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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

## 31 **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](http://www.lansstyrelsen.se)), with generally low abundances (0.4-1.8  
46 pairs per km<sup>-2</sup>; Ottosson et al. 2012) observed between peak years of maximum 5.7 pairs  
47 per km<sup>-2</sup> (Hörnell-Willebrand unpublished data, [www.lansstyrelsen.se](http://www.lansstyrelsen.se)) compared to North  
48 America (up to 15 territories km<sup>-2</sup> in peak years; Sinclair et al. 2003) and Iceland (from 5.9  
49 males per km<sup>-2</sup> in low years up to 21.7 males per km<sup>-2</sup> 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](http://www.ssb.no),  
52 [www.rktl.fi](http://www.rktl.fi), [www.smavilt.se](http://www.smavilt.se), [www.ust.is](http://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<sup>2</sup> (Hörnell-Willebrand unpublished data,  
63 [www.lansstyrelsen.se](http://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](http://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.

## 112 **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<sup>2</sup>) 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](http://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](http://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](http://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 ( $\Delta AIC$ ) 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).

## 265 **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<sup>2</sup>, 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<sup>2</sup>, 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  $\chi^2 = 1502$ , df =  
276 1462, p = 0.22; territory scale, Pearson's  $\chi^2 = 1523$ , df = 1464, p = 0.13; landscape scale,  
277 Pearson's  $\chi^2 = 1562$ , 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 =  $0.73 \pm 0.0053$ ;  
297 territory scale =  $0.75 \pm 0.0025$ ; landscape scale =  $0.75 \pm 0.0037$ ).

## 298 **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<sup>2</sup>), 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.

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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 <sup>a</sup>

<b>Vegetation</b>	<b>Description</b>	<b>N</b>
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 <sup>a</sup> 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) <sup>a</sup>

Scale	Predictor	Level	Unit	Presence	Absence
<b>Observation</b>	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	$1.5 \times 10^{-4}$ ( $5.3 \times 10^{-7}$ – $2 \times 10^{-2}$ )	$1.5 \times 10^{-4}$ ( $3.2 \times 10^{-7}$ – $1.6 \times 10^{-2}$ )
	Aspect		degree	173 (0–360)	171 (0–360)
	Snowfield	presence	–	4	12
		absence	–	487	970
	<b>Territory</b>	Vegetation	dry	–	285
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
<b>Landscape</b>		Habitat	dry	–	284
	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 <sup>a</sup> 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  $\Delta$  AICc  
 721 and AIC weight <sup>a</sup>

Scale	Model	Vegetation	Alt	Alt <sup>2</sup>	VRM	Slope	Snow	Aspect	df	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	AIC <sub>c</sub> weight	R <sup>2</sup>	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 <sup>a</sup> Alt = altitude (m); VRM = Vector ruggedness measure; Snow = presence or absence of a permanent snowfield within the spatial scale; R<sup>2</sup> = Nagelkerke's R<sup>2</sup> (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 <sup>a</sup>

<b>Scale</b>	<b>Predictor</b>	<b>Level</b>	<b>Estimates</b>	<b>SE</b>
<b>Observation</b>	Vegetation	Intercept (dry)	-3.63	1.028
		open	-0.99	0.13
		rock	-1.34	0.22
	Altitude		0.007	0.002
	(Altitude) <sup>2</sup>		-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
<b>Territory</b>	Vegetation	Intercept (dry)	-4.44	1.13
		open	-0.99	0.13
		rock	-1.10	0.22
	Altitude		0.010	0.002
	(Altitude) <sup>2</sup>		-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
<b>Landscape</b>	Vegetation	Intercept (dry)	-5.54	1.19
		open	-0.96	0.13
		rock	-1.37	0.24
	Altitude		0.012	0.002
	(Altitude) <sup>2</sup>		-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 <sup>a</sup> 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 <sup>a</sup>

<b>Scale</b>	<b>Ratio</b>	<b>OR</b>	<b>95% CI</b>
<i>Observation</i>	dry/open	0.37	0.29–0.48
	dry/rock	0.26	0.16–0.40
	open/rock	0.70	0.46–1.08
<i>Territory</i>	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
<i>Landscape</i>	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 <sup>a</sup> 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

## 736 **Figure legends**

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

740 **Fig. 2** Number of Rock Ptarmigan observations by year (1990-2012) and month (June N =  
 741 230; July N = 261) included in the statistical habitat modeling. Mean observation days were  
 742 (Julian day June,  $173.4 \pm 6.8$  [ $\approx$  June 22]; Julian day July,  $192.8 \pm 8.9$  [ $\approx$  July 12]) and  
 743 median observation days were (Julian day June, 175 [ $\approx$  June 24]; Julian day July, 191 [ $\approx$  July  
 744 10]) across years

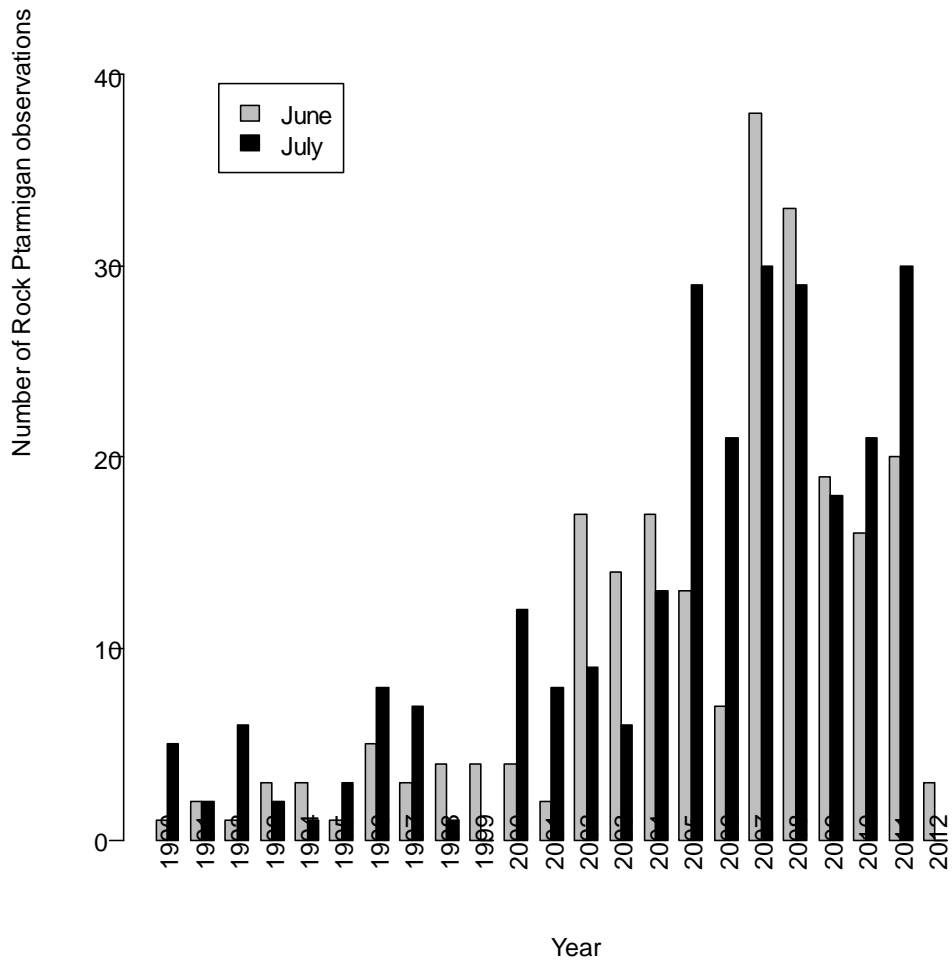
745 **Fig. 3** Marginal plots for the best fitted logistic regression models for probability of Rock  
 746 Ptarmigan presence at (a) observation scale (25 and 75 m neighborhood; 1 and 3 pixels in  
 747 the digital maps with the bird observation in the center); and (b) territory scale (525 m  
 748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

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

760 **Fig. 1**



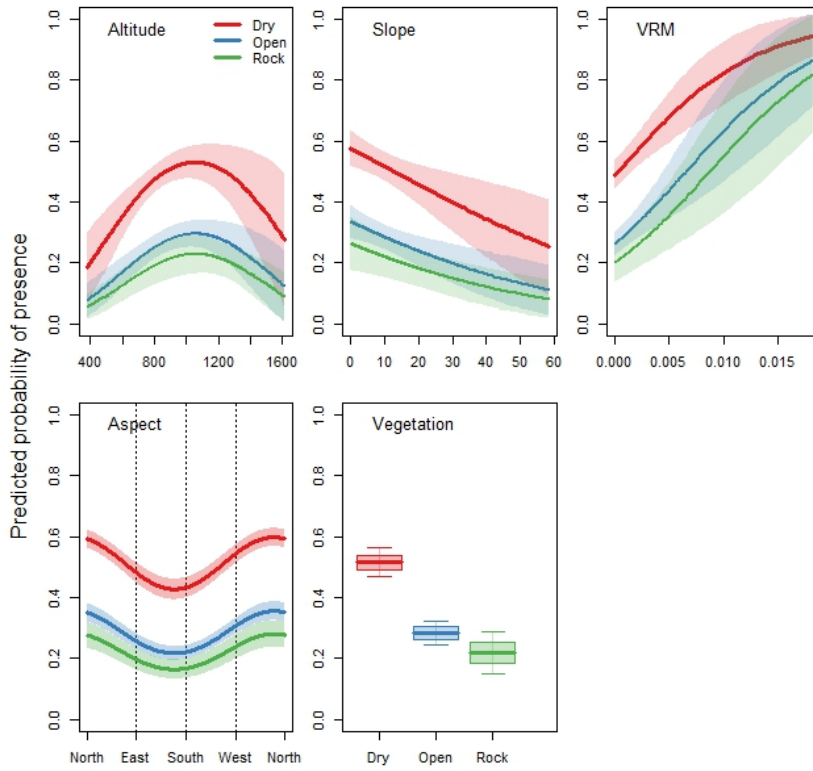
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762 **Fig. 2**

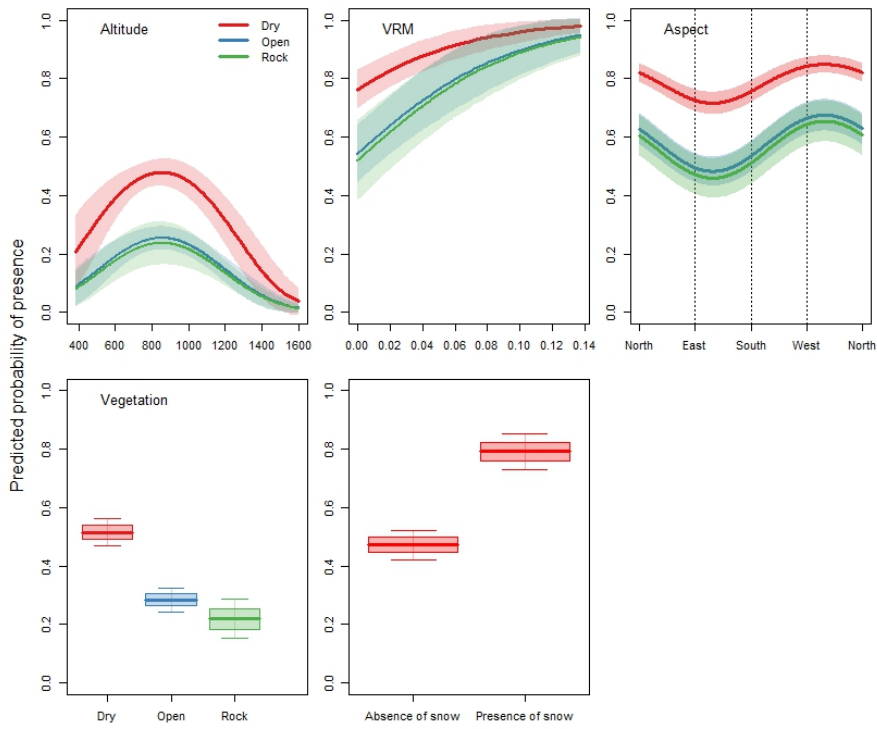
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764 Fig. 3

(a) Observation scale



(b) Territory scale



766 **Fig. 4**



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