

Alpine avifauna facing rapid climate change: foraging micro-habitat selection of the White-winged Snowfinch in the Swiss Alps

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Abstract

Alpine ecosystems and their highly specialised and cold-adapted biodiversity are particularly impacted by climate change, with a warming occurring about twice faster at high than at low elevation. In upland ecosystems, snow cover is a major landscape feature, shaping vegetation growth and arthropod communities, and imposing a strong seasonality in resources availability, notably in food supply for insectivorous species. Yet, at any given elevation in mountainous ranges, the winter snowpack is declining and the spring snowmelt progressively advancing, which might cause phenological mismatches between peaks in invertebrate availability and breeding activity of alpine insectivores. As a result, birds tied to the alpine zone, especially those breeding during the snowmelt period like the White-winged Snowfinch, are predicted to undergo a severe decline in the next decades. Logistic constraints associated to research in high-alpine ecosystems have, however, limited our knowledge of the ecology of these species and hamper building meaningful mechanistic species distribution and habitat suitability models. To address this issue, we investigated the foraging microhabitat selection of breeding Snowfinches in the Swiss Alps in 2015-2017. We located 31 breeding Snowfinch populations in the Valais Alps and recorded their foraging events to compare the habitat characteristics (micro-topography, ground cover, micro-habitat diversity, vegetation height and soil moisture) at their foraging locations to conditions encountered at randomly selected so-called pseudo-absence locations. We show that Snowfinches specifically collect food at the snow field margins, where the melt water, ground cover diversity, high proportion of bare ground and low vegetation height are thought to maximize prey availability. As the snowmelt progresses and the vegetation develops, Snowfinches increasingly rely on the structure and diversity of their foraging grounds to find bare ground patches, concentrations of flowers and locally shorter vegetation. Evaluating the model performances across years showed that the models obtained in Valais can robustly predict foraging occurrences in other years within the same study area. In contrast, the geographical transferability of our final Valais model showed a good fit for the Italian Alps, which are affected by similar snow conditions, but a poor fit when applied to the Cantabrian Mountains, a separate range where snow conditions differ substantially from the Alps. Our study highlights the reliance of the Snowfinch on temporary snow front micro-habitats during the early nesting stage, but also on scarce short vegetation and diverse micro-habitat features in the later nesting stage. This indicates that vegetation management, notably via targeted grazing by cattle, might, to some extent, compensate for the negative impacts of climate warming on this highly specialised alpine bird.

KEYWORDS

White-Winged Snowfinch *Montifringilla nivalis* alpine birds global warming habitat selection snowmelt snow front phenology adaptive management conservation

Introduction

Anthropogenic climate change has been recognized as a major threat to biodiversity globally (Kappelle, Van Vuuren and Baas 1999, Parmesan and Yohe 2003, Rosenzweig et al. 2008, IPCC 2013), with worldwide documented changes in population abundances (Stephens et al. 2016) and range contractions (Parmesan 2006), widespread poleward and upward shifts (Root et al. 2003, Parmesan 2006, Chen et al. 2011), niche alterations due to changes in communities (Parmesan 2006) or phenological changes disrupting species interactions (Cahill et al. 2013, Thackeray et al. 2016). But, so far, climate warming has been unevenly distributed on the surface of the globe, with high latitudes (Meehl et al. 2007) and mountain regions (Brunetti et al. 2009) being most severely affected.

The fast warming affecting mountains will impact a large portion of the world biodiversity as they harbor about half of the hotspots (Myers et al. 2000) and a quarter of the terrestrial species (Korner & Ohsawa 2006), many of them endemic (Myers et al. 2000, Essl et al. 2009) and highly specialised (Reif and Flousek 2012, Reif et al. 2016). The steep climatic gradient of mountains following their elevation gradient, the heterogeneity of solar exposure, terrain and soil have contributed to create this biodiversity (Nagy and Grabherr 2009, Spehn and Korner 2002), which was then reinforced by their fragmented topography pushing the communities of each mountain to diverge and adapt like on isolated islands separated by unsuitable habitats. Not only species compose the diversity in mountains but also ecological traits (Lu et al. 2009), behaviors and specific physiological adaptations (Cheviron and Brumfield 2012) that have emerged in response to their extreme seasonal change in resource availability (Pearce-Higgins and Yalden 2004) and generally cold harsh weather (Lu et al. 2009, Scridel et al. 2018). But, in a context of rapid climate change, this specialisation and isolation of mountain species and populations might well lead to their downfall as the extinction risk largely depends on the capacity to adapt and disperse to other suitable habitats (Pearson 2006, Engler et al. 2009, Ozinga et al. 2009). Today, the first effects of climate change might already be visible with the proportion of endangered species increasing with elevation (Sekericioglu et al. 2008, Viterbi et al. 2013, Gonzalez et al. 2010).

With global warming, distribution ranges of mountain species are expected to shift upwards following their climatic niche (Chen et al. 2011), a process already widely described in plants with the treeline shifting to higher elevation (Harsch et al. 2009), shrub encroachment in open areas (Myers-Smith et al. 2011), the disappearance of open grassland species at the lower edge of their range (Pauli et al. 2007, Parmesan 2006) and the general thermophilization of mountain communities with the replacement of cold- by warm-adapted species (Gottfried et al. 2012). In mountains, such elevational shifts are inherently associated with a reduction of the available area due to their conical shape (Dirnbock, Essl and Rabitsch 2011, Colwell et al. 2008, Elsen and Tingley 2015), less area meaning reduced carrying capacity and declining populations (Preston 1962). However, the dispersion and establishment of species elsewhere depends on a number of complex intrinsic and extrinsic processes (Engler et al. 2011, Reif & Flousek 2012, Brambilla & Gobbi 2014) other than the climatic niche (Cannone, Sgorbati and Guglielmin 2007). For instance, the subalpine zone is expanding fast upwards, contrarily to the alpine zone as it is restrained by the hundreds of years necessary to the formation of new soil above 2000m a.s.l. (Freppaz et al. 2010), which might ultimately leave open alpine grasslands to be compressed between encroaching forests and bare summits (Chamberlain et al. 2012). Not only the progression and extent of alpine habitats is compromised but the habitat itself might be altered by changes in the abundance and distribution of plants and invertebrates - with consequent effects on higher trophic levels (Scridel et al. 2018). Climate change also directly affects the snowpack characteristics, which has other profound effects on alpine ecosystems. As the winter snow depth decreases, so does the snow cover duration. Over the last 45 years, the snowmelt has been largely impacted and has advanced by 26 days on average in the Swiss Alps (Klein et al. 2016). This might affect the

numerous species breeding in spring in alpine regions, possibly altering the fine-tuned match between the peaks of food supply and energy requirement for reproduction. Moreover, a number of other pressures act on mountain species concomitantly with climate warming (Gehrig-Fasel et al. 2007), such as an increased frequency of extreme weather events (Beniston & Rebetez 1996, Liu & Chen 2000, Pepin et al. 2015), land use changes with the intensification of the most accessible parcels and the abandonment of high-elevation pastures (Laiolo et al. 2004) and increasing human disturbance following the development of leisure and sports facilities infrastructure (Arlettaz et al. 2007, Braunisch, Patthey and Arlettaz 2011, Arlettaz et al. 2015).

Data from well-known taxa, such as birds, confirms that high-elevation species are vulnerable to climate change (Sekercioglu et al. 2008, Gonzalez et al. 2010, Lehikoinen et al. 2014). However, little is known about the underlying ecological mechanisms that may lead to habitat loss or species range contractions, as endotherms are not bound to specific climatic zones but rather constrained by the availability of resources (e.g. food, habitats, nesting sites) and interspecific interactions (Archaux 2004, Parmesan 2006, Braunisch et al. 2014). For example, there is currently no evidence – or contradictory evidence - for an upward shift of alpine birds (Archaux 2004, Popy, Bordignon and Prodon 2010, Maggini et al. 2011, Lehikoinen et al. 2014, Scridel et al. 2018, Reif and Flousek 2012), whereas many lowland birds have been documented to move poleward following the temperature increase (Pounds, Fogden and Campbell 1999, Thomas and Lennon 1999, Hitch and Leberg 2007, Harris et al. 2011). Thus, it seems that traditional projections based on temperature clines cannot be sufficient to predict changes in the distribution of alpine birds (Braunisch et al. 2014), underlining the need for a much finer understanding of their habitat requirements (Sekercioglu et al. 2008, Chamberlain et al. 2013, Scridel et al. 2018, Braunisch et al. 2014) and population dynamics (Chamberlain et al. 2012).

The habitat requirements of a species are the range of environmental conditions where it finds the vital resources such as food and habitat features to survive and reproduce. The habitat selection occurs at multiple levels, from a geographical range for a species, to a home range for an individual or group, down to the specific habitat components used within the home range (e.g. foraging or nesting sites) and to the exact resources consumed (Johnson 1980). Our knowledge of species most often follows a top-down approach, with well-defined geographical ranges for each of them, but little awareness of their exact habitat-use, perhaps because it requires more intensive research (Scridel et al. 2018). However, these habitat components used – the breeding sites, the foraging grounds, the shelters (Brambilla et al. 2018) – define how a species is associated to its habitat and are what dictates its breeding success and survival outside its intrinsic physiology and behavior. Thus, studies of the micro-habitat selection provide a mechanistic understanding of the relation of species to their habitat (Brambilla et al. 2018), which is essential to be able to relate the population dynamics to habitat changes and to act on the trends through habitat management (Scridel et al. 2018, Brambilla et al. 2018). In this regard, studies of the foraging habitat selection during the breeding season become crucial as it is a key period during which breeding individuals have their maximal yearly energy requirements to provision their offspring (Stephens and Krebs, 1986; Stephens et al., 2007). In the end, their performance directly depends on the habitat quality and has repercussions on the population dynamics. However, such micro-habitat studies on alpine birds are still scarce (Brambilla et al. 2018, Scridel et al. 2018) due to the evident technical difficulties associated with long-term intensive species monitorings in high-mountain environments (Pearce-Higgins et al. 2009; Chamberlain et al., 2012).

Among alpine birds, the White-winged Snowfinch (*Montifringilla nivalis*; hereafter Snowfinch) is an emblematic passerine that rarely, even in winter, leaves the open habitats of the summits (Cramps and Perrins 1993; Muscio et al. 2005), but that is predicted to lose most of its suitable habitats to climate change and undergo a rapid population decline (Brambilla et al. 2017). Its seven subspecies have a

scattered but wide distribution across the Palearctic mountain ranges, from the Iberian Cantabrian Mountains to the Himalayas and Altaï Mountains (Cramps & Perrins, 1993). The Western European subspecies (*Montifringilla nivalis nivalis*) is breeding in the Cantabrian Mountains, the Pyrenees, the Alps, the Apennine Mountains, Corsica and the Balkans (Cramps & Perrins, 1993). Although traditionally considered as a resident species with short-distance elevational movements in winter, a decade of capture-mark-recapture data has shown that migration can occur, with some individuals from the Alpine population moving south to wintering grounds in the eastern Pyrenees (Resano-Mayor et al., 2017). The Snowfinch inhabits open habitats above the tree-line, like alpine grasslands and barren rocky slopes (Heiniger, 1991; Grangé, 2008; Strinella et al., 2011), where the above-ground primary productivity is low (Antor 1995) and limits the abundance of herbivorous insects (Mani 1969). In response, Snowfinches have evolved to change their diet according to the resource availability: generally granivorous, which notably allows them to spend the winter at high elevation, they switch to a diet of invertebrates in spring and summer, during the chick rearing period (Heiniger 1991, Cramp and Perrins 1994). They also adapted by timing their breeding on the peak abundance of invertebrates following the snowmelt, hence from May to August. They build their nest in cliff cavities between 2000 and 3000m a.s.l in the Alps (Lang, 1946; Cramp & Perrins, 1994), but also frequently in human-made structures, such as ski-lift pylons or mountain buildings (Pedroli, 1967; Isenmann, 2006), which might be strategically closer to the foraging grounds. After two weeks of incubation, they feed their nestling for ca. 20 days with a diet based on invertebrates including Tipulidae larvae (Diptera), a prey providing a high biomass that develops at the melting snow margins (Muscio et al. 2005; Oliso & Oliso, 2006), arthropods blown and trapped on the snow (Antor, 1995; Rosvold, 2016), but also any other invertebrate that they can opportunistically find searching on the ground: Diptera, Orthoptera, Hymenoptera, Heteroptera, Lepidoptera or Coleoptera (Heiniger 1991, Cramp and Perrins 1994). Though usually gregarious and living in flocks of up to a few hundred birds during the winter time, Snowfinches split in smaller groups during the breeding season to form loose colonies or single isolated pairs, and, only after the chicks have fledged, do large groups join together again. The dramatic decline predicted to the Snowfinch in the coming years is directly due to their breeding phenology timed on the snowmelt and their need for cold foraging sites, where prey acquisition is facilitated by their availability (abundance mediated by the accessibility; Brambilla et al. 2018, Getty and Pulliam 1993). The persistence of snow patches and short vegetation throughout the breeding season largely depends on the duration of the snow cover period (Muscio et al. 2005), which is greatly susceptible to rising temperatures, but also to the change in agricultural paradigm causing the abandon of vast numbers of alpine pastures (Laiolo et al. 2004). The extent to which Snowfinches depend on ephemeral cold foraging habitats throughout their breeding season or have the plasticity to switch to others remains to be assessed.

Dedicated to study the habitat selection, foraging ecology and population dynamics of the Snowfinch, the NIVALIS project was started in 2015 at the Conservation Biology department of the University of Bern (Switzerland). With two thirds of its surface being mountains, Switzerland harbors an estimated fifth of the Snowfinch subs. *nivalis* population (BirdLife International, 2015) and, therefore, bears a large responsibility towards its conservation. One of the main aims of the project is to investigate the Snowfinch foraging habitat selection during the breeding season to better grasp the mechanisms through which climate change might affect the species. In 2015 and 2016, the micro-scale foraging habitat selection was assessed from the comparison of the ground cover, vegetation height, soil moisture, topography and invertebrate community between foraging and random pseudo-absence points taken in the close surrounding available habitat. The underlying idea is that if prey availability can be linked to key environmental variables, then these variables could be used on a larger scale in habitat suitability-distribution models to project the future distribution in time and space of suitable foraging grounds for breeding Snowfinches.

Profiting from the ongoing foraging habitat selection study, the aims of this master project are to 1) broaden the geographical coverage and increase the sample size of foraging locations to further investigate the Snowfinch foraging micro-habitat selection and create a model for the whole Valais (southwestern Switzerland), and 2) test the model spatial and temporal performances, first within the study area and second to other geographical areas. Identifying what exact habitat components Snowfinches rely on during the chick rearing period is crucial to understand how climate change may affect them and build the knowledge from which to draw targeted conservation management actions to mitigate its effects.

Methods

Study area and data collection

In 2017, in order to supplement the data collected at 5 sites during 2015-2016 (radiotracking of 14 individuals), potential Snowfinch breeding areas in Valais were visited based on the recorded observations of the species during the 5 previous breeding seasons (database: ornitho.ch) and taking into account the locations' accessibility. In total, 51 sites were explored from late May to early August, which ensued in data collection at 26 (Fig. 1). Sites were visited a single time, except if requiring a second visit because the breeding individuals had not started collecting prey or if the habitat seemed especially favourable but bad weather conditions did not allow the species' detection or data collection. Sites were considered to be different when separated by at least 2-3 hours of walking. At the remaining sites, Snowfinches were either not breeding at the time of the visit ($n=7$) or remained undetected ($n=18$), probably due to an inadequate timing of the visit (before and after the breeding), reduced detectability in adverse climatic conditions or unsuitable habitats. Sites at which data was collected were remote alpine grasslands, alpine pastures, rocky slopes as well as ski slopes ranging between 2000m and 2800m a.s.l.. At these sites, Snowfinches were either breeding in cliffs ($n\approx 19$ sites) or ski pylons ($n\approx 6$), with the exception of a pair breeding in a crevice of a concrete wall.

Data collection was done from late May to late July. From the 1st July and at all sites visited afterwards, adult Snowfinches were not seen anymore flying out to a nest after collecting food and were instead feeding the fledglings present on the feeding grounds among them. This was very different from the 2 previous years, during which data was recorded from nestling feeding events until the 16th (2015) and 26th (2016) of July. Therefore, in 2017, it was decided to continue the sampling throughout the fledgling period ($n = 47$ foraging points) as the adults kept entirely feeding the fledglings until the family groups moved up to higher elevations.

Working during the snowmelt induces an inherent strong seasonality in the habitats and potentially to the habitat selection. Indeed, all sites visited in the very early season were fully covered with snow, then snow receded to multiple melting patches before it became suddenly totally absent from the foraging grounds by the 19th June and at near all sites visited afterwards (Fig. S1). In order to investigate the seasonality of the Snowfinch foraging habitat selection, this natural division between snow-dominated habitats until the 19th June and mostly snow-free habitats from this date onwards was utilised to separate the nestling dataset into an early nestling period ($n = 43$) and late nestling period ($n = 41$). The absence of snow at numerous sites in 2017, again, contrasts with the situation of previous years. The datasets of these two years were separated at their half as there was no obvious natural division to exploit based on the snow cover, with snow present throughout most of the sampling period.

Sampling design

The sampling design was the same during the three years, only with the foraging point acquisition slightly adapted. In 2015-16, foraging points were obtained based on the radio-tracking of eight (2015) and six (2016) breeding Snowfinches from four breeding colonies per year (same three colonies both years, plus one extra colony each year). In 2017, only visual observations were conducted in order to be able to cover a larger geographical area. Breeding colonies were found and sampled on the same day, taking foraging locations from any Snowfinch spotted collecting food to provision its chicks. Snowfinches inhabit open habitats, which usually enables to easily detect them when present at their foraging sites and allows to visually follow their movements throughout their breeding areas. They are also relatively trustful when approached so good observations at the foraging grounds were possible with the use of 10x42 binoculars to register their exact foraging locations. The Snowfinch is a multi-loader species but only the first prey picking event observed per feeding round was recorded to keep independent foraging events. Once an individual had left its foraging site, the observed foraging point was marked, the GPS coordinates were recorded, and the habitat characteristics were mapped (see below). The habitat mapping was done at two different scales: 1m (2015-2017) and 5m radius (2016-2017) around the foraging point. In order to compare foraging points with surrounding available habitats, two pseudo-absence points were randomly generated (Fig. 2) and directly mapped to keep a temporal coherence. Pseudo-absence points were generated from the foraging point with a random azimuth (α : 0 – 359) setting the direction of an axis along which a first pseudo-absence point was defined at a random distance of 5-25m (sampled at 1m radius), and a second pseudo-absence point at 26-100m (sampled within 1m and 5m radius). Habitat mapping was assessed in the same way for both foraging and pseudo-absence points.

Habitat mapping

For each foraging and pseudo-absence point, we assessed the ground cover, distance to snow, topography, vegetation height, and soil moisture (Table 1). The ground cover was described with the following variables summing up to 100%: snow, water, mineral (at the 5m scale, mineral was split into scree: elements of only a few centimeters, boulders: larger elements and bedrock), bare ground, moss and/or lichens (hereafter moss), old grass, new grass, green superficial plants, flowers, shrubs, cow dung and other (e.g. urbanised elements). The ground cover diversity was stated as the number of variables making up the total ground cover of each plot (e.g. 1 if the plot was fully covered by snow, or 3 if it included snow, old and new grass). Distance to snow was only recorded if the plot was within 50m from a snow patch. The topographic variables included slope (angle °) and exposure (aspect, 0-359°), which were measured with a smartphone clinometer and compass, respectively. Vegetation height was measured for both old and new vegetation by taking either 3 (1m scale) or 5 (5m scale) replicates within the plot. The soil moisture was measured with SM150T Soil Moisture Sensor (Delta-T Devices) by applying an electric current at 5cm depth and measuring the difference of potential between the two electrodes (mV), which is proportional to the soil moisture. Soil moisture was only measured at the 1m scale.

Statistical analyses

Foraging micro-habitat selection

To assess the Snowfinch foraging habitat selection, we used hierarchical logistic regressions to compare the environmental characteristics between foraging (presence=1) and pseudo-absence (control=0) plots by fitting generalized linear mixed models (GLMMs) with a binomial error distribution and a logit link function. GLMMs were fitted using the *glmer* function from the *lme4* package of R (Bates et al. 2014). The

environmental variables (Table 1) were included as explanatory variables. Non-independence of clustered observations from the same stratum (i.e. association of the foraging with its pseudo-absence points), study site and year were accounted for as random factors (Hosmer and Lemeshow 2000, Gillies et al. 2006). Before the analyses, the explanatory variables were transformed to improve model fitting (Kay and Little 1987) although the logistic regression is not required to satisfy any assumption on their distribution. The following transformations were done: (1) exclude marginal variables (>90% of zero values) to limit the zero-inflation; (2) arcsine-square-root transformation of all ground cover variables as commonly done for proportional data; and (3) standardization of all variables (centered on their mean and scaled by their standard deviation), which also makes their effect size comparable in the model output. The logarithmic transformation of right-skewed variables (i.e. grass height, soil moisture) was tested but finally discarded because it lowered the explanatory power of the transformed variables and of the models that included them. Collinearity among explanatory variables was tested by Spearman correlations and, when the correlation coefficient was $|r_s| > 0.7$, the least explanatory variable based on univariate models was removed (Hosmer and Lemeshow 2000). The data analyses followed a two-step model selection approach. First, the explanatory variables were divided into two groups to avoid model overfitting: vegetation variables (variables describing all types of vegetation cover and sward height) and other variables (water and mineral ground cover variables, topographic variables and ground cover diversity). A quadratic term was included to the variables suspected to show an optimum at intermediate values (i.e. snow cover and soil moisture). Then, for each group of explanatory variables, multivariate models with all possible variable combinations were fitted using the *dredge* function from the R-package *MuMIn* (Bartoń 2015) in order to find the most parsimonious models. Model selection was based on the Akaike's Information Criterion adjusted for small sample size (AICc) (Burnham & Anderson; 2002) by ranking the models from lowest to highest AICc, and those with $\Delta AICc < 2$ were selected as the most supported ones (Burnham and Anderson 2002) after the exclusion of 'uninformative parameters' (Arnold 2010, Jedlikowski et al. 2016). The Akaike weights (AICcw) were estimated to assess the probability that each selected model was the best of the proposed set (Burnham & Anderson 2002). Finally, the selected models (if more than one) were averaged and the variables showing $P < 0.1$ were selected for the next modelling step. In this second step, the *dredge* function was applied again to create all model combinations with the group of selected variables. In this case, however, only the best model was selected and presented in the final results as model averaging makes interpretation delicate, notably because model averaged regression coefficients can be severely affected by even a slight multi-collinearity (not rejected at $|r_s| > 0.7$) between explanatory variables and because non-linear model averaged coefficients cannot be used to produce model averaged predictions (Cade 2015). The final selected model was used to plot the foraging occurrence probability in relation to each of the significant variables while keeping the other variables at their mean. The plots include the 95% confidence intervals around the regression line drawn from the 2.5% and 97.5% quantiles of the distribution, obtained using 1,000 simulations with the R-package *arm* (Gelman & Su 2015). All the statistical analyses were performed with the R statistical software, version 3.2.1 (R Development Core Team 2015).

The model selection process was separately done with different datasets (years and scales, see Tables S1 and S2). In 2017, for the 1m and 5m scales independently, we considered: (i) the whole nestling period, (ii) the early and (iii) late nestling periods, and (iv) the fledgling period (Fig. S1). Then, a subsequent analysis was run pooling per scale all the data gathered since the beginning of the study (1m scale: 2015-17; 5m scale: 2016-17), and again analyzing (i) the whole nestling period, (ii) the early and (iii) late nestling periods.

Spatio-temporal model evaluation

The principle of a model evaluation is to build a model on a dataset and simply test its performance on another dataset. Here, a first step was to verify how well our models performed within our study area –

Valais – considering that the snow conditions were very different from year to year, plus the study sites and (to some extent) methods changed between 2015-16 and 2017. For this, we confronted the foraging micro-habitat selection model of each year to the datasets of other years, and their ability to distinguish the foraging and pseudo-absence plots gave a measure of their performance. The other important step was to check if our models built in Valais could recognize foraging habitats in other breeding areas of the Alps and other mountain ranges. To achieve this, Snowfinch foraging locations were recorded in the Italian Alps (2016, 5m scale, n=191) and the Cantabrian Mountains (2017, 1 and 5m scale, n=30) in northwestern Spain. This time, the overall models for Valais 2015-17 (1m scale) and 2016-17 (5m scale) were used to be tested on the Italian and Cantabrian datasets. Tests were performed using the function *predict* from the R-package *ROCR* (Sing et al. 2005), which allows a model to predict the response variable (occurrence probability) from an input of explanatory variables. The predicted foraging occurrence probabilities were then compared to the observed occurrences to estimate the sensitivity (true positive proportion) versus the specificity (true negative proportion) over a continuous range of discrimination threshold probabilities (Pearce and Ferrier 2000). The sensitivity was plotted against the specificity to obtain the receiver operating characteristic curve (ROC), and the area under the curve (AUC) was used as an index of the model discrimination ability between foraging and pseudo-absence sites. The AUC may range from 0.5 to 1, from a null to a perfect discrimination ability. AUC values under 0.7 indicate a poor discrimination ability as the true and false positive rates are close, whereas AUC superiors to 0.7 are considered to reflect a good discrimination ability with the benefits of frequent true positives exceeding the cost of few false positives (Pearce and Ferrier 2000).

Within Valais, the tests provide an evaluation of the models' temporal robustness between breeding seasons with very different snow conditions: from the rather normal conditions during the 2016 breeding season following a standard winter and spring, to the early melt in 2015 due to a warm spring and extremely warm summer, to the total disappearance of snow a month early and generally extremely little snow during the 2017 breeding season due to a combination of a sunny dry warm winter and record-high temperatures in spring (MétéoSuisse 2015, 2016a,b,c, 2017a,b,c,d). The evaluations also show how robust the models are to spatial variations in the Snowfinch foraging habitats, particularly between the years 2015/16 and 2017, as none of their breeding sites overlapped and the number and repartition of these sites was imbalanced, with 5 sites sampled in 2015-16 and 26 in 2017 (Fig. 1).

Results

Foraging habitat selection

Valais 2017

Whole nestling period

At the 1m scale, the best and only selected model included the cover of snow (linear and quadratic term), bare ground, moss and soil moisture (linear and quadratic term) (Tables 2A and 3A). All the variables were significant except moss cover. Snow cover had a strong positive and quadratic relation showing a preference for foraging sites with intermediate snow cover (Fig. 3A), like the snow front. Bare ground also had an important effect: absent, the foraging probability was near null, and it strongly increased with its relative cover (Fig. 3B). Finally, the quadratic effect of soil moisture suggested an avoidance of low-intermediate soil moisture conditions and a preference for very high soil moisture (Fig. 3C).

At the 5m scale, the results were similar, with two final competitive models (Tables 2A and 3A). The best supported model had an AICcw = 0.664, and included the variables: snow cover (linear and quadratic term), bare ground cover, mineral cover, ground cover diversity, plus vegetation height, which was the only one with a non-significant effect. The effects of snow (Fig. 3D) and bare ground cover (Fig. 3E) were similar to the 1m scale. Ground cover diversity had a strong positive effect, with most foraging events occurring on plots that summed more than five habitat types within the 5m radius (Fig. 3F). The mineral cover had a clear negative impact on the foraging probability with barely any foraging events where minerals represented more than 30% of the ground cover (Fig. 4G).

Early nestling period

At the 1m scale, the only selected model included snow cover (linear and quadratic term), bare ground cover, vegetation height and soil moisture (linear), all of them with a significant effect (Tables 2B and 3B). Vegetation height had the greatest effect size and was negatively linked to the foraging occurrence probability (Fig. 4C). Snowfinches were almost never recorded foraging on plots with an average vegetation height reaching above 4cm, although the vegetation height at pseudo-absence plots was between 0-13cm. Interestingly, the soil moisture was only selected under its linear term and had a positive effect (Fig. 4D). Typically, the high values between 900 and 1200mV, which are over-represented at the foraging sites, were only measured in the soaked soils at melting snow margins or in water runoffs. The snow and bare ground cover showed a similar effect as for the whole nestling period (Fig. 4A, B).

At the 5m scale, three final competitive models were obtained (Tables 2B and 3B), with the first-ranked one well supported (AICcw = 0.582) against the second (AICcw = 0.257) and the third (AICcw = 0.207). The first model included the cover of snow (linear and quadratic effects), bare ground and water, all of them with a significant effect (Fig. 4E-G). The presence of water, even only 5% of the ground cover, strongly increased the foraging occurrence probability, approximately doubling it.

Late nestling period

In the late season at the 1m scale, there were two competitive models (Tables 2C and 3C), with the first-ranked one only slightly better supported (AICcw = 0.582) than the second one (AICcw = 0.418). Both models positively related the foraging occurrence probability to the proportion of bare ground cover (Fig. 5A), but the first model also included the green superficial plants cover as a marginal variable.

At the 5m scale, the only selected model included bare ground cover, mineral cover, vegetation height, ground cover diversity and slope, all of them with a significant effect (Tables 2C and 3C). The foraging probability in plots without bare ground plunged to a near 0 (Fig. 5B), which is lower than previously seen in the early season and whole dataset. In opposition, the selection for short vegetation seemed slightly less strict than in the early season (1m scale), with the foraging events occurring in areas where the mean vegetation height was up to 10cm (Fig. 5C). The selection for a diverse ground cover (Fig. 5D) and against highly mineral areas (Fig. 5E) remained unchanged. Snowfinches seemed to avoid the steepest slopes (Fig. 5F), although this variable had the weakest effect size in the model and was indeed significant solely in this particular model.

Fledgling period

At the 1m scale, there were two competitive models, with one much better supported (AICcw = 0.691) than the other (AICcw = 0.302) (Tables 2D and 3D). The variables retained in the first model were bare ground cover, vegetation height and ground cover diversity, all of them significant. The absence of bare ground provoked a quasi-total avoidance of the plots, like in the late nestling season (Fig. 6A). Foraging

plots with short vegetation height were strongly selected, but Snowfinches seemed to tolerate a slightly higher sward height (up to 7cm) than in the early nestling season (4cm) (Fig. 6B). Plots with ground cover diversity lower than four habitat types were avoided, but a much higher diversity did not seem to enhance a lot the occurrence probability (Fig. 6C). The second-ranked model included a positive relation with flower cover instead of ground cover diversity, but it remained non-significant.

At the 5m scale, only one model was selected, with the variables: bare ground cover, vegetation height and flower cover (Tables 2D and 3D), similarly to the 1m scale. The presence of bare ground (Fig. 6D) and very short vegetation (Fig. 6E) proved again of foremost importance for the prey collection. Flower cover also had a significant positive effect on the foraging occurrence probability (Fig. 6F), though with a smaller effect size.

Valais 2015-2017: 1m scale & 2016-2017: 5m scale

Whole nestling period

At the 1m scale, a single final model was obtained with six significant variables: the cover of snow (linear and quadratic term), bare ground, flowers, moss and vegetation height (Tables 2E and 3E). The linear term for snow had an effect size twice greater than each of the other variables, and snow cover was the sole variable that resulted in a very high occurrence probability (0.8-1) at its optimum (Fig. 7 A-E). Tough, despite the importance of the linear term of the snow cover, the avoidance of areas fully covered by snow appeared clearer than in the whole nestling period model of the year 2017 alone. The proportion of bare ground remained positively correlated to the foraging occurrence probability, but had a much weaker effect than in the 2017 model, resulting in a maximal foraging occurrence probability of about 0.4-0.7 versus 0.8-1 in 2017. With this extended 3 years dataset, the positive effect of moss and flower cover and negative effect of vegetation height could be detected despite having rather small effect sizes.

At the 5m scale, there were three competitive models (Tables 2E and 3E), with the first-ranked one only moderately better supported ($AIC_{cw} = 0.450$) than the second ($AIC_{cw} = 0.364$) and the third ($AIC_{cw} = 0.186$) ones. In the first model, the cover of snow (linear and quadratic term), bare ground, minerals, the vegetation height and ground cover diversity were significant, while moss cover was included but not significant. In that model, the ground cover diversity (Fig. 7I) and mineral cover (Fig. 7J) had the largest effect sizes, with a positive and negative effect, respectively. Despite this, foraging events remained very likely at the snow front (Fig. 7F) and most of them occurred at a vegetation height below 6cm and never above 12cm (Fig. 7H). Patches without bare ground had a lower foraging occurrence but were not fully avoided, and high bare ground amounts did not seem to be strongly selected for either (Fig. 7G).

Early nestling period

At the 1m scale, there were six competitive models, all of them with similar weights (Tables 2F and 3F). Snow cover (linear and quadratic term), vegetation height and soil moisture appeared in all models with a significant effect (Fig. 8A-C). The cover of bare ground, old vegetation, green superficial plants and slope had a considerably lower effect size and remained non-significant, thus making the different final models conflict on their inclusion. In the first-ranked model, only the green superficial plants cover was excluded. Within the clearly selected snow front, it seems that most foraging events occur on the ground just emerged from the snow, as indicates the snow cover optimum around 25% (Fig. 8A). During the early season, increasing vegetation height made the occurrence probability decrease steeper than during the nestling period as a whole (Fig. 8B). The response to soil moisture was positive, as in the early season of 2017 (Fig. 8C).

Similarly, at the 5m scale there were five final competitive models (Tables 2F and 3F) with very similar weights. Snow cover (linear and quadratic term) and ground cover diversity appeared in all models, with a large but quite variable effect size. Some models also included mineral cover and vegetation height, with a large effect size but not always a significant negative effect, and water cover, which always remained non-significant. The first-ranked model retained all the five variables, but only the snow cover (linear and quadratic term), ground cover diversity and mineral cover were significant (Fig. 8 D-F).

Late nestling period

At the 1m scale, the late season was best described by only two models, with the highly supported first one (AICcw = 0.632) including mineral cover, vegetation height, ground cover diversity and soil moisture (linear and quadratic term) as significant variables, plus flower cover remaining non-significant (Tables 2G and 3G). Vegetation height had the strongest effect size, although late in the season Snowfinches tolerated slightly higher vegetation than in the early season, with a few foraging events occurring in plots with vegetation averaging 10-18cm height (Fig. 9A). Ground cover diversity was the second major component, with a preference for plots summing more than four habitat types (Fig. 9B). Like in the 2017 whole nestling season, the quadratic effect of soil moisture suggested an avoidance of low-intermediate soil moisture conditions and a preference for very high soil moisture (Fig. 9D). Mineral cover was also strongly avoided with most foraging points below 30% cover (Fig. 9C). Interestingly, bare ground was not selected, although it was the only variable selected in the corresponding model of the year 2017 alone.

At the 5m scale, we found three competitive models with the first-ranked one (AICcw = 0.409) only slightly better supported than the second (AICcw = 0.310) and the third (AICcw = 0.280) ones (Tables 2G and 3G). All the models included mineral cover, vegetation height and ground cover diversity, which were always significant. The models differed by the inclusion or not of bare ground and old vegetation, which both had a small effect size and remained non-significant. The best model included the five variables. It showed a particularly strong selection for ground cover diversity, with all foraging points having at least five habitat types but most seven or more (Fig. 9F). Plots with average vegetation height looming above 10cm were avoided (Fig. 9E) and so were plots with more than 25% mineral cover (Fig. 9G). Again, in opposition to the year 2017, bare ground cover showed a weak effect on the foraging occurrence probability when analysing both years (2016-2017) together.

Model performance

Evaluation within Valais

In general, all models (see Table 5) performed reasonably well at predicting the foraging occurrence probabilities in the datasets of the other years (Fig. 10), with AUC values around the standard threshold for a good prediction (AUC $\approx$ 0.7). At the 1m scale, the 2016 and 2017 models performed very well on their own datasets (2016 model: AUC = 0.78; 2017 model: AUC = 0.85), but not the 2015 model (AUC = 0.67). Similarly, the 2016 and 2017 models also predicted the 2015 occurrences poorly (2016 model: AUC= 0.62; 2017 model: AUC= 0.60). However, the 2015 model remains valid as shows its good performance on the 2016 (AUC = 0.75) and 2017 (AUC = 0.74) datasets. The 2016 and 2017 models also predicted relatively well each other's datasets (2016 model: AUC= 0.70; 2017 model: AUC = 0.72). At the 5m scale, both 2016 and 2017 models predicted moderately well the occurrences on the other year, with the 2017 model being just above the threshold (AUC = 0.72) and the 2016 just below (AUC = 0.69), while they performed very well on themselves (2016 model: AUC = 0.78; 2017 model: AUC = 0.87).

Transferability

At the 5m scale, the transferability to the Italian Alps (2016: 5m scales, n=191 foraging points) of the model built on the 2 years of sampling in Valais (2016-17) was good (AUC = 0.72) (Fig. 11A). In return, the Italian Alps model predicted the Valais data slightly worse (AUC = 0.69). Both models predicted very well on their own data (Valais: AUC = 0.80; Italian Alps: AUC = 0.81). The transferability to the Cantabrian Mountains (2017: 1 and 5m scales, n=30) was very poor at the 1m scale (AUC = 0.49) and still low at the 5m scale (AUC = 0.65) (Fig. 11B). Final models used for the transferability analysis are shown in Table 5.

Discussion

Foraging habitat selection

This study compiles an extended temporal and spatial dataset to assess the Snowfinch foraging habitat selection, which was proved to be dynamic across the breeding season and mostly modulated by the strong seasonality that occurs at the alpine and sub-nival belts during the snowmelt (Table 4). Early during the breeding season when snow covered much of the alpine grasslands, Snowfinches collected food at the snow field margins and at sites with a high proportion of bare ground, lichens and moss as well as short vegetation height. Later in the season, these habitats became rarer and Snowfinches increasingly relied on the structure and diversity of their foraging grounds to find persisting bare ground patches, locally shorter vegetation or flower concentrations within the most developed grasslands. Throughout the breeding season, highly mineral areas appeared unsuitable to the collection of prey, certainly due to a lower prey abundance. Though, Snowfinches were often observed using isolated stones in high vegetation as viewpoints to spot prey and swoop on them.

Early season – a habitat selection tied to the snowmelt

Snowfinches largely rely on the melting margins of snow fields to collect prey as shows their selection for foraging sites with intermediate snow cover, but also soaked soils, water runoffs, a high ground cover diversity and bare to mossy ground surfaces as they typically emerge from the snow. This selection for the snow front is also apparent in the feeding strategy of adult Snowfinches during the snowmelt, as they would usually directly fly from the nest to a snow field margin and follow it to pick up the visible prey on the snow or on the ground just emerged from it. At the snow front, the two components of prey availability are thought to maximise. On the one hand, the prey abundance peaks with the seasonal outburst of Tipulid larvae developing in the snowmelt water, a prey that is known to play a major role in the diet of breeding Snowfinches and other alpine birds (Cramp and Perrins 1994, Laiolo et al. 2004). On the other hand, prey at the snow front are generally highly accessible as only flattened very short vegetation or bare-mossy ground usually emerge from the snow.

Snowfinches also venture on the snow and investigate the interiors of the snowfields, often checking the dark debris on the snow for potential arthropod fallout. These prey trapped on the snow might be a valuable resource in areas where they accumulate due to the winds (Antor 1995) and are definitely an easy-catch. However, only about 10% of our foraging events linked to the snow were in the interior of snowfields, which shows that their margins are much preferred, certainly because they are generally richer in invertebrates. Nearly all of these foraging events were recorded in 2017, bringing that occurrence to 20% of the foraging events linked to the snow that year, which shows that there is some variability either in the magnitude of the arthropod fallout across the sites and years, or in our detection of those foraging events.

Nonetheless, if the snow generally provides favourable habitats by limiting the vegetation growth, other factors influence the state of the vegetation as it emerges at the snow front and critically impact the resource availability. Highly vegetated margins with long dense old grass were rare in the foraging grounds – because highly unfavourable – but not around. The presence and repartition of these over-vegetated areas may result from the patterns of grazing pressure during the previous year.

Late season - the micro-scale vegetation development becomes determinant

The time between when foraging grounds are fully covered with snow and when they become totally devoid of it is only about a month, which is short in regards the Snowfinch chick rearing period of ca. 20 days (Cramp and Perrins 1994). As the snow disappears, the patterns of prey abundance and accessibility change in the landscape but the prey acquisition is still optimised towards the highest availability. Late in the season, Snowfinches seem to increasingly rely on a high ground cover diversity to find small favourable patches within the generally overgrown vegetation. The ground diversity is inherently high at the snow margins due to the presence of different vegetation re-growth stages, but it becomes rarer in the landscape as the vegetation develops and has to be actively selected for. Snowfinches were never observed collecting prey in homogeneous alpine grasslands reaching their climactic growth. Indeed, independently of their abundance of invertebrates, their accessibility is very low for a species like the Snowfinch picking prey off the ground. In 2017, a minimum of 5% bare ground surfaces in between patchy vegetation seemed to be necessary to allow foraging events to take place. Snowfinches often used bare ground to navigate around the high vegetation tussocks and find invertebrates hiding within.

In parallel, their strong selection for low vegetation height was evident late in the season. Low vegetation is crucial for easy prey accessibility and near all foraging events occurred in plots with a vegetation height below 10cm, contrasting with the 15-25 cm reached in many pseudo-absence plots. Our pseudo-absence plots, taken at 5-25m and 26-100m from the foraging point, nonetheless mostly remained within the observed foraging grounds – so within the meso-scale areas selected by Snowfinches to collect food – and thus might not show the full contrast to the real baseline vegetation height of areas avoided by Snowfinches when collection food.

In addition to the selection for bare ground and/or very short vegetation, a positive selection for a high flower cover occurred in the late season. Although this seems to indicate a selection for two mutually excluding vegetation stages: barren and blooming, we suggest that the two involve the same mechanisms. In high and dense vegetation, Snowfinches were often observed checking flower after flower for invertebrates, a behaviour which suggests that the prey availability might be higher on flowers than in between grass swards. Indeed, flowers certainly attract many invertebrates but also make them easy targets on their corolla. Nonetheless, the cover of flowers at the 1 or 5m radius plots was often below 5% (ground cover percentages were attributed down to 5% of the total cover), which could hamper the detection of this precise selection and explain its weak effect, even though it was a commonly observed foraging behaviour.

Changing selections - collinearity and confounding factors

Snowfinches show a consistent selection on most factors throughout their breeding season – quadratic for snow cover, positive for bare ground, negative for vegetation height and mineral cover – as they directly connect to profitable or poor habitats. However, we also measured some other factors for which the selection is unclear or even changing throughout the breeding season, such as exposure and soil humidity. It seems that these factors are, in reality, only confounding factors, collinear to some of the habitat types selected or only modulating their availability.

For example, if melting snow patches are the habitat favoured by Snowfinches, then a south-exposure would generally be indirectly selected for in the early season but become avoided in the late season. Other confounding factors, such as elevation, would influence the prevalence of snow patches and therefore indirectly the exposure selection, which could explain why not evident exposure pattern was detected. Similarly, as long as snow patches are present and Snowfinches collect food at their margins, our models show a selection for water cover and soaked soils – evident collinear factors to the presence of melting snow. In opposition, once the snow is gone, this relation to water completely changes as humid sites become those favourable to the vegetation development and thus avoided by Snowfinches. Indeed, weeks after the snowmelt, bare ground and low vegetation persist only through a combination of factors, like high elevation, north exposure, nutrient poor and dry soils – hence the selection for very low soil moisture. This dual soil moisture selection is shown in our results with a curvilinear selection curve (selection for the lowest and highest soil moisture values) in the models that cover periods during which snow was partially present on the foraging grounds: the whole 2017 nestling period (snow only present in the early season) and the 2015-17 late nestling period (snow present throughout the late season but locally absent in parts of the foraging grounds).

Two scales – a scale-dependent selection?

Our results of foraging habitat selection were generally consistent between the two sampling scales (see Table 4). However, the positive selection for ground cover diversity and negative selection for mineral cover showed a stronger signal at the 5m scale. Perhaps, both selection patterns operate on a slightly larger scale than those of the other habitat variables. A high ground cover diversity might be selected for at a rather larger scale so to ensure the presence of enough interesting micro-habitats, like bare ground patches, within the area that Snowfinches cover searching for prey on the ground. At a micro-scale, closer to our 1m scale, the selection would directly be on the profitability of each habitat type, therefore making the ground cover diversity signal less important. Similarly, the mineral cover typically rather varies on a meso-scale, following the local topography, which might be better captured at the 5m scale as it only compared each foraging point to its most distant pseudo-absence point, 26-100m away.

Year effect – an observer bias?

Bare ground was the habitat cover variable whose selection varied the most between the years. Bare ground was ubiquitous in the 2017 foraging habitat selection models, but only significant in the whole nestling period in 2015-17 (1m scale) and 2016-17 (5m scale). On the other hand, in the 2015 and 2016 models alone, a selection for moss cover interestingly replaced the selection for bare ground (Table 5). Rather than reflecting an important environmental change between the years and sites, this might simply be due to an observer bias as barren habitats in the field were typically situated on a spectrum between bare ground and moss, rather than clearly belonging to one of the categories. Moreover, both variables provide a high prey accessibility and are similarly selected for by Snowfinches. Combining the two variables into one, however, only had a minimal overall effect on the predictive performance of the models when tested within Valais (maximal improvement in prediction by 6%; maximal decrease by 2%) and had no effect on model transferability to the breeding areas of the Italian Alps and the Cantabrian Mountains.

Model performance

Evaluation within Valais

The annual foraging habitat selection models in Valais generally showed a good discrimination ability on the foraging occurrences from the other years considering the large spatio-temporal variability affecting

each dataset, from the onset to the completion of the snowmelt and across the sites. Furthermore, using pseudo-absences instead of real absences in our study design inherently increases the false positive rate as pseudo-absences might randomly fall on real presences – an important issue considering that most presence and pseudo-absence points were concentrated together within the same foraging grounds. Therefore, obtaining good model performances suggests that the selected habitat variables can robustly depict the foraging habitats of breeding Snowfinches and could be used as proxies. However, at the 1m scale, the model evaluation showed that none of the annual model could satisfyingly predict the 2015 occurrences, although they all performed well on the other datasets. The 2015 model was no exception and made a poor performance despite originating from this dataset, which suggests that there might be a strong variability in the foraging habitats within the year 2015 in addition to the variability between the years. The timing of the snowmelt does not seem to cause this variability as, although the snowmelt occurred early in 2015, it came even earlier in 2017, which makes the snowmelt dates in 2015 intermediate between 2016 and 2017. Thus, the poor predictions of the 2015 foraging occurrences remain largely unexplained. Finally, the inter-year (temporal) variability seemed to be more important than the spatial variability as the years 2015 and 2016, sampled in relative spatial continuity and with the same method, did not perform better on each other than on 2017, sampled at different sites without radio-tracking.

Transferability

The good transferability of the Valais model to the Italian Alps shows that our model and understanding of the foraging habitat selection of the Snowfinch does not resume to the study area but could be representative of the Alps. However, the transferability to the Cantabrian Mountains was very poor, certainly due to their exceptional lack of snow during the sampling year (2017) and enhanced by the small sample size ($n=30$ foraging points). The absence of snow would have resulted in very different foraging habitats than those in the Alps, whose vegetation is profoundly structured by the heterogeneous disappearance of the snow. This advocates to limit the use of our foraging habitat selection model built in Valais to regions that are similarly affected by the snow and be careful about extrapolations to different mountain systems where snow melting patterns can differ substantially.

Perspectives for conservation

The reliance of Snowfinches on the melting snow field margins to provide their chicks confirms that the species is directly threatened by climate warming as it affects the timing and duration of these ephemeral habitats. However, their foraging habitat selection in the late season showed that they continue to find suitable foraging sites according to the local vegetation characteristics, which gives some ground to potential management actions. Indeed, if the snow duration can hardly be acted upon without global actions, the vegetation height (Brambilla et al. 2018), structure (Peringer et al. 2013), diversity (Hoiss et al. 2013) and stratification (e.g. fight shrub encroachment; (Gehrig-Fasel, Guisan and Zimmermann 2007) are all directly manageable by adaptively controlling the grazing pressure. Unfortunately, the opposite is currently happening with large numbers of high-altitude pastures being abandoned (Laiolo et al. 2004), which shows that more efforts have to be put in to protect and promote mountain agriculture. Wild herbivory, although often ignored in management scheming, could also be used by adapting the hunting quotas and designing reserves in target areas. The effects of an increased grazing pressure on habitat suitability for breeding Snowfinches and other alpine birds remain to be assessed as there is, to date, only little and conflicting scientific evidence (Scridel et al. 2018, Brambilla et al. 2018).

Conclusion

Snowfinches have evolved specific strategies and traits to breed in alpine ecosystems, above the tree-line and up to the nival-belt, where the above-ground primary productivity is low and limits the food resources. In response to the strong seasonality in habitat types and invertebrate abundance, they time their breeding to profit from seasonal outburst of invertebrate prey occurring during the snowmelt. This study of the species' foraging micro-habitat selection during the chick rearing period shows that Snowfinches specifically collect food at the snow field margins, where the melt water, low vegetation height, high proportion of bare ground and ground cover diversity are thought to maximize prey availability. As the snowmelt progresses and the vegetation develops, Snowfinches increasingly rely on the diversity and micro-scale structure of their foraging grounds to find bare ground patches, locally shorter vegetation or flower concentrations within the most developed grasslands, where a sufficient prey availability remains. This specialization towards cold foraging sites disservices them in a fast-warming world, and Snowfinches are now threatened by the expected disappearance of suitable foraging habitats at their breeding sites. With the spring snow cover and duration set to continue declining as our emissions of greenhouse gases are far from curbed, it becomes crucial to find conservation strategies based on local management actions. By showing that scarce short vegetation provides persisting micro-scale suitable foraging habitats after the snowmelt, we suggest that the negative effects of climate change might be mitigated by increasing the grazing pressure in alpine ecosystems. This could be done by promoting the use of mountain pastures and adapting hunting quotas and reserves for wild herbivores in target areas.

This work is a first step on our way to understand and predict the effects of climate change on the Snowfinch. Yet, the link between breeding success, habitat use and food consumption remains to be assessed as the selection of a habitat *per se* does not prove its quality, especially in disturbed and low productive ecosystems. Further investigations on the Snowfinch breeding phenology and the phenology of their preferred prey also have to be conducted to understand whether and how the species will adapt to the advancing snowmelt or encounter phenological mismatches. Finally, management actions aiming to increase the grazing activity at some Snowfinch breeding grounds should be implemented in order to keep their vegetation short and evaluate, in an adaptive management scheme, the potential of such short term conservation measures for the conservation of the species.

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Tables

Table 1: Environmental variables mapped at the 1m and 5m scales.

Variables	1m (2015-17)	5m (2016-17)
Ground cover (%)		
Snow	X	X
Water	X	X
Mineral	X	
Scree		X
Boulders		X
Bedrock		X
Bare ground	X	X
Moss and/or lichens	X	X
Old (brown) grass	X	X
New (green) grass	X	X
Green superficial plants	X	X
Flowers	X	X
Shrubs	X	X
Cow dung	X	X
Other	X	X
Distance to snow/topography		
Distance to the snow (only if $\leq 50\text{m}$)	X	X
Slope	X	X
Exposure (0 -359°)	X	X
northing: cosine of aspect		
easting: sine of aspect		
Vegetation height (mean value of 3 (1m) or 5 (5m) measures)		
Old vegetation height (cm)	X	X
New vegetation height (cm)	X	X
Soil properties (mean value of 3 measures (1m))		
Soil moisture (mV)	X	

Table 2 (part 1): Final foraging habitat selection models resulting from the **1m** and **5m** scales selection: remaining models within 2 units of $\Delta AICc$ of the first-ranked model and excluding the uninformative parameters. The models included the explanatory variables: SNOW1: snow cover; SNOW2: quadratic term of snow cover; BARE: bare ground cover; HEIGHT: vegetation height; GRDIV: ground cover diversity; MINER: mineral cover; MOSS: moss and/or lichens cover; OLDVEG: old vegetation cover; GSPLANTS: green superficial plants cover; FLOWER: flower cover; MOIST1: soil moisture; MOIST2: quadratic term of soil moisture; WATER: water cover; SLOPE: slope; NORTH: north exposure.

1m

Rank	Model	Deviance	K	$\Delta AICc$	AICcw
2017					
A. Whole nestling period					
1	SNOW1 + SNOW2 + BARE + MOIST1 + MOIST2	206.3	8	0.00	1
B. Early nestling period					
1	SNOW1 + SNOW2 + BARE + HEIGHT + MOIST1	99.0	8	0.00	1
C. Late nestling period					
1	BARE + GSPLANTS	121.3	5	0.00	0.582
2	BARE	122.0	4	0.66	0.418
D. Fledgling period					
1	BARE + HEIGHT + GRDIV	134.5	6	0.00	0.691
2	BARE + HEIGHT + FLOWER	136.1	6	1.61	0.302
2015-17					
E. Whole nestling period					
	SNOW1 + SNOW2 + BARE + HEIGHT + MOSS + FLOWER	897.6	10	0.00	1
F. Early nestling period					
1	SNOW1 + SNOW2 + BARE + HEIGHT + MOIST1 + OLDVEG + SLOPE	449.1	11	0.00	0.218
2	SNOW1 + SNOW2 + BARE + HEIGHT + MOIST1 + SLOPE	449.5	10	0.37	0.182
3	SNOW1 + SNOW2 + BARE + HEIGHT + MOIST1 + OLDVEG	449.7	10	0.55	0.166
4	SNOW1 + SNOW2 + HEIGHT + MOIST1 + OLDVEG + GSPLANTS + SLOPE	449.8	11	0.68	0.156
5	SNOW1 + SNOW2 + HEIGHT + MOIST1 + OLDVEG + SLOPE	449.9	10	0.84	0.143
6	SNOW1 + SNOW2 + HEIGHT + MOIST1 + OLDVEG	450.1	9	0.96	0.135
G. Late nestling period					
1	HEIGHT + GRDIV + MOIST1 + MOIST2 + MINER + FLOWER	472.5	10	0.00	0.632
2	HEIGHT + GRDIV + MOIST1 + MOIST2 + MINER	473.6	9	1.08	0.368

Table 2 (part 2).

5m

Rank	Model	Deviance	K	$\Delta AICc$	AICcw
2017					
A. Whole nestling period					
1	SNOW1 + SNOW2 + BARE + HEIGHT + GRDIV + MINER	171.7	9	0.00	0.664
	SNOW1 + SNOW2 + BARE + GRDIV + MINER	173.1	8	1.36	0.336
B. Early nestling period					
1	SNOW1 + SNOW2 + BARE + WATER	82.2	7	0.00	0.536
2	SNOW1 + SNOW2 + WATER + NORTH	83.6	7	1.47	0.257
3	SNOW1 + SNOW2 + GRDIV + WATER + MINER	84.1	8	1.91	0.207
C. Late nestling period					
1	BARE + HEIGHT + GRDIV + MINER + SLOPE	87.4	8	0.00	1
D. Fledgling period					
1	BARE + HEIGHT + FLOWER	112.9	6	0.00	1
2016-17					
E. Whole nestling period					
1	SNOW1 + SNOW2 + BARE + HEIGHT + GRDIV + MINER + MOSS	356.3	11	0.00	0.450
2	SNOW1 + SNOW2 + BARE + HEIGHT + GRDIV + MINER	356.7	10	0.42	0.364
3	SNOW1 + SNOW2 + HEIGHT + GRDIV + MINER	358.1	9	1.77	0.186
F. Early nestling period					
1	SNOW1 + SNOW2 + HEIGHT + GRDIV + WATER + MINER	176.7	10	0.00	0.243
2	SNOW1 + SNOW2 + HEIGHT + GRDIV + MINER	176.7	9	0.00	0.243
3	SNOW1 + SNOW2 + GRDIV + WATER + MINER	176.7	9	0.01	0.241
4	SNOW1 + SNOW2 + GRDIV + MINER	177.7	8	0.98	0.149
5	SNOW1 + SNOW2 + GRDIV + WATER	178.1	8	1.34	0.124
G. Late nestling period					
1	BARE + HEIGHT + GRDIV + MINER + OLDVEG	182.6	9	0.00	0.409
2	BARE + HEIGHT + GRDIV + MINER	183.2	8	0.55	0.310
3	HEIGHT + GRDIV + MINER	183.4	7	0.76	0.280

Table 3 (part 1): Estimates of the regression, standard errors and P-values of the final first-ranked models for the 2017 whole, early and late nestling period and fledgling period, and for the 2015-17 or 2016-17 whole, early and late nestling period at the **1m** and **5m** scales.

1m

Model	Estimate	Standard error	P-value
2017			
A. Whole nestling period			
Snow	1.1715	0.2664	<0.001
Snow square	-0.6344	0.2054	0.002
Bare ground	0.9792	0.2111	<0.001
Moisture	0.3880	0.2238	0.071
Moisture square	0.5388	0.2336	0.021
B. Early nestling period			
Snow	0.7987	0.2885	0.006
Snow square	-0.4970	0.2190	0.023
Bare ground	0.7726	0.2985	0.010
Height	-1.4924	0.7605	0.050
Moisture	0.8802	0.3705	0.018
C. Late nestling period			
Bare ground	1.3441	0.3242	<0.001
Green superficial plants	-0.4256	0.2573	0.098
D. Fledgling period			
Bare ground	1.0882	0.2994	<0.001
Height	-1.0298	0.4077	0.012
Ground cover diversity	0.6952	0.3235	0.032
2015-17			
E. Whole nestling period			
Snow	0.77972	0.10122	<0.001
Snow square	-0.39442	0.08690	<0.001
Bare ground	0.35962	0.09333	<0.001
Flowers	0.34128	0.09431	<0.001
Moss	0.36826	0.09219	<0.001
Height	-0.31537	- 0.12521	0.012
F. Early nestling period			
Snow	0.4880	0.1131	<0.001
Snow square	-0.3319	0.0875	<0.001
Bare ground	0.1961	0.1227	0.078
Old vegetation	-0.2124	0.1315	0.106
Height	-0.6585	0.2114	0.002
Slope	0.208 2	0.1257	0.098
Moisture	0.45789	0.1644	0.003
G. Late nestling period			
Mineral	-0.3875	0.1296	0.003
Flowers	0.2179	0.1206	0.071
Height	-0.6952	0.1584	<0.001
Ground cover diversity	0.4444	0.1389	0.001
Moisture	0.3380	0.1521	0.026
Moisture square	0.3366	0.1485	0.023

Table 3 (part 2).

5m

Model	Estimate	Standard error	P-value
2017			
A. Whole nestling period			
Snow	0.8220	0.2960	0.005
Snow square	-0.5484	0.2582	0.034
Bare ground	0.7581	0.2494	0.002
Mineral	- 0.8859	0.3330	0.008
Height	-0.5025	0.2879	0.083
Ground cover diversity	1.0707	0.3433	0.002
B. Early nestling period			
Snow	1.0804	0.3287	0.001
Snow square	-1.0533	0.2722	<0.001
Bare ground	0.7727	0.3556	0.030
Water	1.3474	0.4953	0.007
C. Late nestling period			
Bare ground	1.2444	0.4534	0.006
Mineral	-1.3818	0.5195	0.008
Height	-1.0115	0.4144	0.015
Ground cover diversity	1.1589	0.5195	0.018
Slope	-0.7360	0.3516	0.036
D. Fledgling period			
Bare ground	1.07823	0.30105	<0.001
Flowers	0.53948	0.26064	0.038
Height	-0.87327	0.36554	0.017
2016-17			
E. Whole nestling period			
Snow	0.50170	0.21140	0.018
Snow square	-0.55789	0.18665	0.003
Bare ground	0.31230	0.15649	0.046
Mineral	-0.71229	0.21733	0.001
Moss	0.23947	0.15076	0.112
Height	-0.40103	0.20485	0.050
Ground cover diversity	0.80493	0.23625	<0.001
F. Early nestling period			
Snow	0.5235	0.2679	0.051
Snow square	-0.7632	0.2180	<0.001
Mineral	-0.6807	0.3204	0.034
Water	0.3745	0.2583	0.144
Height	-0.6608	0.4603	0.151
Ground cover diversity	0.8447	0.3474	0.015
G. Late nestling period			
Bare ground	0.4167	0.2420	0.085
Mineral	-0.7514	0.3134	0.016
Old vegetation	0.4626	0.2826	0.102
Height	-0.9810	0. 2908	<0.001
Ground cover diversity	1.0351	0.3195	0.001

Table 4: Summary of our results of the Snowfinch foraging habitat selection. The significant variables and their effect are shown for each **1m** and **5m** scale model. The variables were: SNOW1: snow cover; SNOW2: quadratic term of snow cover; BARE: bare ground cover; HEIGHT: vegetation height; GRDIV: ground cover diversity; MOSS: moss and/or lichens cover; MINER: mineral cover; FLOWER: flower cover; MOIST1: soil moisture; MOIST2: quadratic term of soil moisture; WATER: water cover; SLOPE: slope.

1m

		SNOW1	SNOW2	BARE	HEIGHT	GRDIV	MOSS	MINER	FLOWER	MOIST	MOIST2
2017	Whole nestling	+	∩	+							∩
	Early nestling	+	∩	+	-					+	
	Late nestling			+							
	Fledgling			+	-	+					
2015-17	Whole nestling	+	∩	+	-		+		+		
	Early nestling	+	∩		-					+	
	Late nestling				-	+		-		+	∩

5m

		SNOW1	SNOW2	BARE	HEIGHT	GRDIV	MINER	FLOWER	WATER	SLOPE
2017	Whole nestling	+	∩	+		+	-			
	Early nestling	+	∩	+				+		
	Late nestling			+	-	+	-			-
	Fledgling			+	-			+		
2016-17	Whole nestling	+	∩	+	-	+	-			
	Early nestling		∩			+	-			
	Late nestling				-	+	-			

Table 5: Summary of the variables included in the final models tested in the model evaluation: at the **1m** scale the 2015, 2016, 2017 and 2015-17 models, and at the **5m** scale the 2016, 2017 and 2016-17 in Valais, and 2016 in Italy. The variables were: SNOW1: snow cover; SNOW2: quadratic term of snow cover; BARE: bare ground cover; HEIGHT: vegetation height; GRDIV: ground cover diversity; MOSS: moss and/or lichens cover; MINER: mineral cover; FLOWER: flower cover; OLDVEG: old vegetation cover; NEWVEG: new vegetation cover; MOIST1: soil moisture; MOIST2: quadratic term of soil moisture; SLOPE: slope. Non significant variables are visible in *italic*. The variables SNOW1 and SNOW2 had to be excluded of the 2015-17 and 2016-17 models when tested on the Cantabrian Mountain dataset as it was devoid of snow. Similarly, the variable MOSS had to be excluded when testing the 2016-17 model on the Italian Alps dataset in which it was not recorded.

1m

Model	Variables
2015	SNOW1 + SNOW2 + <i>HEIGHT</i> + MOSS + FLOWER
2016	SNOW1 + SNOW2 + MOSS + <i>SLOPE</i>
2017	SNOW1 + SNOW2 + BARE + <i>MOIST1</i> + MOIST2
2015-17	SNOW1 + SNOW2 + BARE + HEIGHT + MOSS + FLOWER

5m

Model	Variables
2016	<i>SNOW1</i> + SNOW2 + MOSS + SLOPE
2017	SNOW1 + SNOW2 + <i>HEIGHT</i> + BARE + GRDIV + MINER
2016-17	SNOW1 + SNOW2 + HEIGHT + BARE + GRDIV + <i>MOSS</i> + MINER
Italy 2016	SNOW1 + SNOW2 + BARE + HEIGHT + OLDVEG + NEWVEG + FLOWER

Figures

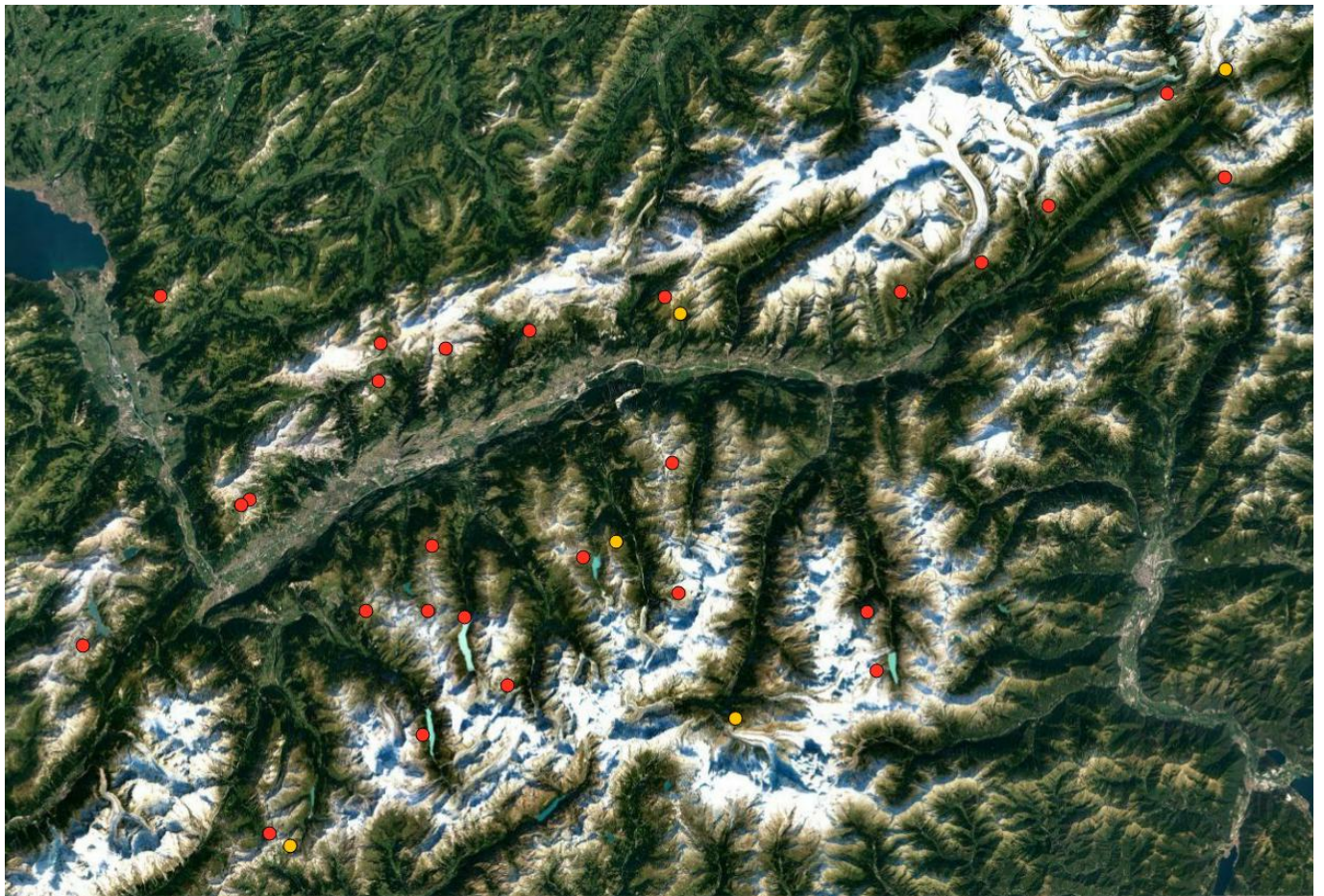


Figure 1: Location of the study sites of 2015-16 (yellow) and 2017 (red) in canton Valais, southwestern Switzerland.

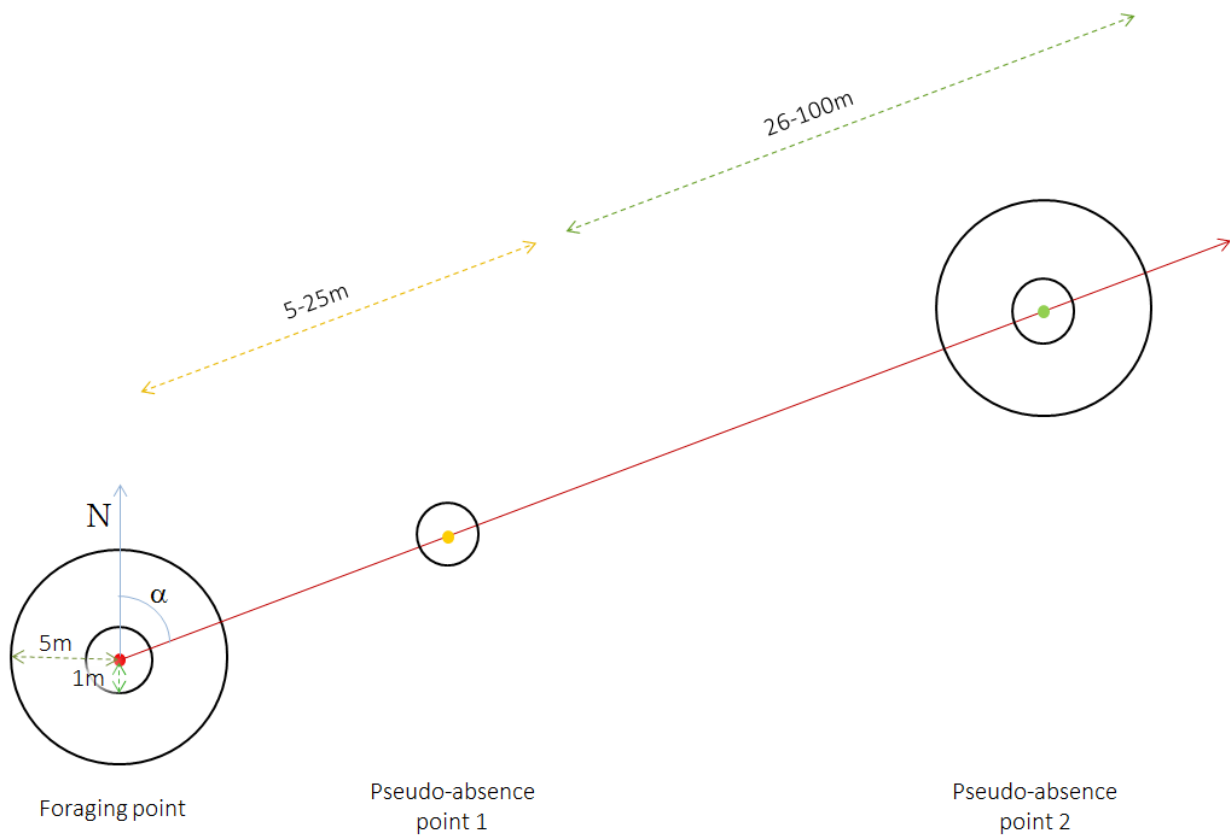
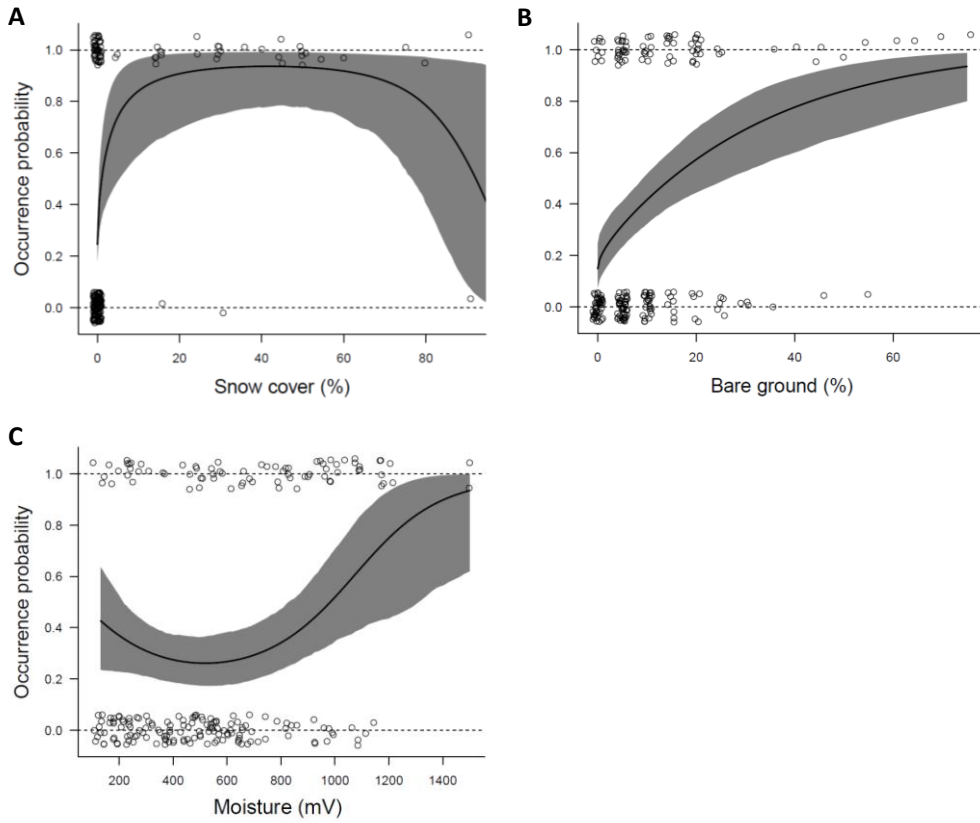


Figure 2: Sampling design based on the foraging point (red) and two random pseudo-absence points (short-distance: 5-25m, yellow; long-distance: 26-100m, green). At each foraging point, habitat mapping is done at both 1m and 5m radius. The pseudo-absence points are generated from the foraging point by taking a random angle (α) from the North (0° azimuth), which sets the direction of the sampling transect (red arrow), and selecting a random distance from the foraging point between 5-25m (pseudo-absence point 1, mapped at 1m radius) and 26-100m (pseudo-absence point 2, mapped at both 1m and 5m radius).

1m



5m

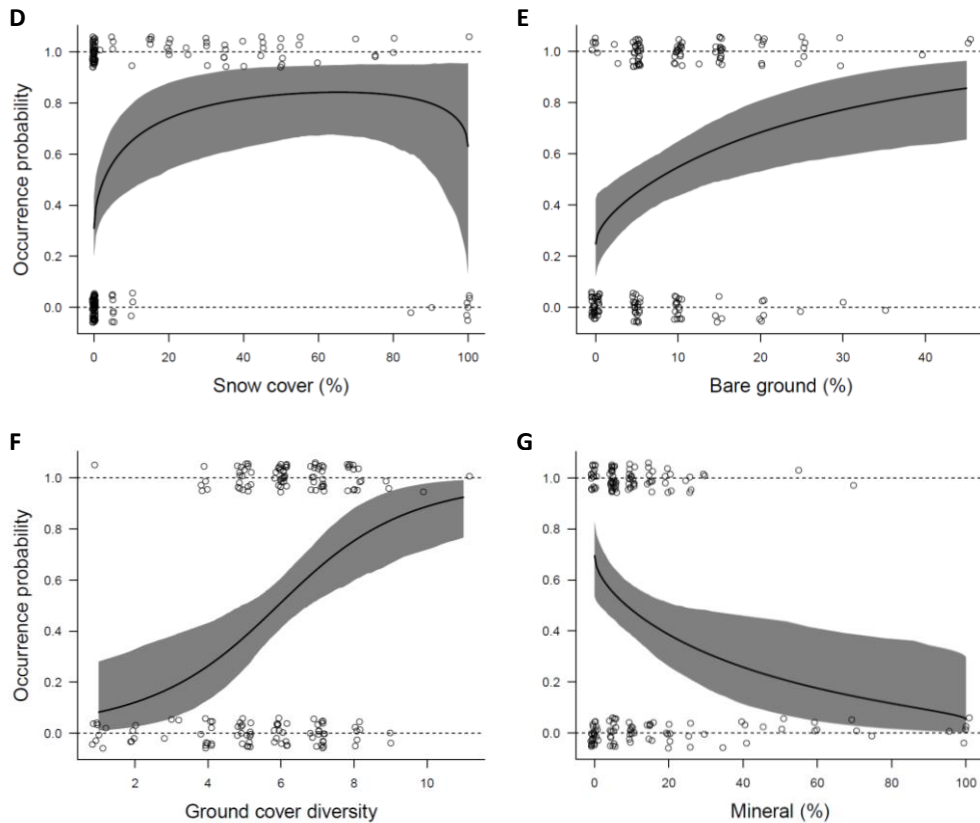
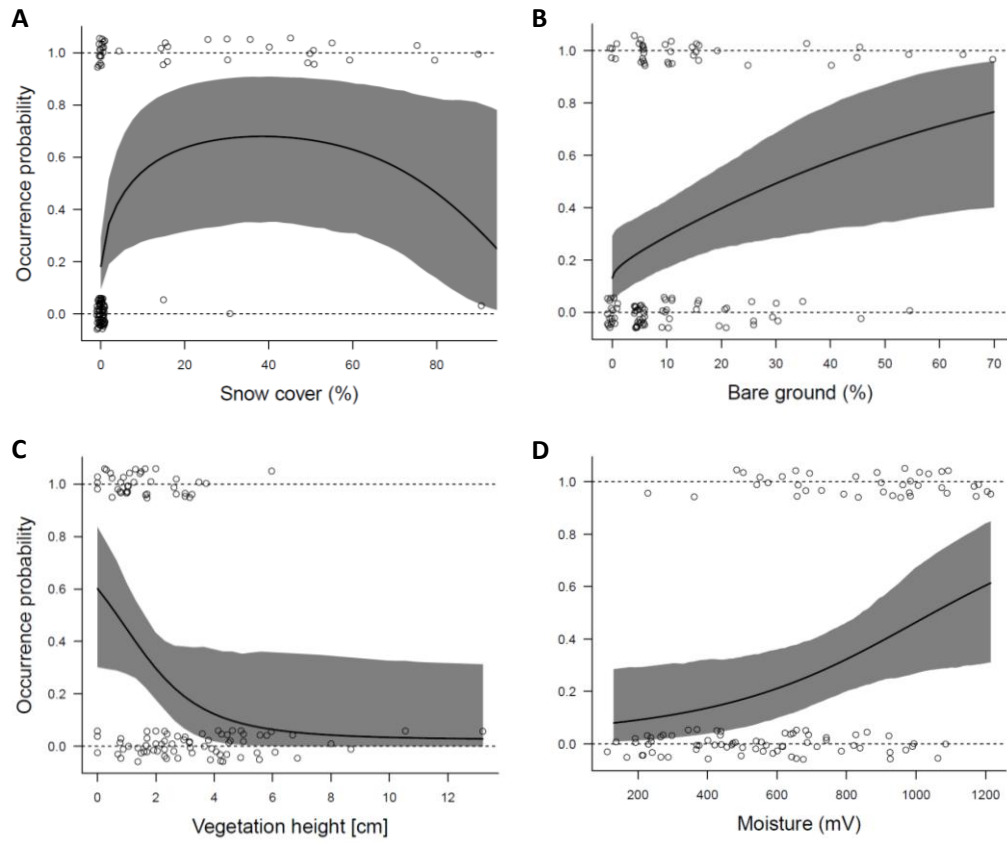


Figure 3: Plots of the marginal foraging occurrence probability in relation to A) snow cover (%), B) bare ground cover (%) and C) soil moisture (mV) in the **1m scale** and D) snow cover (%), E) bare ground cover (%), F) ground cover diversity and G) mineral cover (%) in the **5m scale 2017 whole nestling period model**. The regression is made on each variable separately while keeping the others at their mean. The 95% confidence intervals are obtained from 1,000 simulations.

1m



5m

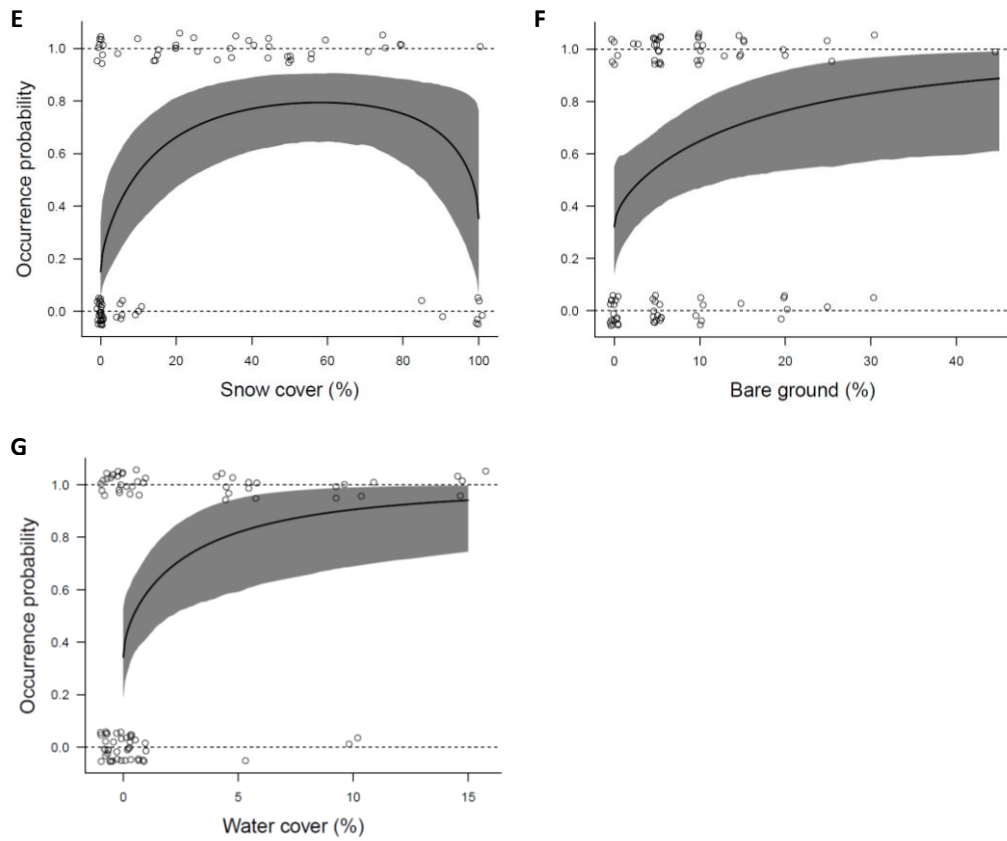
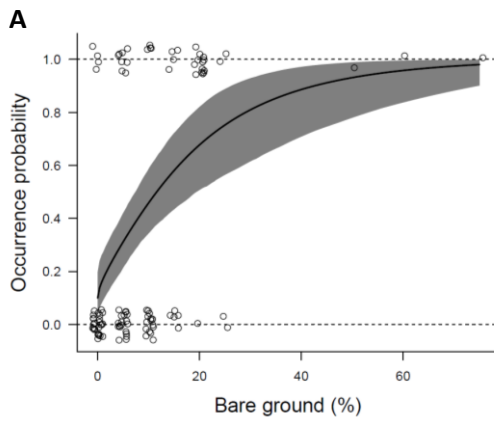


Figure 4: Plots of the marginal foraging occurrence probability in relation to A) snow cover (%), B) bare ground cover (%), C) vegetation height (cm) and D) soil moisture (mV) in the **1m scale** and E) snow cover (%), F) bare ground cover (%) and G) water cover (%) in the **5m scale 2017 early nestling period model**.

1m



5m

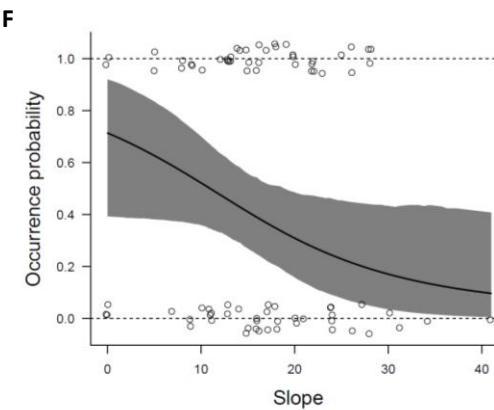
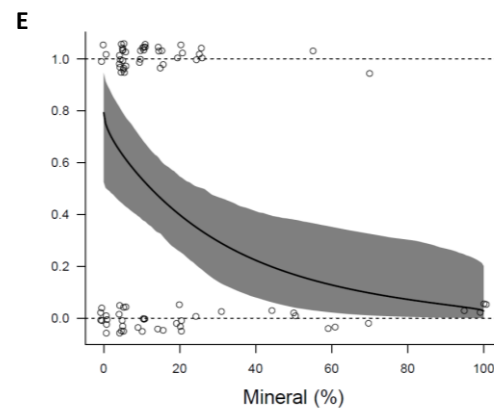
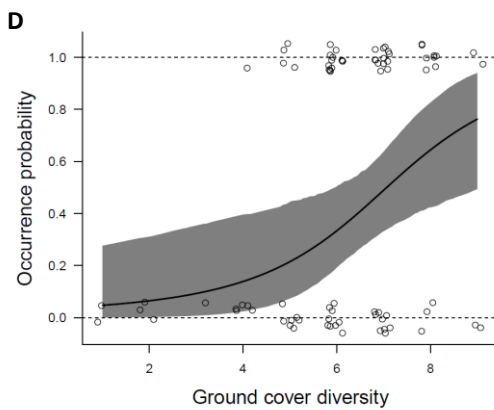
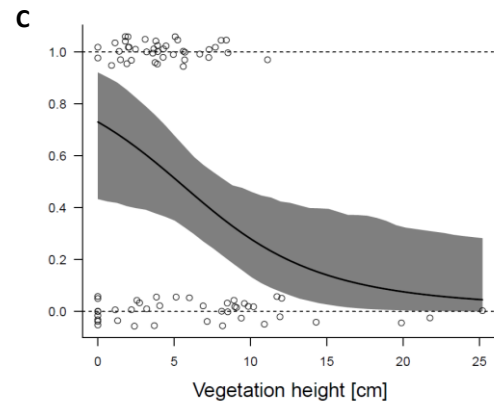
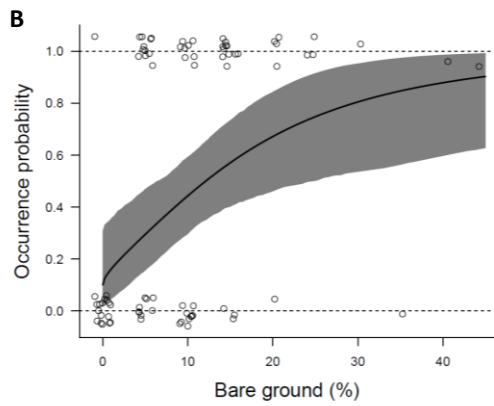
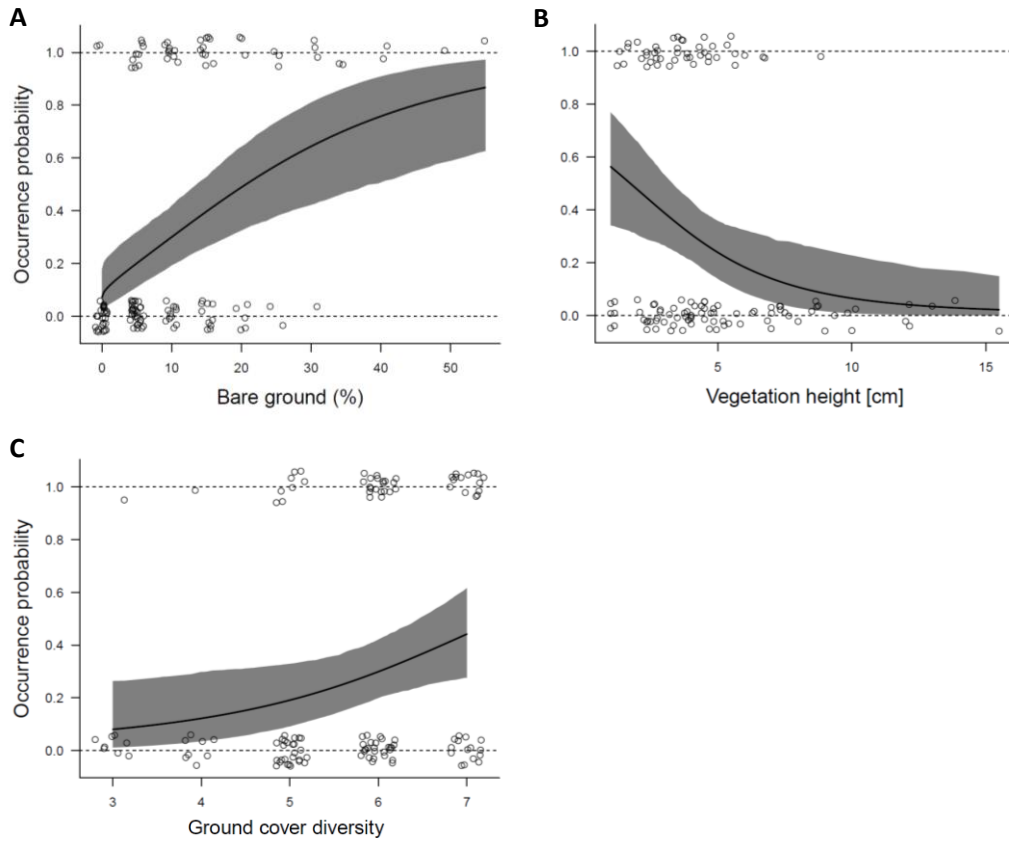


Figure 5: Plots of the marginal foraging occurrence probability in relation to A) bare ground cover (%) in the **1m scale** and B) bare ground cover (%), C) vegetation height (cm), D) ground cover diversity, E) mineral cover (%) and F) slope in the **5m scale 2017 late nestling period model**.

1m



5m

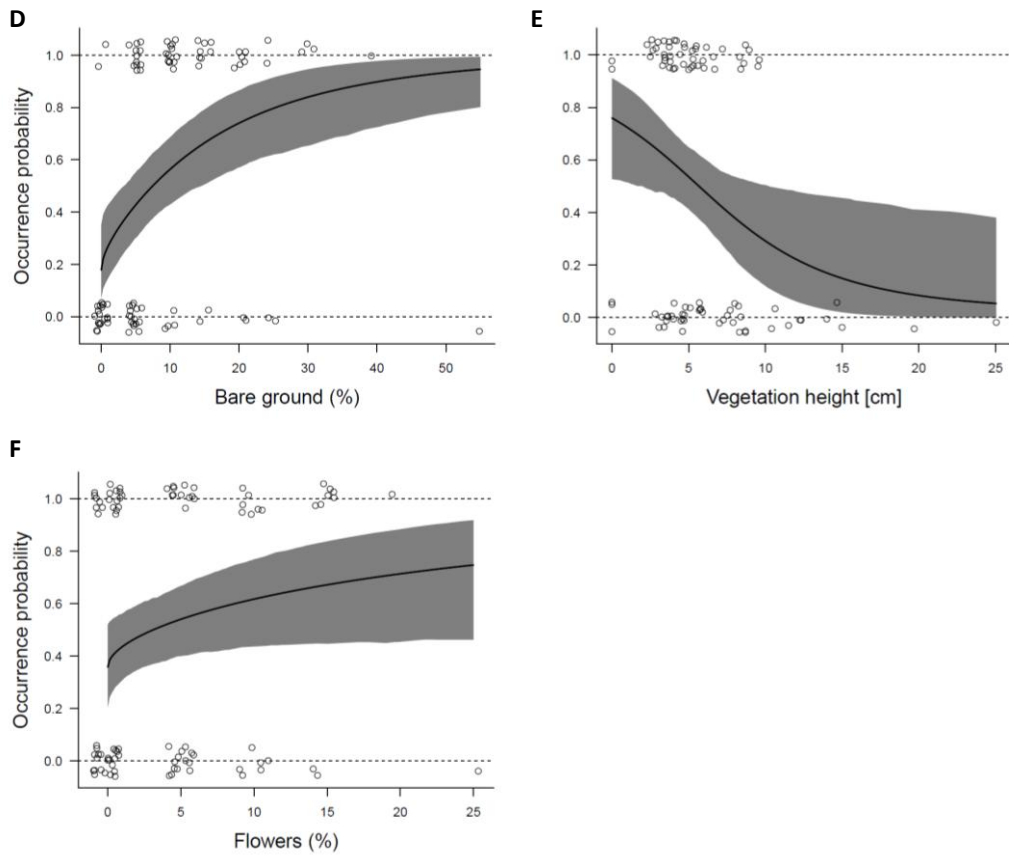


Figure 6: Plots of the marginal foraging occurrence probability in relation to A) bare ground cover (%), B) vegetation height (cm) and C) ground cover diversity in the **1m scale** and D) bare ground cover (%), E) vegetation height (cm) and F) flower cover (%) in the **5m scale 2017 fledgling period model**.

1m

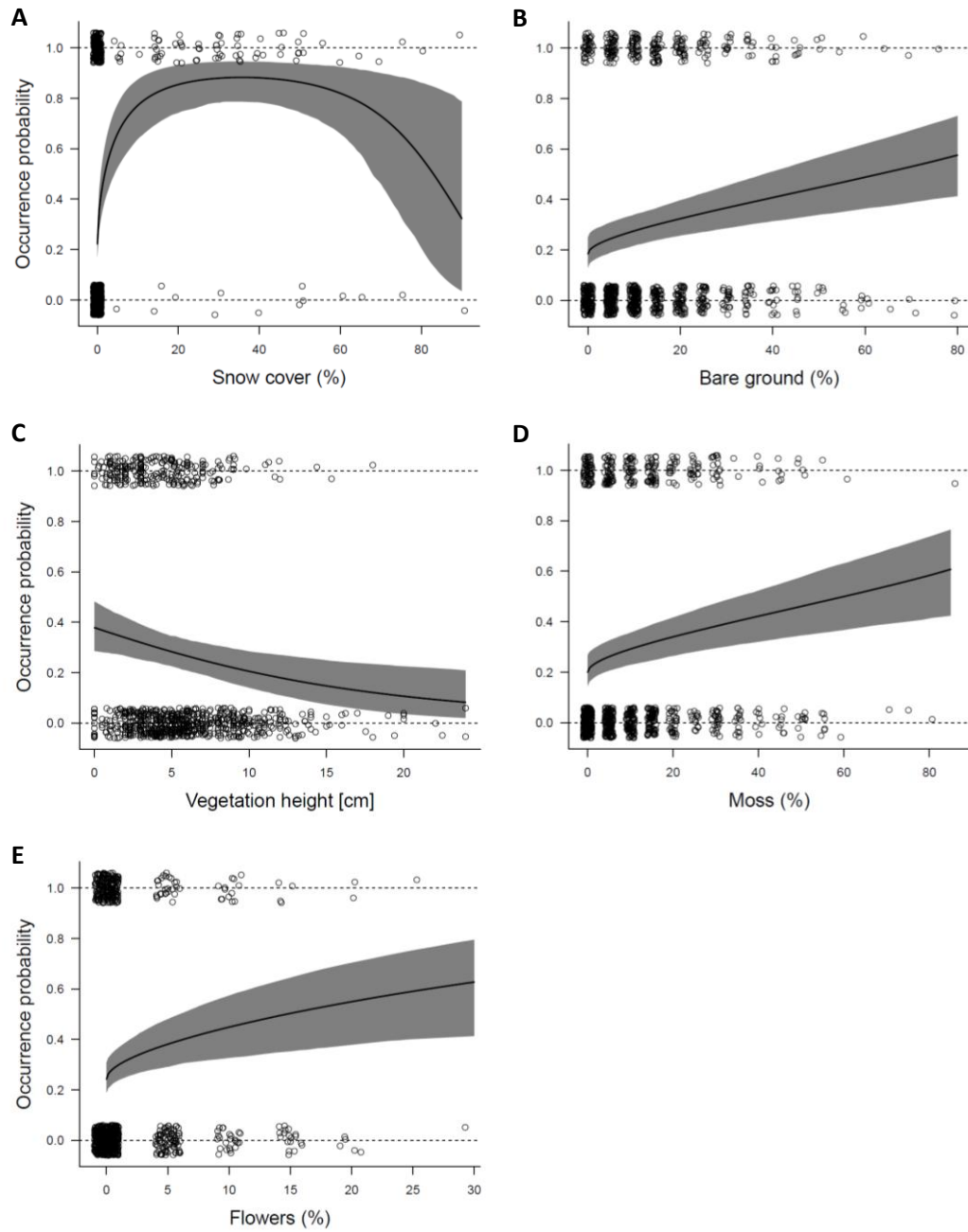


Figure 7 (part 1): Plots of the marginal foraging occurrence probability in relation to A) snow cover (%), B) bare ground cover (%), C) vegetation height (cm), D) moss cover (%) and E) flower cover (%) in the **1m scale 2015-17 whole nestling period model**.

5m

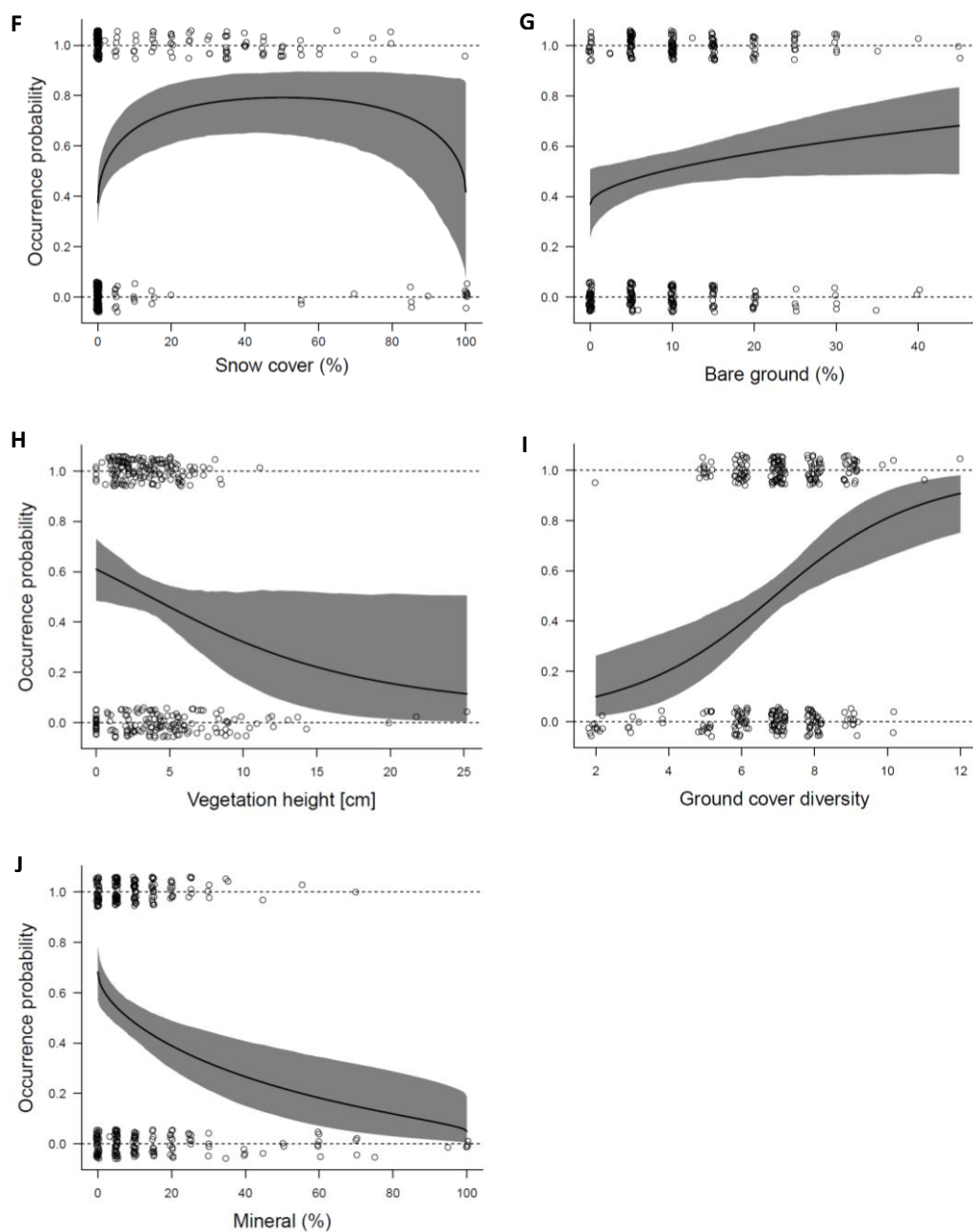
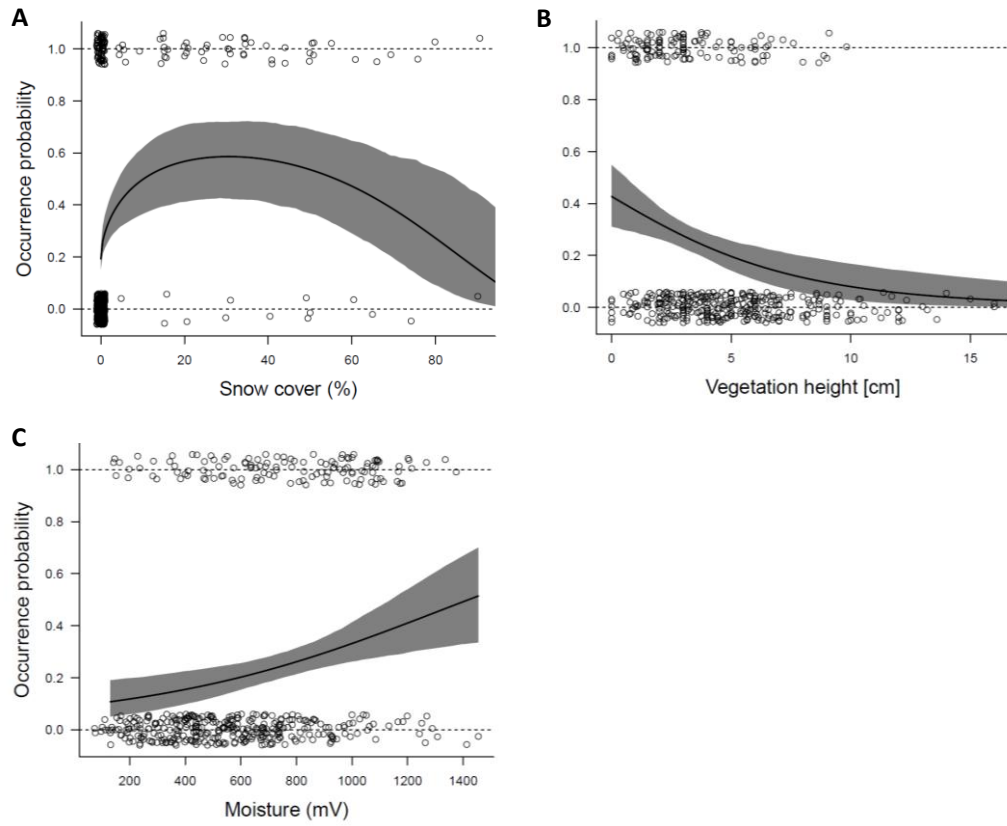


Figure 7 (part 2): Plots of the marginal foraging occurrence probability in relation to F) snow cover (%), G) bare ground cover (%), H) vegetation height (cm), I) ground cover diversity and J) mineral cover (%) in the **5m scale 2016-17 whole nestling period model**.

1m



5m

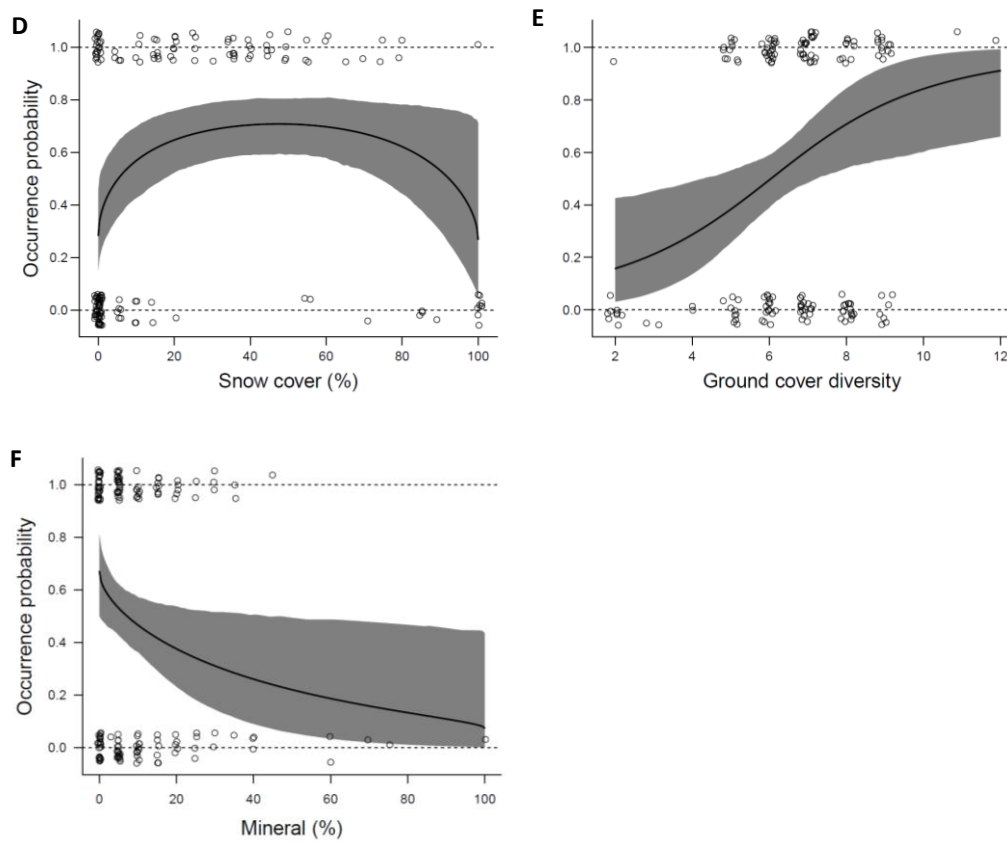
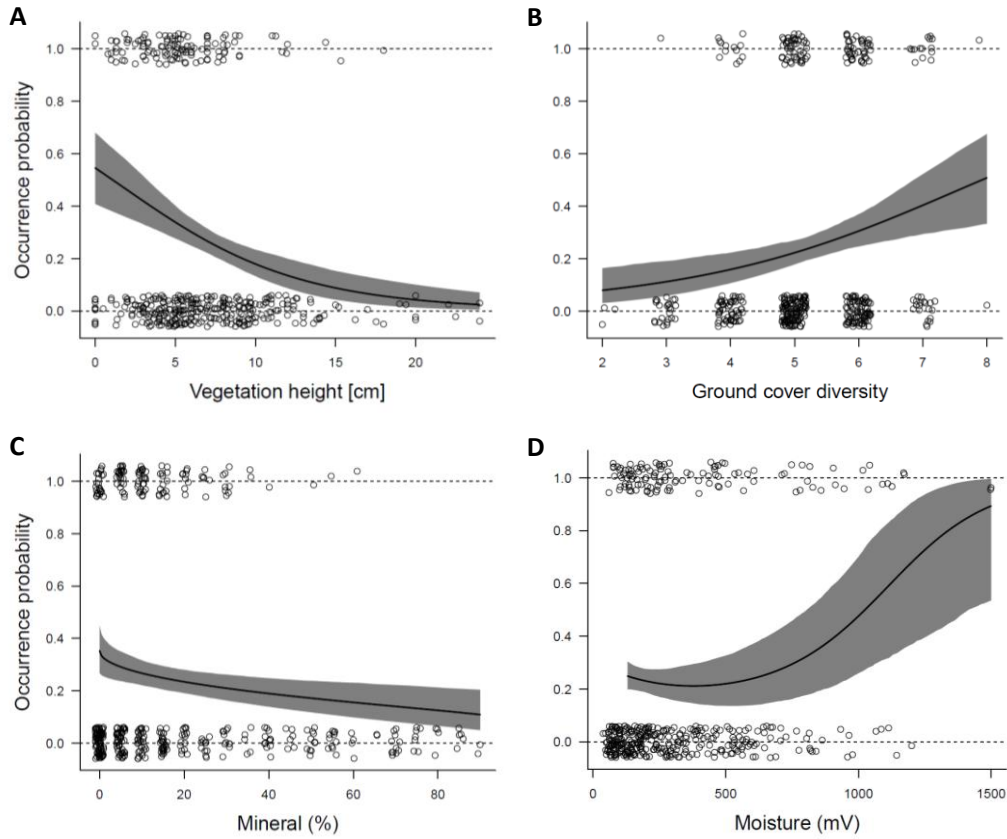


Figure 8: Plots of the marginal foraging occurrence probability in relation to A) snow cover (%), B) vegetation height (cm) and C) soil moisture (mV) in the **1m scale 2015-17 early nestling period model** and E) snow cover (%), F) ground cover diversity and G) mineral cover (%) in the **5m scale 2016-17 early nestling period model**.

1m



5m

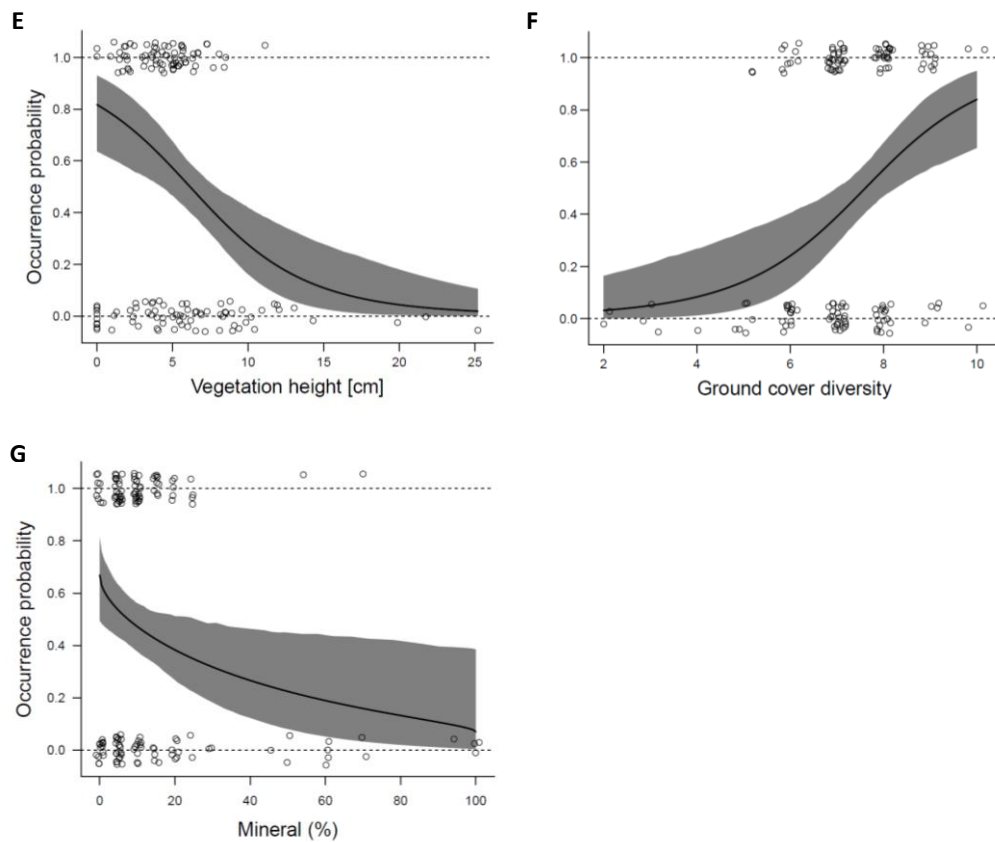
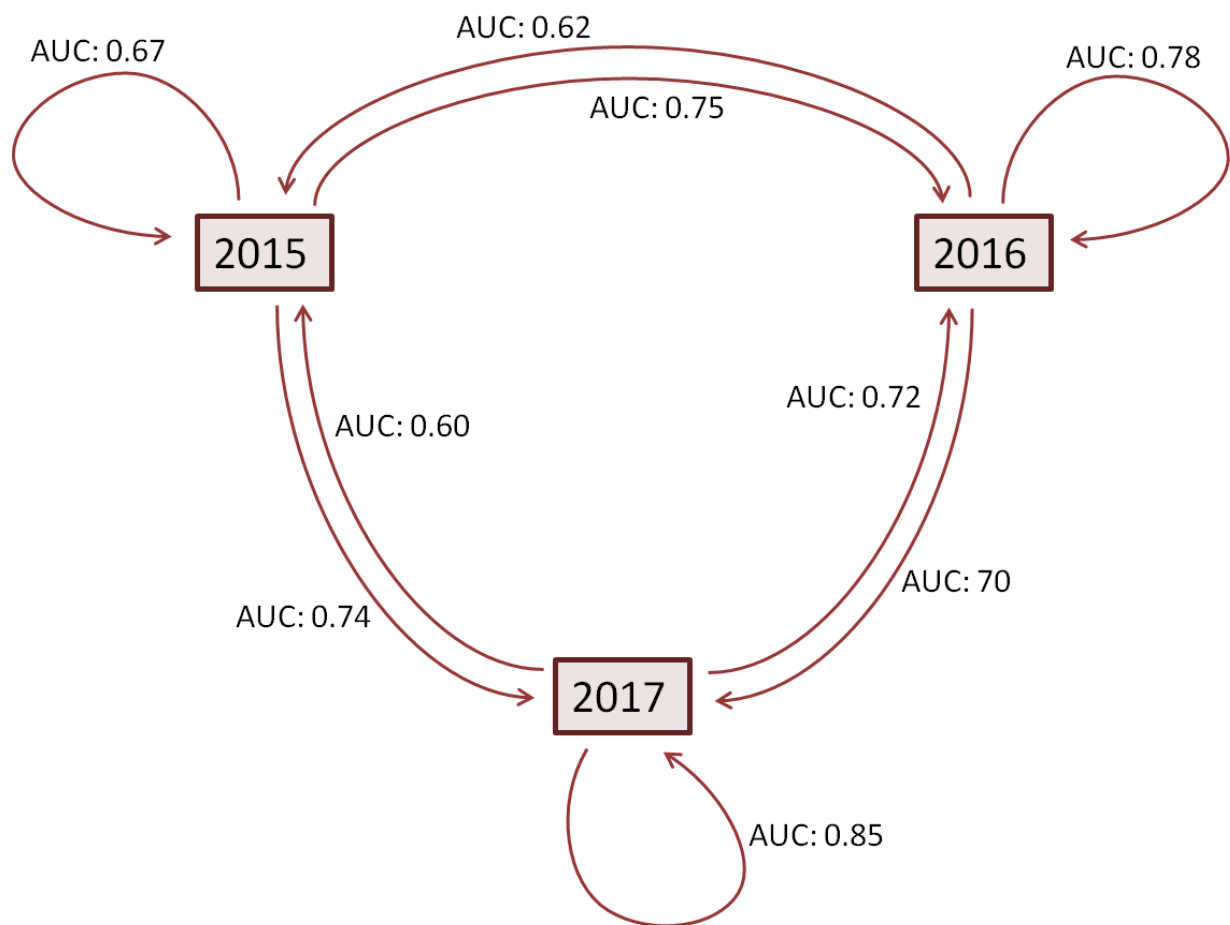


Figure 9: Plots of the marginal foraging occurrence probability in relation to A) vegetation height (cm), B) ground cover diversity, C) mineral cover (%) and D) soil moisture (mV) in the **1m scale 2015-17 late nestling period model** and E) vegetation height (cm), F) ground cover diversity and G) mineral cover (%) in the **5m scale 2016-17 late nestling period model**.

1m



5m

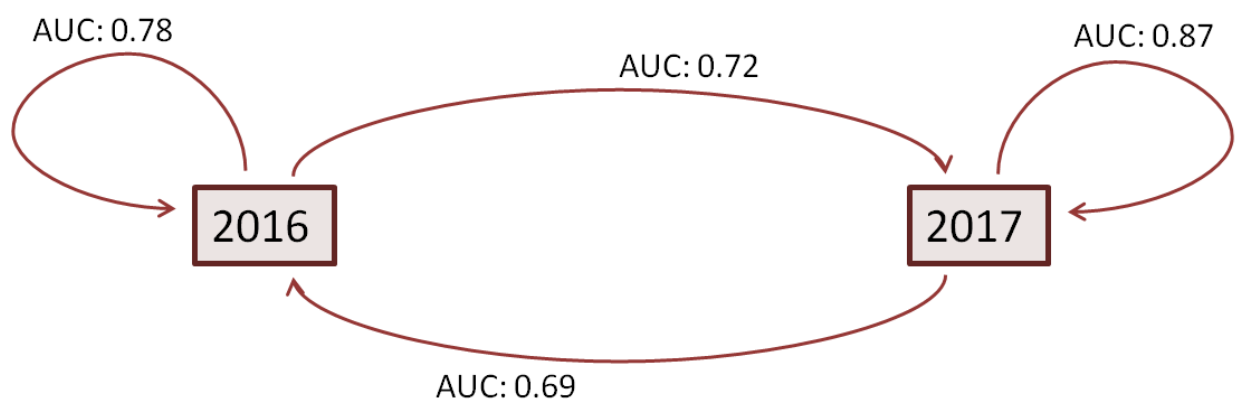
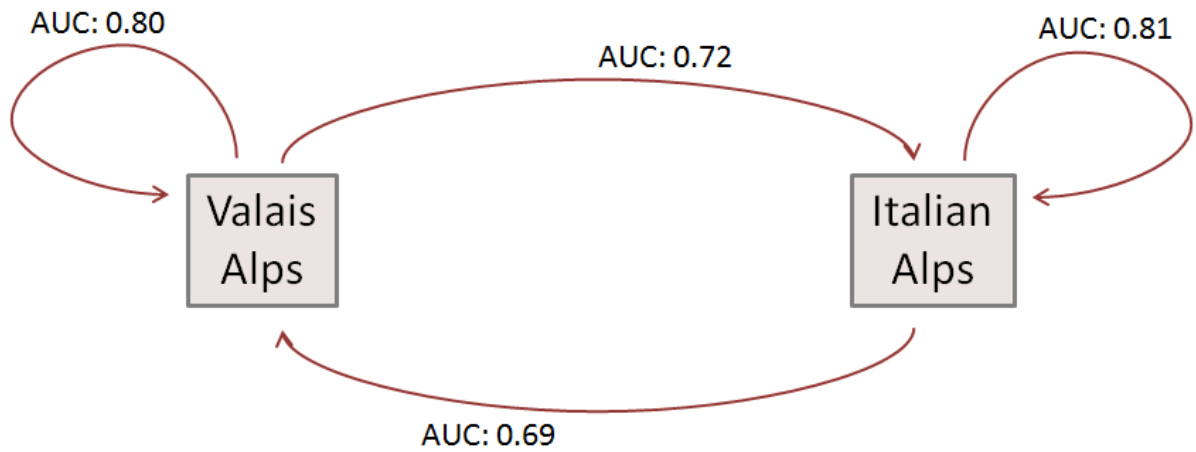


Figure 10: Results of the model performance evaluation within Valais at the 1m and the 5m scales.

A



B

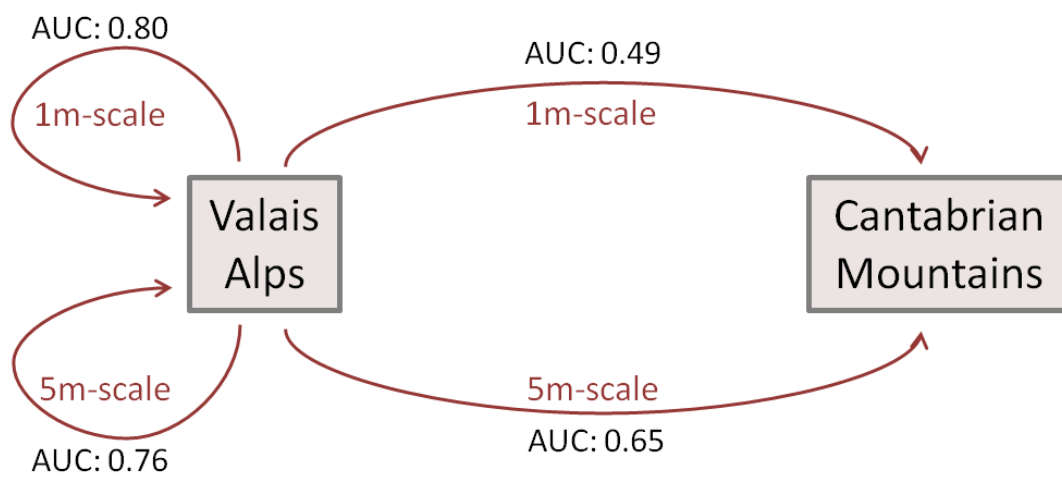


Figure 11: Results of the model transferability to A) the Italian Alps at the 5m scale, and B) to the Cantabrian Mountains at the 1m and 5m scales.

Supplementary material

Tables

Table S1: Time periods analysed and the corresponding datasets (years) per scale.

Period analysed	Corresponding dataset	
	1m scale	5m scale
Whole nestling period	2017 & 2015-17	2017 & 2016-17
Early nestling period	2017 & 2015-17	2017 & 2016-17
Late nestling period	2017 & 2015-17	2017 & 2016-17
Fledgling period	2017	2017

Table S2: Sample size for each model selection at the **1m** scale and **5m** scale after removing the plots containing missing values. The different periods include (i) the whole nestling period; (ii) early and (iii) late nestling period split in two halves; and (iv) the fledgling period (fledged chicks present among the adults, but still being fed by their parents). At the 1m scale, the nestling and early nestling period were the most affected by missing values as the variable “soil moisture” could not be measured on plots fully covered by snow (n=39 plots in 2015-17: 3 presence and 36 pseudo-absence) and therefore those plots could not be considered.

1m

Model period		Number of presence plots	Number of pseudo-absence plots
2017			
	Whole nestling period	77	139
	Early nestling period	39	70
	Late nestling period	38	69
	Fledgling period	45	84
2015-17			
	Whole nestling period	249	645
	Early nestling period	129	330
	Late nestling period	120	314

5m

Model period		Number of presence plots	Number of pseudo-absence plots
2017			
	Whole nestling period	84	84
	Early nestling period	43	43
	Late nestling period	41	41
	Fledgling period	43	43
2016-17			
	Whole nestling period	158	155
	Early nestling period	82	80
	Late nestling period	76	75

Table S3: Results of the Snowfinch foraging habitat selection in relation to the distance to snow only (both linear and quadratic effects). Estimate of the regression, standard error and P-values are given for each model at the **1m** and **5m**-scales.

1m

Model	Estimate	Standard error	P-values
2015-17 A. Snow linear			
Snow	-0.5002	0.1078	<0.001
B. Snow linear and quadratic			
Snow	-0.4569	0.0966	<0.001
Snow square	0.4703	0.0994	<0.001

5m

Model	Estimate	Standard error	P-values
2016-17 A. Snow linear			
Snow	-0.8694	0.1801	<0.001
B. Snow linear and quadratic			
Snow	-0.8149	0.1683	<0.001
Snow square	0.2273	0.1598	0.155

Figures

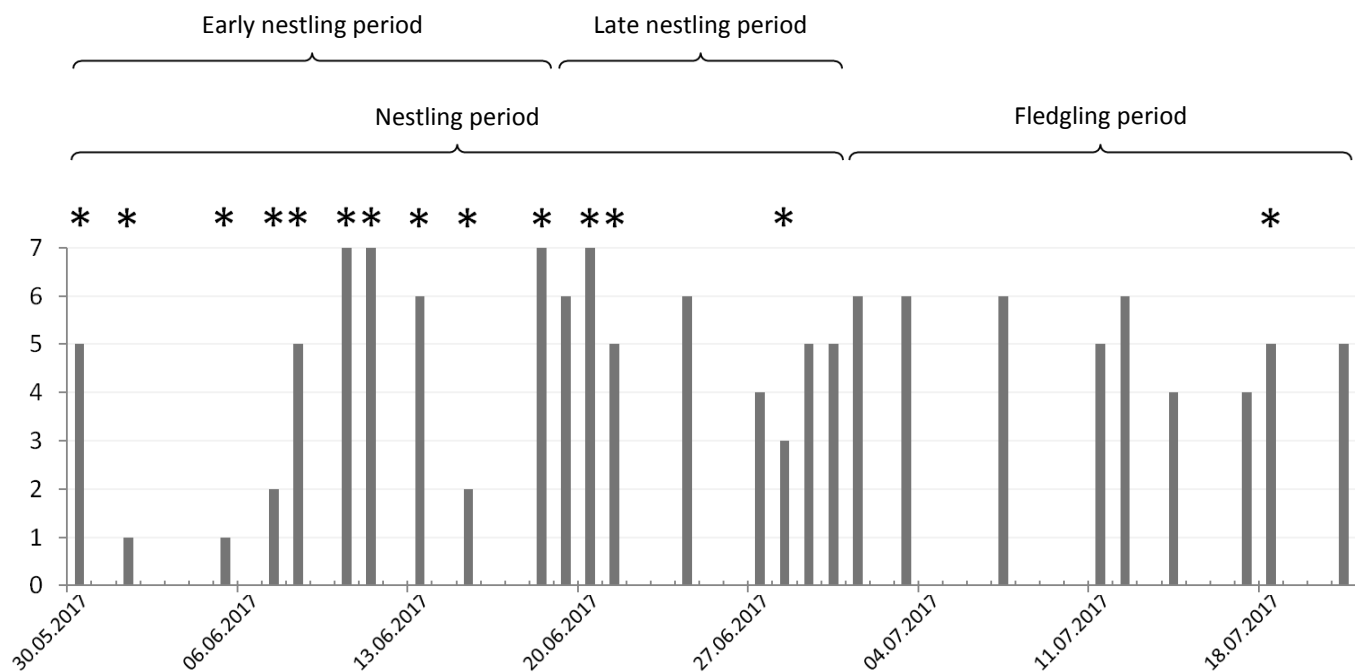


Figure S1: Visualization of the 2017 dataset with the number of foraging points collected per day and the division into nestling ($n = 84$ foraging points) and fledgling periods ($n = 47$). The presence of snow at the sites is indicated by a star (*) above the corresponding day. At the first site without snow (19th June), the nestling period was further divided into 2 seasons: early nestling period ($n = 43$) and late nestling period ($n = 41$). The absence of snow at numerous sites contrasts with the situation of 2015 (1 absence) and 2016 (2 absences).

Declaration of consent

on the basis of Article 30 of the RSL Phil.-nat. 18

Name/First Name: Binggeli Anaïs

Registration Number: 12411765

Study program: Master of Science in Ecology and Evolution

Bachelor ☐

Master ☒

Dissertation ☐

Title of the thesis: Alpine avifauna facing rapid climate change: foraging micro-habitat selection of the White-winged Snowfinch in the Swiss Alps

Supervisor: Prof. Dr. Raphaël Arlettaz
Dr. Jaime Resano-Mayor

I declare herewith that this thesis is my own work and that I have not used any sources other than those stated. I have indicated the adoption of quotations as well as thoughts taken from other authors as such in the thesis. I am aware that the Senate pursuant to Article 36 paragraph 1 letter r of the University Act of 5 September, 1996 is authorized to revoke the title awarded on the basis of this thesis.

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