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Nest site selection of the White-winged Snowfinch *Montifringilla nivalis* in the Swiss Alps

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Summary

Time and place of reproduction are crucial determinants of the reproductive success, especially in mountain ecosystems where the diverse topography and pronounced seasonality result in a high degree of spatial and temporal variation of environmental conditions. Species inhabiting high-elevation ecosystems have thus evolved strategies to adjust their breeding effort according to the prevailing environmental conditions. In mountain environments, the pattern of snowmelt often determines the onset of the reproductive period by governing access to key resources such as food. Yet, climate change may disrupt the fine-tuned species-habitat associations because of altered snow conditions and therewith changes in food availability, modification of the microclimatic conditions or increased predation pressure. We used a combination of habitat mapping and satellite remote sensing to assess the small-scale and broad-scale nest site selection of the White-winged Snowfinch *Montifringilla nivalis*, a declining alpine passerine. We observed considerable temporal variation of nest site selection in response to environmental conditions. In the first half of the breeding season, Snowfinches selected weather-protected, morning sun exposed nest cavities while they used nest cavities according their availability later on. Nests were often located close to snow patches which typically offer abundant and accessible food supply. Our results highlight the risk of a phenological mismatch that may arise from ongoing shifts in spring snow conditions, which could increase the spatial disconnection between suitable nest sites and optimal foraging grounds, with potentially negative effects on reproductive success and population dynamics. We suggest that nest box supplementation could to some extent help Snowfinches to cope with climate change if installed with the right orientation and next to suitable foraging grounds.

Key words: species-habitat association, nest site selection, environmental conditions, mountain ecosystem, White-winged Snowfinch, snow cover

1 Introduction

Temperate mountain ecosystems are characterised by a strong seasonality where snowmelt is one of the main factors determining the onset of the reproductive period. The environmental conditions often exhibit high variability over short distances due to a complex topography and the steep elevational gradients. A selective habitat use allows a fine-tuned response to the heterogeneous environmental conditions and is linked to different fitness parameters such as survival and reproductive success (Bollmann & Reyer 2001; Arlettaz *et al.* 2017). In this context, habitat selection describes the overproportioned use of some habitat in relation to their availability and should relate to the ecological requirements of a species (Johnson 1980). For birds, the nest site selection is particularly important as the nest location, directly and indirectly, influences the time and energy budget during reproduction (Johst *et al.* 2001; Catry *et al.* 2013). The microclimate of the nest can affect the incubation cost (Rauter & Reyer 2000; Catry *et al.* 2013) and nestling development (Ardia *et al.* 2006; Mueller *et al.* 2019) while the surrounding habitat determines the distance to foraging grounds (Fournier & Arlettaz 2001; Berthier *et al.* 2012; Catry *et al.* 2013) and thus the energetic cost of foraging. Furthermore, the nest location can influence predation risk (Rauter *et al.* 2002). Nest site selection should therefore reflect a trade-off between different selective forces in a way that maximises the overall fitness. The current environmental changes will potentially disrupt the fine-tuned habitat associations and high-elevation species might be particularly vulnerable due to their high degree of specialisation (Martin & Wiebe 2004; Chamberlain *et al.* 2012).

The effects of climate change are particularly strong in alpine regions. During the last decades, the rate of warming in the European Alps was twice the global average (Auer *et al.* 2007). Higher ambient temperatures in spring alter the timing and duration of snowmelt (Steger *et al.* 2013; Klein *et al.* 2016) resulting in cascading effects on the ecosystem (Keller *et al.* 2005). The phenological response to climate change can vary across trophic levels, creating a mismatch between the reproductive period and the peak of food availability (Thackeray *et al.* 2016; Cohen *et al.* 2018). Moreover, foraging habitat suitability is often strongly seasonal (Resano-Mayor *et al.* 2019; Barras *et al.* 2020) and suitable foraging grounds might be

distributed patchily. Global change can alter the extent and spatial distribution of foraging sites and therefore disrupt the interaction between the nesting habitat and suitable foraging grounds i.e., the distance between them. An increased distance can translate to lower provisioning rates of the young and consequently a lower reproductive success (Fournier & Arlettaz 2001; Kerbiriou *et al.* 2006; Catry *et al.* 2013).

White-winged Snowfinch *Montifringilla nivalis* (hereafter Snowfinch) is a typical species of high-elevation environments. The European sub-species inhabits the alpine and nival zone of central and southern European mountain ranges (Keller *et al.* 2020) and breeds in rock crevices, cavities in buildings, in ski lift pylons and nest boxes (Heiniger 1991; Grangé 2008). Within the Alps, Snowfinches are distributed patchily. While more than eight pairs can breed in some kilometre-squares, it is totally absent from other areas (Knaus *et al.* 2018). Snowfinches are therefore well suited to study the factors influencing nest site selection in a highly specialist high-elevation bird species. Also, studying Snowfinch is of conservation relevance. Over the last years, the breeding populations of Snowfinch has showed a declining trend in various parts of its range (Issa & Muller 2015; Nardelli *et al.* 2015; Knaus *et al.* 2018). Furthermore, a decrease of the distribution range by up to 97% is predicted until 2050 for the Italian Alps, assuming a steady increase in greenhouse gas emission (Brambilla *et al.* 2016). Around 14% of the Alpine population breeds in Switzerland (Keller *et al.* 2010), resulting in a high responsibility of this country for the conservation of the species. The population decline has been more pronounced where the species occurs at lower elevations (Knaus *et al.* 2018), indicating that climate-induced effects might be responsible for the observed general decline. In the Central Apennine, females disappear in years of warm and dry summers, pinpointing the vulnerability of the species to climate warming (Strinella *et al.* 2020). Reduced food availability and temperature stress are among the potential reasons for this phenomenon. Yet, many aspects of the species' ecology remain poorly understood and this incomplete knowledge hampers the development of sound conservation measures. We studied nest site selection in relation to the nest cavity characteristics. We specifically compared the nest entrance exposition between nest sites and pseudo-absences. For nest boxes, we assessed

how nest box occupancy relates to the next box exposure, time since installation and height above ground. Moreover, we compared the surrounding habitat of nest sites with the one of pseudo-absence sites in order to assess the preferred habitat types in the nest surrounding. Finally, we looked at the effects of seasonal environmental conditions, namely snow conditions, on nest site selection to better understand potential effects of climate change on breeding behaviour of Snowfinch. We used a combination of habitat mapping and satellite remote sensing to measure the potential abiotic drivers of the nest site selection.

Understanding the nest site selection can provide guidance for efficiently designing and placing artificial nest sites in the Alpine landscape. In fact, nest boxes are one of the most widely implemented tools for the conservation of cavity-nesting birds (Arlettaz *et al.* 2010). Knowing where nest boxes should be mounted can therefore potentially provide a directly applicable conservation measure for Snowfinch.

2 Material and Methods

2.1 Study areas

We defined six core study areas (Fig. 1) that were selected according to breeding records of Snowfinch on a citizen science platform (*ornitho.ch*) in the five years before our study. Snowfinch records were filtered based on their breeding code including records that correspond to used nests (active or inactive), nests with incubating adult, and nests with eggs or chicks. All core areas were visited approximately every second week to search for active nests. Every nest that we found was observed from the ground to assess the stage of the brood (incubation, nestling period, fledged). We estimated hatching and fledging dates for every nest based on these observation histories (Appendix A). Besides, we also visited additional sites to achieve a broader spatial coverage of the collected data (Fig. 1). These sites were again selected based on nests from previous years. We selected the nest records of which the precise location was documented as we needed this information to locate them in the field. Subsequently, we manually checked the coordinates of the nest records to assure

that they match a potential nest structure, e.g. building, ski lift pylon or rock cliff (Glutz von Blotzheim & Bauer 1997).

All study sites were located above the tree line and covered an elevational gradient between 1800 – 3100 m a.s.l., corresponding to the breeding range of Snowfinch in Switzerland (Knaus *et al.* 2018). All field data were collected between May and August 2020.

2.2 Cavity characteristics

We mapped the cavity characteristics (nest entrance exposition and height above ground) of all occupied Snowfinch nests located during fieldwork in 2020. A nest was considered occupied if we observed at least one feeding event or heard calls of nestlings. We generated a pseudo-absence site (PA) for every nest and measured the same variables (details: Appendix B). To measure which factors correlate with nest box occupancy, we also mapped all occupied and unoccupied Snowfinch nest boxes that we knew of. We measured the exposition of the nest entrance, height above ground and the exposure of the nest boxes. Exposure was defined as the sum of the distances to the next structures above, left, right and in front of the nest box (Appendix B).

We used a binomial model with a logit link function to estimate correlations between nest box characteristics and nest box occupancy (Table 1). Numeric predictors were centred and scaled (mean set to 0 and standard deviation to 1) before the analysis to allow comparison of the model coefficients. For analysing the selection of nest entrance exposition, we divided the broods into early and late broods based on the median hatching date. The nests were then assigned to morning sun exposition (including NE, E, SE and S exposed nests) or afternoon sun (including SW, W, NW and N exposed nests). The proportion of nest sites in each exposition category for early and late broods and for used and pseudo-absence sites was analysed by a multinomial model.

2.3 Habitat characteristics

2.3.1 Ground cover

We measured ground cover in a 300m radius around the nest representing the approximate home range of Snowfinches (Brambilla *et al.* 2017). We included nests found during fieldwork in 2020 and nests recorded on ornitho.ch between 2015-2019 for this part of the analysis. As some nests were close to each other, we used density-based spatial clustering with a maximum distance of 300m to avoid spatial pseudo-replication. A random pseudo-absence site was generated for every cluster. The PA sites were located within a 1.5 km radius around the nest and restricted to the elevational range of Snowfinch during the breeding period (Knaus *et al.* 2018). The habitat mapping in the field was conducted between July and August 2020 after complete snowmelt or when the snow cover was less than 2% within the 300m radius. If a PA site was inaccessible, we moved it by keeping the same distance from the corresponding nest but using the opposite cardinal direction. Ground coverage was estimated visually and consisted of seven categories: grass, bushes, stones, bare ground, rocks, infrastructure and water (definitions: Table 2). The average slope and exposition within a 100m radius and their standard deviations respectively were retrieved from a digital elevation model with a 25m spatial resolution (Swisstopo 2005).

A binomial model with a logit link function was used to relate nest site use (1=nest site, 0=pseudo-absence site) to the ground cover and topography. The brood identity was used as a random factor to take the paired design into account (Table 1). We used the sum of rock and infrastructure cover since both typically contain potential nest structures for Snowfinch (Glutz von Blotzheim & Bauer 1997). To account for the importance of changes at low values, a log-transformation was applied to this variable. Bare ground, stone cover and water were removed from the model to avoid that the ground cover variables sum up to 100%. All numeric predictors were standardised before the analysis. The model residuals were analysed visually to check how well the model assumptions were met and to assess if interactions or quadratic terms

were necessary. We plotted the residuals against the study area and the x and y coordinates in order to detect spatial autocorrelation.

2.3.2 Snow cover interpolation

We used remote-sensed snow cover to assess the relationship between snow and the nest site use of Snowfinch. The snow cover was retrieved from a raster-based, binary snow cover map with a spatial resolution of 20m x 20m. The product called *Theia snow collection* (Gascoin *et al.* 2018; Gascoin *et al.* 2019) is based on the normalized difference snow index (NDSI). This part of the analysis was based on nests from 2020 for which we had sufficient data to measure the hatching date (n=100). We used satellite images taken between the 1st of March to the 31st of August 2020. Dynamic pseudo-absence sites were used, meaning that the PA could also be at places where a nest was at any other time during the breeding season as long as there was no overlap in the nestling period (details: Appendix C). Apart from that, the PA were generated as for the ground cover estimates. The relative snow cover was extracted from within a 100m radius around the nest sites and PA sites, respectively. We excluded days for which more than 20 % of the pixel values were missing within the 100m radius. Missing values mainly resulted from optically thick clouds masking the sight on the ground surface. The data was subsequently checked for implausible values that can for example arise from subpixel clouds or errors in the cloud masking process. Obvious erroneous values (e.g. snow cover of 0% but 100% directly before and after or evident outliers) were removed. We linearly interpolated snow cover for days without satellite images. The snowmelt duration was calculated as the sum of subsequent days with a snow cover between 90% and 10%. The thresholds were chosen to account for areas where snow never melted completely or places where snow cover did not reach 100%, even at the beginning of the breeding season.

We assumed that the difference in snow cover at nest sites and PA sites would be largest at the time when the nest site is selected (e.g. before nest building starts). To find this time point, we calculated the absolute snow cover difference between the corresponding nests and PA sites on a daily basis in relation to the hatching date. The proportion of snow cover was logit

transformed. Because the logit function of 0 and 1 are not defined, we replaced these values with 0.025 and 0.975 respectively. Next, we modelled the relationship between the nest site use and the snow cover at hatching, using a binomial model with a logit link function. The relationship was modelled for all nests together as well as for early and late nests separately. Elevation and its quadratic term were included as covariables and brood identity was used as a random factor to take the paired design into account.

We modelled the snow cover at hatching over the course of the breeding season. We used independent linear models for nest sites and PA sites (Table 1) to allow for more flexible model fitting. The snow cover at hatching was logit transformed to assure that the predicted values range between 0% and 100%. The model additionally included the snowmelt duration and elevation (linear and quadratic term) as predictors (Table 1). The numeric predictor variables were again centred and scaled before the analysis (mean = 0, sd = 1).

2.3.3 Snow-corrected habitat cover

We assessed how different our results would have been if we had sampled the ground cover at the hatching date instead of after snow had totally melted. To do so, we combined a ground cover map (Swisstopo 2009) with the snow cover data (Gascoin *et al.* 2018). The ground cover map was downscaled from a 25m to a 20m resolution using a modal function and was then aligned with the snow cover map. We extracted the ground cover composition on a 100m radius around the nest at the date closest to hatching, excluding nests that did not have data available within ± 6 days from hatching. Snow cover was again manually checked for plausibility and nests with more than 20% of missing data on a given day were discarded. We used a logistic regression to relate nest site use (nest sites vs. PA) to grass cover (linear and quadratic terms), its interaction with the hatching date and elevation as predictor variables (Table 1). Due to the limited sample size ($n = 56$) we did not add further predictors to the model.

We used R 4.0.5 (R Core Team 2020) and QGIS 3.10.4 (QGIS Development Team 2020) for the analyses. All linear models were fitted with the *brm* function of the *brms* package (Bürkner 2018) using uninformative priors. Convergence of the MCMC simulations was assessed based

on the \hat{R} value and visually (Brooks & Gelman 1998). The 95% credible intervals are based on 10'000 samples drawn from the joint posterior distribution.

3 Results

3.1 Cavity characteristics

We mapped 85 nest boxes in 12 different locations. A breeding attempt of Snowfinch was recorded in 37.6% of the nest boxes in the time since they were installed. Based on the logistic regression, nest box occupancy probability was negatively correlated with the nest box exposure (Fig. 2). Moreover, our results suggest a positive correlation between the time since installation and the probability of use of the nest boxes. The probability that a nest box was used at least once was 44.4% (CrI: 25.9% - 63.7%) for nest boxes that were installed six years ago.

Of all nest cavities in 2020 ($n_{\text{ski lift pylons}} = 64$, $n_{\text{buildings}} = 19$, $n_{\text{nest boxes}} = 8$, $n_{\text{cliffs}} = 8$), 55.3 % were exposed to the morning sun and 44.7% were exposed to the afternoon sun. The distribution of nest cavity expositions changed however throughout the breeding season. The comparison of nests cavities with PA-cavities revealed a preference for morning sun in the first half of the breeding season with 72.4 % (CrI: 58.8% – 84.1%) of the nests and 38.4% (CrI: 24.9% – 51.9%) of the PA-cavities exposed toward the morning sun (Fig. 3). In the second half of the breeding season, the majority (mean: 61.7 %; CrI: 48.1% - 75.1%) of the nest cavities were exposed to the afternoon sun and 56.5 % (CrI: 42.6% - 69.8%) of the PA-cavities had the same exposition. The similar expositions of nest and PA-cavities in the second half of the breeding season indicate that Snowfinch used cavity expositions according to their availability (Fig. 3).

3.2 Habitat characteristics

3.2.1 Ground cover variables

The habitat composition after snowmelt was measured for 68 nest sites and the corresponding number of PA sites. Grass was the most dominant ground coverage type (median, 1st – 3rd

quartile: 70.8%, 54.25 – 80.9%) followed by bare ground (median, 1st – 3rd quartile: 8.5%, 4 – 16.4%). Ground coverage at nest sites and PA sites is summarised in Table 3.

The combination of rock and infrastructure cover correlated strongly with the nest site preference of Snowfinch (Fig.4). Grass cover was positively correlated with nesting preference (Fig 5a). The highest preference index was estimated at the maximum grass coverage of 95%. The estimates the model coefficients of all response variables are summarised in table 3.

3.2.2 Snow cover interpolation

The median hatching date in 2020 was June 9th ± 4 days ranging from May 1st to August 7th. The elevational distribution of the nests corresponded to the elevational breeding range of Snowfinch in Switzerland (Knaus *et al.* 2018).

A comparison of the absolute difference of snow cover at nest sites and PA sites revealed a maximum difference at 15 days before hatching (Fig. 6). The median snow cover at hatching date was 25.4% (1st- 3rd quartile: 0.6% – 54.9%) in a 100m radius around the nests and 0.05% (1st- 3rd quartile: 0.0% - 45.7%) at PA sites. Snowfinch preferentially used nest sites in snow-rich areas early during the breeding season (Fig. 7b + Fig 8). At nest sites, the snowmelt period was slightly shorter than at the pseudo-absence sites (mean ± sd: 39.6 ± 14.4 days and 44.3 ± 23.5 days) The snowmelt duration was slightly negatively correlated with the nesting preference.

3.2.3 Snow-corrected habitat composition

Due to high cloud coverage on satellite pictures close to the hatching date or general gaps in the availability of satellite images, only 56 nests and their corresponding PA sites were included in this part of the analysis. Grass and snow were the most dominant habitat types at hatching (± 6 days) with a median cover of 57.2% (1st-3rd quartile: 16.8 - 91.8%) and 1.3% (1st – 3rd quartile: 0.0 - 46.5%), respectively. Ground cover composition at nests and PA sites is summarised in Table 5. Note that the definition of the habitat categories differs from the habitat

categories used for the habitat cover variables measured in the field (chapter 2.3.1), explaining the discrepancy for some variables.

When we considered the ground cover composition at hatching date derived from the snow-corrected ground cover map, grass cover showed a quadratic relationship with the nest sites use (Fig 5b). The results suggest a grass cover optimum at 47.5% which is in contrast to a steady increase up to maximal cover evidenced from the analyses of the field measurements. The model suggests an interaction between grass cover and the hatching date. Moreover, the model revealed a slight, positive correlation between nest site use and elevation (Table 6).

4 Discussion

This study sheds light on the abiotic drivers of nest site selection in Snowfinch, a declining mountain passerine. The results highlight the role of seasonal environmental factors, namely snow and the role of the cavity entrance exposition. Moreover, the nest site use was correlated to rock and infrastructure cover and the results indicate a preference for intermediate to high grass cover in the nest surrounding.

4.1 Cavity characteristics

Our results suggest that the average nest cavity exposition changed throughout the breeding season with a preference for morning sun exposed nests in early broods. We assume that this preference relates to the microclimatic conditions of the nest sites. The microclimate in the nest, especially the temperature, can affect incubation costs (Vleck 1981; Rauter & Reyer 2000), nestling development (Pérez *et al.* 2008; Mueller *et al.* 2019) and breeding success (Gibson *et al.* 2016). Its link to the nest site choice has been evidenced for several species (Hooge *et al.* 1999; Wiebe 2001; Ardia *et al.* 2006). Ardia *et al.* (2006) found a preference for south and east exposed nests at the start of the breeding season in a nest box population of Tree Swallows. They showed that occupied nest boxes were characterised by higher temperatures, especially in the morning hours. In the cold conditions typically encountered at high elevation, the warming effect of the sun might provide fitness benefits for adults and their

nestlings. The female brooding the nestlings can potentially increase the number and duration of foraging trips as a response to higher nest temperatures (Rauter *et al.* 2002; Walters *et al.* 2016). Moreover, the energy-related costs of incubation and brooding might be reduced (Mueller *et al.* 2019). Yet, this temperature effect ought to be demonstrated in the case of Snowfinch as we did not measure microclimate in the cavities. Especially, it remains unclear if the temperature effect would hold true for all nest types as the temperature inertia might vary considerably among them (Grüebler *et al.* 2014; Larson *et al.* 2018).

The selection for nest boxes with low exposure, as found in this study, might similarly provide more suitable microclimatic conditions. Nest boxes located close to the roof might experience less extreme temperature, both high and low, due to the insulation effect. Moreover, these nest boxes are also less exposed to precipitation and wind.

4.2 Habitat characteristics

4.2.1 Nest site availability

Rocks and infrastructure typically offer nest sites for snowfinch. The pronounced positive correlation between the nest site use and rock and infrastructure cover thus indicates that the availability of suitable nest sites might be scarce. Nest site availability is often considered a limiting factor for the breeding density of cavity-nesting birds (Newton 1994) and was demonstrated for several species e.g. for Lesser Kestrels (Franco *et al.* 2005) and Tree Sparrows (Post & Smith 2015). An increase of nest sites in a before-after control experiment in a forest ecosystem similarly revealed a massive increase of cavity-nesting birds (Aitken & Martin 2012). So far, nest site limitation was rarely looked at in non-managed habitats such as high elevation systems. In an alpine environment, nest structures are inherently scarce for cavity breeding birds. Locally high breeding densities at places providing suitable nesting structures (personal obs.) could hence indicate that food resources in the alpine habitat would be sufficient to support higher local population sizes, but the availability of nest sites may limit Snowfinch density at many places. While it is unlikely that the number of nest sites recently changed, upward shifts of other species with similar nest site preferences could potentially

increase interspecific competition. Providing nest boxes, targeted for the specific needs of Snowfinch, could therefore be a possibility to support Snowfinch populations.

4.2.2 Food availability

Our results suggest a selection of snow-rich areas in the first half of the breeding season. A synchronisation of breeding effort with snowmelt has been evidenced for several bird species breeding at high elevations or high latitudes (Liebezeit *et al.* 2014; Kwon *et al.* 2019), including Snowfinch (Resano-Mayor *et al.* 2019; Brambilla *et al.* 2017). Especially ground-nesting birds are constrained by the availability of snow-free patches for brood initiation (Martin & Wiebe 2004; Madsen *et al.* 2007) and might delay breeding in response to inclement weather (Morrisette *et al.* 2010; Wilson & Martin 2010; Liebezeit *et al.* 2014). As cavity nesters, Snowfinches are presumably less constrained by snow cover for brood initiation. Nevertheless, Heiniger (1991) reported that Snowfinch delayed or skipped breeding in years of late and heavy snowfall. Our results suggest a maximum difference in snow cover between nest sites and pseudo-absence around 15 days before hatching. We interpret this point as the potential time of the nest site selection. Given the 12 days incubation period of Snowfinch (Glutz von Blotzheim & Bauer 1997) the timing of the nest site selection happens very shortly before the brood initiation. Selecting the nest site just before brood initiation might be an adaptation to the strongly variable conditions in its habitat and support the hypothesis that Snowfinch synchronise breeding with snowmelt.

Snow cover can affect plant and invertebrate phenology and hence modify food availability and abundance at higher trophic levels (Liebezeit *et al.* 2014; Kwon *et al.* 2019). Therefore, the timing of reproduction as well as the choice of the nest sites in relation to the habitat composition might be crucial for successful reproduction. Different insect larvae, especially Tipulids are important components of the nestling diet of Snowfinch (Heiniger 1991). Brambilla *et al.* (2017) and the detailed study of Resano-Mayor *et al.* (2019) demonstrated the importance of snowfield margins for the foraging habitat selection of Snowfinch. The abundance of Tipulidae larvae tends to be particularly high next to the melting snow front

(Resano-Mayor *et al.* 2019). The preference for high snow cover around nest sites might therefore reflect the Snowfinch's foraging preferences. High snow cover at hatching might provide good foraging conditions, e.g. long-lasting availability of snowfield margins throughout the three week nestling period. Moreover, invertebrate fall out on snow can additionally offer easily accessible food (Antor 1995). Our results indicate a change from snow-dominated to grass-dominated habitats later during the breeding season. This change in habitat preference might be linked to a change in prey availability as indicated from their foraging habitat selection (Resano-Mayor *et al.* 2019).

4.3 Climate change and future research

The link between the nest site selection and the snow conditions in the nest surrounding highlights the dependence of the species on seasonal environmental conditions. Climate change is expected to alter the snow cover extent but also the timing of snowmelt (Steger *et al.* 2013; Klein *et al.* 2016). These changes could temporally shift or shorten the breeding period of Snowfinch but the consequences for the species depend on their ability to react to environmental shifts. Such reaction may include advancing the breeding period or shifting the breeding sites to higher elevations where the timing of snowmelt may still coincide with their physiologically determined breeding period. Species inhabiting high-elevation ecosystems are considered particularly vulnerable to environmental changes due to their high degree of specialisation (Martin & Wiebe 2004; Chamberlain *et al.* 2012). Heiniger (1991) showed that Snowfinch typically breed in narrow and deep rock cavities pointing out the highly selective nest site choice of this species. Our results indicate that suitable nest sites are distributed patchily in the European Alpine landscape and might be limiting the breeding distribution of snowfinch already now. Upwards distribution shifts could entail further nest site shortage.

The sensitivity to climate change further depends on the reliance on seasonal resources such as prey (Miller-Rushing *et al.* 2010; Halupka & Halupka 2017). Snowfield margins might provide abundant prey early in the season, while Snowfinch potentially switch to other resources after snowmelt. We suggest that future research investigates how snow cover at the

nest site affects the fitness of adults and nestlings, respectively. A better understanding of the link between breeding success and seasonal environmental conditions could help to anticipate the potential effects of climate change. Moreover, information about the diet and the dietary flexibility of Snowfinch could provide a more mechanistic understanding of the observed relationships.

4.4 Limitations

We analysed snow cover at the nest sites based on satellite images. Satellite remote sensing is a powerful tool to investigate species-habitat associations, especially in areas that are otherwise hard to access and monitor tightly. Yet, there are some limitations that are in particular the high prevalence of optically thick clouds in mountain regions and some methodological caveats such as thresholds for snow cover detection. Binary snow cover maps tend to underestimate snow cover as subpixel snow is not represented accurately (Gascoin *et al.* 2019). However, due to the high spatial resolution of the snow cover maps, and the fact that the underestimation affects both nests and PA, these effects should not strongly affect our inference.

5 Conclusion

Our results shed light on the challenges Snowfinch are facing during the breeding period. On one hand, Snowfinch need to have a high degree of flexibility to match the timing and location of breeding with snowmelt in order to track suitable foraging conditions. On the other hand, suitable nesting sites are possibly limited. We therefore, expect that climate warming will enlarge the distance between breeding sites and feeding grounds and, consequently, reduce breeding success at current nesting sites, while new nesting sites may be difficult to find. Our study demonstrates that supplementing nest boxes could benefit Snowfinch populations by enhancing the availability of nest sites and potentially mitigate the expected effect of climate warming on the distance between nest sites and foraging sites. Furthermore, the results can help delineating areas where nest boxes should be placed to provide suitable conditions for Snowfinches.

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Tables

Table 1 Overview of models used in the analysis of the different sections of the main text.

Exposure EXPOS, years since installation INSTALLATION, Height above ground HEIGHT, Grass cover GRASS, Bush cover BUSH, potential nest structures NEST, elevation ELEV, mean exposition EXP, mean slope SLOPE, standard deviation of the exposition SD EXP, standard deviation of the slope SD SLOPE, brood identity BROOD, Interpolated snow cover at the day of hatching SNOW, Hatching day (day of the year) HATCH, Snowmelt duration (days) MELT, days since hatching DAYS, nest type (building, cliff, nest box, ski lift pylon).

Section	Response variable	Model
cavity characteristics	probability of use	EXPOS + INSTALLATION+ HEIGHT
habitat characteristics	probability of use	GRASS + BUSH + log(NEST) + EXP + SLOPE + SD EXP + SD SLOPE + ELEV + (1 BROOD)
	probability of use	SNOW + MELT + ELEV + ELEV ^{2*} + (1 BROOD)
	snow cover	HATCH + (HATCH) ^{2*} + ELEV
	probability of use	GRASS*HATCH + GRASS ² + ELEV + DAYS

* added if the residual analysis indicates a quadratic relationship

Table 2 Definitions of the habitat categories recorded in the field and variables retrieved from the digital elevation model.

Variable	Definition	Source
grass cover	non-woody vegetation including grasses, forbs and flowers	field
bush cover	woody vegetation (mainly <i>Juniperus communis</i> and <i>rhododendron</i> sp.)	field
rock cover	vertical and near-vertical solid rock formation (e.g. cliffs)	field
bare ground*	non-vegetated surfaces including scree, boulders, bare soil and roads	field
stone cover	stones with a diameter < 20cm	field
infrastructure cover	buildings and ski lift infrastructure	field
nest structures	sum of rocks and infrastructure	field
water*	water surface cover	field
elevation	elevation of the nest sites	digital elevation model
exposition / sd exposition	mean / sd exposition in °N on 100m radius	digital elevation model
slope / sd slope	mean / sd slope in ° on 100m radius	digital elevation model
nest type	buildings, rock cavities (natural), nest boxes, ski lift pylons	

* not included in the linear regression to avoid model singularity

Table 3 Mean and standard deviation of ground cover variables and topographic variables at nests and pseudo-absence sites. Definitions of habitat categories in table 2. $n_{\text{nests}} = 68$, $n_{\text{pseudo-absence}} = 68$

	nests		pseudo-absences	
	median	1st -3rd quartile	median	1st - 3rd quartile
snow cover [%]	0.0	0.0-0.0	0.0	0.0-0.0
grass cover [%]	70.8	51.5-78.5	67.0	4.0-16.4
rock cover [%]	0.5	0.0-3.0	0.5	0.0-1.0
stone cover [%]	3.0	1.0-8.0	43.0	1.0-13.1
bush cover [%]	3.5	0.0-10.0	4.8	0.9-15.0
water cover [%]	0	00.0-0.13	0.0	0.0-0.5
infrastructure cover [%]	1	0.5-3.5	0.0	0.0-0.3
bare ground cover [%]	10.0	6.8-16.6	6.0	4.0-16.4
elevation [m asl]	2307	2206-2503	2279	2080-2521
mean slope [°]	18.1	11.7-27.0	16.1	11.5-24.1
sd slope [°]	7.1	4.3-9.5	5.4	4.1-6.6
mean exposition [°N]	1175	130-239	174	121-257
sd exposition [°N]	68.6	23.1-113	33.1	16.3-78.5

Table 4 Estimated model coefficients from a multiple logistic regression fitted to the nest presence and pseudo-absence data with ground cover and the topographic variables as predictors. Mean, 2.5% and 97.5% quantile based on 10'000 samples drawn from the joint posterior distribution are given. Variables were centred and scaled (mean = 0, sd = 1) prior to the analysis. $n_{\text{nests}} = 67$, $n_{\text{pseudo-absences}} = 67$

	mean	2.5% quantile	97.5% quantile
intercept	0.32	-0.32	0.97
grass cover	0.96	0.27	1.75
bush cover	0.47	-0.20	1.18
rocks + infrastructure	1.70	1.06	2.47
mean slope	-0.13	-0.74	0.47
sd slope	0.44	-0.16	1.13
mean exposition	-0.20	-0.73	0.30
mean aspect²	-0.33	-0.83	0.15
sd aspect	0.26	-0.24	0.77
elevation	0.05	-0.44	0.55

Table 5 Summary of the ground cover composition at hatching (± 6 days) based on snow corrected ground cover map for nests and pseudo-absence sites. $n_{\text{nest}} = 56$, $n_{\text{pseudo-absence}} = 56$

	nests		pseudo-absences	
	median	1st-3rd quartile	median	1st-3rd quartile
snow [%]	10.7	0.0-70.3	0.0	0.0-29.5
grass [%]	46.8	17.7-87.0	73.8	16.5-96.0
buildings [%]	0.0	0.0-0.0	0.00	0.0-0.0
forest [%]	0.0	0.0-0.0	0.0	0.0-0.0
water [%]	0.0	0.0-0.0	0.0	0.0-0.0
rocks [%]	0.0	0.0-0.0	0.0	0.0-11.3
bare ground [%]	0.0	0.0-5.2	0.0	0.0-10.3
missing data [%]	0.0	0.0-0.0	0.0	0.0-0.0

Table 6 Estimated model coefficients from a multiple logistic regression fitted to the nest presence and pseudo-absence data with grass cover at hatching, hatching date and its interaction with grass cover, elevation and days since hatching as predictors. All variables were centred and scaled before the analysis (mean = 0, sd = 1). The quantiles are based on 10'000 samples drawn from the joint posterior distribution. $n_{\text{nest}} = 56$, $n_{\text{pseudo-absence}} = 56$.

	mean	2.5% quantile	97.5% quantile
intercept	0.48	-0.29	1.27
grass	-0.25	-0.74	0.22
hatching date	0.05	-0.44	0.53
grass ²	-0.77	-1.48	-0.08
elevation	0.40	-0.02	0.84
days since hatching	0.09	-0.32	0.52
grass : hatching date	0.66	0.15	1.24

Figures

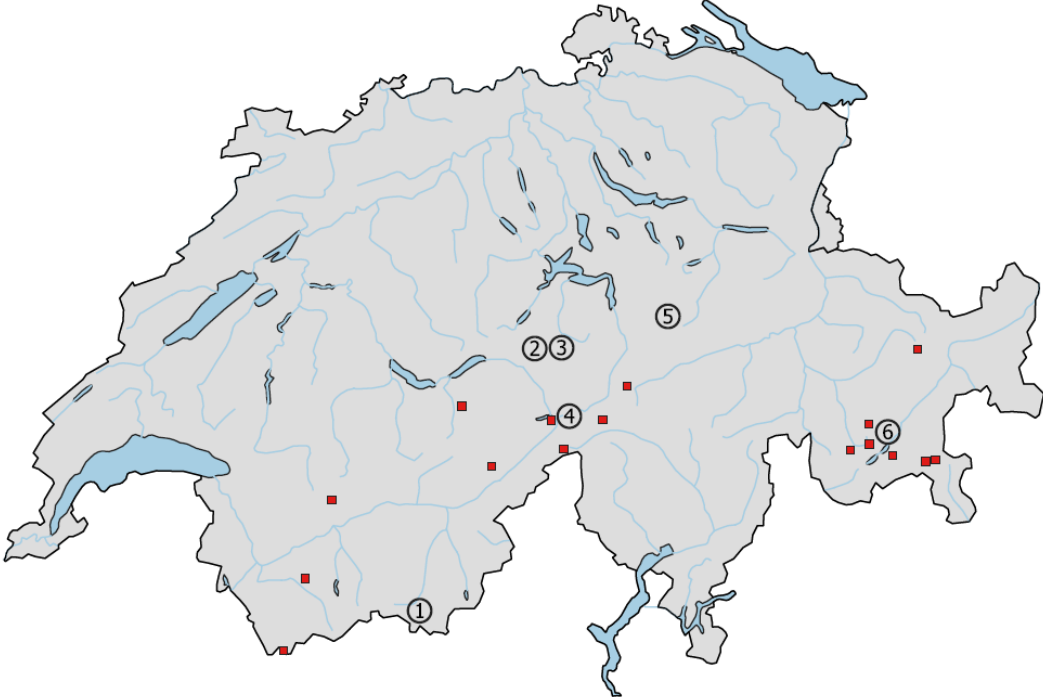


Fig 1. Location of the core study areas (numbers) and additional sites (red squares): 1 Zermatt, 2 Melchsee-Frutt, 3 Jochpass, 4 Furkapass, 5 Klausenpass, 6 St. Moritz.

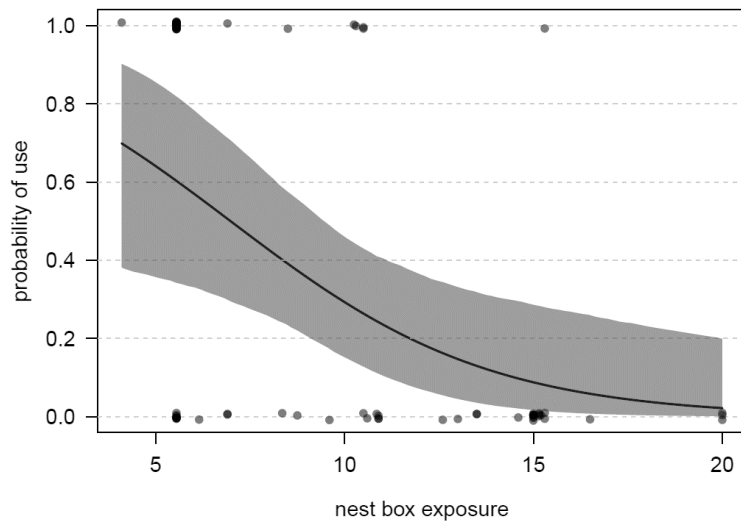


Fig. 2. Probability of use of nest boxes based on a logistic regression. Model specification is given in table 1. Nest box exposure is the sum of the distances from the nest box to the closest structure above, left, right and in front with a maximum value of 5. Low numbers of nest exposure indicate good protectedness against weather (e.g. snow, rain and wind). Shaded area shows the 95% credible interval. $n_{\text{occupied nest boxes}} = 32$ $n_{\text{unoccupied nest boxes}} = 53$.

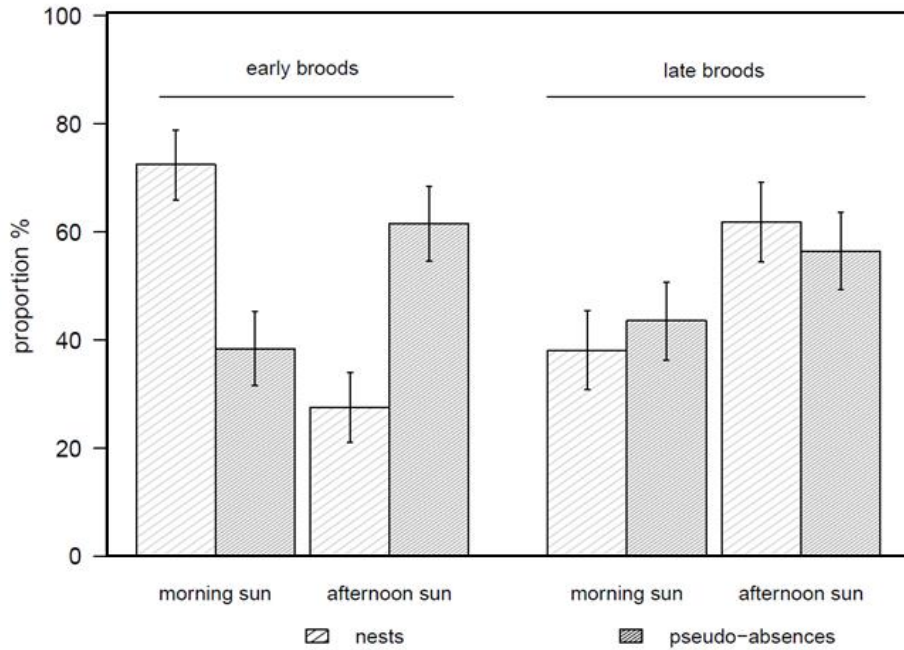


Fig. 3 Nest exposition divided into morning sun (NE, E, SE and S exposed) and afternoon sun (SW, W, NW and N exposed) exposition for nest sites and pseudo-absence sites. Broods were divided into early hatching broods (hatching date < median hatching date) and late hatching broods (hatching date > median hatching date) based on the median hatching date. Pseudo-absences were assigned the hatching date of their corresponding brood. Error bars indicate the standard deviation derived from a multinomial model with 2'000 iterations. $n_{\text{early}} = 47$ $n_{\text{late}} = 47$, $n_{\text{nests}} = 94$, $n_{\text{pseudo-absences}} = 94$.

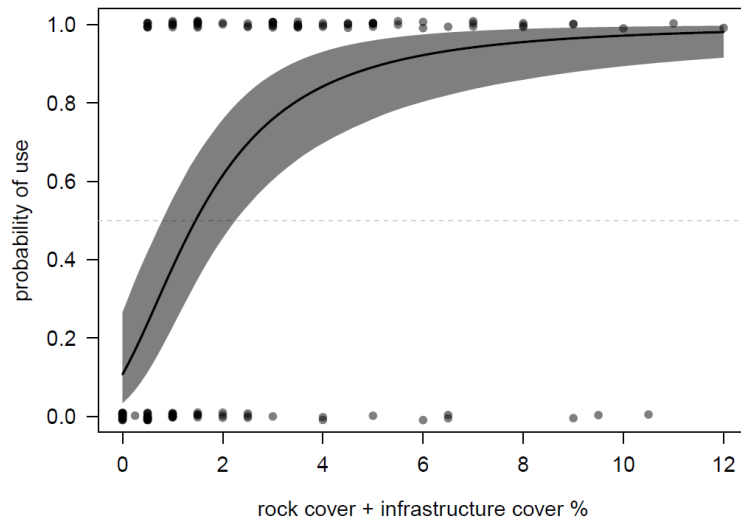


Fig. 4 Estimated probability of use (1 = occupied nest sites, 0 = PA sites) in relation to the linear logistic regression with 95% confidence interval grey shaded. Model estimates in table

4. $n_{\text{nests}} = 67$, $n_{\text{pseudo-absences}} = 67$

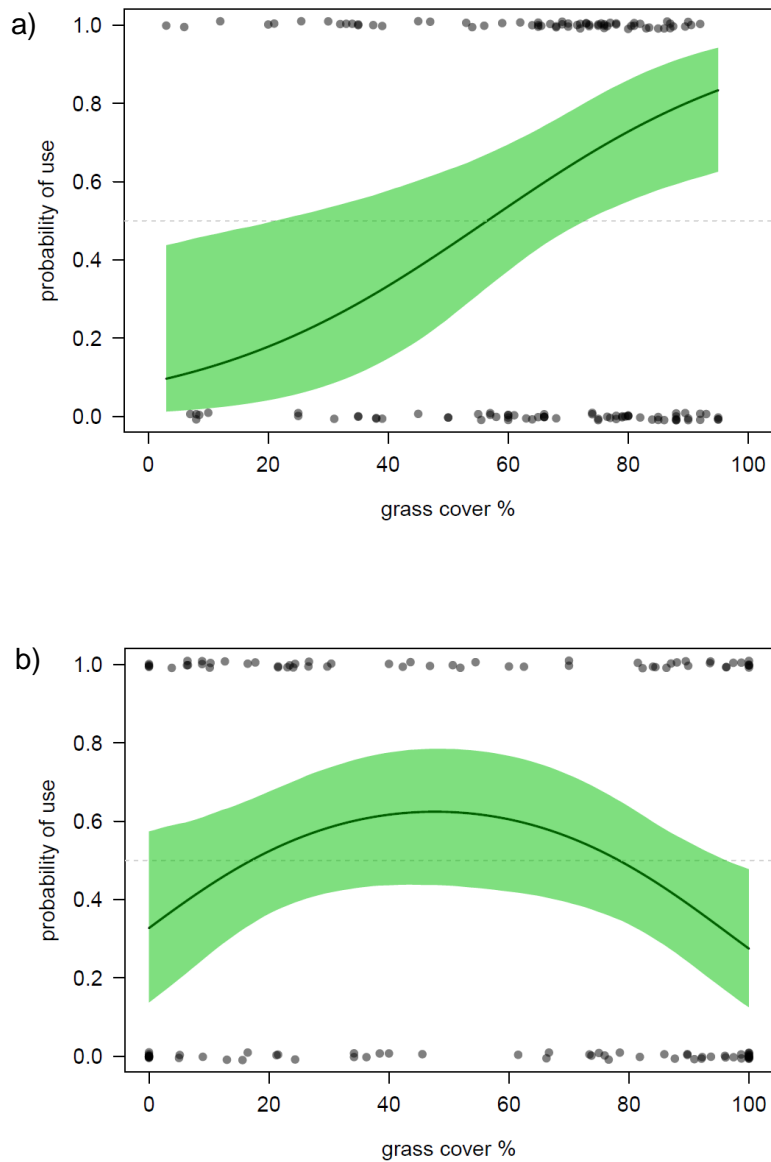


Fig. 5 Estimated probability of use in relation to grass cover based on a) the ground cover measurements in the field (nest clusters of years 2015-2020) and b) the snow-corrected ground cover model at hatching from remote sensing data. The 95% credible intervals are green shaded. Field data: $n_{\text{nests}} = 67$, $n_{\text{pseudo-absence}} = 67$; remote sensing data: $n_{\text{nest}} = 56$, $n_{\text{pseudo-absence}} = 56$

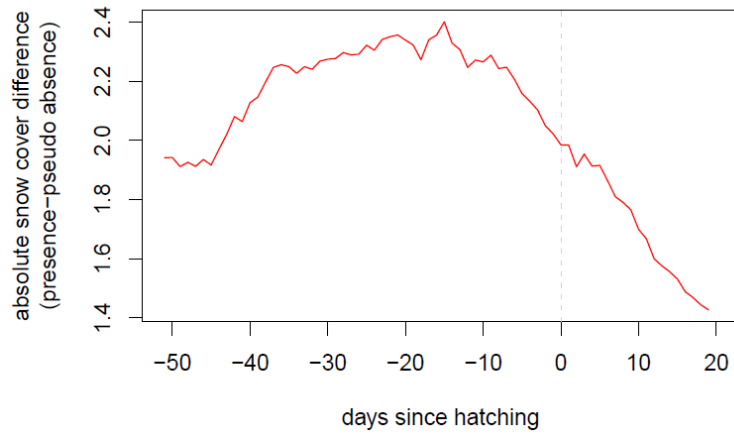


Fig. 6 Relationship between the day since hatching and the daily, absolute snow cover difference between nests and pseudo-absence sites. High values are interpreted as an indication of strong selective choice of nest sites regarding snow cover. The snow cover values were logit transformed before the analysis. The absolute difference is highest at hatching -16 days. $n_{\text{nests}} = 100$, $n_{\text{pseudo-absences}} = 100$.

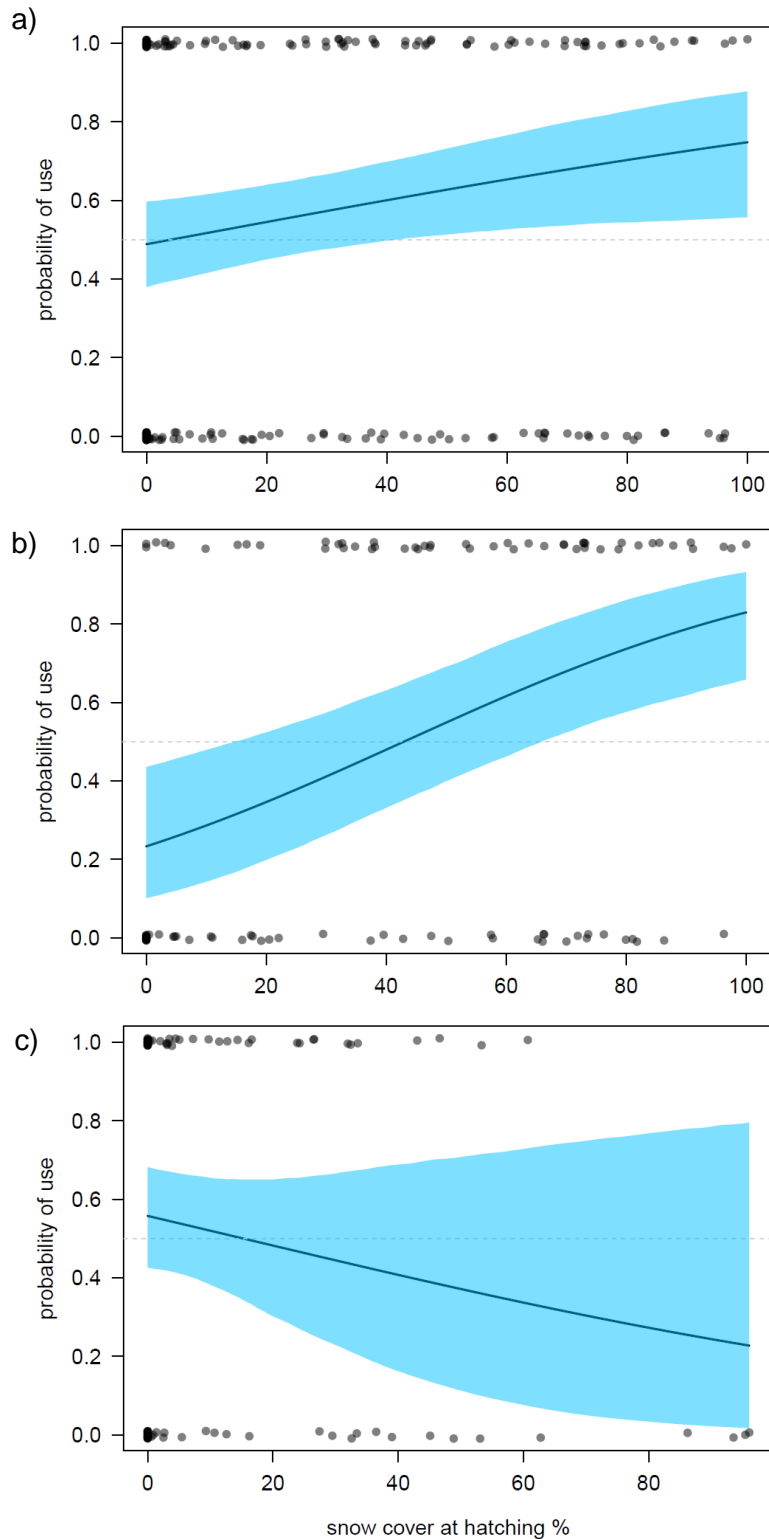


Fig 7. Probability of use in relation to snow cover at hatching for a) all broods b) early broods (hatching date < median hatching date) and c) late broods (hatching date > median hatching date) based on logistic regressions. $N_{\text{nests}} = 100$, $N_{\text{pseudo-absences}} = 100$. $N_{\text{early}} = 50$, $N_{\text{late}} = 50$

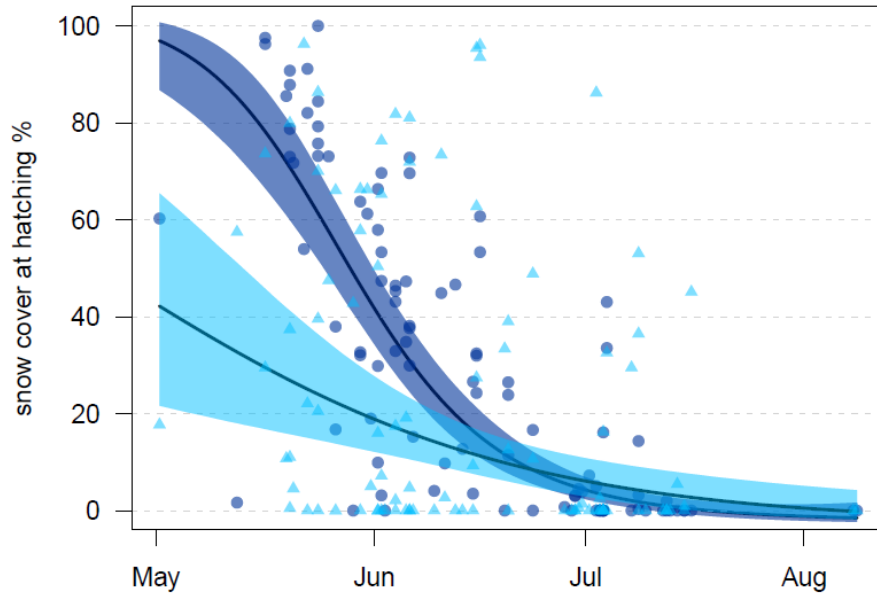
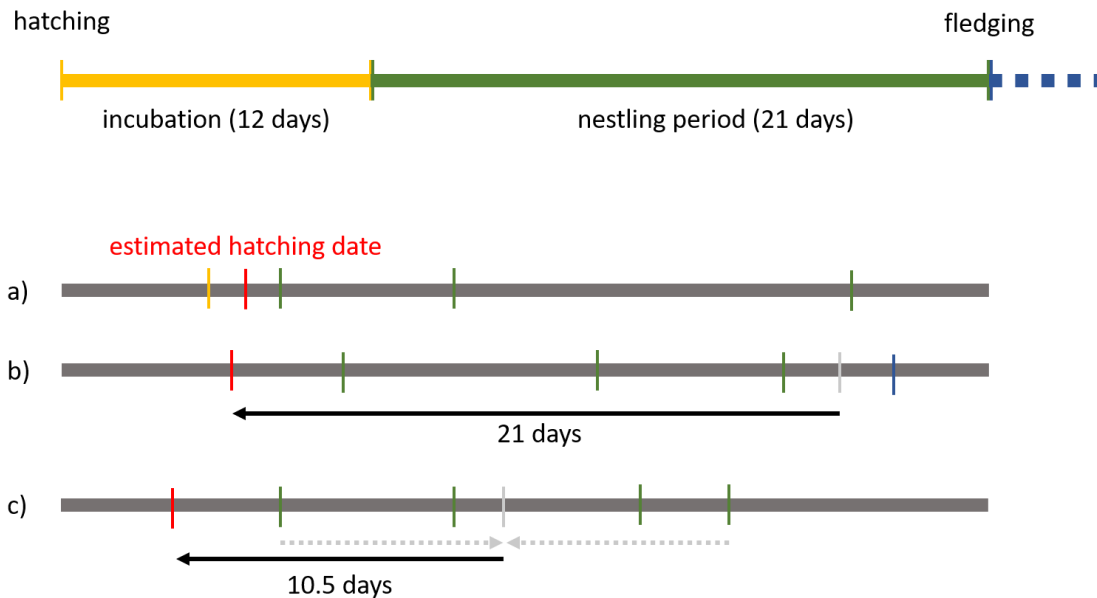


Fig. 8 Snow cover (100m) at hatching date throughout the breeding season for nest sites (dark blue) and the corresponding pseudo-absence sites (light blue); 95% credible interval as shaded areas. The regression lines are based on independent linear models including elevation as a covariable. $N_{\text{nests}} = 100$, $N_{\text{pseudo-absences}} = 100$

Appendix A



To derive possible hatching dates, we assumed an incubation period of 12 days and a nestling period of 21 days (Glutz von Blotzheim & Bauer 1997). Hatching dates were obtained from nest observation histories (a-c). In case a), the hatching date is estimated as the mean day between last time incubation was observed and the first day on which the nestlings were feed (nestling period). In case b) we first estimated the fledging date as mean day between last observation day of the nestling period and the first observation day after fledging. The hatching date was then calculated by subtracting 21 days (= duration of nestling period). If we only recorded observations during the nestling period (c), we used the mean date of the nestling period and subtracted 10.5 days (= 50% of the nestling period) to estimate the hatching date. In all cases, we used the additional information of all observations to refine the estimation.

Appendix B

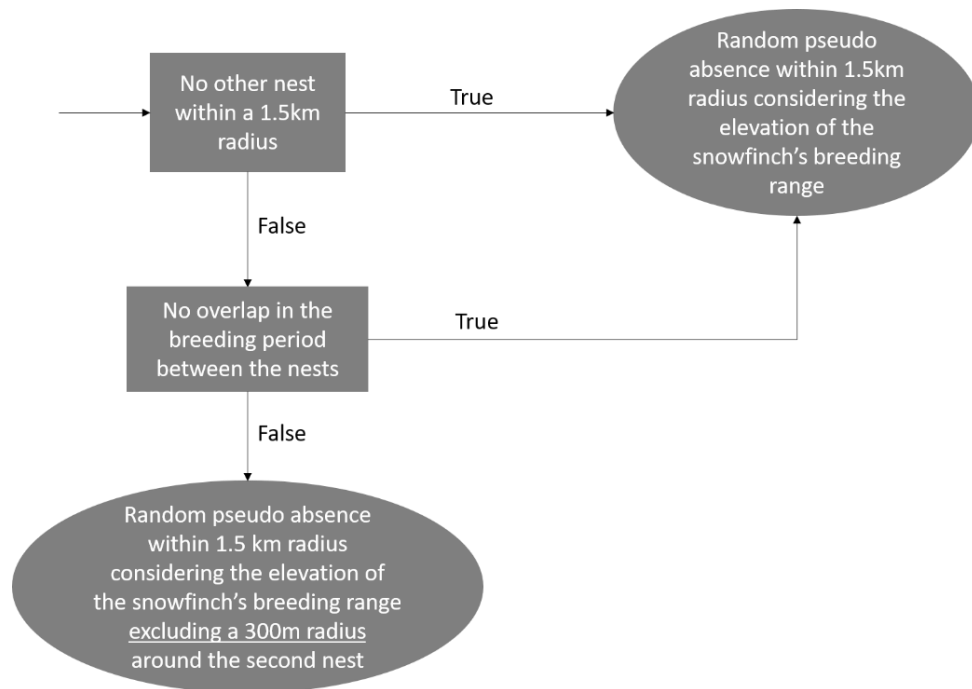
Habitat mapping of the cavity characteristics

Structure	Pseudo-absence point
Buildings	Random distance (max distance = perimeter of building) and random height (max height = building height). PA was defined as the crevice/hole closest to the random point.
Nest box	Unoccupied nest box e.g. nest box for which no Snowfinch breeding attempt was recorded since installation (no paired design)
Rock crevice	Random distance and angle from nest cavity (min distance = 20m; max distance = 100m). Pseudo-absence point was determined as cavity closest to the random point.
Ski lift pylon	All cavity entries of the same pylon were numbered and a random number was drawn determining the pseudo-absence cavity.

Nest box exposure: Sum of the distance to the left, right, in front and above the nest box (max. distance = 5m). Here, nest box exposure = 16m



Appendix C



Scheme for dynamic pseudo-absence sites: The PA sites for the snow cover retrieval of nests from 2020 were allowed to be at any place within a 1.5 km radius where no other nest was active at the same time and within an elevational boundary between 1900 – 3100m a.s.l.