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Short Communication

Nest orientation and proximity to snow patches are important for nest site selection of a cavity breeder at high elevation

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Timing and location of reproduction are central to reproductive success across taxa. Among birds, many species have evolved specific strategies to cope with environmental variability including shifts in timing of reproduction to track resource availability or selecting suitable nest location. In mountain ecosystems, complex topography and pronounced seasonality result in particularly high spatiotemporal variability of environmental conditions. Moreover, the risk of climate-induced resource mismatches is particularly acute in mountain regions given that temperature is increasing more rapidly than in the lowlands. We investigated how a high-elevation passerine, the white-winged snowfinch *Montifringilla nivalis*, selects its nest site in relation to nest cavity characteristics, habitat composition and snow condition. We used a combination of field habitat mapping and satellite remote sensing to compare occupied nest sites with randomly selected pseudo-absence sites. In the first half of the breeding season, snowfinches preferred nest cavities oriented towards the morning sun while they used cavities proportional to their availability later on. This preference might relate to the nest microclimate offering eco-physiological advantages, namely thermoregulatory benefits for incubating adults and nestlings under the harsh conditions typically encountered in the alpine environment. Nest sites were consistently located in areas with greater-than-average snow cover at hatching date, likely mirroring the foraging preferences for tipulid larvae developing in meltwater along snowfields. Due to the particularly rapid climate shifts typical of mountain ecosystems, spatiotemporal mismatches between foraging grounds and nest sites are expected in the future. This may negatively influence demographic trajectories of the white-winged snowfinch. The installation of well-designed nest boxes in optimal habitat configurations could to some extent help mitigate this risk.

Keywords: cavity nesting, climate change, mountain ecosystem, nest microclimate, white-winged snowfinch



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Introduction

Selecting the right place and time for reproduction is crucial, especially so for species inhabiting highly variable environments (McFarland et al. 2017). For altricial birds, nest site selection is particularly important because the nest location influences the time-and energy budget of provisioning adults (de Zwaan et al. 2019), as well as the growth and body condition of the chicks (Johst et al. 2001, Catry et al. 2013). Microclimate of the nest can affect the incubation cost (Rauter and Reyer 2000), nestling development (Mueller et al. 2019) and post-fledgling survival (Greño et al. 2008). The quality and composition of the habitat in the nest surroundings on the other hand influences the foraging distance and therefore with time and energy invested in provisioning and self-maintenance. Increasing distance to high quality foraging habitat can reduce the provisioning rates, chick conditions and fledgling success (Catry et al. 2013). Furthermore, nest location can influence predation risk (Rauter et al. 2002).

Mountain ecosystems are characterised by a high temporal and spatial variability in environmental conditions. The onset of snowmelt governs foraging habitat suitability during the reproduction period of most mountain birds. Many ground-foraging mountain birds rely on soil invertebrates, notably insect larvae that develop in the meltwater, to raise their young (Antor 1995, Brodmann and Reyer 1999, Resano-Mayor et al. 2019). Therefore, snowmelt and the following brief time window that provides short vegetation, enabling efficient ground feeding, result in a peak of optimal foraging conditions (Resano-Mayor et al. 2019, Barras et al. 2020). Winter snowfall and therewith the snowpack in spring further contributes to interannual variation in snow conditions. On top of temporal variability, snow cover is also variable in space. Snow melt occurs at different rates on ridges compared to depressions because of wind dynamics and the snow cover depth varying with these topographic features. Due to the interplay between the topography and weather conditions, suitable foraging sites are patchily distributed in space and time. Bird species breeding in high-elevation biomes have therefore evolved strategies to cope with the variability and stochasticity of their environment to optimise reproductive success (Bollmann and Reyer 2001, Rauter et al. 2002, Arlettaz et al. 2017). Such strategies include for example to skip breeding in years with unfavourable conditions, adjusting the timing of reproduction to match resource peak or to select a nest location with favourable microclimatic conditions (Martin and Wiebe 2004).

These fine-tuned behavioural and physiological adaptations of specialised high-elevation species might be disrupted by ongoing environmental changes (Martin and Wiebe 2004, Chamberlain et al. 2012). Climate change effects are particularly strong in mountain regions which have experienced a faster rate of ambient temperature increase compared to the global average (Auer et al. 2007, Pepin et al. 2015). Higher temperatures in spring alter the timing and duration of the snowmelt process (Steger et al. 2013, Klein et al. 2016), thus modifying the availability of food sources during the

reproduction period (Barras et al. 2021). Shifts in peak food availability might lead to a phenological mismatch or enlarge the distance between high quality foraging habitat and suitable nest sites and consequently increase time and energy necessary for provisioning. Moreover, rising temperatures can influence the suitability of nest cavities as their temperature profile might depend on the prevailing weather conditions. Basic knowledge of nest site selection is thus needed to evaluate the potential impact of global warming on the population dynamics of high-elevation bird species.

We investigated nest-site selection of the white-winged snowfinch *Montifringilla nivalis* (hereafter snowfinch), a typical species of high-elevation environments in the Swiss Alps to assess spatial association of nest sites and foraging habitats and characterize the small-scale cavity characteristics. We compared nest sites with randomly generated pseudo-absence site (hereafter PA sites) to infer about the nest site selection. While much is already known about this species' foraging habitat requirements (Brambilla et al. 2017, Resano-Mayor et al. 2019), we still lack information about nest site selection and the association between nest sites and foraging habitat, which is the focus of this study. The European sub-species inhabits the alpine and nival zones 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). The nestling diet of snowfinch mainly consists of arthropods, especially tipulid larvae (Glutz von Blotzheim and Bauer 1997). These larvae develop in meltwater next to snowfields which make snowfield margins important foraging habitat. Long term data suggests that snowfinch hatching dates have no longer coincided with an earlier snowmelt in recent years, particularly at low elevations (Schano et al. 2021) where populations declined the strongest (Knaus et al. 2018). We expected that 1) snowfinches select nest cavities according to microclimatic conditions e.g. cavity temperature. We expect a selection for east and south exposed cavities as these orientation typically provide higher internal temperatures (Ardia et al. 2006). Furthermore, we expected that 2) snowfinches prefer higher above ground nest cavities to avoid predation. Given the importance of snowfield margins as foraging habitats, we expected 3) a preference to nest in areas with high snow cover. Short distance to high quality foraging habitat might reduce the time and energy the adults need to invest in feeding the nestlings.

Material and methods

Study areas

We searched for snowfinch nest sites in four (2018, 2019) and six (2020) core study areas across the Swiss Alps (Supporting information). The areas covered an elevational gradient ranging between 1900 and 3100 m a.s.l. which corresponds to the breeding range of snowfinches in Switzerland (Knaus et al. 2018). The core areas were visited at least once every second

week between 1 June and 15 August to search for active nests. Content could not be checked except for nest boxes due to inaccessibility of the nest cavities. Potential nest sites were observed repeatedly throughout the breeding season to assess the stage of the brood (nest building, incubation, nestling period, fledged) from behavioural observations. Only nests where we observed at least one feeding event (i.e. an adult entering the nest with food), heard begging calls of the nestlings or where we could detect at least an egg or nestlings (for nest box broods) were subsequently considered occupied nest sites. Feeding occurred on average every 6 min (Niffenegger unpubl.). Observing nests for 30 min therefore allowed us to assess the stage of the brood. From these observations we calculated hatching and fledging dates for every brood (Supporting information).

Cavity characteristics

Sun orientation

We recorded the nest orientation expressed as cardinal direction of all occupied snowfinch nests located during the surveys of 2020 using a magnetic compass. For 102 broods ($n_{\text{ski lift pylons}} = 66$, $n_{\text{buildings}} = 21$, $n_{\text{nest boxes}} = 7$, $n_{\text{cliffs}} = 8$) we had information on hatching and fledging dates from repeated observations. We randomly selected one PA site for each nest in the same structure as the occupied nest (rock, building, ski lift pylon, nest box) within 2 to 20 m distance to measure the orientations in alternative available cavities. Based on cardinal direction of the entrance, nests and PA sites were assigned to morning sun orientation (NE, E, SE and S) or afternoon sun orientation (SW, W, NW and N). We divided nests into early and late, based on the median hatching date to look at changes in selection throughout the breeding season. To analyse the selection of nest cavity orientation, we used a generalized linear mixed effect model with a Bernoulli distribution and a logistic link function using sun orientation as response variable (1 = morning sun, 0 = afternoon sun). Presence versus PA and its interaction with early versus late breeding were included as fixed effects.

Nest box characteristics

In several study sites, nest boxes were mounted between 2012 and 2018. Out of 73 nest boxes, 30 were occupied by snowfinches at least once since their installation. For these nest boxes, we measured sun exposition (morning and afternoon sun), exposure and height above ground. Exposure is an index of the degree of protection of the nest box against weather (e.g. rainfall or direct sun exposition). It was measured as the sum of distances to any structure on the left, right and above the nest with a maximum distance of 5 m. We compared the characteristics of used and unused nest boxes to specifically assess the nest box selection.

We use a generalized mixed effects model with a Bernoulli distribution and a logistic link function using nest box use (1 = occupied nest boxes, 0 = unoccupied nest boxes) as response variable. Sun exposition (morning versus afternoon),

exposure and height above ground were included as fixed effects in the model.

Habitat composition

Ground cover type

Ground cover data (grassland, bushes, bare ground, rocks, stones, infrastructure, water) was collected for nests located during surveys between 2018 and 2020. Additionally, we also included nest sites in our study sites from an online data base (www.ornitho.ch) occupied between 2015 and 2019 ($n_{\text{total}} = 67$). The goal was to characterize the ground cover composition on the home-range scale. We only included nest records that corresponded to confirmed breeding, i.e. nests with eggs or chicks. The PA sites for all nests were randomly selected within a 1.5 km radius. Furthermore, the PA sites were restricted to the elevational range between 1800 and 3100 m.

We visually estimated the ground cover variables (Supporting information) in a 300 m radius around the nest and PA sites. This radius corresponds to the normal foraging distance of snowfinches during the breeding season (Grangé 2008). The habitat mapping in the field was conducted in 2020 between July and August after complete snowmelt or when snow cover was less than 2% within the 300 m radius. The average elevation, slope and exposition (aspect) on a 100 m radius and their standard deviations were retrieved from a digital elevation model with a 25 m spatial resolution (Swisstopo 2005). The topographic variables were collected on a smaller scale compared to ground coverage to reflect the local conditions more accurately.

A generalized mixed effects model with a Bernoulli distribution and the logistic link function was used to relate nest site use (1 = nest site, 0 = PA site) to the ground cover and topography in the nest surroundings. The nest identity was used as a random factor.

Remote-sensed snow cover

We used remote-sensed snow cover data to assess the relationship between snow cover at hatching date and use of nest site. Snow cover was retrieved from a raster-based, binary snow cover map with a spatial resolution of 20 m (Gascoïn et al. 2018, 2019). This analysis was based on broods located during nest surveys in 2018–2020 for which we had sufficient data to calculate the hatching date ($n_{\text{nests 2018}} = 12$, $n_{\text{nests 2019}} = 25$, $n_{\text{nests 2020}} = 102$). Snow cover was extracted from images taken between 1 March and 31 August. We extracted the proportion of snow-covered pixels within a 100 m radius around nests and PA sites. We excluded days for which more than 20% of pixel values were missing within the 100 m radius. The data was subsequently checked for implausible values that can for example arise from subpixel clouds or errors in the cloud masking process. Obvious and inexplicable outliers were removed. We linearly interpolated snow cover for days without satellite images and extracted the snow cover at the hatching date therefrom. We extracted snow cover at hatching dates from the snow cover at the nest sites and its

corresponding PA sites. PA sites were randomly generated and did not overlap within a 300 m radius around other active nests.

A generalized mixed effects model with a Bernoulli distribution and the logistic link function was used to correlate the nest site use (nest site versus PA site) with the snow cover at the hatching date for all broods as well as for early and late broods separately. Year and elevation were included as a fixed factor in the models. The brood identity was used as a random factor to take the paired design into account.

Statistical analysis

All linear models were fitted with the *brm* function of the 'brms' package (Bürkner 2018) with 4 chains and 2000 iterations. The minimum effective sample size was 2377. We used flat, so called improper priors, for all fixed effects, a folded-t distribution with 3 degrees of freedom, mean 0 and standard deviation of 2.5 for random effects and a student-t distribution with 3 degrees of freedom, mean 0 and standard deviation of 2.5 for the intercept. The convergence of the MCMC simulation was assessed both visually and based on the \hat{R} value. All \hat{R} value were smaller or equal to 1.01. The model residuals were analysed visually to check how well the model assumptions were met. We first fitted models without quadratic effects and subsequently added quadratic terms if they were deemed necessary. This can be assessed by plotting residuals against each predictor (Korner-Nievergelt et al. 2015). Based on the residual analyses, we included the quadratic term of elevation and snow cover in the snow cover model. We assessed spatial autocorrelation based on semi-variograms and Moran's I. We used R ver. 4.1.2 (www.r-project.org) and QGIS ver. 3.10.4 (QGIS Development Team 2020) for all analyses.

Results

Cavity characteristics

Sun orientation

Out of 102 nest cavities, 54 were oriented towards the morning sun. Cavity exposition towards SE and NW were most common with 33.3% and 26.5% of all occupied cavities. In the first half of the breeding season, nest sites had a probability of being oriented towards the morning sun of 68.0% (95% CrI: 53.2–80.7%) compared to PA cavities 38.4% (25.0–53.4%) (Fig. 1), indicating a preference for morning sun oriented cavities. In the second half of the breeding season, a similar proportion of nest cavities and PA sites were morning-sun oriented. Nest cavities had a probability of 38.4% (25.1–53.2%) to be morning-sun oriented, while PA sites had a probability of 44.7% (30.4–59.5%) for the same orientation in the second half of the breeding season (Fig. 1).

Nest box characteristics

The comparison of used and unused nest boxes did not indicate a clear association between nest box height and use. However, less exposed e.g. more weather protected nest boxes were clearly preferred (Supporting information).

Habitat composition

Ground cover type

Cover of rock and infrastructure (e.g. buildings and ski lifts) and grass cover were most strongly correlated with nest site use. Cover of rock and infrastructure was, on average, higher at nest sites (median: 3.25%, 1st and 3rd quartile: 1.5–5%, $n=67$) compared to PA sites (median: 0.5%, 1st and 3rd quartile: 0.0–1.6%) and the model indicates a strong

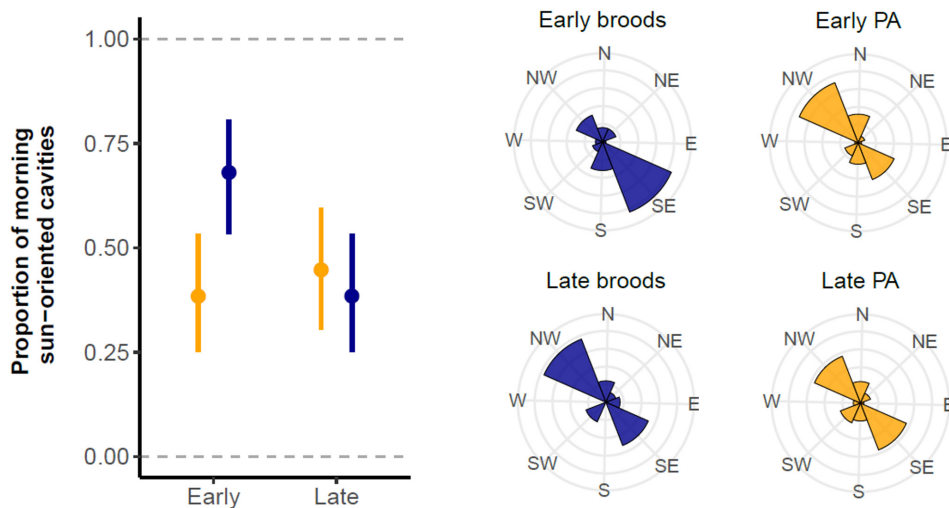


Figure 1. Proportion of morning sun-oriented nest cavities (blue) and pseudo-absence sites (orange). Broods were divided into early and late hatching broods based on the median hatching date in 2020 (early: hatching date < median hatching date; late: hatching date \geq median hatching date). PA cavities were assigned the hatching date of their corresponding brood. Left: Proportion of morning sun orientation and error bars indicating the 95% credible interval based on a generalized linear mixed effect model. Right: Distribution of nest orientations for early and late broods and the PA cavities. $n_{\text{early}}=51$, $n_{\text{late}}=51$.

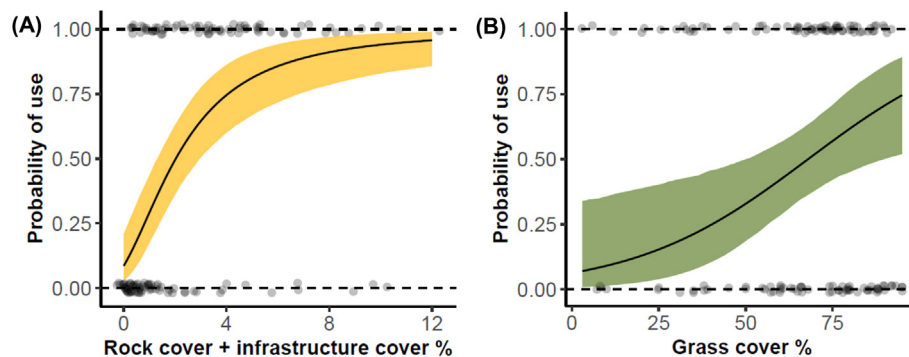


Figure 2. Probability of nest site use (nest site: $y=1$, PA site: $y=0$) in relation to coverage of rocks and infrastructures and coverage of grassland within a 300 m radius around the nest. All other predictors in the model (Table 1) except coverage of rocks and infrastructure (A), and coverage of grassland (B), respectively, were fixed at their mean values for calculating the regression line. Shaded area denotes the 95% credibility interval. $n_{\text{nest sites}}=67$, $n_{\text{pseudo-absence sites}}=67$.

selection for such structures (Fig. 2a). Median grass cover at nest sites was 71.5% (1st and 3rd quartile: 53.5–79%) and 68% (1st and 3rd quartile: 55.3–84.5%) at PA sites. Based on a logistic regression model, nest location with a high grass cover were preferred (Fig. 2b, Table 1). Bush cover and topographic variable did not show clear correlations with nest site selection.

Remote-sensed snow cover

The median snow cover at hatching varied strongly across the three-year study period ranging between 23.9% (1st and 3rd quartile: 0.00–53.3%) in 2020 and 69.9% (1st and 3rd quartile: 48.8–79.0%) in 2019. The median hatching date instead was similar across years (2018 = 14 June, 2019 = 16 June, 2020 = 9 June). Overall, 56.8% of broods ($n=79$) hatched when snow cover was at least 25% in a 100 m radius around the nest sites. Snowfinch nest sites were consistently located in areas with intermediate to high snow cover, particularly in the case of early broods (Fig. 3a–b, Table 2), indicating a preference for more than average snow cover. This trend was consistent throughout the study period but was not evident for late broods (Fig. 3c).

Discussion

This study sheds light on the abiotic drivers of nest site selection in a declining high-elevation passerine. It thereby complements the results of former investigations on foraging and dietary biology of the species. Our results show that snowfinches in the Alps select nest sites in areas with intermediate to high snow cover, which have been shown to offer optimal foraging conditions (Brambilla et al. 2017, Resano-Mayor et al. 2019). We could further evidence a preference for nest sites oriented to morning sun early in the breeding season.

Cavity characteristics

The selection of nest sites oriented towards the morning sun early during the breeding season might relate to the microclimatic conditions inside the nest cavity. Nest boxes oriented towards the morning sun have higher inside temperatures, especially in the morning hours (Ardia et al. 2006), potentially providing eco-physiological advantages in a cold environment. Nest microclimate, especially temperature, can

Table 1. Estimated model coefficients and the 95% credibility interval from a generalized mixed effect model for the nest site use in relation to the habitat composition and topography. Habitat composition was measured within a 300 m radius, topographical variables within a 100 m radius. All numeric predictors except sin and cos exposition were centred and scaled before the analysis (original data: Supporting information). $n_{\text{ests}}=67$, $n_{\text{pseudo-absences}}=67$.

Predictor variable	Standardized estimate	2.5% quantile	97.5% quantile	Unstandardized estimate	2.5% quantile	97.5% quantile
Grass cover (%)	1.01	0.32	1.78	0.04	0.01	0.08
Bush cover (%)	0.51	-0.18	1.22	0.04	-0.01	0.09
Log (rock and infrastructure cover (%))	1.72	1.08	2.47	2.40	1.51	3.45
Slope (°)	-0.16	-0.74	0.43	-0.02	-0.08	0.05
SD slope (°)	0.46	-0.12	1.12	0.14	-0.04	0.34
Eastness (°N) (sin exposition)	0.18	-0.46	0.82	0.18	-0.46	0.82
Northness (°N) (cos exposition)	-0.68	-1.57	0.18	-0.68	-1.57	0.18
SD exposition (°N)	0.25	-0.24	0.76	0.01	-0.01	0.02
Elevation (100 m)	0.05	-0.25	0.55	0.02	-0.17	0.22

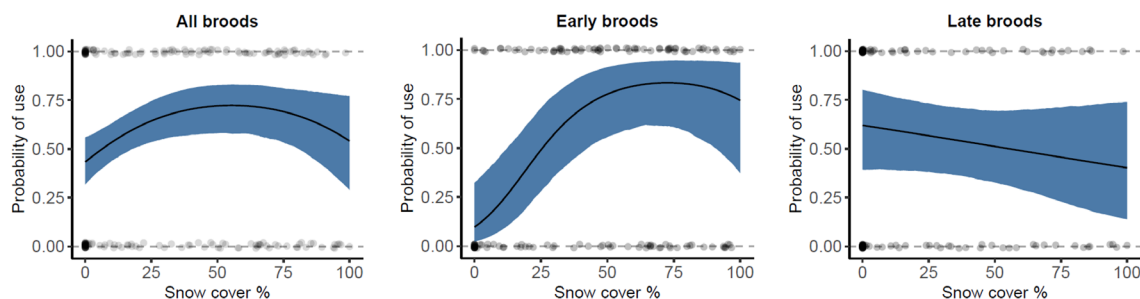


Figure 3. Probability of nest site use (nest site: $y = 1$, pseudo-absence-site: $y = 0$) in relation to snow cover at hatching within a 100 m radius around the nest. Pseudo-absences were assigned the hatching date of their corresponding brood. All continuous predictors (elevation, hatching date) except snow cover were fixed at their mean values for obtaining the regression line. Shaded area denotes the 95% credibility interval. (Left) all broods. (Middle) early broods (hatching date < median hatching date 2018–2020). (Right) late broods (hatching date > median hatching date 2018–2020). $n_{\text{neests } 2018} = 12$, $n_{\text{neests } 2019} = 25$, $n_{\text{neests } 2020} = 102$, $n_{\text{PA}} = 139$.

affect incubation costs (Vleck 1981, Rauter and Reyer 2000, Nord and Nilsson 2011), nestling development (Pérez et al. 2008, Mueller et al. 2019, de Zwaan et al. 2020) and breeding success (Dawson et al. 2005, Burton 2006, Gibson et al. 2016). Higher nest temperatures can reduce the time needed for incubation or brooding the nestlings (Mueller et al. 2019). Therefore, adults could potentially increase the number and

Table 2. Estimated model coefficients with standard errors (SE) and the 95% credibility interval from a generalized linear effect model for the nest site use in relation to the snow cover at the hatching date, hatching date, elevation and year. Separate models were fitted for all broods, early and late broods. All numeric predictors were centred and scaled before the analysis. $n_{\text{neests } 2018} = 12$, $n_{\text{neests } 2019} = 25$, $n_{\text{neests } 2020} = 102$.

Predictor variable	Estimate	SE	2.5% quantile	97.5% quantile
All broods				
Intercept	0.85	0.48	-0.06	1.81
Snow cover	0.5	0.22	0.08	0.93
Snow cover ²	-0.43	0.18	-0.78	-0.06
Hatching day	0.2	0.16	-0.13	0.53
Year 2019*	-0.47	0.56	-1.56	0.64
Year 2020*	-0.3	0.47	-0.95	0.9
Elevation	0.1	0.14	-0.17	0.38
Elevation ²	-0.26	0.11	-0.48	-0.04
Early broods				
Intercept	0.26	0.68	-1.07	1.59
Snow cover	1.18	0.30	0.61	1.77
Snow cover ²	-0.68	0.24	-1.18	-0.21
Hatching day	0.23	0.48	-0.72	2.27
Year 2019*	-0.29	0.86	-2.03	1.35
Year 2020*	0.68	0.69	-0.67	2.05
Elevation	-0.19	0.24	-0.65	0.26
Elevation ²	-0.34	0.19	-0.73	0.02
Late broods				
Intercept	0.67	0.79	-0.83	2.29
Snow cover	-0.36	0.30	-0.95	0.22
Hatching day	-0.18	0.29	-0.75	0.40
Year 2019*	-0.13	0.89	-1.86	1.61
Year 2020*	-0.62	0.76	-2.21	0.81
Elevation	0.36	0.22	-0.06	0.79
Elevation ²	-0.24	0.15	-0.55	0.05

* Reference year is 2018.

duration of foraging trips as a response to higher nest temperatures (Rauter et al. 2002, Walters et al. 2016). This might not only lead to higher provisioning rates but also increase the time spent for self-maintenance.

Yet, this temperature effect still ought to be demonstrated for snowfinch nest sites as we did not measure microclimate inside the nest cavities. Especially, it remains unclear if the temperature effect would hold true for all types of nests (rocks, pylons and buildings) as the temperature inertia might vary considerably among them (Grüebler et al. 2014, Maziarz et al. 2017, Larson et al. 2018, Fontaine et al. 2021).

Habitat composition

Generally, we found many snowfinch nest sites in ski lift pylons and buildings. These nest locations might differ in their proximity to foraging habitats. Especially the vertical distance to foraging grounds can be considerably larger for nest sites in cliffs compared to other nest types. Furthermore, snow grooming and artificial snow in ski resort might alter the quality of foraging habitats. Our results suggest that snowfinch nest sites are located in areas with above-average snow cover at hatching, especially during the first half of the breeding season. This trend was consistent during the three-year study period but the average snow cover at hatching varied strongly between years, ranging from 23.9% (1st and 3rd quartile: 0.00–53.3%) in 2020 to 69.9% (1st and 3rd quartile: 48.8–79.0%) in 2019. These results are in line with a study of the long-term trend of the breeding phenology of snowfinches in Switzerland (Schano et al. 2021). The long-term data suggests that two thirds of the broods hatch during the snow melting period, but this proportion decreased with the advancement of the snowmelt at lower elevations in recent years (Schano et al. 2021).

Snowmelt typically governs plant and invertebrate phenology at high elevation and hence modifies food availability and abundance at higher trophic levels (Liebezeit et al. 2014, Kwon et al. 2019, Barras et al. 2020). Therefore, the timing of reproduction as well as the choice of the nest location in relation to the habitat composition and, especially to snow cover, might be crucial for successful reproduction. Different insect

larvae, particularly tipulids, are important components of the nestling diet of snowfinches (Heiniger 1991). The abundance of tipulid larvae is particularly high next to the melting snow front (Resano-Mayor et al. 2019) and snow patches hence represent an important foraging habitat for snowfinches (Brambilla et al. 2017, Resano-Mayor et al. 2019). The selection of areas with high snow cover might reflect the foraging preference of the species. High snow cover on the hatching date might provide good foraging conditions, e.g. long-lasting availability of snowfield margins and thus food throughout the three week nestling period. Moreover, invertebrate fall-out on snow can additionally offer easily accessible food (Antor 1995).

Climate change is expected to alter the snow cover extent and the timing of the snowmelt (Steger et al. 2013, Klein et al. 2016). Snow cover changes and therewith potential changes in food availability may affect the timing and duration of the breeding period. Yet, the consequences for alpine species depend on their ability to react to environmental shifts. Such reactions may include advancing the breeding period or shifting the breeding sites to higher elevation where the timing of snowmelt still coincides with their physiologically determined breeding period. In snowfinches, population declines in the lower parts of the elevational distribution suggest that an adaption to an earlier snowmelt may not occur (Schano et al. 2021). Furthermore, the current overall negative population development suggests that an upward shift could not compensate for the population losses at low elevations (Knaus et al. 2018).

In conclusion, supplementing nest boxes oriented towards the morning sun and sheltered from weather could benefit snowfinch populations by enhancing the availability of suitable nest sites, e.g. along an elevation gradient, and to some extent mitigate the expected negative effect of climate warming on the distance between nest sites and foraging grounds.

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Author contributions

Carole A. Niffenegger: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Writing – original draft (lead); Writing – review and editing (lead). **Christian Schano:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Raphaël Arlettaz:** Conceptualization (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Fränzi Korner-Nievergelt:** Conceptualization (supporting); Data

curation (equal); Formal analysis (equal); Project administration (lead); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/jav.03046>.

Data availability statement

Data are available on <https://doi.org/10.5281/zenodo.7258122> (Niffenegger et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Antor, R. J. 1995. The importance of arthropod fallout on snow patches for the foraging of high-alpine birds. – *J. Avian Biol.* 26: 81–85.
- Ardia, D. R., Pérez, J. H. and Clotfelter, E. D. 2006. Nest box orientation affects internal temperature and nest site selection by tree swallows. – *J. Field Ornithol.* 77: 339–344.
- Arlettaz, R., Christe, P. and Schaub, M. 2017. Food availability as a major driver in the evolution of life-history strategies of sibling species. – *Ecol. Evol.* 7: 4163–4172.
- Auer, I., Böhm, R., Jurkovic, A., Lipa, W., Orlik, A., Potzmann, R., Schöner, W., Ungersböck, M., Matulla, C., Briffa, K., Jones, P., Efthymiadis, D., Brunetti, M., Nanni, T., Maugeri, M., Mercalli, L., Mestre, O., Moisselin, J.-M., Begert, M., Müller-Westemeier, G., Kveton, V., Bochnicek, O., Stastny, P., Lapin, M., Szalai, S., Szentimrey, T., Cegnar, T., Dolinar, M., Gajic-Capka, M., Zaninovic, K., Majstorovic, Z. and Nieplova, E. 2007. HISTALP – historical instrumental climatological surface time series of the Greater Alpine Region. – *Int. J. Climatol.* 27: 17–46.
- Barras, A. G., Marti, S., Ertlin, S., Vignali, S., Resano-Mayor, J., Braunisch, V. and Arlettaz, R. 2020. The importance of seasonal environmental factors in the foraging habitat selection of Alpine Ring Ouzels *Turdus torquatus alpestris*. – *Ibis* 162: 505–519.
- Barras, A. G., Niffenegger, C. A., Candolfi, I., Hunziker, Y. A. and Arlettaz, R. 2021. Nestling diet and parental food provisioning in a declining mountain passerine reveal high sensitivity to climate change. – *J. Avian Biol.* 52.
- Bollmann, K. and Reyer, H.-U. 2001. Reproductive success of water pipits in an alpine environment. – *Condor* 103: 510–520.
- Brambilla, M., Cortesi, M., Capelli, F., Chamberlain, D., Pedrini, P. and Rubolini, D. 2017. Foraging habitat selection by alpine white-winged snowfinches *Montifringilla nivalis* during the nestling rearing period. – *J. Ornithol.* 158: 277–286.
- Brodmann, P. A. and Reyer, H.-U. 1999. Nestling provisioning in water pipits *Anthus spinoletta*: do parents go for specific nutrients or profitable prey? – *Oecologia* 120: 506–514.
- Bürkner, P.-C. 2018. Advanced Bayesian multilevel modeling with the R package brms. – *R J.* 10: 395–411.
- Burton, N. H. K. 2006. Nest orientation and hatching success in the tree pipit *Anthus trivialis*. – *J. Avian Biol.* 37: 312–317.

- Catry, I., Franco, A. M. A., Rocha, P., Alcazar, R., Reis, S., Cordeiro, A., Ventim, R., Teodósio, J. and Moreira, F. 2013. Foraging habitat quality constrains effectiveness of artificial nest-site provisioning in reversing population declines in a colonial cavity nester. – *PLoS One* 8: e58320.
- Chamberlain, D. A. N., Arlettaz, R., Caprio, E., Maggini, R., Pedrini, P., Rolando, A. and Zbinden, N. 2012. The altitudinal frontier in avian climate impact research. – *Ibis* 154: 205–209.
- Dawson, R. D., Lawrie, C. C. and O'Brien, E. L. 2005. The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. – *Oecologia* 144: 499–507.
- de Zwaan, D. R., Camfield, A. F., MacDonald, E. C. and Martin, K. 2019. Variation in offspring development is driven more by weather and maternal condition than predation risk. – *Funct. Ecol.* 33: 447–456.
- de Zwaan, D. R., Drake, A., Greenwood, J. L. and Martin, K. 2020. Timing and intensity of weather events shape nestling development strategies in three alpine breeding songbirds. – *Front. Ecol. Evol.* 8: 570034.
- Federal Office of Topography swisstopo 2005. The digital height model of Switzerland (DHM25 <https://www.swisstopo.admin.ch/en/geodata/height/dhm25.html>).
- Fontaine, A., Simard, A., Dubois, B., Dutel, J. and Elliott, K. H. 2021. Using mounting, orientation and design to improve bat box thermodynamics in a northern temperate environment. – *Sci. Rep.* 11: 7728.
- Gascoïn, S., Grizonnet, M., Bouchet, M., Salgues, G. and Hagolle, O. 2019. Theia snow collection: high-resolution operational snow cover maps from Sentinel-2 and Landsat-8 data. – *Earth Syst. Sci. Data* 11: 493–514.
- Gascoïn, S., Grizonnet, M., Klempka, T. and Salgues, G. 2018. Algorithm theoretical basis documentation for an operational snow cover product from Sentinel-2 and Landsat-8 data (Let-it-snow) (v1.0). Zenodo. <https://doi.org/10.5281/zenodo.1414452>
- Gibson, D., Blomberg, E. J., Atamian, M. T. and Sedinger, J. S. 2016. Nesting habitat selection influences nest and early offspring survival in greater sage-grouse. – *Condor* 118: 689–702.
- Glutz von Blotzheim, U. N. and Bauer, K. M. 1997. *Handbuch der Vögel Mitteleuropas*. Band 14, Passeriformes. Teilband 1. – Aula-Verlag.
- Grangé, J.-L. 2008. Biologie de reproduction de la niverolle alpine *Montifringilla nivalis* dans les Pyrénées occidentales françaises. – *Nos Oiseaux* 55: 67–82.
- Greño, J. L., Belda, E. J. and Barba, E. 2008. Influence of temperatures during the nestling period on post-fledging survival of great tit *Parus major* in a Mediterranean habitat. – *J. Avian Biol.* 39: 41–49.
- Grüebler, M. U., Widmer, S., Korner-Nievergelt, F. and Naef-Daenzer, B. 2014. Temperature characteristics of winter roost-sites for birds and mammals: tree cavities and anthropogenic alternatives. – *Int. J. Biometeorol.* 58: 629–637.
- Heiniger, P. H. 1991. Anpassungsstrategien des Schneefinken *Montifringilla nivalis* an die extremen Umweltbedingungen des Hochgebirges. – *Ornithol. Beobach.* 88: 193–207.
- Johst, K., Brandl, R. and Pfeifer, R. 2001. Foraging in a patchy and dynamic landscape: human land use and the white stork. – *Ecol. Appl.* 11: 60–69.
- Keller, V., Herrando, S., Voříšek, P., Franch, M., Kipson, M., Milanesi, P., Marti, D., Anton, M., Klvanova, A., Kalyakin, M., Bauer, H. and Foppen, R. 2020. European breeding bird atlas 2: distribution, abundance and change. – Lynx Edicions.
- Klein, G., Vitasse, Y., Rixen, C., Marty, C. and Rebetez, M. 2016. Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than to later snow onset. – *Clim. Change* 139: 637–649.
- Knaus, P., Antoniazza, S., Wechsler, S., Guélat, J., Kéry, M., Strelbel, N. and Sattler, T. 2018. Swiss Breeding Bird Atlas 2013–2016. Distribution and population trends of birds in Switzerland and Liechtenstein. – Swiss Ornithological Inst.
- Korner-Nievergelt, F., Roth, T., Von Felten, S., Guélat, J., Almasi, B. and Korner-Nievergelt, P. 2015. Bayesian data analysis in ecology using linear models with R, BUGS and Stan. – Academic Press.
- Kwon, E., Weiser, E. L., Lanctot, R. B., Brown, S. C., Gates, H. R., Gilchrist, G., Kendall, S. J., Lank, D. B., Liebezeit, J. R., McKinnon, L., Nol, E., Payer, D. C., Rausch, J., Rinella, D. J., Saalfeld, S. T., Senner, N. R., Smith, P. A., Ward, D., Wiseman, R. W. and Sandercock, B. K. 2019. Geographic variation in the intensity of warming and phenological mismatch between Arctic shorebirds and invertebrates. – *Ecol. Monogr.* 89: e01383.
- Larson, E. R., Eastwood, J. R., Buchanan, K. L., Bennett, A. T. D. and Berg, M. L. 2018. Nest box design for a changing climate: the value of improved insulation. – *Ecol. Manage. Restor.* 19: 39–48.
- Liebezeit, J. R., Gurney, K. E. B., Budde, M., Zack, S. and Ward, D. 2014. Phenological advancement in arctic bird species: relative importance of snow melt and ecological factors. – *Polar Biol.* 37: 1309–1320.
- Martin, K. and Wiebe, K. L. 2004. Coping mechanisms of alpine and arctic breeding birds: extreme weather and limitations to reproductive resilience. – *Integr. Comp. Biol.* 44: 177–185.
- Maziarczyk, M., Broughton, R. K. and Wesolowski, T. 2017. Microclimate in tree cavities and nest-boxes: implications for hole-nesting birds. – *For. Ecol. Manage.* 389: 306–313.
- McFarland, H. R., Kendall, S. and Powell, A. N. 2017. Nest-site selection and nest success of an Arctic-breeding passerine, Smith's Longspur, in a changing climate. – *Condor* 119: 85–97.
- Mueller, A. J., Miller, K. D. and Bowers, E. K. 2019. Nest microclimate during incubation affects posthatching development and parental care in wild birds. – *Sci. Rep.* 9: 5161.
- Niffenegger, C. A., Schano, C., Arlettaz, R. and Korner-Nievergelt, F. 2022. Data from: Nest orientation and proximity to snow patches are important for nest site selection of a cavity breeder at high elevation. – Zenodo, <https://doi.org/10.5281/zenodo.7258122>.
- Nord, A. and Nilsson, J.-Å. 2011. Incubation temperature affects growth and energy metabolism in blue tit nestlings. – *Am. Nat.* 178: 639–651.
- Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M. Z., Liu, X. D., Miller, J. R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M. B., Williamson, S. N., Yang, D. Q. and Mountain Research Initiative, E. D. W. W. G. 2015. Elevation-dependent warming in mountain regions of the world. – *Nat. Clim. Change* 5: 424–430.
- Pérez, J. H., Ardia, D. R., Chad, E. K. and Clotfelter, E. D. 2008. Experimental heating reveals nest temperature affects nestling condition in tree swallows *Tachycineta bicolor*. – *Biol. Lett.* 4: 468–471.
- QGIS Development Team 2020. QGIS geographic information system. – Open Source Geospatial Foundation Project.

- Rauter, C. and Reyer, H. U. 2000. Thermal and energetic consequences of nest location and breeding times in water pipits *Anthus spinoletta*. – J. Ornithol. 141: 391–407.
- Rauter, C. M., Reyer, H.-U. and Bollmann, K. 2002. Selection through predation, snowfall and microclimate on nest-site preferences in the water pipit *Anthus spinoletta*. – Ibis 144: 433–444.
- Resano-Mayor, J., Korner-Nievergelt, F., Vignali, S., Horrenberger, N., Barras, A. G., Braunisch, V., Pernolet, C. A. and Arlettaz, R. 2019. Snow cover phenology is the main driver of foraging habitat selection for a high-alpine passerine during breeding: implications for species persistence in the face of climate change. – Biodivers. Conserv. 28: 2669–2685.
- Schano, C., Niffenegger, C., Jonas, T. and Korner-Nievergelt, F. 2021. Hatching phenology is lagging behind an advancing snowmelt pattern in a high-alpine bird. – Sci. Rep. 11: 22191.
- Steger, C., Kotlarski, S., Jonas, T. and Schär, C. 2013. Alpine snow cover in a changing climate: a regional climate model perspective. – Clim. Dyn. 41: 735–754.
- Vleck, C. M. 1981. Energetic cost of incubation in the zebra finch. – Condor 83: 229–237.
- Walters, L. A., Webber, J. A., Jones, B. A. and Volker, C. L. 2016. Taking a break: the relationship between ambient temperature and nest attendance patterns of incubating Carolina chickadees *Poecile carolinensis*. – Wilson J. Ornithol. 128: 719–726.