The importance of seasonal environmental factors in the foraging habitat selection of Alpine Ring Ouzels *Turdus torquatus alpestris*

Arnaud G. Barras[1], Sophie Marti[1], Sarah Ettlin[1], Sergio Vignali[1], Jaime Resano-Mayor[1], Veronika Braunisch[1, 2] & Raphaël Arlettaz[1]

[1] Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland

[2] Forest Research Institute of Baden-Wuerttemberg, Wonnhaldestrasse 4, 79100 Freiburg, Germany

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ABSTRACT

Species inhabiting mountain ecosystems are expected to be particularly vulnerable to environmental change, yet information on their basic ecology is often lacking. Knowledge from field-based empirical studies remains essential to refine our understanding of the impact of current habitat alterations and for the consequential development of meaningful conservation management strategies. This study focuses on a poorly investigated and vulnerable mountain bird species in Europe, the Ring Ouzel *Turdus torquatus*. Our aim was to identify the species' key ecological requirements during the crucial period of nestling provisioning in the context of environmental change. We radiotracked and observed Alpine Ring Ouzels in a high-density population, investigating their pattern of foraging habitat selection in 2015 & 2017, and evaluated the transferability of these results over a wider geographic range across the SW Swiss Alps. Foraging birds selected, consistently in space and time, short grass swards (< 10 cm) with interspersed patches of accessible and penetrable soils, at intermediate moisture levels (around 40–65% volumetric water content). In Alpine ecosystems, this microhabitat configuration is typically widespread during the spring snowmelt, but extremely seasonal, with a rapid decrease in its availability over the course of the breeding season. This underlines the high vulnerability of the Ring Ouzel to environmental change: an earlier snowmelt could generate a temporal mismatch between the peak of the breeding effort and optimal foraging conditions; however, abandoning grazing activities on semi-wooded Alpine pastures may further decrease foraging habitat suitability through taller and denser grass swards, and subsequent woody vegetation encroachment. This study provides a mechanistic appraisal of the challenges Ring Ouzels will face in the future, as well as initial guidelines for targeted habitat management within treeline ecotones.

Keywords: alpine birds, conservation, seasonality, snowmelt, soil conditions, treeline

INTRODUCTION

There is growing awareness that mountain ecosystems are facing steadily increasing threats. Those most commonly identified across mountain ranges are climate change (La Sorte & Jetz 2010; Scridel *et al.* 2018), changes in land-use, in particular farming practices (Laiolo *et al.* 2004; Guo, Lenoir & Bonebrake 2018), and the increase in anthropogenic disturbance (Rolando *et al.* 2007; Arlettaz *et al.* 2015). Nevertheless, there is still a paucity of research on how species of higher elevations will be affected. Contrary to the European lowland and forest avifauna, knowledge on the basic ecology and demography of alpine bird species is still lacking (Chamberlain *et al.* 2012; Lehikoinen *et al.* 2019). This precludes both predictions about their response to environmental change and framing management recommendations (Chamberlain *et al.* 2012).

Predictions of future distributions under different scenarios of climate change exist for most European bird species nowadays (e.g. Huntley *et al.* 2008), even combined with land-use change for specific regions (e.g. Maggini *et al.* 2014). These predictions mostly result from species distribution models that rely on coarse-grained environmental data, and therefore do not capture small-scale functional species-habitat associations (Braunisch *et al.* 2014; Brambilla *et al.* 2018). This is potentially problematic in alpine ecosystems where coarse-grained predictions are mainly driven by the steep macroclimatic gradient, whereas a very complex topography leading to a high diversity of microclimates and microhabitats may buffer general trends (Beniston 2003; Chamberlain *et al.* 2016; Brambilla *et al.* 2018). The harsh environment and remoteness of high elevation ecosystems have hampered fine-grained empirical studies in the past (Chamberlain *et al.* 2012), although such studies represent an absolute prerequisite for meaningful predictions of future distributions (Chamberlain *et al.* 2016; Jähnig *et al.* 2018), and ought to serve as the basis for conservation management at the local scale (Morris *et al.* 2001; Arlettaz *et al.* 2012). In addition to high spatial resolution, information should also be collected at a fine temporal resolution, such that seasonal patterns of habitat selection can be assessed (Brambilla *et al.* 2017; Resano-Mayor *et al.* 2019). This is of paramount importance in highly seasonal environments like temperate mountain ecosystems where birds are expected to be particularly vulnerable to changes in vegetation phenology (Inouye *et al.* 2000) but where very few asynchronies have actually been documented (Scridel *et al.* 2018).

The Ring Ouzel *Turdus torquatus* is a good example of an alpine species for which information on small-scale ecological requirements is still largely lacking across its breeding range. UK uplands represent the exception, as the sharp decline of the subspecies *T. t. torquatus* in the last 50 years and its status of high conservation concern (Wotton, Langston & Gregory 2002) have prompted some studies on its autecology and population dynamics (e.g. Burfield 2002; Beale *et al.* 2006; Sim *et al.* 2013; Sim *et al.* 2015). In central and southern Europe, where the subspecies *T. t. alpestris* breeds in a rather different habitat, in semi-open coniferous forests at the treeline, studies on its ecology are scarce (von dem Bussche *et al.* 2008; Ciach & Mrowiec 2013). Over the whole distribution range, the current population trend appears stable (BirdLife International 2018), but the well-monitored population in Switzerland, which represents around 15% of the European population (Knaus *et al.* 2018), has decreased by 36% over the period 1990–2018 (Swiss Ornithological Institute 2019). It is hence red-listed in the country, and is one of the seven bird species with the highest priority for the development of a recovery programme (Keller *et al.* 2010). In addition, its vulnerability index calculated from different large-scale scenarios of land-use and climate change is one of the highest across all Swiss breeding birds (Maggini *et al.* 2014). Nonetheless, while factors determining habitat selection at the territory and landscape scale in the Alps have been identified to some extent (von dem Bussche *et al.* 2008), information about the key drivers of local-scale habitat selection during the breeding period is still lacking. Only high-resolution studies may allow the underlying ecological mechanism of the observed decline to be deciphered (Morris *et al.* 2001). In this way, the vulnerability of the species can be better assessed in order to frame recommendations for future conservation.

One of the main determinants of habitat use during the reproduction period is the selection of feeding grounds, i.e. the foraging habitat selection. Parents must indeed supply large quantities of food to chicks for optimal somatic growth, representing a true energy bottleneck in the species' life cycle. Feeding grounds providing high prey availability represent therefore a *sine qua non* for successful reproduction (Naef-Daenzer, Naef-Daenzer & Nager 2000). For ground-foraging insectivorous birds, prey accessibility is often limited by ground vegetation structure (Atkinson, Buckingham & Morris 2004; Schaub *et al.* 2010), whereas soil conditions have a large influence on both abundance and accessibility of soil-dwelling invertebrates (Peach *et al.* 2004; Gilroy *et al.* 2008). Extensive research on the Ring Ouzel in the UK has shown that both adults (Burfield 2002) and fledglings (Sim *et al.* 2013) indeed favour foraging grounds with high soil pH and short grass swards within a heather-grass

mosaic. Moreover, it has been hypothesized that soil conditions, such as soil moisture (Beale *et al.* 2006) and soil penetrability (Burfield 2002), could also play a key role, as they are known to influence the abundance and activity of earthworms (Oligochaeta; Edwards & Bohlen 1996), the staple food of Ring Ouzel nestlings (Glutz von Blotzheim & Bauer 1988; Burfield 2002; Sim *et al.* 2015).

Using radiotracking and direct visual observations, we investigated how fine-scale habitat characteristics influence the foraging habitat selection by Ring Ouzels during the nestling provisioning period in the European Alps. For this purpose, we focused on the selection of foraging grounds within the home-range (hereafter home-range scale) and on the resource acquisition within a foraging site (hereafter site scale), which correspond to the third and fourth orders of selection respectively, following the definition of Johnson (1980). Our aim was to identify key drivers of foraging microhabitat selection, and to characterize their seasonality so as to detect changes in the availability of suitable foraging habitat, all this in the perspective of future environmental change.

MATERIALS AND METHODS

Study area

The study was conducted in the central Swiss Alps, in the canton of Valais. This region is characterized by a continental climate, with warm and dry summers, and cold and wet winters. The site where radiotracking took place (46.33 N, 7.43 E), hereafter referred to as Serin, encompassed 205 ha, ranging from 1700–2200 m above sea level (asl), at the interface between the subalpine and the alpine belts. The zone is used for summer pasturing, with the continuous presence of cattle between mid-June and mid-September, which is a widespread traditional farming practice at these elevations in the Swiss Alps (Schulz, Lauber & Herzog 2018). Extensive pasturing results in a habitat mosaic consisting of open grasslands interspersed with isolated or groups of coniferous trees (predominantly larches *Larix decidua* and spruce *Picea abies*). The configuration of these semi-wooded pastures is particularly attractive for breeding Ring Ouzels (von dem Bussche *et al.* 2008), and the average density at the study area estimated from standardized monitoring is 40.7 territories/km^2, which is among the highest observed in the country (Knaus *et al.* 2018).

Foraging locations sampling

Ring Ouzels (n = 41) were captured using mistnets and equipped with radio-transmitters (PD-2P; Holohil Systems Ltd., Carp, Canada; 3.0–3.7g — corresponding to 3.0–3.7% of the species mean body mass — life span 3–4 months) between mid-April and mid-May: 11 males and 10 females in 2015, and 10 males and 10 females in 2017. The permit for bird capturing was delivered by the Swiss Federal Office for the Environment (F044-0799) and authorisation for radiotracking by the Swiss Federal Food Safety and Veterinary Office. The radiotags were mounted with a leg-loop harness (loop span 76 mm, diameter 0.6 mm) made out of stretch-nylon tubes, following the method of Rappole and Tipton (1991). We tracked the birds during the whole breeding period (mid-April to the end of June) with the 'homing-in' technique, i.e. obtaining a series of repeated bearings using a radio-receiver (Australis 26k, Lawnton, Australia) coupled with a three-element hand-held Yagi antenna to approach and visually locate an individual. Each radiotagged individual was located at least twice a week to monitor its breeding status and, if possible, find its nest. From the first observations of adults provisioning chicks (2015: May 16th; 2017: May 24th), we started to track breeding adults more intensively (every 1–3 days per individual) until fledging of the brood occurred. Once a radiotracked bird was visually located, it was carefully approached (at 30–50 m distance), taking care not to influence its behaviour. From that moment, the exact spot of the first observed successful prey capture event was recorded with binoculars and marked with a labelled flag as soon as the bird had left the area. We referred to this visually evidenced prey capture as a 'foraging location'. To avoid, as far as possible, spatio-temporal correlation between the foraging locations, i.e. to achieve data independency, we left a time span of at least 30 min between two recordings from the same individual. This was enough to ensure that the bird had been provisioning nestlings in the meantime and had therefore started a new foraging bout. In 2017, several radiotagged individuals were particularly shy and showed increased flight-initiation distances, so that it was particularly difficult to obtain foraging locations for those birds. To increase our sample size, we therefore also recorded foraging locations of provisioning parents randomly encountered during radiotracking sessions. We are confident that this did not introduce any detection bias in our analysis, as all habitat types and sectors of the study area were visited regularly during the radiotracking sessions.

In 2016, 16 areas situated outside the main study area of Serin were visited once or twice along a predefined transect (1.5–3 km) during the reproductive season (May 15th –June 27th) to collect additional foraging locations from untagged provisioning individuals. These

data, spanning from 1650 to 2200 m asl, served for external model evaluation on a wider area across the Swiss Alps with different climatic conditions (Fig. 1).

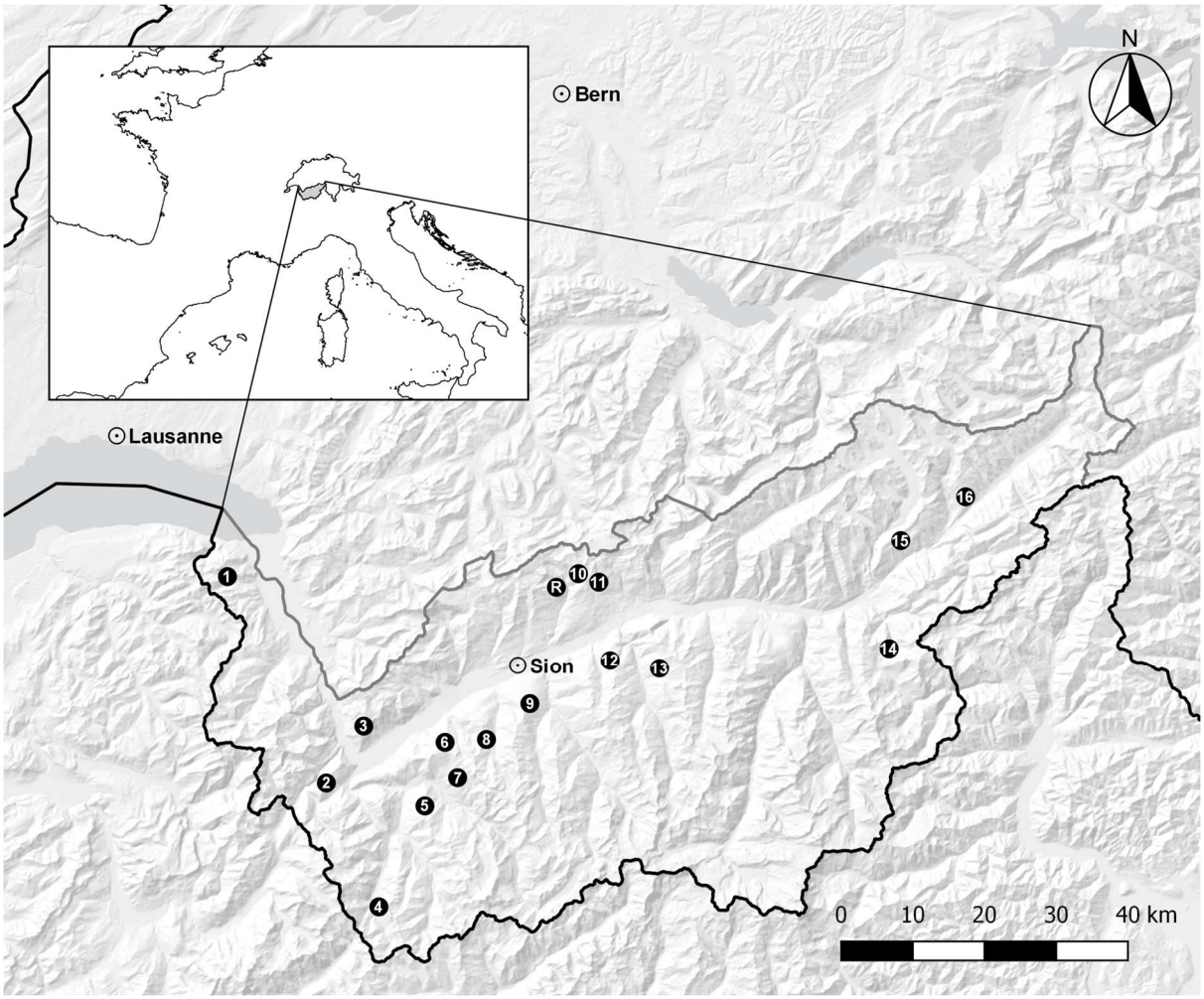

Figure 1 Map of the study region (Valais, Switzerland; shaded in the inset). The area where the radiotracking took place is symbolized with the letter R, and those for the collection of data for model evaluation are numbered from 1 to 16.

Habitat measurements

The habitat selection pattern was assessed by comparing the characteristics of the habitat at actual foraging locations with neighbouring locations, which were assumed to represent less suitable habitat because they were apparently not used for foraging. For that purpose, we randomly selected two pseudo-absences (PA) in the surroundings of a foraging location following a standard procedure. A random bearing (α: 0–359°) was generated, which defined the direction from the actual foraging location in which two PA locations were placed, the first one at a random distance between 5 and 14 m, and the second between 15 and 50 m. The former range (5–14 m) was chosen so as to investigate habitat selection at the foraging site scale. In

effect, these distances from an actual location are within the range of a hopping bird, as typically observed during a single foraging bout (Burfield 2002; own pers. obs.). In contrast, the latter range (15–50 m) is more likely to express foraging habitat selection at the wider scale of the home-range, as the chosen distance is within the typical range of a Ring Ouzel flying from one part of its home-range to another (Burfield 2002). The PA locations were generated instantly after each recorded foraging location, so that the habitat measurements could occur during the same or the next day, and hence accurately reflect the environmental conditions encountered by a foraging bird. This represents a fundamental aspect of the sampling design, as several habitat variables showed strong temporal variations due to the high seasonality of the ecosystem at these elevations, in particular as regards snow cover.

Measurements of predefined habitat variables were taken in the same way at foraging and PA locations and restricted to a plot of 1-m radius around each location, so as to describe the microhabitat. Habitat variables were classified into four main categories: ground cover, topography, vegetation height and soil conditions (Table 1). Ground cover consisted of eight classes: brown grass (dry, i.e. dead annual herbaceous plants from the previous year), green grass (new annual living plants), accessible ground (cover of bare ground and leaf/needle litter combined; hereafter AG cover), mineral (gravel and rocks), dead wood (lying trunks and branches), snow, woody plants (shrubs and bushes below head height) and mosses. Topographic variables included slope inclination and aspect (as northness and eastness — see Table 1), both measured with a compass, and distance to the nearest snow patch if present within a radius of 50 m. Herbaceous vegetation height was measured for the brown and green grass swards separately. Two soil condition variables were also considered. Soil penetrability was measured with a penetrometer (EL 29-3729, ELE International, Loveland, USA), a device that indicates the force (kg/cm^2) needed to insert a metal tip into the soil to a depth of 6.35 mm, with high values thus indicating low soil penetrability. For soil moisture, we measured the volumetric water content (VWC) of the soil, calculated from its conductivity using a specific dual probe with two 51-mm rods (SM150, Delta-T, Cambridge, UK). For each soil variable, three measurements were taken within 10 cm of the centre of the plot, i.e. where prey capture occurred, with their means retained for subsequent analyses.

Statistical analyses

We assessed foraging habitat selection as a function of habitat variables measured at foraging vs. PA locations, using hierarchical logistic regression, which corresponds to a generalized

linear mixed-effects model (GLMM) with a binomial error distribution and a logit link function. The habitat variables were included as fixed effects. Non-independence of the data coming from the same stratum (a triplet consisting of a given actual foraging location and its two associated PA locations), or the same individual, was accounted for with nested random effects (Gillies *et al.* 2006), i.e. stratum nested within individual, as several foraging locations per individual had been recorded. Data from untagged and therefore unidentified individuals were given unique factor values. All analyses were performed using the software R 3.5.1 (R Development Core Team 2018) and logistic models were fitted using the *glmer* function in the R-package 'lme4' (Bates *et al.* 2015).

Prior to model selection, several variables were transformed: marginal ground cover variables (> 90% of zero values) were not considered in the analysis, and those with more than 70% of zero values were transformed to binary presence/absence (1/0) variables. The other ground cover variables were arcsine-square-root transformed, and vegetation height variables log-transformed. Moreover, all variables were standardized to visualize and compare the effect size directly from the coefficient estimates. We also tested the addition of squared terms to variables for which we hypothesized a hump-shaped relationship in relation to occurrence probability: soil moisture, soil penetrability, AG and green grass cover. Finally, to avoid collinearity, we checked for Pearson's correlation coefficients between the variables, retaining only those with $|r| < 0.7$, and we carefully checked that all variables had variance inflation factors (VIF) < 3 in all fitted models.

To characterize each order of selection separately, we fitted two different sets of models. First, foraging locations were compared to PA in the closer range (5–14 m) and, second, to PA in the wider range (15–50 m). For each analysis, we adopted a model selection approach in two steps. First, for each of the four categories of variables, we generated a list of candidate models from all possible variable combinations and ranked them based on the Akaike Information Criterion with correction for small samples (AICc) using the function *dredge* of the package 'MuMIn' (Bartoń 2018). We defined the set of best-supported models as those within ΔAICc < 2 from the first-ranked one, after the exclusion of models with uninformative parameters, i.e. models that contained additional parameters compared to better-ranked models, but that have a higher AICc value (Arnold 2010). We then retained all variables appearing in at least one model of this set. In a second step, retained variables from every category were combined into a single model. The interaction term between AG cover and height of green grass was added to this model, to check for the potentially higher importance of AG cover

within high ground vegetation. We then carried out the same model selection procedure as above to identify the set of best-supported models within ΔAICc < 2. The AICc weight (w_i) of each possible candidate model was calculated, and variable importance was assessed by summing the w_i of all the models where it appeared following Burnham and Anderson (2002). To evaluate the performance of the best-ranked model, we calculated R-squared with the function *r.squaredGLMM* from the package 'MuMIn', as well as the area under the receiver operating curve (AUC) using a five-fold cross-validation. Finally, we assessed model spatial transferability by calculating the AUC on the evaluation data collected in 2016. Plots of occurrence probability against a given habitat variable were based on the best-ranked model, while setting all other retained variables to their empirical mean. 95% credible intervals around the regression line were drawn from the 2.5% and 97.5% quantiles of the posterior distribution, obtained with 10,000 simulations with the package 'arm' (Gelman & Su 2018).

Table 1 Habitat variables measured at each foraging and pseudo-absence (PA) plot. Mean ± sd values are displayed for each group, except for woody plants and moss cover, which were transformed into binary factors as they contained > 70% of zero values, with resulting 0/1 counts shown here. Variables in brackets were removed from the analysis as they contained too many NAs or zero values (> 90%).

	Habitat variables	Unit	Foraging	PA (5–14m)	PA (15–50m)
Ground cover					
1	Brown grass	%	12.7 ± 14.0	12.2 ± 16.4	10.6 ± 12.4
2	Green grass	%	44.6 ± 28.3	50.3 ± 30.5	57.3 ± 30.7
3	Accessible ground	%	32.4 ± 25.6	25.2 ± 25.7	20.7 ± 23.9
4	Mineral	%	2.4 ± 4.2	3.6 ± 8.0	3.3 ± 8.2
5	Dead wood	%	3.2 ± 5.3	3.4 ± 6.8	3.0 ± 7.3
6	(Snow)	%	0.9 ± 5.1	1.1 ± 7.2	0.8 ± 8.1
7	Woody plants	0/1	155/53	165/42	164/44
8	Moss	0/1	159/49	167/41	172/36
Topography					
9	Slope	°	18.2 ± 8.9	18.4 ± 9.6	18.2 ± 9.9
10	Northness	cos(aspect[a])	0.5 ± 0.6	0.4 ± 0.6	0.2 ± 0.7
11	Eastness	sin(aspect[a])	0.4 ± 0.5	0.5 ± 0.5	0.4 ± 0.5
12	(Distance to snow if < 50 m)	m	10.6 ± 17.2	10.4 ± 13.4	14.3 ± 17.1
Vegetation height					
13	Brown grass height	cm	2.5 ± 1.6	2.7 ± 2.0	3.1 ± 3.2
14	Green grass height	cm	5.9 ± 3.3	7.9 ± 4.8	8.9 ± 5.7
Soil conditions					
15	Soil moisture	VWC[b]	49.9 ± 12.3	41.9 ± 14.3	41.1 ± 14.4
16	Soil penetrability	kg/cm^2	0.9 ± 0.5	1.2 ± 0.7	1.3 ± 0.6

[a]Expressed in radians
[b]Volumetric water content

Finally, we investigated the seasonal pattern of the best predictors of foraging habitat selection, i.e. those for which a significant relationship was detected in at least one of the two orders of selection. We built linear mixed-effects models with each key predictor as a response variable, using *lmer* from package 'lme4' (Bates *et al.* 2015). When necessary, we transformed the response variable to meet a normal distribution and checked model assumptions looking at standard residual plots (residuals vs. fitted values, QQ-plot of the residuals). As explanatory variables, we included date and year of sampling, as well as plot type, which was either foraging or PA (PAs of both distance ranges were grouped together). In addition, interaction terms between date and year, and date and plot type, were included in all models as fixed effects, and individual identity and stratum as nested random effects; 95% credible intervals were again drawn from simulations.

RESULTS

In total, we collected 137 foraging locations from 19 radiotagged individuals in 2015, and 71 locations from nine tagged and several untagged individuals in 2017 (ratio 26/45). For 13 radiotagged individuals, we could not record any foraging locations, as we either lost the signal, they did not breed, or the brood failed early on. For model evaluation over a wider range, we collected 53 foraging locations from untagged individuals across 16 different areas (1–11 locations per area). Out of the measured habitat variables, only AG cover and green grass cover were strongly correlated (r = -0.75). We excluded the latter, as the mean cover percentage was the highest across all plots, and removing it relaxed the unit-sum constraint of ground cover variables. All variables in our models had a VIF < 3.

Foraging habitat selection at the site scale

A final set of 4 models (ΔAICc < 2) was obtained for the analysis of habitat selection at the scale of the foraging site. The best-ranked model explained a relatively low proportion of variance R^2 = 0.19, with an AUC ± sd from the cross-validation equal to 0.70 ± 0.07. Performance based on the evaluation dataset was also fairly low (AUC = 0.64). All variables showed consistent coefficient estimates in the four different models, and hence their respective effects were considered to be well represented by the first-ranked model (Table 2). AG cover had a positive effect on occurrence probability ($\beta \pm \text{se} = 0.24 \pm 0.11$, $P = 0.03$), but the quadratic term was retained as well, suggesting a hump-shaped relationship (Fig. 2), despite not being significant ($\beta \pm \text{se} = -0.17 \pm 0.11$, $P = 0.12$). For soil moisture, the presence of an optimum was

clear (linear: $\beta \pm$ se = 0.65 ± 0.12, $P < 0.001$; quadratic: -0.33 ± 0.12, $P < 0.01$) with a peak in occurrence probability at 64% VWC (Fig. 2), whereas soil penetrability had a negative effect ($\beta \pm$ se = -0.34 ± 0.13, $P < 0.01$), i.e. birds avoided impenetrable soils. These two soil condition variables were ranked as the most important (Table 2). A negative relationship with green grass height was highlighted only in the third-ranked model (Supplementary Materials, Table S1) and had the lowest variable importance overall (Table 2).

Table 2 Variables retained in the set of best models within ΔAICc < 2, in the analysis of foraging habitat selection at the site and the home-range scale, respectively. Coefficient estimates, *Z*- and *P*-values are from the best-ranked model in each analysis, whereas importance of the variable (from 0 to 1) is the sum of Akaike weights from the models where it appears out of all model combinations.

	Variable	Estimate ± se	*Z*-value	*P*-value	Importance
Site scale					
	AG cover	0.24 ± 0.11	2.14	0.033	0.85
	AG cover^2	-0.17 ± 0.11	-1.55	0.121	0.51
	Soil penetrability	-0.34 ± 0.13	-2.67	0.008	0.96
	Soil moisture	0.65 ± 0.12	5.24	< 0.001	1.00
	Soil moisture^2	-0.33 ± 0.12	-2.77	0.006	0.95
	GG height	–	–	–	0.51
Home-range scale					
	AG cover	0.22 ± 0.13	1.70	0.089	0.94
	AG cover^2	-0.27 ± 0.12	-2.19	0.028	0.69
	Soil penetrability	-0.64 ± 0.15	-4.41	< 0.001	1.00
	Soil moisture	0.49 ± 0.14	3.62	< 0.001	1.00
	Soil moisture^2	-0.42 ± 0.12	-3.44	< 0.001	1.00
	GG Height	-0.37 ± 0.15	-2.49	0.013	0.91
	Mineral cover	-0.21 ± 0.13	-1.55	0.122	0.49
	Northness	0.21 ± 0.12	1.76	0.078	0.63
	GG height x AG cover	–	–	–	0.36

AG cover: accessible ground cover; GG height: green grass height; ^{2}: quadratic term of a variable;
x: interaction between two variables

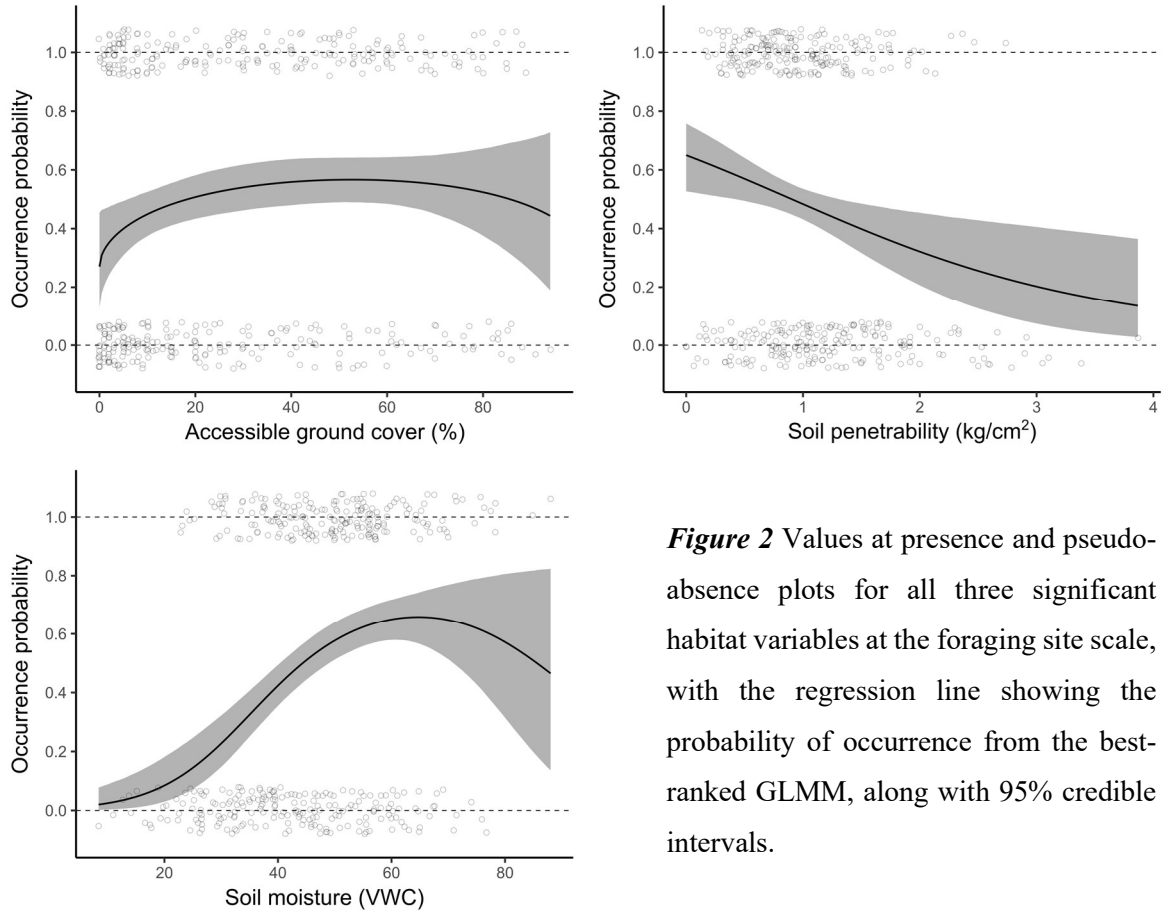

Figure 2 Values at presence and pseudo-absence plots for all three significant habitat variables at the foraging site scale, with the regression line showing the probability of occurrence from the best-ranked GLMM, along with 95% credible intervals.

Foraging habitat selection at the home-range scale

The analysis of foraging habitat selection at the home-range scale yielded a final set of four models. The best-supported model showed a higher performance than the site scale model for all three evaluation metrics considered: R^2 = 0.33, cross-validation AUC ± sd = 0.77 ± 0.10 and evaluation dataset AUC = 0.69. All variables showed consistent coefficient estimates in the four models, so that we again considered the first-ranked model to be representative of the set (Table 2). Again, soil moisture (linear: β ± se = 0.49 ± 0.14, $P < 0.001$; quadratic: -0.42 ± 0.12, $P < 0.001$) and penetrability (β ± se = -0.64 ± 0.15, $P < 0.001$) were the most important predictors (Table 2), with, in addition, a potential optimal range of moisture around a peak at 41% VWC (Fig. 3), i.e. somewhat lower than at the foraging site scale. At this order of selection, green grass height (β ± se = -0.37 ± 0.15, $P = 0.01$) was much more important than at the site scale (0.91; Table 2), with a clear selection for short grass swards (Fig. 3). The hump-shaped relationship with AG cover (linear: β ± se = 0.22 ± 0.13, $P = 0.09$; quadratic: β ± se = -0.27 ± 0.12, $P = 0.03$) was more supported than at site scale (Fig. 3; Supplementary Materials, Table S1). Finally, we detected a positive effect of northness (β ± se = 0.21 ± 0.12, $P = 0.08$),

indicating a selection for north-facing slopes, and a negative effect of mineral cover ($\beta \pm$ se = -0.21 ± 0.13, P = 0.12), although those variables were not significant and ranked among the last in importance (Table 2).

Seasonality of key habitat variables

Models of seasonality were fitted only for the key habitat predictors retained in the dual foraging habitat selection analysis, namely, AG cover, green grass height, soil moisture and soil penetrability. The type of plot had a significant effect in all four models (Table 3), which means that the difference between foraging and PA plots was consistent throughout the breeding season for all four habitat variables (Fig. 4). The significant effect of date indicated a clear seasonal change in AG cover ($\beta \pm$ se = -0.15 ± 0.08, P = 0.05) and soil moisture ($\beta \pm$ se = -0.35 ± 0.07, $P < 0.001$), both decreasing, whereas grass height ($\beta \pm$ se = 0.44 ± 0.07, $P <$ 0.001) progressively increased (Table 3; Fig. 4). For soil penetrability, the effect of date was positive but marginally significant ($\beta \pm$ se = 0.12 ± 0.07, P = 0.07). Furthermore, an effect of year on AG cover, soil moisture and soil penetrability was evident, with different intercepts in different years (Table 3), indicating a varying spring phenology. Only for soil moisture did the slope of the regression line differ significantly between 2015 and 2017, as indicated by the interaction between year and date ($\beta \pm$ se = 0.35 ± 0.12, $P < 0.01$; Table 3). Finally, the interaction between the type of plot and date was never significant ($P > 0.25$ for all variables), which indicates a similar seasonal pattern in both actual foraging and PA plots.

Table 3 Summary table of the coefficient estimates ± se from the linear mixed-effect models fitted for each of the four key habitat predictors. Explanatory variables are type of plot (presence/pseudo-absence), year (2015/2017) and date, as well as their interaction terms.

	Response variable			
	Soil moisture	Soil penetrability	Green grass height	AG cover
Presence	0.59 ± 0.06 ***	-0.49 ± 0.07 ***	-0.46 ± 0.06***	0.42 ± 0.06***
Date	-0.35 ± 0.07 ***	0.12 ± 0.07 °	0.44 ± 0.07***	-0.15 ± 0.08*
Year 2017	0.30 ± 0.14 *	0.42 ± 0.13 **	-0.31 ± 0.19	0.46 ± 0.17**
Date x Year 2017	0.35 ± 0.12 **	-0.15 ± 0.12	0.16 ± 0.13	-0.17 ± 0.13
Date x Presence	-0.07 ± 0.06	-0.03 ± 0.07	-0.03 ± 0.06	0.01 ± 0.06

Level of significance is indicated with symbols: ° $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

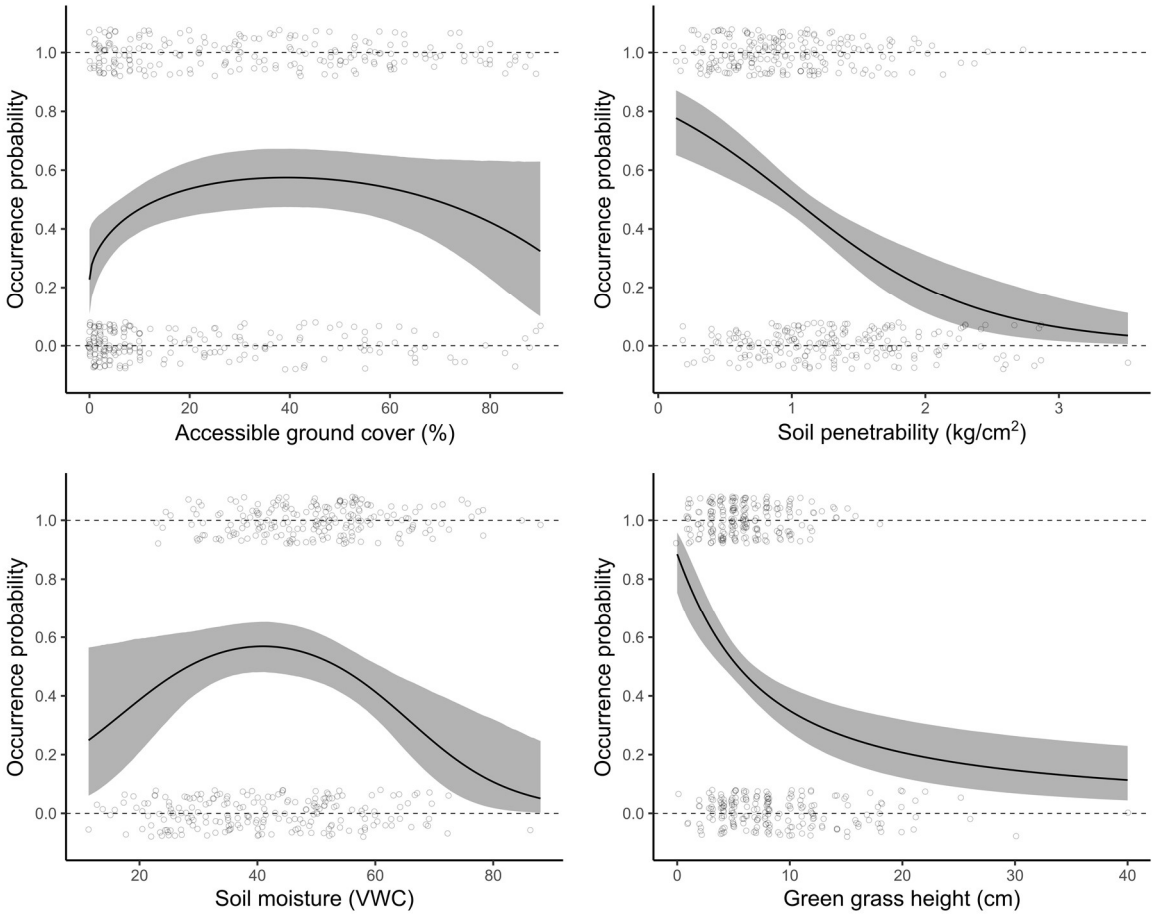

Figure 3 Values at presence and pseudo-absence plots for all four significant habitat variables at the home-range scale, with the regression line showing the probability of occurrence from the best-ranked GLMM, along with 95% credible intervals.

DISCUSSION

The present study delivers new insights into the fine-grained species-habitat associations of Alpine Ring Ouzel parents during the energetically critical period of nestling provisioning. It sheds light, in particular, on the challenges this emblematic passerine of treeline ecosystems is likely going to face in an era of rapid environmental change. Birds preferentially foraged in sites with intermediate soil moisture, high soil penetrability and short ground vegetation interspersed with accessible ground. Our models further emphasize the sheer spatio-temporal variability in these key variables, highlighting in particular the need to finely match reproductive effort with the narrow time window of optimal foraging conditions.

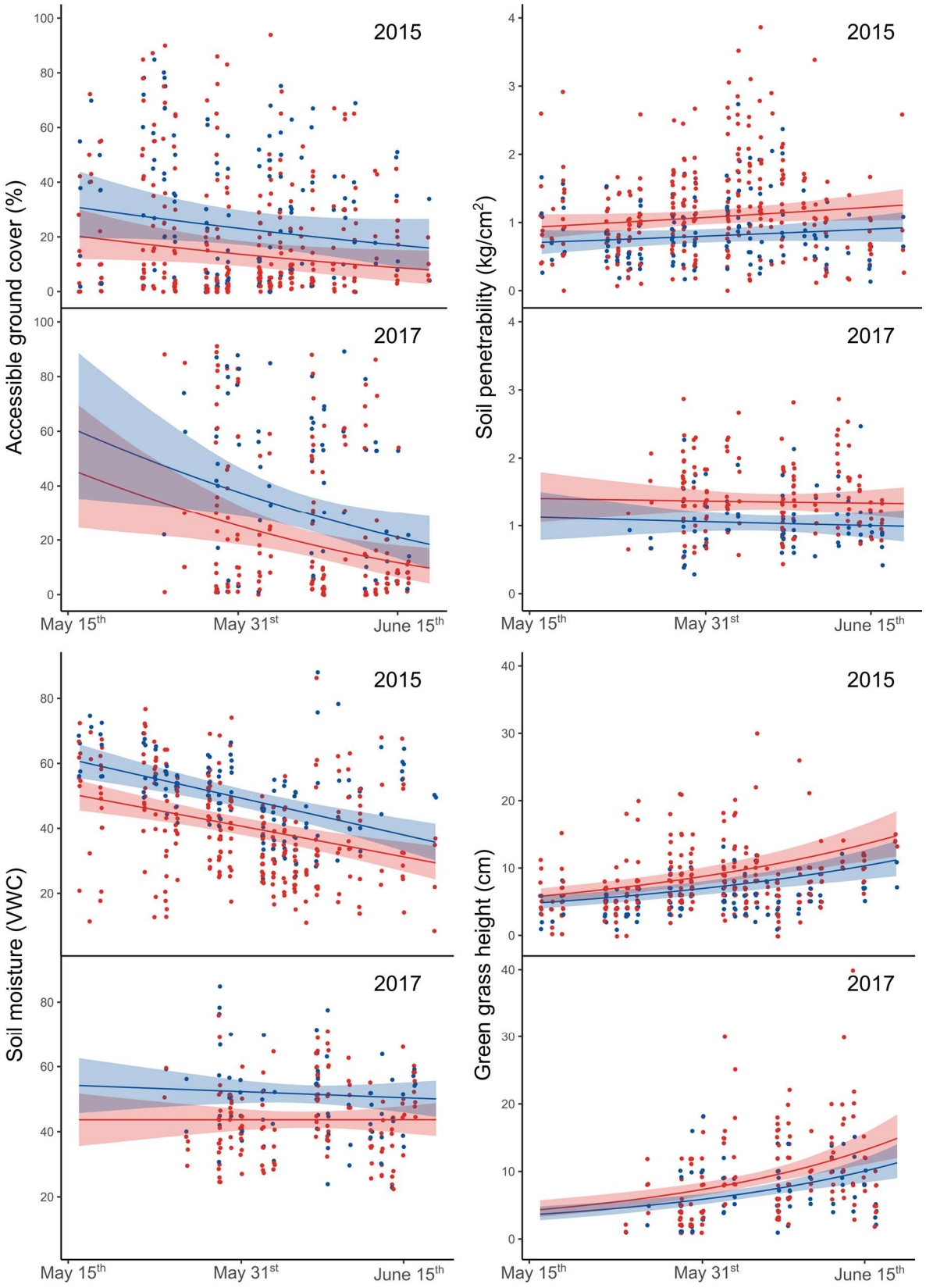

Figure 4 Relationship between each of the four key predictors and date during two different breeding seasons (2015 and 2017) at foraging (in blue) and pseudo-absence plots (in red) from the respective fitted linear-mixed models, along with 95% credible intervals.

When comparing the two different orders of habitat selection considered here (Johnson 1980), the model of habitat selection at the foraging site scale was unsurprisingly less accurate than at the home-range scale. An increasing predictive difficulty towards higher orders of selection, i.e. finer scales, is common in studies of habitat use (Fattebert *et al.* 2018) and can be explained by the fact that PA plots that are randomly selected in the close surroundings of the foraging plot are more likely to present habitat characteristics similar to those of the foraging plot itself. Indeed, we cannot rule out that our PA plots, although reflecting true absences at the very time of a given foraging observation, might have been visited by the same bird earlier or later on for foraging. Therefore, the metrics considered for evaluating model predictive performance, which assume no false negatives (i.e. false absences), are usually underrated (e.g. maximum AUC < 1). In addition, as regional evaluation data were collected in a different year (2016) to radiotracking data (2015 and 2017) due to logistic constraints, inter-annual variability in snowmelt phenology may also have influenced the predictive performance of our models. When taking these limitations into account, as well as the fine scale of our analysis (1-m radius), the overall performance of our models from the cross-validation and on the regional evaluation dataset can be deemed to be fairly good. Therefore, we consider that the significant selection patterns evidenced here are temporally consistent and can be generalized to the western central Alps, which harbour a significant fraction (ca. 20%) of the Swiss Alps, if not beyond to the entire Alpine massif.

Soil conditions and ground vegetation cover and structure were the most important predictors of foraging habitat selection in our study. Those parameters have been repeatedly highlighted as crucial for several ground-foraging bird species (Atkinson, Buckingham & Morris 2004; Gilroy *et al.* 2008; Schaub *et al.* 2010). Most of those studies have shown that these relationships are driven by prey availability, i.e. prey abundance modified by its accessibility. In the case of the Ring Ouzel, prey accessibility is probably driven by both soil penetrability, as prey is extirpated from the upper soil layers via beak probing, and opportunities for terrestrial foraging, which chiefly depends on ground vegetation structure. Even if we did not collect data on invertebrate prey abundance and distribution across our study area, food availability most likely explains the pattern we observed, especially because we restrained our foraging locations to ascertained prey captures.

The two soil condition variables measured here, moisture and penetrability, were the most important predictors of foraging occurrence at both scales considered (site and home-range), with birds selecting soft soils with intermediate moisture levels. Soil moisture is indeed

known to strongly influence the biomass and activity of some soil invertebrates, notably earthworms (Edwards & Bohlen 1996; Peach *et al.* 2004). Most species of terrestrial earthworms favour a clear optimum of soil moisture and go either deeper into the soil in response to drought or emerge on the soil surface following heavy rainfall (Edwards & Bohlen 1996). Earthworms have been identified as a main component of the diet of Ring Ouzel chicks across the species' breeding range (Glutz von Blotzheim & Bauer 1988; Burfield 2002), which seems to be corroborated in our study area (ca. 90% of the biomass provisioned by parents). The avoidance of dry and very moist soils by Ring Ouzels may hence result from reduced earthworm availability under these conditions. This is further supported by a clear avoidance of impenetrable soils that are probably suited neither for earthworms nor for beak probing (Peach *et al.* 2004; Gilroy *et al.* 2008).

The selection for intermediate levels of accessible ground, as provided here by patches of bare soil surfaces and vegetation litter, underlines the importance of small-scale substrate heterogeneity in the foraging microhabitat. Similar requirements were evidenced for a variety of ground-foraging, insectivorous farmland birds (Atkinson, Buckingham & Morris 2004; Schaub *et al.* 2010; Arlettaz *et al.* 2012), but also for some alpine specialists such as the White-winged Snowfinch *Montifringilla nivalis* (Brambilla *et al.* 2017; Resano-Mayor *et al.* 2019). The preference for a heterogeneous microhabitat mosaic has already been demonstrated for foraging Ring Ouzels in the UK (Burfield 2002; Sim *et al.* 2013). The likely mechanism at play is that dense grass swards host a greater abundance of above- and belowground invertebrates (Atkinson, Buckingham & Morris 2004), including earthworms (Edwards & Bohlen 1996), and that walking birds profit from the interspersed open-ground patches enhancing prey detectability and accessibility (Schaub *et al.* 2010). Yet, the strong selection for short grass swards evidenced in this and other studies on the Ring Ouzel (Burfield 2002; Sim *et al.* 2013) indicates that prey accessibility may be traded-off against prey abundance during foraging. Interestingly, the importance of vegetation height was only clearly detected at the larger home-range scale, suggesting that, in the hierarchical process of selection, birds first elect to forage at sites with predominantly short grass, while suitable prey extraction sites are secondarily chosen within the grassy matrix.

Three out of the four key habitat variables driving Ring Ouzel foraging dramatically changed with season: soil moisture and AG cover gradually decreased, whereas ground vegetation height increased. At treeline elevation in the Alps (ca. 1800–2300 m asl), the depth and temporal duration of the snow cover constitute the main environmental drivers (Beniston

2003). In addition to its insulation property in winter, which is appreciated by overwintering Alpine wildlife (Arlettaz *et al.* 2015), the snowpack plays another crucial ecological role in spring, when its melt provides much of the water supply in subalpine and alpine ecosystems (Beniston 2003; Klein *et al.* 2016). First, the water supply resulting from snow, mirrored in our measurements of 2015, showed a progressive seasonal decrease in both average soil moisture and penetrability, while snow was almost fully melted at the study site when the first broods hatched. In 2017, despite a similar snowmelt phenology, both soil condition variables were much more constant across the season, probably as a result of regular precipitation and/or reduced soil desiccation during the entire breeding season. Second, the snowmelt also triggers the onset of the annual vegetation cycle (Inouye *et al.* 2000), thus defining the timing of vegetation growth. Ring Ouzels essentially foraged in very short grass swards, with 90% of the selected foraging sites offering ground vegetation shorter than 10 cm. According to our seasonality model, the mean green grass height in PA plots had already exceeded this value on June 5th and 8th, in 2015 and 2017, respectively. This points to a fairly brief period with suitable foraging conditions and is supported by our own field observations: parents left the breeding grounds towards higher elevations as soon as the brood had fledged, most probably to track suitable feeding grounds. However, we could not collect foraging information after this abrupt change in their whereabouts, as tagged birds became highly mobile and some rapidly left the study area.

Altogether, it appears that highly seasonal variables drive the foraging microhabitat selection of Ring Ouzels in the Alps. As a consequence, the availability of optimal foraging habitat progressively decreases across the period of nestling provisioning, resulting in a restricted time window with suitable conditions for breeding. High elevation specialists are adapted to such extreme environments (Martin & Wiebe 2004), but global environmental change, in particular climate change, represents a new challenge for matching the reproductive period with optimal environmental conditions. Climatic changes are particularly marked in the spring in the Alps, with higher solar radiation and ambient temperatures causing an earlier snowmelt (Klein *et al.* 2016), thereby potentially affecting the breeding success of alpine birds (Martin & Wiebe 2004). In the case of the Ring Ouzel, there is a risk of phenological mismatch due to a possible discordance between the spring peak in prey availability and the timing of breeding, as already predicted for other temperate mountain birds such as the American Robin *Turdus migratorius* (Inouye *et al.* 2000), another species of thrush. However, it is as yet unknown to which extent the Ring Ouzel may adapt to such changes by either advancing its

breeding phenology or moving to higher elevations. We can expect that the migration schedule of the species, as a short-distance migrant, could be shifted so as to arrive earlier in the Alps. Moreover, an elevational shift of the breeding population has been observed in Switzerland in the last decades (Knaus *et al.* 2018). This process may nonetheless be limited by the growth of trees, in which most Alpine Ring Ouzels build their nests (Glutz von Blotzheim & Bauer 1988), and, higher up, by the formation of suitable soils, which is a very slow process at high elevations (Chamberlain *et al.* 2012).

Nevertheless, if, as suggested by our results, prey accessibility is vital, adaptive habitat management may to some extent buffer these detrimental effects if not compensate for them (see Braunisch *et al.* 2014; Brambilla *et al.* 2018). Initial measures should consist of maintaining a variegated habitat mosaic, which would be beneficial not only for the Ring Ouzel (von dem Bussche *et al.* 2008), but also for other emblematic species of the Alpine treeline (Jähnig *et al.* 2018), notably the Black Grouse *Lyrurus tetrix* (Patthey *et al.* 2012; Braunisch, Patthey & Arlettaz 2016). In effect, habitat heterogeneity guarantees the retention of suitable foraging sites, which probably explains the close association observed between the Ring Ouzel and the highly diverse and finely structured habitat matrix of the treeline ecotone in the Alps. In this respect, traditional extensive grazing practices, still widespread today in the Alps (Laiolo *et al.* 2004; Schulz, Lauber & Herzog 2018), are expected to benefit this species as well as other ground-foraging birds, notably by reducing the grass sward height and by increasing the availability of patches of bare ground through livestock trampling (Pittarello *et al.* 2016). Traditional pasturing would also limit the risk of encroachment by the woody vegetation of these valuable semi-open wooded grasslands (Laiolo *et al.* 2004; Schulz, Lauber & Herzog 2018). Another risk of habitat degradation stems from the progressive intensification of grasslands through slurry application, which results in a more homogeneous grass sward growing high and dense earlier in the season (Andrey *et al.* 2014). Finally, the development of ski infrastructure could also represent an additional threat, as the use of artificial snow and snow-grooming machines have wide-ranging negative effects on soil characteristics (Rixen, Haeberli & Stoeckli 2004) and their biodiversity (Rolando *et al.* 2007). All this points to a high vulnerability of the Ring Ouzel to the prevailing scenarios of climate and land-use change, which may act either singly or synergistically. In this context, the extent to which suitable alpine breeding habitat can be maintained via management, e.g. targeted grazing, needs further investigations which should optimally consider the potential evolution of agricultural practices and be carried out in controlled experimental setups. Additionally, whether other sympatric

species with similar ecological requirements benefit from such practices should be evaluated, as habitat management recommendations formulated here may have far-reaching positive effects for the biodiversity of treeline ecosystems.

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SUPPLEMENTARY MATERIALS

Table S1 Set of best-ranked models from the model selection process within ΔAICc < 2, at the site and home-range scale, respectively.

#	Model	df	AICc	ΔAICc	weight
	Site scale				
1	AGC + AGC^2 + SMoist + $SMoist^2$+ SPen	8	529.79	0.00	0.37
2	AGC + SMoist + $SMoist^2$+ SPen	7	530.13	0.34	0.31
3	SMoist + $SMoist^2$ + SPen + GrGH	7	531.38	1.59	0.17
4	SMoist + $SMoist^2$ + SPen	6	531.70	1.91	0.14
	Home-range scale				
1	AGC + AGC^2 + SMoist + $SMoist^2$+ SPen + GrGH + MinCov + North	11	482.67	0.00	0.35
2	AGC + AGC^2 + SMoist + $SMoist^2$ + SPen+ GrGH + North	10	483.03	0.36	0.29
3	AGC + AGC^2 + SMoist + $SMoist^2$ + SPen + GrGH	9	483.63	0.96	0.22
4	AGC + SMoist + $SMoist^2$ + SPen + GrGH + MinCov + North + GrGH x AGC	11	484.62	1.95	0.13

AGC: accessible ground cover; SMoist: soil moisture; SPen: soil penetrability; GrGH: green grass height; MinCov: mineral cover; North: northness; ^{2}: quadratic term; x: interaction