



OPEN Potential effect of early snowmelt on nestling growth and first-year apparent survival in an alpine bird

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Climate change is shifting the environmental conditions during key life cycle events such as during reproduction. The shift in the environmental conditions can change for example the food availability and therewith influence growth and survival of offspring. We used nine years of ringing data of white-winged snowfinches *Montifringilla nivalis nivalis*, a high-elevation bird species, to assess how variation in temperature and snow conditions affected nestling growth and first-year apparent survival (probability that an individual survives and returns to the study area). We used linear mixed models and a path analysis to estimate the effect of environmental conditions on nestling growth and a multi-state mark-recapture model to estimate apparent survival. Nestlings raised during snowmelt tended to have slightly higher body mass, longer tarsi and longer wings than nestlings raised after snowmelt and apparent first-year survival was lower in years when snowfinches breed late relative to the timing of snowmelt. These findings suggest that advancing snowmelt may be associated with reduced offspring fitness and potentially contributed to observed population declines in this high-elevation species.

Keywords Snowmelt, Climate change, Nestling development, High elevation, White-winged snowfinch

In seasonal habitats, animals reproduce when resources are most abundant. Climate change has altered the timing of resource peaks and therewith, many animals have adjusted the onset of reproduction^{1,2}. However, these adjustments in the timing of reproduction may be insufficient to track the extent of environmental change^{3–6}. The breeding phenology of thick-billed murres *Uria lomvia*, for example, depends on the timing of sea-ice breakup in the Arctic. They reproduce earlier as the sea-ice break-up advances. However, they only advanced their phenology by around 7 days while sea-ice breakup advanced by more than a month during the same period⁷. As a consequence, the peak of resource demand mismatches the peak in resource availability.

Missing the optimal timing for reproduction can affect offspring development by altering the balance between energy intake and energy expenditure. Low temperature, for example, can increase the cost of thermoregulation and might therefore slow down offspring development⁸. On the other hand, mistimed reproduction can also indirectly affect nestling growth via the quality or quantity of available food^{9–12}. Reduced nestling growth and smaller size of fledglings can lead to negative effects beyond the nestling period. It has been shown that fledglings with a lower body mass have lower survival¹³. Furthermore, smaller size, especially shorter wings, can impair the ability to escape from predators through poorer flight performance, thereby reducing survival¹³. Mistimed reproduction and the associated reduction in growth can thus have a long-lasting negative impact on offspring^{8,14,15}.

Mistiming is more likely to occur in habitats with fast warming and is therefore expected to be strongest in arctic regions and high-elevation habitats^{16,17}. However, often we have less data from these habitats¹⁸ because they are remote, and research is logistically demanding.

Here, we studied nestling growth and first-year apparent survival of a high-elevation bird species, the white-winged snowfinch *Montifringilla nivalis nivalis* in the Swiss and Austrian Alps. Snowfinches breed above the treeline, typically at elevations between 1900 and 3000 m a.s.l.¹⁹ and the population is declining in the lower parts of its range¹⁹. Snowfinches breed in cavities either in large rock faces, in buildings or in ski lift pylons²⁰. They typically lay eggs between mid-May and early June but the timing of reproduction can vary considerably

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between years²¹. The offspring are mainly feed with arthropod prey, especially Tipulidae larvae which are often collected along the edges of snowfields^{20,22}.

Snowmelt in the Swiss Alps has on average advanced 26 days between 1970 and 2015²³ which would require snowfinches to breed almost a month earlier in order to keep track with the snowmelt timing. However, snowfinches hatching dates advanced by less than a day per decades at elevations below 2200 m.a.s.l.²⁴. The aim of this study is to investigate how environmental conditions, especially snowmelt timing and temperature, influence nestling growth and first-year apparent survival of snowfinches. While previous studies have already investigated the effect of environmental conditions on phenology and nestling success^{11,12,25}, there is very little information about the effects of environmental conditions on first-year survival in alpine songbirds.

We collected morphometric measurements of snowfinch nestlings in a nestbox population in the Swiss Alps and one population in the Austrian Alps. The data was collected during nine years in the Swiss Alps and two years in Austria. We used linear models and a path analysis to assess how temperature and snowmelt influenced nestling growth in terms of body mass, tarsus length and wing length shortly before fledging. Secondly, we ringed nestlings and adult snowfinches and collected recapture and resighting data to estimate apparent survival. Apparent first-year survival (probability that an individual survives and returns to the study area) was estimated using a multi-state mark recapture model based on ringing data collected in the Swiss Alps ($n = 1603$). We assessed how first-year apparent survival was related to temperature and snow conditions during the breeding season. Due to a sexual dimorphism in size, we differentiated between males and females in our analyses. Females, which are on average smaller than males, might be impacted more strongly by adverse environmental conditions. In both sexes, nestling growth rate and apparent survival were expected to be higher for nestlings growing up during snowmelt and to be positively associated with temperature. Growing up during the time of snowmelt should provide optimal foraging conditions^{22,26} while thermoregulatory costs are reduced at higher temperature²⁷.

The results of this study advance the understanding of how altered environmental conditions affect the fitness of snowfinches, particularly through their influence on first-year apparent survival. The results about the link between environmental conditions and demographic parameters provide insights for predicting how climate change may influence the population dynamics of this characteristic high-elevation species.

Materials and methods

Nestling growth

Data collection

We collected data on morphometrics of snowfinch nestlings at a site in the Swiss Alps (46.58°N, 8.42°E, 2430.4 m a.s.l.) and a site in the Austrian Alps (47.11°N, 12.83°E, elevation between 2198 and 2535 m a.s.l.). The data set from Switzerland encompassed eight years of data collected between June 2016 and August 2023 while the Austrian data set consists of data collected in June and July 2022 and 2023. In both populations, morphometrics data was collected from broods in wooden nest boxes, as these are the only accessible nest sites of snowfinches. We started to check nestboxes between mid-May and early June depending on the accessibility of the study area. The nestboxes were subsequently checked every three to seven days with shorter intervals towards the expected hatching date. We took morphometric measurements of the nestling once the youngest nestling was at least 12 days old. Nestlings were weighed to the nearest 0.1 g, tarsus length was measured to the nearest 0.1 mm using a calliper, and wing length was measured to the nearest 1 mm using a ruler²⁸. Due to logistic constraints, data on tarsus length and wing length is available only for a subset of the nestlings. For body mass, we had 202 measurements ($n_{\text{during snowmelt}} = 125$, $n_{\text{after snowmelt}} = 77$), for tarsus length we had 177 measurements ($n_{\text{during snowmelt}} = 103$, $n_{\text{after snowmelt}} = 74$) and for wing length we had 129 measurements ($n_{\text{during snowmelt}} = 87$, $n_{\text{after snowmelt}} = 42$).

We collected saliva samples using sterile swabs to genetically determine the sex of the nestlings. The swabs were subsequently transferred to collection tubes containing ethanol and stored in a freezer at -18 °C until further processing²⁹, in prep]. For some nestlings, genetic sexing failed. We included these nestlings in the analysis assigning the category “unknown” for sex ($n_{\text{females}} = 98$, $n_{\text{males}} = 74$, $n_{\text{unknown}} = 22$).

Bird handling was authorised by Swiss Veterinary Service (Licence numbers LU02/16, LU02/19 and LU02/2022) and by county Salzburg (Amt der Salzburger Landesregierung Abt. Natur- und Umweltschutz, Gewerbe: 205-05RI/8-2022), county Carinthia (Bezirkshauptmannschaft Spittal an der Drau Bereich Bau und Umwelt: SP3-NS-3959/2022 (007/2022)) and the “Nationalpark Hohe Tauern”. Bird handling was carried out according to legal regulations and guidelines of the Swiss Federal Food Safety and Veterinary Office FSVO and the Austrian Federal County regulations of Carinthia and Salzburg.

We visually estimated snow cover during field visits or from pictures. Snow cover was defined as the percentage of snow-covered surface in a 300 m radius around the nest sites. This radius encompasses the main foraging radius of snowfinches during the nestling rearing period³⁰. Based on the snow cover data, we calculated the snowmelt intensity per brood. The snowmelt intensity was defined as the daily average of snow cover loss between hatching and the day of ringing. To assess the effect of temperature on the nestling development, we calculated the mean temperature between hatching and the day of morphometric measurements of nestlings, e.g., the temperature during the nestling period. We used temperature data recorded at meteorological stations close to our study sites. We used daily mean temperature at the meteorological station Grimselhospiz (46.57°N, 8.33°E, 1980 m a.s.l.) (Source: MeteoSwiss) for the Swiss data set and daily mean temperature values measured at Sonnblick meteorological station in Austria³¹ (47.05°N, 12.96°E, 3.106 m a.s.l.). To account for elevation difference between the meteorological station and the nest locations, we used an elevation correction of -0.65 °C /100 m.

Statistical analyses

All models were fitted in a Bayesian framework in the R environment version 4.4.3³². We used the *brm* function from the *brms* package version 2.22.0³³ for all linear models. The models were fitted with four chains and 2000 iterations per chain using default weakly informative priors. Convergence of the MCMC chains was assessed visually and with $\hat{R}$ values which had a maximum of 1.01.

The analysis of nestling growth had two aims. On one side, we aimed to describe the difference in growth for nestlings growing up during snowmelt vs. nestlings growing up after snowmelt. On the other side, we aimed to describe the mechanisms of how temperature and snowmelt influence nestling growth. We defined that nestlings grew up after snowmelt if most snow had melted before they hatched, i.e. when snow cover was less than 10% on the hatching day. We use the body mass, tarsus length and wing length at age of 15 days as three variables that describe nestling growth, and we analyse these three variables separately because growth in body mass and size variables may react differently to environmental variables.

We aimed to quantify the effect of temperature and snowmelt intensity on growth of snowfinch nestlings at an age of around 15 days. This age was chosen because the body mass of snowfinch nestlings usually peaks at an age of around 15 days before it slightly decreases again towards fledging (Supp. Info. 1). Tarsus length already reaches the maximum between day 10–12 while the wings continue to grow even after fledging. We included nestlings of age 12 to 17 and accounted for age within the analyses.

The linear mixed models to describe the difference in growth during and after snowmelt, included a binary variable for snow condition (during vs. after snowmelt), sex, the nestling age (range: 12–17 days) and the interaction between snow conditions and sex as fixed effect and a random effect of the brood identity to account for non-independence of data from siblings. The sex of the nestlings was included because females and males might differ in size.

To understand the mechanism of how temperature and snowmelt intensity influence growth, we used a path analysis. We divided the data into “during” and “after” snowmelt and analysed the data sets separately because the predictor variable snowmelt intensity was not available after snowmelt. The path analysis contained two linear models, one model to estimate the relationship between temperature and snowmelt (temperature-snow model), and a second linear model (environment-growth model) to estimate the effect of snowmelt and temperature on the nestling growth. This approach allowed to differentiate a direct effect of temperature on nestling growth from an indirect effect of temperature via snowmelt intensity. We accounted for the effect of hatching day, age of the nestling, time of the day and sex of the nestling by including these variables as fixed effects in the environment-growth model. Furthermore, we included the brood identity as a random factor in the environment-growth model to account for non-independence of data from siblings. All continuous variables were centred and scaled (i.e. standardized) for the analysis and model estimates were reported both on the standardized scale as well as on the scale of the original units. The indirect effect of temperature on growth parameters was estimated by multiplying the standardised model coefficient from temperature on snowmelt intensity with the standardised model coefficient of snowmelt intensity on any of the growth parameters³⁴.

For those nestlings that grew up after snowmelt, a linear mixed model was used with temperature, hatching date, sex and nestling age as fixed effects and the brood as random factor.

First-year apparent survival

Data collection

We collected mark-recapture data of nestling and adult snowfinches in the Swiss Alps between 2015 and 2024. The data set included in total 1603 individuals ($n_{\text{males}} = 1132$; $n_{\text{females}} = 471$) of which 119 were ringed as nestlings and 1484 birds were ringed as adults. The nestlings that were ringed, are the same individuals for which morphometric measurements were collected. They stem from broods in nestboxes (46.58°N, 8.42°E, 2430.4 m a.s.l.) and were ringed when they were at least 12 days old. Adult birds were captured mainly during winter from December to April when they aggregate in flocks and visit bird feeders. Winter captures occurred in four study sites in the Swiss Alps (Supp. Info. 2). We used mist nets and whoosh net traps to capture the birds. During the breeding season from June to August, we ringed occasionally adults at the nest site using nest traps. Birds were marked individually using a unique aluminium ring and an alphanumeric plastic ring with a three-digit code. The plastic rings can be read from distance with a scope and help to resight birds without the need to capture them. From the 1603 ringed birds, 597 individuals were recaptured or resighted (identified based on the alphanumeric plastic ring without recapture) again and 122 lost their alphanumeric plastic ring. The number of reencounters (recaptures and resightings) ranged from 0 to 7 per individual. Bird ringing was authorized by the Swiss Veterinary Service (Licence numbers LU02/16, LU02/19 and LU02/2022).

Temperature and the timing snowmelt were taken from the meteorological station Grimselhospiz: 46.57°N, 8.33°E, 1980 m a.s.l.) (Source: MeteoSwiss). We extracted automated daily snow depth measurements and daily mean temperature. Timing of snowmelt was defined as the day when snow depth was less than 15 cm for the first time in spring. We then calculated the days between snowmelt and the mean hatching date in each year (days since snowmelt) which can be interpreted as a proxy for phenological mismatch. We calculated the mean temperature during the breeding season of snowfinches. The breeding season was defined based on first and last hatching date from the nest box checks in a given year and therefore varied between years. As for the analyses of nestling growth, we adjusted temperature to the elevation of the nest sites using an elevation correction of $-0.65^\circ\text{C} / 100\text{ m}$.

Statistical analyses

We used Stan³⁵ via the Rstan package version 2.32.7³⁶ to fit a multi-state mark-recapture model^{37–39} that accounted for resighting probability and ring loss^{40,41}. Based on individual capture and resighting histories, the multi-state model allowed estimating the apparent survival, the resighting probability, and the ring loss probability separately.

Apparent survival means that the model can't differentiate between mortality and permanent emigration. The alphanumeric plastic rings sometimes break and get lost resulting in a lower detection probability of birds which lost their plastic ring. For every plastic ring number, or for individuals that were released without plastic ring, for the aluminium ring number i , a capture history $y_{i,1:l_i}$ was constructed that contained the observation history of ring i . l_i is the last occasion when ring i could be observed (last occasion of the study period for most rings except when the individual got a new plastic ring). We used a multinomial likelihood for the counts of the different observation histories C_{y_i} . $C \sim \text{Multinomial}(\mathbf{p}, N)$ where N is the number of releases, i.e., the number of plastic rings plus the number of individuals released without plastic ring.

The vector $\mathbf{p}$ contained the probability of each capture history which is calculated from the apparent survival probability ϕ , the probability to lose a plastic ring τ and the detection probability p as follows. The transition matrix contains the probabilities with which the birds change their states from 1=alive with both rings on, 2=alive with the plastic ring lost, 3=dead.

$$T_{i,t} = \begin{bmatrix} \phi_{i,t}(1-\tau_{i,t}) & 1-\phi_{i,t} & 0 \\ \phi_{i,t}\tau_{i,t} & \phi_{i,t} & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

And the observation matrix describes how individuals are detected.

$$O_{i,t} = \begin{bmatrix} p_{\text{marked}} & 0 & 1-p_{\text{marked}} \\ 0 & p_{\text{unmarked}} & 1-p_{\text{unmarked}} \\ 0 & 0 & 1 \end{bmatrix}$$

Based on the transition and observation matrices, the probability for the observation $y_{i,t}$ can recursively be calculated⁴²: $\zeta_{i,t,j} = \zeta_{i,t-1,1:3} \cdot T_{1:3,i,t,j} \cdot O_{j,i,t,y_{i,t}}$ where $\cdot$ is the scalar product (dot product). For the first occasion when a plastic ring on a bird was released f_i , $\zeta_{i,f_i,1} = 1$ if the bird was released with plastic ring and $\zeta_{i,f_i,1} = 0$ if the bird was released without plastic ring, $\zeta_{i,f_i,2} = 1$ if the bird was released without plastic ring and $\zeta_{i,f_i,2} = 0$ if the bird was released with plastic ring, and $\zeta_{i,f_i,3} = 0$ in all cases, because no bird was released when it was dead. Finally, the sum over the state-specific probabilities that the bird is observed $\zeta_{i,l_i,1:3}$ is the probability p_i of observation history i : $p_i = \sum_{j=1}^3 \zeta_{i,l_i,j}$

We estimated the apparent survival separately for sex, year and age classes (first-year vs. adult). We assumed resighting probability to vary by sex and year. Although we were only interested in first-year apparent survival, the model was substantially improved by including data of first-year and adult birds. Some birds were equipped with lightweight loggers for a different research project. We included whether a bird was equipped with a logger in the linear predictor of the apparent survival probability to account for potential effects of the logger.

$$\text{logit}(\phi_{[i,t]}) = \beta_{0 \text{ sex}[i], \text{age}[i,t], \text{year}[t]} + \beta_{1 \text{ logger}[i,t]} + \beta_{2 [i,t]} \text{ first occasion}$$

$$\text{logit}(p_{[i,t]}) = \beta_{0 \text{ sex}[i]} + \sigma_{\text{year}[t]}$$

Apparent survival could only be estimated between 2015 and 2023 because in the last year, it was not possible to disentangle apparent survival from resighting probability as we specified the model to have yearly resighting probability. First-year apparent survival of females could not be estimated in 2015 because all nestlings ($n=5$) were males.

We used linear mixed models to assess how environmental conditions affect the first-year apparent survival of snowfinches. Therefore, we correlated yearly apparent survival as the response variable and days since snowmelt and temperature during the breeding season as predictor. We fitted a separate model for the apparent survival probabilities of males and females. We used a beta model since the apparent survival is bounded between zero and one. This however meant that we couldn't include the uncertainty of the apparent survival estimate from the apparent survival model, which is only possible to implement with a normal error distribution. Results with a normal error distribution and accounting for the uncertainty of the apparent survival estimates were similar to the one using the beta error distribution.

Results

Nestling growth

Effect of snowmelt on nestling growth

We distinguished between nestlings growing up during and after snowmelt based on the snow cover on the hatching date. On the day of hatching, snow cover was on average 24.7%, ranging between 0% and 93.9%. In total, 75 out of 202 nestlings (37.1%) hatched after snowmelt. Based on the results from the linear mixed model, snowfinch nestlings growing up during snowmelt had a slightly higher body mass, longer tarsi and slightly longer wings at an age of 15 days than nestlings growing up after snowmelt (Fig. 1). The difference in body mass was slightly larger for males (mean: -1.6 g, 95%CrI: -3.2 – 0.10 g) than for females (mean: -0.72 g, 95%CrI: -2.3 – 0.85 g). Females growing up during snowmelt had on average a 0.43 mm longer tarsus (95% CrI: 0.15–0.73 mm) than nestlings growing up after snowmelt, while the difference was 0.32 mm (95% CrI: 0.02–0.6 mm) in males. The difference in wing length for nestlings growing up after vs. during snowmelt was small (females: -1.6 mm, 95% CrI: -4.3 – 0.93 mm; males: 1.1 mm, 95% CrI: -3.8 – 1.5 mm). The 95% uncertainty interval of

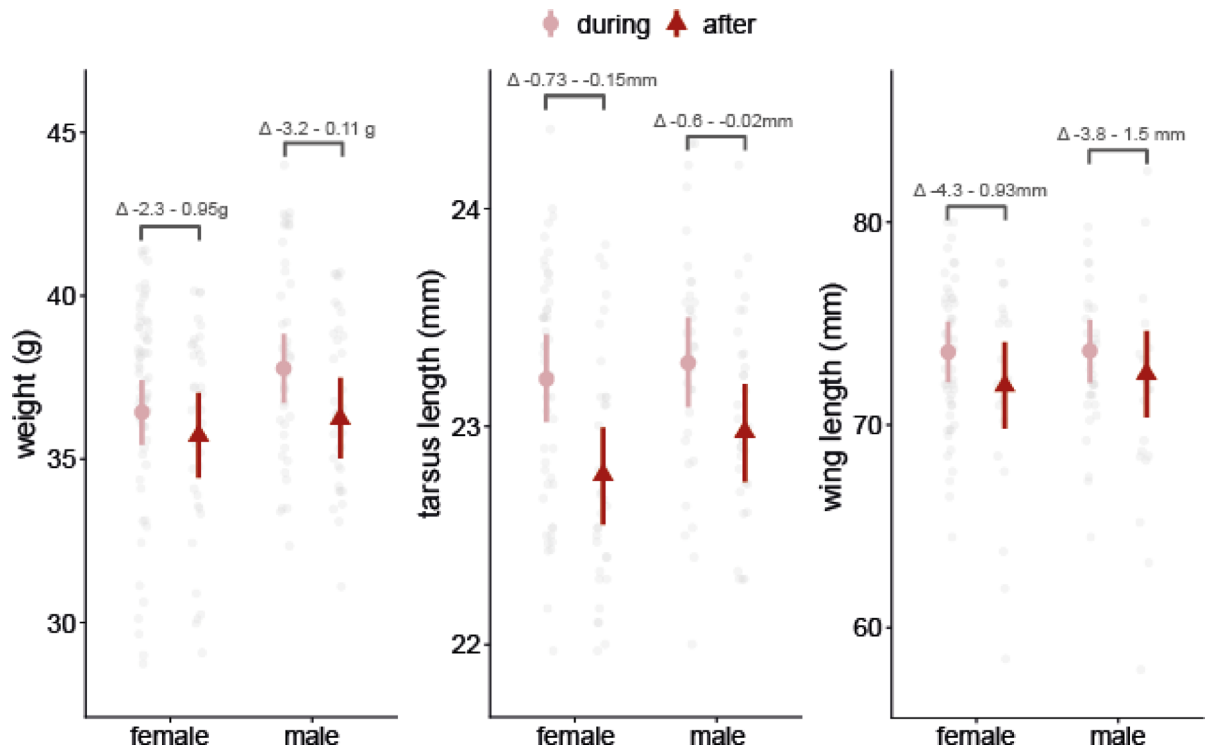


Fig. 1. Body mass (A), tarsus length (B) and wing length (C) of snowfinch nestling growing up during or after snowmelt (pink: during, red: after) for females and males. The coloured symbols depict the means corrected for nestling age (linear mixed effect model). The results are displayed for a nestling age of 15 days. The 95% uncertainty interval is displayed as coloured lines. The 95% uncertainty interval of the differences between the means are displayed (delta value) above the respective means. Grey dots depict the normed raw data e.g. the raw data adjusted for the nestling age based on the model coefficient for age. $n_{\text{weight}} = 202$, $n_{\text{tarsus length}} = 179$, $n_{\text{wing length}} = 125$.

the difference in body mass and wing length for individuals growing up after vs. during snowmelt included zero indicating uncertainty around the direction and magnitude of the effects.

The snowmelt intensity varied between 0.03% and 5.1% per day. The results from the path analysis suggest that snowmelt intensity had a slight positive effect on body mass and tarsus length but a negative effect on wing length (Fig. 2; Table 1). The 95% uncertainty intervals of the estimates included zero indicating uncertainty around the direction and magnitude of the effects.

Effect of temperature on nestling growth

Overall, the average temperature during the nestling period was 7.6 °C (minimum = 2.4 °C, maximum = 12.2 °C). Temperature during the nestling period was on average lower for nestlings growing up during snowmelt (mean = 7.2 °C, sd = 2.3 °C) than for nestlings growing up after snowmelt (mean = 8.2 °C, sd = 2.0 °C).

By using a path analysis, we can differentiate between the direct and indirect effect (via snowmelt) of temperature on growth. The sum of the direct and indirect temperature effect is total effect of temperature. The indirect effect was smaller than the direct effect of temperature and the total effect of temperature was positively for all growth variables (Fig. 2). The 95% uncertainty intervals include zero, indicating uncertainty around the direction and magnitude of the effect.

For nestlings raised after snowmelt, we used a linear mixed effect model to estimate the effect of temperature. In this case, there is just one effect of temperature (equivalent to the direct temperature effect in the path analysis). Temperature after snowmelt was positively correlated with wing length while the effect of temperature on body mass and tarsus length was small and uncertain (Fig. 2).

First-year apparent survival

Hatching occurred on average 17 days after snowmelt (range: 1.4–31.4 days). The average breeding season temperature during the study period from 2015 to 2023 ranged from 4.7 °C to 8.7 °C. Average apparent first-year survival of females was 0.28 (range: 0.12–0.46) and 0.40 (0.11–0.87) for males (Table 2).

The variation in apparent survival was partially explained by variation in the timing of snowmelt (Fig. 3A). First-year apparent survival of both sexes was lower in years when breeding season was late relative to the timing of snowmelt. Apparent survival of females decreased from 0.49 to 0.20 when comparing the year with least to most days since snowmelt. For males, the apparent survival decreased from 0.57 to 0.29. The effect of

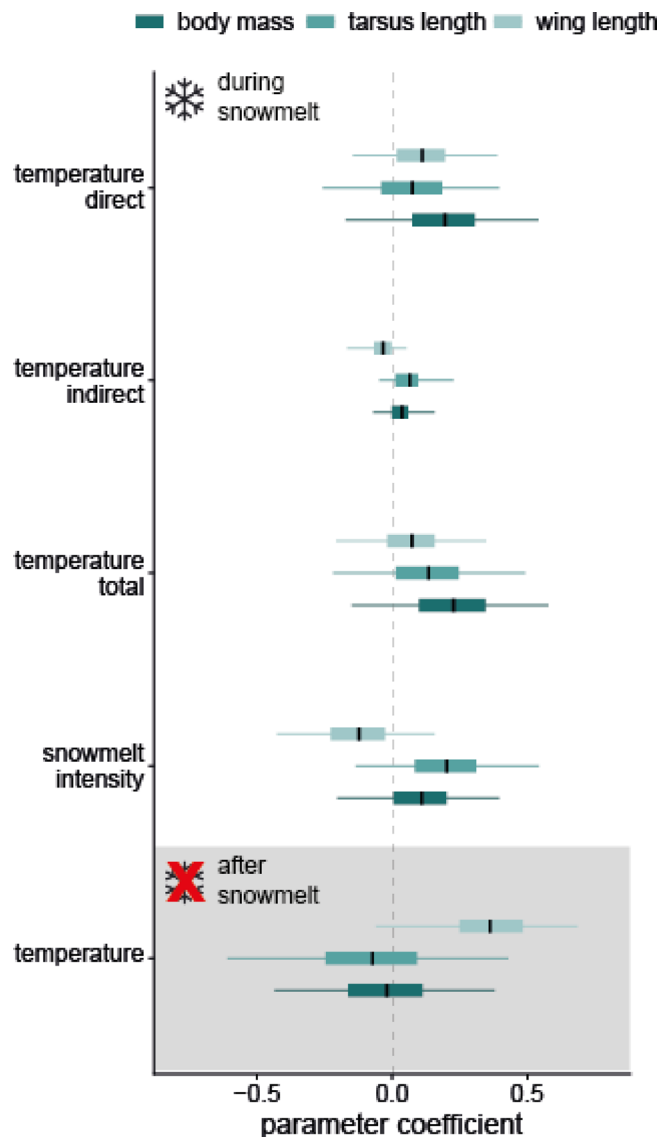


Fig. 2. Effects of temperature and snowmelt on nestling growth (body mass, tarsus length and wing length on day 15). For nestlings growing up during snowmelt, results are coming from a path analysis to incorporate the indirect effect of temperature via its effect on snowmelt intensity. The total temperature effect is the sum of the direct and indirect effects of temperature. For nestlings growing up after snowmelt, the temperature effect was estimated using a linear mixed model. To allow for comparing the effects among the different environmental variables and across the three morphological variables, all variables were centered and scaled. Therefore, the mean coefficients indicate a change in the weight or size (measured in standard deviations) if the environmental variable is increased by one standard deviation. Multiplying the estimated effect size (given in the Figure) with the standard deviation of the variable gives the effect size in the respective unit. The lines depict the 95% uncertainty interval of the estimates, the boxes depict the 25% to 75% quantile, and the black bar depicts the mean estimate. For body mass, we had 202 measurements ($n_{\text{during snowmelt}} = 125$, $n_{\text{after snowmelt}} = 77$), for tarsus length we had 177 measurements ($n_{\text{during snowmelt}} = 103$, $n_{\text{after snowmelt}} = 74$) and for wing length we had 129 measurements ($n_{\text{during snowmelt}} = 87$, $n_{\text{after snowmelt}} = 42$).

temperature during the breeding season on apparent survival was small with a high uncertainty for females and males (Fig. 3B).

Discussion

Despite broad uncertainty intervals, the results of the different analyses consistently support the same hypothesis, i.e. that snowfinch nestlings have an advantage when growing up during snowmelt compared to after. Because the species breeding phenology has already been shown to lag behind the advancing snowmelt over the last decades²⁴ our result imply that the delayed reproduction could have negative fitness consequences.

		Body mass		Tarsus length		Wing length	
		During	After	During	After	During	After
Snowmelt intensity	Std	0.36 g/sd(melt) (− 0.71 to 1.4)		0.11 mm/sd(melt) (− 0.07 to 0.29)		− 0.56 mm/sd(melt) (− 1.9 to 0.69)	
	Original scale	0.39 g/% melt (− 0.76 to 1.5)		0.12 mm/%melt (− 0.08 to 0.32)		− 0.62 mm /%melt (− 2.1 to 0.76)	
Temperature direct	Std	0.67 g/sd(temp) (− 0.60 to 1.9)	− 0.07 g/sd(temp) (− 1.3 to 1.1)	0.04 mm/sd(temp) (− 0.14 to 0.21)	− 0.04 mm/sd(temp) (− 0.32 to 0.23)	0.47 mm/sd(temp) (− 0.64 to 1.7)	2.4 mm/sd(temp) (− 0.40 to 4.5)
	Original scale	0.29 g/°C (− 0.26 to 0.81)	− 0.03 g/°C (− 0.62 to 0.54)	0.02 mm/°C (− 0.09 to 0.13)	− 0.02 mm/°C (− 0.16 to 0.11)	0.27 mm/°C (− 0.37 to 1.0)	1.0 mm/°C (− 0.17 to 2.0)
Temperature indirect	Std	0.11 g/sd(temp) (− 0.24 to 0.55)		0.03 mm/sd(temp) (− 0.03 to 0.12)		− 0.17 mm/sd(temp) (− 0.73 to 0.23)	
	Original scale	0.05 g/°C (− 0.10 to 0.23)		0.02 mm/°C (− 0.02 to 0.08)		− 0.10 mm/°C (− 0.43 to 0.14)	
Temperature total	Std	0.78 g/sd(temp) (− 0.52 to 2.0)		0.07 mm/sd(temp) (− 0.12 to 0.27)		0.30 mm/sd(temp) (− 0.91 to 1.5)	
	Original scale	0.33 g/°C (− 0.22 to 0.86)		0.04 mm/°C (− 0.07 to 0.16)		0.18 mm/°C (− 0.53 to 0.89)	
Hatching date	Std	− 0.70 g/sd(day) (− 1.9 to 0.51)	− 0.25 g/sd(day) (− 1.5 to 1.0)	− 0.09 mm/sd(day) (− 0.28 to 0.10)	0.01 mm/sd(day) (− 0.27 to 0.30)	− 0.60 mm/sd(day) (− 1.9 to 0.73)	− 3.1 mm/sd(day) (− 5.5 to − 0.42)
	Original scale	− 0.08 g/day (− 0.23 to 0.06)	− 0.01 g/day (− 0.08 to 0.06)	− 0.01 mm/day (− 0.04 to 0.01)	− 0.00 mm/day (− 0.02 to 0.02)	− 0.07 mm/day (− 0.22 to 0.09)	− 0.22 mm/day (− 0.38 to − 0.03)

Table 1. Effect of snowmelt, temperature and hatching date on nestling morphometrics based on path analysis (during snowmelt) and a linear mixed effect model (after snowmelt). We present both standardized coefficients for comparison of the effect size of different predictors and on the original scale for easier interpretation. For temperature, we calculated direct effects, indirect effects through the effect of temperature on snowmelt intensity and the total temperature effect which is the sum of the direct and indirect effect. The 95% uncertainty intervals of the estimates are presented in brackets.

Year	Survival of first-year females (95%CrI)	N females	Survival of first-year males (95%CrI)	N males
2015	n.a.	0	0.87 (0.62–0.99)	5
2016	0.39 (0.07–0.82)	5	0.53 (0.21–0.84)	7
2017	0.18 (0.02–0.50)	7	0.11 (0.01–0.32)	13
2018	0.17 (0.02–0.48)	8	0.47 (0.09–0.89)	3
2019	0.43 (0.11–0.82)	7	0.34 (0.07–0.72)	5
2020	0.25 (0.05–0.58)	10	0.33 (0.09–0.64)	10
2021	0.46 (0.13–0.85)	7	0.40 (0.04–0.63)	1
2022	0.11 (0.01–0.34)	15	0.11 (0.01–0.30)	15

Table 2. Sex-specific first-year apparent survival probabilities based on estimates from Cormack-Jolly-Seber model.

The results suggest that nestling growth is influenced by temperature and snowmelt. The positive correlation between nestling growth and temperature supports our hypothesis that higher temperature reduces the cost of thermoregulation and therefore allows for more energy investment in growth. The effect of temperature on growth was primarily driven by direct temperature effects. For nestlings growing up after snowmelt, the effect of temperature was positive for wing length and uncertain for body mass and tarsus length. The weaker temperature effect after snowmelt compared to before may indicate that temperature is no longer a limiting factor for growth later in the breeding season when average temperatures are higher. It is important to note that we looked at the average temperature between hatching and the date when we measured the nestlings which encompassed 12–17 days. Catch-up growth after inclement weather might mask the immediate effect of weather phenomena such as cold spells⁴³. Furthermore, we could only collect data from broods in nestboxes, because other nest types such as rock crevices are inaccessible. We know, however, that the microclimate differs between different nest types²⁷. While rock crevices provide low but constant thermal environment, temperature in nest boxes are subject to daily temperature fluctuations closely linked to ambient temperature²⁷. Direct effects of temperature on the cost of thermoregulation might thus differ between nest types.

The negative effect of breeding late relative to snowmelt has also been found in other arctic and alpine species^{6,44}. Insufficient food availability could potentially lead to the observed reduction in nestling growth after snowmelt. Previous studies found that, larval prey, especially Tipulidae larvae are an important part of the nestling diet of snowfinches²⁰. As these prey items are most abundant and accessible next to melting snow

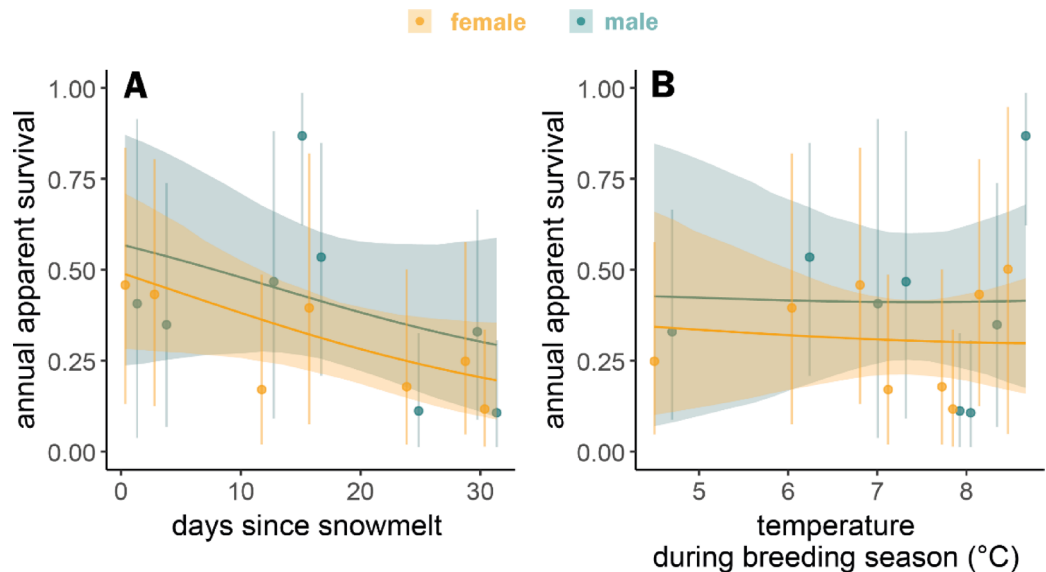


Fig. 3. Annual apparent first-year survival in relationship to (A) the days since snowmelt (i.e. the difference between the hatching date and the timing of snowmelt) and (B) the temperature during the breeding season. Apparent survival probabilities were estimated in a multi-state mark-recapture model and subsequently correlated with snow conditions and temperature. Shaded areas indicate the 95% uncertainty intervals of the regression model whereas the 95% uncertainty intervals of the survival estimates are displayed as vertical lines.

fields^{20,22}, snowfinches are at risk of a phenological mismatch if they breed late relative to the timing of snowmelt. In line with this hypothesis, our results suggest a potential positive association of snowmelt intensity with body mass and tarsus length, which could be the result of optimal foraging conditions. It remains unclear, why wing length has a weak negative association with snowmelt intensity. Our results suggest that the effect of snowmelt was similar for female and male nestlings, despite that females were on average smaller than males.

The average first-year survival probability estimated in this study was 0.24 (range: 0.12–0.46) for females and 0.40 (0.11–0.87) for males which is higher than reported in a study from the Abruzzi Mountains in Italy. Moreover, the study from the Abruzzi mountains found a weak negative effect of summer temperature on apparent survival while our results suggest a potential negative effect of the timing since snowmelt but no strong support for an effect of temperature on first-year survival. Because our model included both snowmelt timing and temperature, we were able to distinguish between these two environmental variables, while the study from the Abruzzi Mountains focused on summer temperature. Furthermore, as the Abruzzi population is located farther south, the overall environmental conditions likely differ, which may explain the differing importance of temperature and snowmelt between the two regions.

Unfavourable conditions during the nestling period can have carry-over effects on later life stages. Carry-over effects of fledgling body conditions to post-fledgling survival and recruitment have been demonstrated in other species^{45–47} and might explain why we found potential negative effects of breeding after snowmelt on both growth and survival. Typically, mortality risk is highest during several days or weeks after fledging which is mainly related to high predation risk during this time. Therefore, physiological or morphological traits that allow to escape from predators are likely correlated with post-fledgling survival. Wing development for example correlates with flight ability and post-fledgling survival⁴⁸. Moreover, heavier nestlings have been shown to have a higher survival than lighter conspecifics^{49,50}. This could also explain why females in our study, which were on average lighter, had a lower first-year apparent survival than males. Because apparent survival probabilities cannot differentiate between permanent emigration and death, the sex-specific apparent survival could also result from a sex-biased dispersal strategy with a higher dispersal probability of females which is a widespread phenomenon in birds.

Breeding late after snowmelt potentially also reduces the food availability¹² for fledglings and could therewith explain lower first-year survival. Snowfinches switch to a granivorous diet after fledging. An early snowmelt can reduce the seed production of alpine plants. This can for example happen if early snowmelt and therewith early plant phenology increase the risk of frost damage^{51,52}. Reduced survival of snowfinches in years when breeding is late relative to the timing of snowmelt could therefore be a consequence of the insufficient food availability in the critical time window after fledging.

Snowmelt has advanced considerably over the last decades in the Alps, and this trend is expected to continue^{23,53}. The change of snowmelt but also altered temperature and precipitation patterns have profound implications for high-elevation ecosystems as these factors have cascading effects across trophic levels^{54,55}. Snowfinches seem to increasingly mismatch the timing of reproduction with the timing of snowmelt²⁴ potentially causing negative effects on the population dynamics through reduced first-year survival. Further studies are needed to evaluate the sensitivity of the population to changes in first-year apparent survival.

At the moment, there are limited scientifically supported mitigation strategies available to protect high-elevation species threatened by climate change⁵⁶. Therefore, we highlight the need for more research targeted at developing strategies to mitigate climate-change induced effects on high-elevation species. This could include, for example, spatial prioritisation of areas which are expected to provide climate refuges⁵⁷ or assessments of the role of habitat structures and especially the active management of the habitat that is anyway under human influence as for example grazed areas or ski resorts⁵⁸.

Data availability

R codes and data are available on zenodo [<https://doi.org/10.5281/zenodo.18195339>].

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Author contributions

C.N. designed the study, collected and curated data and lead the analysis and writing process. S.H. designed the study, lead the data collection in Austria and supported the analysis and writing process. S.D. collected and curated data and supported the analysis and writing process. A.G. collected data and supported the analysis and writing process, F.I. helped designing the study questions. C.K. collected and curated data and supported the analysis and writing process. C.P. helped designing the study and collected and curated data. C.S. collected and curated data and supported the analysis and writing process. F.K. designed the study, lead the data collection in Switzerland and supported the analysis and writing process. F.K. and S.H. have jointly supervised the study. All authors contributed to developing and improving the manuscript.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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