and the presence of permanent snowfield (as a factor

234   with two levels: presence or absence). Only one interaction (altitude × aspect) was assumed

235   to have biological relevance and was tested (see summary statistics of predictors in Table 2).

236   Initially, we checked whether predictor variables were correlated using a two-sided

237   Spearman's rank correlation test. If two variables were correlated ($|r_s|>0.7$), we included the

238   one with most likely biological relevance to ptarmigan spatial distribution in the habitat

239   modelling. We assessed the linearity of relations between the response variable (probability

240   of used versus available on logit scale) and the predictor variable by graphically examining

241   the distribution of a given response variable within the two response variable classes. Only

242   one predictor variable, altitude, showed evidence of a nonlinear relation with the response

243   variable, and this was adequately described using a second-order polynomial. We selected

244   models at each spatial scale using the Akaike Information Criterion (AIC), differences in AIC

245 (ΔAIC) and AIC weights (Burnham and Anderson 2004). Goodness of fit was assessed by

246 calculating Nagelkerke's R^2, which quantifies the proportion of the total variance explained by

247 the model (Nagelkerke 1991). We tested model discrimination by calculating the area under

248 the receiver operating characteristics curve (AUC; Fielding and Bell 1997) using the library

249 'PresenceAbsence' for R (Freeman and Moisen 2008). An AUC value of 0.5 indicates that

250 the model was not able to discriminate between sites with presence of ptarmigan and

251 pseudo-absence sites whereas an AUC value of 1.0 indicates perfect ability to discriminate

252 (Pearce and Ferrier 2000). AUC scores between 0.8 and 0.9 indicate good discrimination

253 and above 0.9 excellent discrimination. We internally cross-validated predictive accuracy (i.e.

254 proportion of observations correctly classified in a random sample of data), using the library

255 DAAG for R (Maindonald and Braun 2013), for the best models at all scales by randomly

256 assigning the data to a number of 'folds' (termed 'training data set' containing 90 % of the

257 data and a 'test data set' containing the remaining 10 % of the data) since we lacked an

258 independent rock ptarmigan data. Each fold was removed, in turn, while the remaining data

259 was used to re-fit the logistic regression model and to predict at the deleted observations.

260 We repeated the procedure 25 times and cross-validated estimates are presented as means

261 of the 25 iterative runs. Variable importance (VI) for each predictor variable was assessed

262 using the sum of the AIC_c weights for the models including this variable using the 40 best

263 models (Anderson et al. 2001). For comparison within factorial levels, estimates of effect

264 sizes were given as odds ratios (OR) with 95 % confidence intervals (CI).

Results

266 At the observation scale, none of the predictor variables were strongly correlated and

267 therefore, all could be entered in the models. Slope and VRM were highly correlated ($|r_s|>0.7$)

268 at the territory and landscape scales and, therefore, were entered as alternatives in the

269 habitat models. The best model at the observation scale contained one categorical

270 (vegetation type) and four continuous ($altitude^2$, aspect, slope and VRM) significant predictor

271 variables (Table 3). Models at the territory and landscape scales were similar and contained

272   two categorical (vegetation type and presence of permanent snowfield) and three continuous

273   (altitude^2, VRM and aspect) significant predictor variables (Table 3). The interaction term

274   (altitude × aspect) was not selected in either of the models. There was no indication of

275   overdispersion in the models at any scale (Observation scale, Pearson's χ^2 = 1502, df =

276   1462, p = 0.22; territory scale, Pearson's χ^2 = 1523, df = 1464, p = 0.13; landscape scale,

277   Pearson's χ^2 = 1562, df = 1462, p = 0.3).

278   Vegetation cover was an important variable in the selected habitat models at each of the

279   three scales (Tables 3 and 4). The probability of Rock Ptarmigan presence was positively

280   influenced by open vegetation, rock-dominated areas and dry heath at all study scales (Fig.

281   3; only observation and territory scale are shown with marginal plots; Table 4). The effects of

282   rock and open vegetation on the probability of presence of Rock Ptarmigan were of similar

283   magnitude, whereas the effect of the presence of dry heath was significantly stronger (Table

284   5). This pattern was consistent across spatial scales. Altitude and terrain heterogeneity were

285   important variables at all scales, with higher probabilities of presence of Rock Ptarmigan

286   being predicted for intermediate altitude ranges (800-1100 m) with a high degree of terrain

287   heterogeneity and low slope values (the latter only at the observation scale) (Fig. 3, Table 4).

288   The presence of a permanent snowfield had a positive influence on the probability of

289   ptarmigan presence (Table 5), but only at the territory and landscape scales (Table 3).

290   Aspect was the least important variable, but had a consistent effect across scales, with

291   ptarmigan showing a slight preference for north-facing slopes (Fig. 3, Table 4). The models

292   attained Nagelkerke's R^2 from 0.14 to 0.17, indicating a low proportion of the total variance

293   explained, and AUC values from 0.69 to 0.72, indicating a low to fair ability to discriminate

294   correctly between the presence (used sites) and pseudo-absence (available sites) for Rock

295   Ptarmigan (Table 3). The proportion of observations correctly classified ranged from 0.73-

296   0.75 (internal cross-validation for predictive accuracy; observation scale = 0.73±0.0053;

297   territory scale = 0.75±0.0025; landscape scale = 0.75±0.0037).

Discussion

299 This article describes for the first time the breeding distribution of the Rock Ptarmigan in

300 Fennoscandia using a large opportunistic data set covering the entire northern mountain

301 region of Sweden. Patterns of habitat use were similar across all three scales studied,

302 although at the territory and landscape scale we found presence of permanent snowfields to

303 positively influence the occurrence of Rock Ptarmigan.

304 Vegetation cover in the form of dry heath, dominated by low-growing ericaceous

305 shrubs commonly interspersed by patches of exposed gravel, rocks and boulders in the

306 study area (Anderson et al. 1985; Lantmäteriet 2008), increased the probability of occurrence

307 of ptarmigan compared with open rock-covered terrain and open tundra vegetation at all

308 spatial scales. The use of the heath vegetation type might be related to shelter against

309 predators (i.e. low vegetation height enabling early detection of predators; Sawa et al. 2011),

310 access to look-out points and structural diversity of microhabitats which creates patchy

311 landscapes (Zohmann and Wöss 2008; Schweiger et al. 2012; Revermann et al. 2012)

312 facilitating foraging opportunities at edges . Rocky areas characterized by sparse vegetation

313 cover of mosses and lichens (Anderson et al. 1985; Lantmäteriet 2008) (termed 'rock' in the

314 models) also contributed positively to the occurrence, but less so than the dry heath

315 vegetation probably because of the more sporadic vegetation cover limiting foraging in this

316 habitat type. The open vegetation class comprised various vegetation types including among

317 others, various types of mires, heaths and alpine meadows (Table 1), which likely provide

318 good access to high-quality food for Rock Ptarmigan. The lower occurrence of ptarmigan in

319 open habitat types might demonstrate a trade-off between, on the one hand, access to this

320 high-quality foraging patches and, on the other hand, fewer lookout points and less shelter

321 for predator detection and avoidance (Zohmann and Wöss 2008). The lack of statistical

322 difference between two distinctly different vegetation types, the 'rock' and 'open' vegetation

323 type (Table 5) and the consistent responses across scales, might be linked to the

324 opportunistic feeding pattern of the Rock Ptarmigan, with limited preferences for certain

325   foraging plants (Weeden 1969). One could speculate that there might be intraspecific

326   competition between Willow ptarmigan and Rock Ptarmigan explaining the low preference for

327   the open vegetation type. Where the Rock Ptarmigan co-exists with sympatric and

328   congeneric species (i.e. White-tailed Ptarmigan and Willow Ptarmigan), they have species-

329   specific breeding habitat use (Weeden 1969; Wilson and Martin 2008; Wong 2010), but are

330   found overlapping in chick rearing habitats (Wong 2010) and on wintering grounds, although

331   segregated on sex (Weeden 1964; Weeden 1969). We could not find any study comparing

332   habitat selection in similar habitats for Willow Ptarmigan and Rock Ptarmigan, and cannot

333   exclude that Rock Ptarmigan would show a higher preference for the open vegetation type in

334   the absence of Willow Ptarmigan. However, Weeden (1967) described that competition in the

335   shrubby interface between wood and tundra winter habitat in Alaska, where all ptarmigan

336   species live, may have noticeable effects on food selection by each species.

337   In terms of terrain variables, the strongest response was seen in relation to altitude

338   and terrain heterogeneity. The significant second-order polynomial term suggests a peak in

339   the probability of Rock Ptarmigan presence at intermediate altitude ranges (800 – 1100 m),

340   and this was further positively influenced by higher terrain heterogeneity at all scales. Higher

341   terrain heterogeneity is associated with increased vegetation diversity and spatial variation

342   across short distances (Kudo 1991). This creates a patchy heterogeneous landscape with

343   more habitat edges available as foraging sites for Rock Ptarmigan (Favaron et al. 2006;

344   Novoa et al. 2008). Additionally, higher terrain heterogeneity might create conditions for the

345   accumulation of snow, which provides snowfield edges with cavities for Rock Ptarmigan

346   shelter (Fig. 4). At the observation scale, flat or gentle sloping areas had the highest

347   probability of presence of Rock Ptarmigan, compared with steep slopes. Although, this might

348   be biased by gentle slopes having a higher likelihood of being searched as compared to the

349   steep slopes where walking may be difficult. Earlier studies have found heterogeneous

350   terrain on elevated valley slopes to be favoured breeding habitat (Unander and Steen 1985;

351   Frederick and Gutierrez 1992; Pedersen et al. 2007). In a similar habitat use approach,

352   Revermann et al. (2012) found topographic variables, such as altitude, aspect and terrain

353   variability, to be important at the territory scale, but not at the mesoscale (1 km^2), which is in

354   contrast to our results.

355   Rock Ptarmigan preference for north facing terrain at the two largest scales was

356   probably related to the fact that these areas provide continuous access to snowfields for a

357   longer period. The slower and more gradual snowmelt in north-facing slopes would provide

358   stable access to fresh, nutritional vegetation and insects as the season progresses (Kaler et

359   al. 2010). Favaron et al. (2006) found that Rock Ptarmigan females with chicks in the

360   European Alps preferred habitats where vegetation growth was in an early stage and insects

361   easier to find. Similarly, Frederick and Gutiérrez (1992) found that the sympatric White-tailed

362   Ptarmigan (*Lagopus leucura*) used north-facing slopes more than expected, and linked this

363   to the greater availability of late-developing plant communities in snow-free depressions.

364   Thus, if females match localization of nest sites and chick-rearing areas with access to

365   snowfields, they could reduce foraging time and limit their exposure to predators (Wiebe and

366   Martin 2000; Yoder et al. 2004). In agreement with other studies (Frederick and Gutierrez

367   1992; Martin 2001; Martin and Wilson 2011), we believe that it is the snowfield edges or

368   habitat features in the vicinity of persistent snowfields that are important for camouflage and

369   vicinity forage opportunities, rather than the snowfields themselves.

370   To counterbalance the risk of empirical bias, we excluded 18 observations of Rock

371   Ptarmigan located on permanent snow, assuming that the vegetation close to the snowfields

372   and the snowfield edges, rather than the snowfields themselves, represented suitable Rock

373   Ptarmigan breeding habitat. This might explain the lack of influence of snowfield presence at

374   the smallest scale because few snowfields were included in the neighborhood of the

375   observation. The findings might underestimate the importance of snow because, in our static

376   habitat model, we only included presence of permanent snowfields. Snow patches and

377   permanent snowfields differ in size and extent according to the onset of spring and summer,

378   and will diminish with climate warming. Booms et al. (2011) developed a retrospective model

379   of the fundamental niche for the Rock Ptarmigan in Alaska and found that the area of the

380   niche had decreased by 40% and had become more fragmented over the past 200 years.

381 Therefore, we recommend integrating inter-annual snow dynamics in a more comprehensive

382 study of snow as an important determinant of the Rock Ptarmigan breeding distribution in

383 Fennoscandia.

384   The environmental predictors explained a relatively small proportion of the variation in

385 Rock Ptarmigan occurrence in our habitat models which could relate both to the use of

386 pseudo-absences (Stokland et al. 2011; Barbet-Massin et al. 2012) and failure to select one

387 or more biologically relevant environmental variables at the appropriate scales. However, we

388 also believe that the presence of individuals in a given habitat may not necessarily be

389 indicative of habitat quality (Pulliam 1991; Caughley 1994; Jones 2001). Rettie and Messier

390 (2000) proposed that animals make trade-offs among multiple factors related to space use

391 and population limitation when their effects occur at the same scales. The dominant factors

392 affecting ptarmigan survival is predation (Novoa et al. 2011; Wilson and Martin 2012) and in

393 some areas for closed populations of willow ptarmigan, human hunting mortality (Pedersen

394 et al. 2004; Sandercock et al. 2011). The general lack of scale differences in our habitat

395 models could be attributed to predators operating at large spatial scales, thereby influencing

396 the distribution pattern of ptarmigan at these larger scales. In terms of their relative

397 consequences for fitness, predator avoidance might be more important than foraging

398 decisions when the risk of predation is greater than the risk of starvation owing to food

399 shortage (Mayor et al. 2009). For instance, Byholm et al. (2012) found strong evidence that

400 the spatial distribution of Flying Squirrels (*Pteromys volans*) was affected by predators and

401 argued that the influence of the predator community might override landscape composition in

402 explaining the local distribution of prey species. We suggest that the same might be true for

403 the Rock Ptarmigan. Future research on Rock Ptarmigan should therefore focus on

404 dynamical predator-prey interactions, because the spatial distribution of Rock Ptarmigan in

405 the breeding season might be explained by factors other than habitat characteristics alone.

406 Such studies should ideally focus on the main Rock Ptarmigan predators, including

407 generalist predators such as the Red Fox *(Vulpes vulpes)*, Golden Eagle (*Aquila chrysaetos*),

408 Stoat and Weasel (*Mustela ermine and Mustela nivalis*), Common Raven (*Corvus corone*),

409 Hooded Crow (*Corvix cornix*) and Peregrine Falcon (*Falco peregrines*) (Cotter and Gratto

410 1995; Rosenfield 1995; Watson et al. 1998; Pedrini and Sergio 2002; Nystrom et al. 2006),

411 as well as the ptarmigan specialist, Gyrfalcon (*Falco rusticolus*) (Cotter and Boag 1992;

412 Tømmeraas 1993; Nielsen 1999).

413   The multi-scale approach used in this study allowed us to examine the complex

414 pattern of habitat use of rock ptarmigan where both food availability and predation risk are

415 likely to influence the spatial and temporal distribution. The distribution of Rock Ptarmigan

416 can only be understood in the context of the environment in which they exist. There was no

417 big difference in habitat use between the different scales which suggest that Rock Ptarmigan

418 respond primarily to overall resource abundance within a larger area rather than to local

419 variation in resources. By investigating multiple scales (see also Reverman et al. 2012 for

420 another example), in addition to the observation scale, we got information about the

421 importance of snow-fields in the landscape which makes it possible to develop habitat

422 conservation strategies that operate at the appropriate spatial scale relevant to the rock

423 ptarmigan breeding habitat use. Collecting high-quality data on wild birds on large spatial and

424 temporal scales is logistically difficult and expensive, particularly on low-abundance species

425 inhabiting remote areas, thus leaving opportunistic data collection, as in this study, a good

426 alternative compared to systematic surveys (Braunisch and Suchant 2010; Snall et al. 2011;

427 Sarda-Palomera et al. 2012). Based on prior knowledge of Rock Ptarmigan biology and

428 habitat use, we attempted to limit any bias by actively removing observations that were

429 probably due to, for example, erroneous registered positions for observations. As an

430 example we assumed all observations of Rock Ptarmigan in the birch forest to be

431 misidentification of Willow Ptarmigan. This suggests that improvements in species

432 recognition should be a priority for future collection of data through the Swedish Species data

433 base, and also highlights the need for more extensive data quality control. The observational

434 sampling did not primarily focus on Rock Ptarmigan sightings, and did not follow a structured

435 survey design, thus making observer bias with respect to the habitat types searched

436 unavoidable (i.e. habitats close to trails may be more likely to be searched than habitats

437 away from trails). Potential biases associated with opportunistic surveys (e.g. observers not

438 moving randomly in the terrain, and detection biases between habitat types; Yoccoz et al.

439 2001) can be minimized with more observers and an increased spatial coverage (Hauser et

440 al. 2006). Our habitat models classified correctly around seven out of ten observations as

441 true presence or absence of Rock Ptarmigan, which indicate a level of fair prediction, which

442 supports the conclusion by Sardà-Palomera et al. (2012) that opportunistic data sources

443 might offer sufficient predictions, especially for the distribution of uncommon species and for

444 data with large spatial coverage (Hauser et al. 2006). One way of improving datasets similar

445 to the one used in this study is to encourage the volunteers who are collecting the data to

446 submit a set of systematically selected reference points where the species in question were

447 not observed. It would then be possible to use these locations as a more realistic sample of

448 absence observation and allow for proper development of predictive maps of the Rock

449 Ptarmigan spatial distribution.

450 In Fennoscandia, both Willow and Rock Ptarmigan are likely to be affected by a

451 reduction in alpine habitat (i.e. elevated tree lines and shrubification of alpine tundra) owing

452 to climate warming (Myers-Smith et al. 2011; Hofgaard et al. 2012) and, although this might

453 increase the potential for intraspecific competition, the interactions between Rock and Willow

454 Ptarmigan have not been studied explicitly. The Rock Ptarmigan is expected to experience

455 range contractions, whereas the Willow Ptarmigan might expand its range. In a recent study,

456 Revermann et al. (2012) found that increased summer temperature was the main driving

457 factor for Rock Ptarmigan population distribution in Switzerland, and concluded that the

458 predicted change in climate will have a severe negative effect on their distribution. In

459 Fennoscandia, there will probably be both a direct effect on the Rock Ptarmigan distribution

460 owing to a warmer climate and changes in the predator community and an indirect effect

461 depending on the interaction with Willow Ptarmigan. Finally, results from our habitat models

462 give information on what environmental predictors are important for the spatial distribution of

463 Rock Ptarmigan in the breeding season. The likely impact on Rock Ptarmigan habitats of

464 development projects, such as wind turbines in the mountain areas, can be assessed and

465 preliminary mitigation guidelines created. When planning conservation efforts, this

466 information should be used to identify and rank suitable areas to act as core areas with no

467 hunting allowed. These areas could function as buffer zones in relation to conservation and

468 harvest management of the Rock Ptarmigan similarly as recommended by Willebrand and

469 Hörnell (2001) for the sympatric Willow Ptarmigan.

Acknowledgments

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707 **Tables**

708 **Table 1** Overview of the five vegetation classes considered for modeling of Rock Ptarmigan

709 summer habitat use at the observation, territory and landscape scales [a]

Vegetation	Description	N
Birch forest	Short and sparse birch forests (3)	105
Dry heath	Dry heath (1) and extreme dry heath (1)	277
Open	Mire (7) alpine meadows (2) mesic grass and wet heath (4) snow bed vegetation (1)	157
Rock	Boulders and rocky areas with sparse vegetation cover of mosses and lichens (1)	57
Shrub	Willow shrub vegetation (1)	3
Unsuitable	Open water (1) cultivated land (3) coniferous forests (6) glaciers (1) and permanent snowfields (1)	129

710 [a] The classes were re-classified based on vegetation structure from 33 original classes from the Swedish

711 mountain vegetation map (Anderson 2008). The numbers in brackets represent the number of original vegetation

712 types included in each of the re-classified classes evaluated. N = number of ptarmigan observations in each class

713 at the observation point scale.

714 **Table 2** Summary statistics (median and range) of the predictor variables assessed for Rock

715 Ptarmigan spatial distribution at the three selected study scales (observation, territory and

716 landscape scale) [a]

Scale	Predictor	Level	Unit	Presence	Absence
Observation	Vegetation	dry	–	277	291
		open	–	157	457
		rock	–	57	234
	Altitude		meter	886 (301–1618)	812 (338–1601)
	Slope		degree	7.6 (0–58)	7.1 (0–54)
	Terrain heterogeneity		none	$1.5*10^{-4}$ ($5.3*10^{-7}$–$2*10^{-2}$)	$1.5*10^{-4}$ ($3.2 *10^{-7}$–$1.6\ 10^{-2}$)
	Aspect		degree	173 (0–360)	171 (0–360)
	Snowfield	presence	–	4	12
		absence	–	487	970
Territory	Vegetation	dry	–	285	303
		open	–	144	451
		rock	–	62	228
	Altitude		meter	891 (301–1537)	813 (336–1598)
	Slope		degree	8.1 (0–50)	7.5 (0–44)
	Terrain heterogeneity		none	0.002 (0–0.1)	0.002 (0–0.1)
	Aspect		degree	194 (0–360)	186 (0–360)
	Snowfield	presence	–	100	79
		absence	–	391	903
Landscape	Habitat	dry	–	284	323
		open	–	150	432
		rock	–	57	227
	Altitude		meter	889 (301–1459)	818 (340–1580)
	Slope		degree	8.7 (0–40)	7.7 (0.5–40)
	Terrain heterogeneity		none	0.005 (0–0.18)	0.005 (0–0.14)
	Aspect		degree	207 (0–360)	182 (0–360)
	Snowfield	presence	–	125	183
		absence	–	366	799

717 [a] The column 'Presence' refers to the rock ptarmigan observations and the column 'Absence' to the pseudo-

718 random sites. The levels for the categorical variables (vegetation class and presence of snowfield) are expressed

719 as number of observations within each category.

720 **Table 3** The three best habitat models including the predictor variables at observation, territory and landscape scales according to AICc Δ AICc

721 and AIC weight [a]

Scale	Model	Vegetation	Alt	Alt^2	VRM	Slope	Snow	Aspect	df	AIC$_c$	Δ AIC$_c$	AIC$_c$ weight	R^2	AUC
Observation	1	X	X	X	X	X		X	9	1737	0.00	0.36	0.14	0.69
	2	X	X	X	X	X	X	X	10	1739	2.00	0.12	0.14	0.69
	3	X	X	X	X			X	8	1743	6.30	0.01	0.13	0.69
Variable importance		1.00	1.00	0.97	1.00	0.94	0.26	0.52						
Territory	1	X	X	X	X		X	X	9	1698	0.00	0.79	0.17	0.71
	2	X	X	X	X		X		7	1713	15.20	0.00	0.16	0.70
	3	X	X	X			X	X	8	1716	18.60	0.00	0.16	0.69
Variable importance		1.00	1.00	1.00	1.00		1.00	0.79						
Landscape	1	X	X	X	X		X	X	9	1726	0.00	0.58	0.15	0.72
	2	X	X	X	X		X		7	1738	12.00	0.00	0.14	0.70
	3	X			X		X	X	7	1750	23.90	0.00	0.13	0.70
Variable importance		1.00	1.00	1.00	1.00		1.00	0.58						

722 [a] Alt = altitude (m); VRM = Vector ruggedness measure; Snow = presence or absence of a permanent snowfield within the spatial scale; R^2 = Nagelkerke's R^2 (Nagelkerke

723 1991); AUC = Receiver operating characteristics curve

724 **Table 4** Parameter estimates and standard error (SE) for the predictor variables in the

725 selected habitat models for Rock Ptarmigan spatial distribution in the breeding season at the

726 tree scales [a]

Scale	Predictor	Level	Estimates	SE
Observation	Vegetation	Intercept (dry)	−3.63	1.028
		open	−0.99	0.13
		rock	−1.34	0.22
	Altitude		0.007	0.002
	(Altitude)^2		−0.0000034	0.0000011
	VRM		158.50	37.17
	Slope		−0.024	0.008
	Aspect cos		0.32	0.08
	Aspect sin		−0.12	0.08
Territory	Vegetation	Intercept (dry)	−4.44	1.13
		open	−0.99	0.13
		rock	−1.10	0.22
	Altitude		0.010	0.002
	(Altitude)^2		−0.0000057	0.0000013
	VRM		20.06	4.41
	Snow presence	present	1.45	0.20
	Aspect cos		0.19	0.09
	Aspect sin		−0.35	0.09
Landscape	Vegetation	Intercept (dry)	−5.54	1.19
		open	−0.96	0.13
		rock	−1.37	0.24
	Altitude		0.012	0.002
	(Altitude)^2		−0.0000068	0.0000014
	VRM		17.56	3.39
	Snow presence	present	0.91	0.17
	Aspect cos		0.14	0.09
	Aspect sin		−0.33	0.09

727 [a] Reference level was set to vegetation type 'dry' and 'absence of snow' for models including these variables and

728 the estimates are differences (contrasts) between the intercept and the estimated effect. Note that the estimates

729 are on the logit scale

730 **Table 5** Odds ratios (OR) and 95 % confidence intervals (CI) for each level of the categorical

731 variables (vegetation and presence of a permanent snowfield) in the best models describing

732 probability of Rock Ptarmigan presence at the three spatial scales [a]

Scale	Ratio	OR	95% CI
Observation	dry/open	0.37	0.29–0.48
	dry/rock	0.26	0.16–0.40
	open/rock	0.70	0.46–1.08
Territory	dry/open	0.37	0.28–0.48
	dry/rock	0.33	0.21–0.52
	open/rock	0.91	0.59–1.40
	snow A/snow P	4.27	2.85–6.38
Landscape	dry/open	0.38	0.16–0.49
	dry/rock	0.25	0.15–0.41
	open/rock	0.67	0.42–1.06
	snow A/snow P	2.48	1.77–3.46

733 [a] The reference levels for the two categorical variables are 'dry' and 'absence of a snowfield' (Snow A = absence

734 of snow field; Snow P = presence of a snow field). Note that the odds ratio snow A / snow P is calculated for the

735 level 'dry' and only for the two larger scales. CI of significant estimates do not intersect the value 1

Figure legends

Fig. 1 The study area in Norrbotten county in northern Sweden. Each black dot represents a Rock Ptarmigan observation during 1990-2012 (N = 491). Illustration: Oddveig Øien Ørvoll Norwegian Polar Institute 2012

Fig. 2 Number of Rock Ptarmigan observations by year (1990-2012) and month (June N = 230; July N = 261) included in the statistical habitat modeling. Mean observation days were (Julian day June, 173.4 ± 6.8 [≈ June 22]; Julian day July, 192.8 ± 8.9 [≈ July 12]) and median observation days were (Julian day June, 175 [≈ June 24]; Julian day July, 191 [≈ July 10]) across years

Fig. 3 Marginal plots for the best fitted logistic regression models for probability of Rock Ptarmigan presence at (a) observation scale (25 and 75 m neighborhood; 1 and 3 pixels in the digital maps with the bird observation in the center); and (b) territory scale (525 m neighborhood; 21 pixels). The marginal plots for the best logistic regression models at landscape scale (1025 m neighborhood; 41 pixels). are not shown because estimated effects were similar to the territory scale. The effect of each variable on the predicted probability of presence of a Rock Ptarmigan in the study area is shown by letting the predictor variable take a set of values from the data while the other variables are held constant at an average value. The marginal effect of each predictor variable is shown with the 95% CI (shaded area) for each level of the vegetation cover variable (dry, open or rock). At the territory scale the marginal plots are shown only for the factor level 'presence of a permanent snowfield within a square of 525 m *x* 525 m. The influence of the presence of a permanent snowfield at the territory scale is shown only for the factor level 'dry'

Fig. 4 Rock Ptarmigan feathers remaining at the snowfield-boulderfield edge after birds were observed sheltering during the summer. Photo: Maria Hörnell-Willebrand
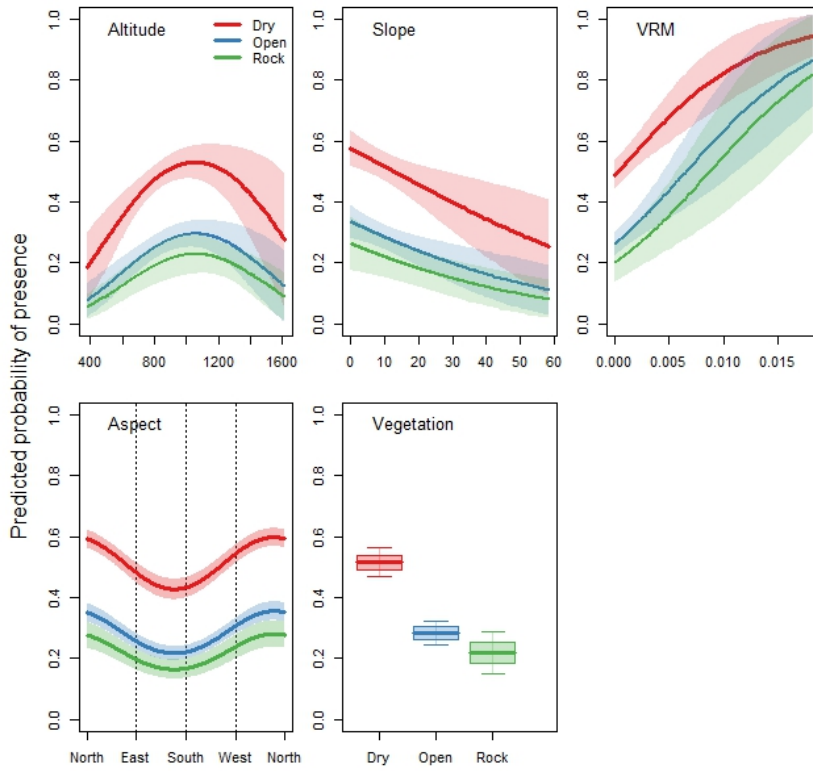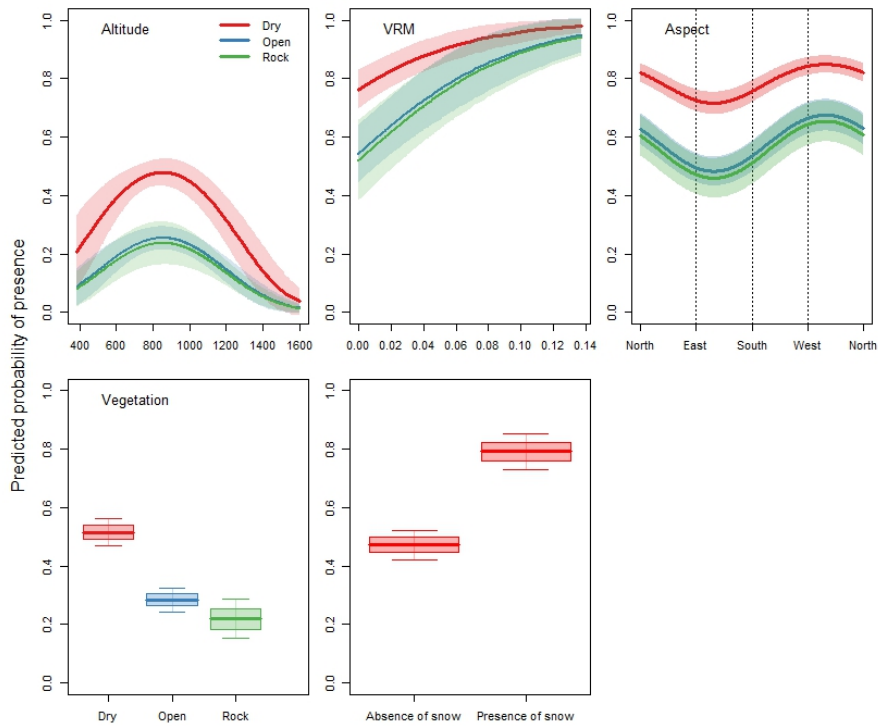
760 **Fig. 1**

761

762 **Fig. 2**
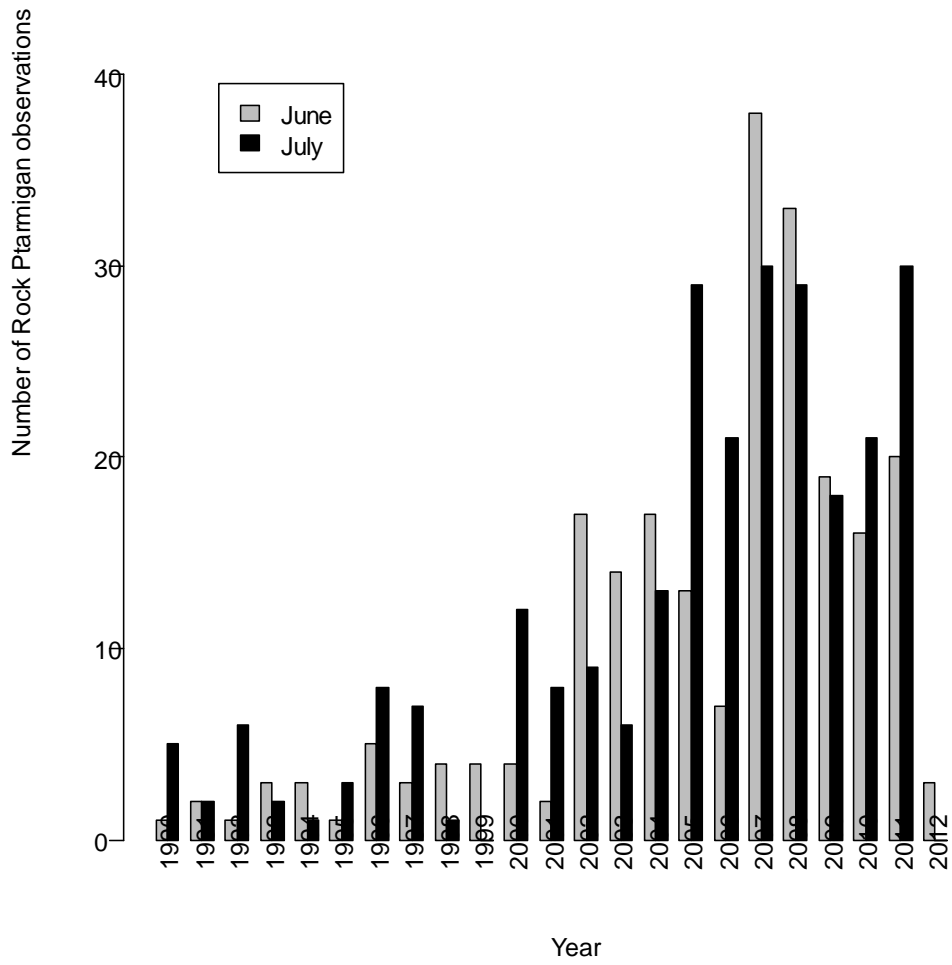
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764 **Fig. 3**

(a) Observation scale

(b) Territory scale

765

766 **Fig. 4**

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