High nest failure but better nestling quality for early breeders in an alpine population of Northern Wheatear (*Oenanthe oenanthe*)

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Climate change is leading to the advancement of spring conditions, resulting in an earlier snowmelt and green-up, with highest rates of change in highly seasonal environments, including alpine habitats. Migratory birds breeding at high elevations need to time their arrival and lay dates accurately with this advancement, but also with the annually variable spring conditions at their breeding sites, to maximize nest survival probabilities and reproductive output. Nest survival probability and mean nestling mass were analysed in relation to lay date and habitat conditions in an alpine population of the migratory Northern Wheatear *Oenanthe oenanthe* collected over six consecutive breeding seasons in the Western Italian Alps. This open grassland species showed the lowest nest survival probability in years with an early onset of spring conditions. Within-season, nest survival was highest when breeding late, at lower elevations, and when grass cover and grass height were higher. Both across- and within-season, severe weather conditions may indirectly lead to higher early season nest failure rates by increasing predation risk. By contrast, mean nestling mass, and thus the quality of the fledglings, was lower when breeding late. This might be driven by a mismatch with the peak in food abundance. Breeding early is thus generally advantageous in terms of chick quality in our high-elevation population, but reproductive success is limited by the risk of nest failure that is higher in early springs and early in the season. This trade-off between breeding early and late may thus allow Northern Wheatears to maximize fitness under highly variable spring conditions. However, climate change may cause disruption to this trade-off, and shifts in phenology could become a threat for migratory alpine birds that might not be able to keep track of advancing spring conditions.

Keywords: alpine, climate change, grassland, phenology, songbird, trophic mismatch.

At high latitudes or elevations, which show a strong seasonality in the availability of food resources, animal reproduction needs to be timed with local environmental conditions and the expected peak in food abundance within a narrow time window (Lisovski *et al.* 2017). In birds, this is fundamental to increase the probability that nestlings fledge, and thus to have a successful breeding attempt (Martin & Wiebe 2004, Kristensen *et al.* 2015). Additionally, the timing of spring progression can show a very high variability between years, and alpine animals need to adapt to annual changes in plant phenology and weather conditions (Martin & Wiebe 2004). Across the globe and

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across living organisms, climate change results in changes in phenology due to the advancement of spring conditions (Thackeray *et al.* 2016), resulting in earlier snowmelt and green-up dates (Parmesan & Yohe 2003), and bringing the risk of a trophic mismatch (Visser *et al.* 2012). This phenological shift seems especially fast in highly seasonal environments including alpine habitats (Oyler *et al.* 2015, Vitasse *et al.* 2021) and is likely to impact alpine breeding birds in particular, as their population dynamics and reproductive success are strongly connected to climate variability (DeSante & Saracco 2021). Thus, understanding the drivers and consequences of climate change for the reproductive success of species inhabiting these fragile habitats is crucial for effective conservation (Chamberlain *et al.* 2013, Boyle & Martin 2015, Lehikoinen *et al.* 2018).

Strategies used by birds to adapt to environmental cues include adjusting the number of broods per year, adjusting lay date, delaying the start of incubation once eggs have been laid, adjusting clutch size or the interval between laying of eggs, or adjusting incubation time itself via nest attentiveness by the female (Higgot *et al.* 2020). Choosing the right timing for laying, which needs to be done well in advance of hatching and of the estimated food peak, is not trivial. Often there is a trade-off in costs between early and late breeding. Generally, individuals breeding early in the season have a higher fitness by matching the time of chick-rearing with the food peak (Perrins 1970, Both 2010). However, early clutches may have a higher risk of nest failure. This is caused directly by environmental conditions such as late snowfall, higher precipitation, low temperatures and more variable weather (Martin *et al.* 2017), or when females are prevented from laying due to low food abundance when their own survival is at risk (Perrins 1970, Both 2010, MacDonald *et al.* 2013). Despite these direct environmental factors limiting breeding success, predation is assumed to be the most common cause of nest failure in songbirds (Martin 1995, Martin & Briskie 2009), and for alpine and ground-nesting birds such as the Horned Lark *Eremophila alpestris* (MacDonald *et al.* 2016), Water Pipit *Anthus spinoletta* (Rauter *et al.* 2002) and Rock Partridge *Alectoris graeca* (Bernard-Laurent *et al.* 2017). Furthermore, the risk of predation might be linked to environmental conditions (MacDonald *et al.* 2016, Sander *et al.* 2021). A delay in hatching exposes nests to

predators for longer, the higher demand for food increases begging behaviour (Leech & Leonard 1997), and the number of nest visits by the adult and/or longer food search times increases the likelihood of detection by a predator (Rauter & Reyer 1997). Indirect variation in predation risk across the season might also occur when alternative prey species, such as voles, become active above ground and more abundant in summer than in spring (Yoccoz *et al.* 1998, Hille & Rödel 2014). The timing of breeding at high elevations, where breeding conditions are particularly challenging, may therefore have severe consequences for the reproductive output and fitness of the individual (MacDonald *et al.* 2013, 2016).

Recent literature reflects that climate-driven adaptations in breeding phenology are evident in several songbird species in that they advance the onset of breeding in warmer springs (Kluen *et al.* 2011, Fossøy *et al.* 2015, Bründl *et al.* 2020, Hoover & Schelsky 2020, Shipley *et al.* 2020, Nicolau *et al.* 2021). The arrival of migrants at the breeding grounds is strictly connected to their migration schedule (Schmaljohann 2019), bringing an additional challenge to the successful timing of life-history events and determining the ability to adjust lay date to the local green-up (Low *et al.* 2019, Amélineau *et al.* 2021, Lamarre *et al.* 2021, Sander *et al.* 2021). In some long-distance migrant songbirds, the timing of breeding events shows high flexibility (Le Vaillant *et al.* 2021), with lay dates being adapted by adjusting the arrival–laying interval. The latter has been found to be shorter in northern populations without negative effects on fecundity (Nicolau *et al.* 2021) and in late-arriving individuals (Low *et al.* 2019). One strategy to cope with variable spring onset times in migrant alpine birds is to arrive early at sites close to the breeding grounds, from where it is probably possible to estimate environmental conditions (de Zwaan *et al.* 2019) or even periodically to visit the breeding habitat and temporarily defend territories (Barras *et al.* 2021).

In the Nearctic, climate change and extreme weather events have been found to affect the phenology and reproductive success of migratory species breeding at high elevations. Birds showed later lay dates in colder springs or following cold snaps, but generally had higher reproductive success when breeding early (Martin *et al.* 2009, 2017, de Zwaan *et al.* 2019, 2020, 2022). Comparable studies investigating these effects on Palaearctic long-distance migrants, and in particular on mountain

populations of holarctic generalist species breeding under a highly variable environment, are lacking. However, previous European studies conducted in alpine environments have investigated weather and temperature effects (mountain populations of Eurasian Blue Tit *Cyanistes caeruleus*, Bründl *et al.* 2020), and the effects of nesting habitat and invertebrate food resources on breeding success and nestling growth (Water Pipit; Bollmann *et al.* 1997, Brodmann *et al.* 1997, Rauter *et al.* 2002). No study to date has investigated the combined effects of nesting habitat and breeding phenology on these traits in a long-distance migrant. It remains to be investigated which trade-offs migratory mountain generalists are facing and how climate change could disrupt the equilibrium in timing their life-history events. To develop future strategies for the conservation of migratory species inhabiting high-elevation habitats, it is crucial to understand the factors that drive their productivity.

Our model species, the Northern Wheatear *Oenanthe oenanthe* (henceforth Wheatear), is considered a mountain generalist (Scridel *et al.* 2018) and an open grassland species that breeds mostly above the tree line in Southern Europe, migrating *c.* 3500 km to its wintering grounds in sub-Saharan Africa (Conder 1989, Bairlein *et al.* 2012, Schmaljohann *et al.* 2016, Sander *et al.* 2021). Despite having a potentially high resilience to environmental and climate variability, this species represents a system that is threatened in two ways: species of open grasslands are especially vulnerable to habitat loss caused by climate change, with a warming rate in alpine habitats twice as high as in lowlands (Chamberlain *et al.* 2013, Ferrarini *et al.* 2017, Scridel *et al.* 2018, Bani *et al.* 2019); and long-distance migrants are showing the strongest population declines among all bird species (Sanderson *et al.* 2006, Kirby *et al.* 2008, Vickery *et al.* 2014), for which phenological mismatch is likely to be a key driver (Both *et al.* 2010, Saino *et al.* 2011). Nest and environmental data were collected over six consecutive breeding seasons in high-elevation open grassland. It is crucial to assess both breeding success (expressed as nest survival probability) and the quality of fledglings (e.g. using mean nestling mass as a measure of predicted fledgling condition) when studying breeding productivity, as overall breeding success and thus population productivity cannot be estimated using only one of these parameters (Streby *et al.* 2014).

In the present study, whether nest survival probability and mean nestling mass were related to an early or late start of breeding was assessed. Furthermore, the relationship between reproductive success and local environmental conditions, in particular those related to snowmelt and spring green-up, was analysed. As these vary significantly between years with an early or late spring onset, this approach can be used to assess potential future impacts of environmental and climate change, and to better understand the constraints faced by high-elevation migrant species.

METHODS

Study species and study area

The Wheatear is a typical species of alpine open grassland in our study area, ground-foraging and nesting in rock crevices or holes covered by dwarf shrubs (*Juniperus nana*, *Rhododendron ferrugineum*, henceforth juniper and rhododendron) and soil. Unlike lowland populations of this species, birds in our study area usually (98% of nests with colour-ringed adults, $n = 97$) have only one brood per season with on average five eggs ($n = 108$), which is incubated by the female only, but both adults feed nestlings (e.g. Conder 1989). Its presence at the high-elevation breeding grounds (most commonly from 1900 to 2800 m asl, on south-eastern slopes) is restricted to the snow-free period, and spans from mid- to late May (arrival) to the beginning of September (post-breeding moult; for more information on the study population see Sander *et al.* 2021). Adults seem highly variable in their timing of breeding, with some individuals initiating attempts in late May when much of the area can be snow-covered, whereas others seem to arrive and begin breeding much later in June (Martha Maria Sander, Susanne Jähnig, pers. obs.).

Data on breeding phenology and success and on environmental conditions were collected from 2016 to 2021 between May and August in Parco Naturale Val Troncea, 44°57′28″N, 6°56′28″E, Western Alps, Piedmont, Italy. Monitoring of the species was conducted in most parts of the protected area over an elevation gradient from 1560 to 2700 m asl. The landscape structure of the valley is characterized by forests (predominantly larch *Larix decidua*), with shrubby patches and grazed pastures at lower elevations, and larches and woody shrubs (juniper and rhododendron)

interspersed with open grasslands at around 2200 m asl, followed by grassland interspersed with rocky areas above the tree line. Across all elevations, grazing cows influence the distribution and availability of potential open grassland habitat (for more details of the study area, see Masoero *et al.* 2016, Jähnig *et al.* 2018, 2020, Sander *et al.* 2021).

Nest monitoring and ringing of nestlings

Nests were monitored that were searched for and found on a daily basis throughout the whole breeding season in the same study area across all years (in 2016, a smaller site was covered within the same larger study area) and during the same period of the year with, mostly, two to three field-workers (in 2016, only one), starting the season upon snowmelt at the end of May and ending when the last nestlings fledged and adults started to moult at the beginning of August. Nests were found by observing males showing territorial and mating behaviour in likely breeding habitat, females building or returning to the nest for incubation, or feeding adults. Very few female and male identities were known (from individual colour-ringing of all captured birds in the years 2019–2021) for the replacement broods or second attempts, and therefore adult identity could not be accounted for in the analysis. Second broods are very rare in our study area, and in general in alpine populations (Conder 1989), but replacements are frequent, especially in years with higher nest failure rates (Sander *et al.* 2021). Lay and hatch dates were estimated from nestling age (*cf.* Low *et al.* 2019) and the known mean duration of incubation within our population, if not observed directly (for details on estimation of breeding parameters, see Sander *et al.* 2021). To account for differences in reproductive output in nests located at different elevations and in different microhabitats, as well as with differing breeding phenologies, chicks were ringed and measured between the ages of 6 and 14 days. Reproductive output is described here as the mean nestling mass per nest, corrected for the age of the nestling (as a fixed effect in the models described below). It was assumed that nestling mass can be used as a proxy for nestling quality and hence reproductive output, as many studies have demonstrated a link between mass and subsequent survival probability in passerines (e.g. Tinbergen & Boerlijst 1990, Magrath 1991, Streby *et al.* 2014).

Environmental conditions and microclimate

To describe whether the spring in each year was 'early' or 'late', the day of spring green-up and snowmelt was estimated for each year using the method described in more detail in Sander *et al.* (2021): higher-resolution snow-free and green-up dates for the actual nest-sites in the study area (using GPS locations of 133 nests found in 2019 and 2020 as a representative set of potential nest-sites in the study area for all years) were derived from the remotely sensed Sentinel-2 MSI MultiSpectral Instrument Level-2A dataset with a spatial resolution of 10 m (Drusch *et al.* (2012). First, all images taken in the years 2016–2021 (Google Earth Engine Server) that intersected at least one of the nest-sites were selected. Cloud pixels were masked using the Sentinel-2 Cloud Probability layer with a probability threshold of 60. The normalized difference snow index (NDSI, Band 8 & 4) and the normalized vegetation index (NDVI, Band 3 & 11) were calculated, and for each nest-site and each image, the mean NDSI and NDVI values of all pixels within a 10-m radius ($n = 2$–4) around the nest were extracted. For each nest-site and for all years, a smooth line was fitted (loess fit with span = 0.2 from the R package stats) to the NDVI and NDSI values over the day of the year, the day when the line fell below 0.1 NDSI (snowmelt) and exceeded 80% of the NDVI annual amplitude (green-up) was extracted. The annual day of snowmelt and green-up presented in the results for each year is the median ($\pm$ sd) of all nest locations. In Sander *et al.* (2021), this method was combined with on-site data (grass height) collected at nest-sites and points distributed across a grid, and it was shown that it was representative of the estimation of spring onset in the whole study area.

In addition to the remote sensing data of the environment, temporally variable habitat features (hereafter nest habitat parameters) that were found to impact habitat selection and breeding success (e.g. Tye 1992, Arlt & Pärt 2007), i.e. grass height, grass cover and snow cover, were recorded in the field throughout the active period of each nest in 2019, 2020 and 2021 (see details

in Sander *et al.* 2021). Measurements of nest habitat parameters that were closest to the individual point in time of laying and hatching (at least two measurements per nest) were selected for the analyses.

To characterize the microclimate of the nest location, temperature was recorded in 2019 using hygro buttons (Plug & Track™) placed in silicon capsules and a plastic cup upside down to protect them from direct sunlight, rain, moisture and wind. They were then placed on a bamboo stick at 50–70 cm above the ground, 5 m distant from the nest using randomly chosen directions (see methods described in Jähnig *et al.* 2020). Temperature was recorded every 5 min throughout the active period of the nest. For the analyses, the average day and night temperatures during the egg period (incubation) were used.

Data analysis and statistics

All analyses were carried out in R version 4.0.5 (R Core Team 2021). As the aim was to understand ecological relationships, the confirmatory modelling approach was used, i.e. model selection was based on predictive model checking and comparing Akaike's Information Criterion (AIC) and biological reasoning (Korner-Nievergelt *et al.* 2015). The assessment of model assumptions (residual analysis, checking for overdispersion and zero-inflation) and the interpretation of the models was performed by following the analytical procedures proposed by Korner-Nievergelt *et al.* (2015). For the latter, the Bayesian approach using improper prior distributions, namely $p(\beta) \propto 1$ for the coefficients and $p(\sigma) \propto \frac{1}{\sigma}$ for the explanatory variables, was used. The posterior distribution was obtained by simulation of 5000 values from the joint posterior distribution of the model parameters (using the function *sim* of the package arm; Gelman & Hill 2007). Variables were considered to have a significant effect on the response variable when their 95% credible intervals did not include zero.

Nest survival probability, quantified by using daily failure rates (DFRs; Mayfield 1975), was calculated for a single nest with: DFR = fate/exposure days−fate, with 'fate' (nest failure or success, respectively 1 or 0) and 'exposure days' as number of days from the date a nest was found until the date between the last visit and the penultimate visit. With this method, DFRs were corrected for the variable duration of monitoring of individual nests. To model DFR for the whole population and test for effects of variables, binomial general linear mixed models were used as described by Aebischer (1999). Total nest survival probability for the whole population was then calculated to compare nest survival between the years of the study. For each year separately, total nest survival probability was calculated by 1−(DFR^32 days), as in our population the combined laying, incubation and nestling period spans about 32 days (Sander *et al.* 2021). Here, the DFR estimates from intercept-only general linear models were used, with the structure DFR ~ 1 based on year subsets.

In the next step, DFR was analysed in relation to environmental and phenological factors, including the nest data from all 6 years. The explanatory variables considered in the general linear models were elevation, grass height at lay and hatch date, grass and snow cover at lay and hatch date, median day and night temperature during egg stage, lay and hatch date, and the time difference between snowmelt and lay date, and green-up and hatch date (in days). Lay and hatch dates were transformed to day of year (doy) and scaled within the respective year to account for between-year differences in phenology. Depending on data availability (which varied between the years of study), we performed different models for the study periods 2016–2021, 2019–2021, 2020–2021 and 2019 (Table 1), trying to include as many of the above-mentioned variables as possible. When sample size did not allow the inclusion of all variables, the effects on DFR were tested beforehand in univariate models and included only those with significant effects. The possibility of including the random term year (at least three levels) dictated whether binomial mixed models or binomial models were used.

For the study period 2016–2021, DFR was modelled by fitting a binomial mixed model, using the function *glmer* (logit link) and including lay date (scaled within years) and elevation (scaled) as explanatory variables. The random term year (six levels) was included to account for between-year variation in overall nest survival not captured by the fixed effects. Additionally, the effect of the difference between snowmelt (for the respective year) and lay date (for each nest), and between green-up and hatch date, was tested in univariate binomial models (function *glm* (logit link)), as there was collinearity when these variables were included in the full model.

Table 1. Sample sizes of phenological and environmental data throughout the study period 2016–2021 (grey), and sample sizes (*n*) of each variable (representing the number of nests for which the type of data was recorded).

Study period	Lay date	Hatch date	Mean nestling mass	Snowmelt	Green-up	Elevation	Grass cover	Snow cover	Grass height	T
2016–2021 (6 years)	195	180	114	+	+	224				
2019–2021 (3 years)	146	131	78	+	+	164	131	131		
2020–2021 (2 years)	85	78	41	+	+	97	78	78	43	
2019	62	54	38	+	+	68				30

Temperature (*T*) was recorded close to the nest (5-m radius) with hygro buttons. Elevation data were available for all nests monitored, and as such these values represent the total number of nests available for analysis in the respective period. Sample sizes of lay and hatch dates differ, as some nests failed prior to the hatching event or the lay and/or hatch date was not known at all. Not every nest was accessible, so that mean nestling mass was not measurable for all nests monitored. Snowmelt and green-up dates were derived from remote sensing images and therefore were available for all years. Grass and snow cover data were collected in 3 years at hatch date, and equal the latter's sample size. Due to field constraints, grass height was not collected for all nests.

In the years 2019–2021, grass cover was also recorded and included in the models for this subset. Here, a binomial mixed model was fitted, using the function *glmer* (logit link), with the response variable DFR and the explanatory variables elevation (scaled), lay date (doy, scaled within years), grass cover (scaled) and year as a random term (three levels, although we acknowledge that caution is needed in interpreting mixed models with relatively few levels for a given random factor; Harrison *et al.* 2018). In 2020 and 2021, additionally, grass height at lay date (scaled) was recorded, and this habitat feature was included in a binomial model, but without including year as a random term, but as a fixed effect (only two levels). Due to constraints in the field, or to nest failure prior to the nestling period, in many cases there was not sufficient data to include all variables. Therefore, grass cover and lay date were excluded from the analysis of the 2-year subsample to understand whether grass height had an effect on nest survival. Based on the conclusions drawn from the full dataset, we controlled for the differences along the elevational gradient and between years. In 2019, temperature data loggers were used to model the effect of the average day and night temperature during the egg stage, including elevation and lay date (binomial models with logit link function).

All analyses were run on the probabilities calculated separately for the whole nesting period, the incubation period (egg period) and the nestling period. Trends in the models for DFR during the egg and nestling period mirrored the trends in the models for the whole nest period. As our sample size was larger when including the whole nest period, results are shown only for the whole nest period. As a former study on our population highlighted 2020 as an exceptional year in terms of spring phenology and breeding success (Sander *et al.* 2021), the influence of this year was checked by excluding it from all analyses, and by performing all models on a subsample with data from 2020 only. However, excluding 2020 did not have a clear effect on the conclusions of the full dataset.

Mean nestling mass was modelled with linear models, using the function *lm*, due to the normal distribution of the response variable; explanatory variables were included according to data availability for the different year subsets (Table 1). First, differences between years were checked by modelling mean nestling mass in a separate linear model including age (nestling mass is a function of age, e.g. Bründl *et al.* 2020) and year as fixed effects. For the study period 2016–2021, mean nestling mass (scaled) was modelled by fitting linear models with hatch date (scaled within years), elevation (scaled), age of nestlings (in days, as quadratic and linear terms) and number of nestlings (per nest) as explanatory variables. Model selection was performed by comparing AICs of models with different combinations of these variables. Grass cover was included in the models for the data collected in 2019–2021, grass height for the data from 2020–2021, and mean day and night temperatures for data from 2019. Due to the low sample size of 30 nests (Table 1), all other variables except age were excluded in this dataset. Additionally, the relationship between hatch date (doy, response variable) and these temperatures (explanatory variables) was modelled in linear models.

RESULTS

Spring phenology and nest survival probabilities

There were 93 failed nests between 2016 and 2021, of which the cause of failure was determined in 88 nests: six failed during building (6%), 33 during laying and incubation (38%) and 46 (52%) in the nestling period (Fig. 1, Supporting Information Table S1). In total, at least 75 nests were predated (85%), 12 (14%) were abandoned and one failed due to being buried in mud after an event of strong precipitation (Fig. 1, Table S1). Between-year differences in nest survival were high, ranging from survival probabilities of 23% (2020) to 53% (2018). The high variability across years might be driven by the between-year variability in median snowmelt (ranging from 25 April in 2016 to 9 June in 2018) and green-up (Fig. 2a). Although there were only 6 years of data, there were nevertheless some interesting patterns, in that we observed the lowest nest survival in 2020 and 2021 when spring started early (snowmelt and green-up were about 1 month earlier than in 2018). In the earliest spring in 2020, lay dates in our population were advanced by 1 week, compared with the latest spring in 2018, and were highly variable (Fig. 2b, median: 30 May, 1st quartile: 25 May, 3rd quartile: 26 June). We observed the highest survival in 2018 when lay date (median: 6 June, 1st quartile: 2 June, 3rd quartile: 13 June) co-occurred with snowmelt, and hatch dates (median: 22 June) were before the peak in
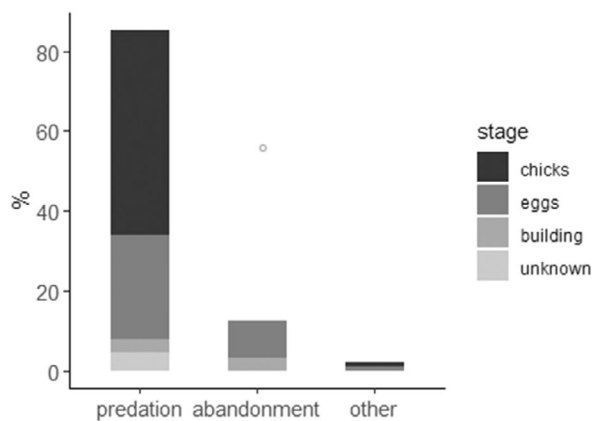

Figure 2. (a) Linear regressions of nest survival probabilities (based on a yearly estimate for all nests monitored respectively, Table S1) with median snowmelt (blue, $\beta = 0.005 \pm 0.003$, $P = 0.12$, $R^2 = 0.4$) and green-up (green, $\beta = 0.008 \pm 0.003$, $P = 0.07$, $R^2 = 0.5$) for each year ($n = 6$), drawn with the function *geom_smooth (method = "lm")*. (b) Raw lay dates (black dots), raw hatch dates (orange dots), median snowmelt dates $\pm$ sd (blue diamond) and median green-up dates $\pm$ sd (green triangle) are shown. Sample sizes are given in Table 1. Boxplots show the median, the 1st and 3rd quartile, and whiskers represent the minimum and maximum of all lay dates in the respective year.

vegetation (green-up: 19 July). This pattern was also found in 2017 and 2019 (Fig. 2a,b). Conversely, we observed the lowest nest survival in the early years 2016, 2020 and 2021 when snowmelt was well before the lay dates (Fig. 2a). Across the study period of 6 years, median lay dates did not vary as much as median snowmelt and green-up dates (Fig. 2b).

Daily failure rate

Lay and hatch dates were correlated, so lay date as the measure for breeding phenology was selected

Figure 1. Cause of failure and stage (grey shades) at failure for all failed nests ($n = 93$) monitored during 2016 to 2021. Sample sizes for each year are provided in Table S1.
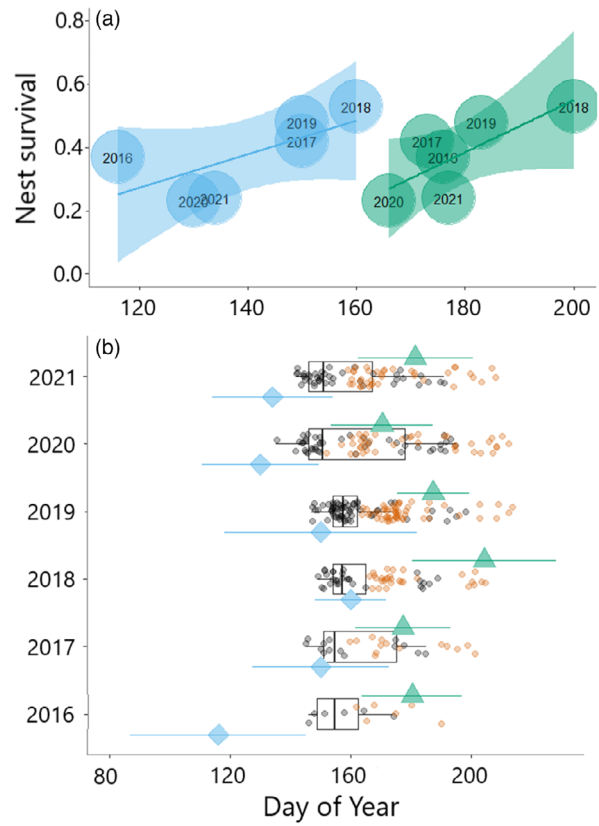
in all models, as done in previous studies in alpine environments (e.g. Bründl *et al.* 2020). There was no evidence of collinearity (using the function *vif*, variance inflation factor) in any model for DFR and mean nestling mass. Therefore, breeding parameters as well as nest habitat parameters were included in all analyses according to the limits of data availability and sample size in different study years (Table 1). Interactions between year and lay date, lay date/hatch date and elevation, and between all of these variables and any of the habitat variables were not significant and thus no interactions were included in the selected models. Furthermore, the difference between snowmelt and lay date did not have any effect on DFR or mean nestling mass in the univariate models, and was thus excluded from further analyses. Snow cover (2019–2021) did not improve the model fit in any model and was never significant. Therefore, this variable was also not included in the selected models.

The selected model for the data from all years (2016–2021) showed a decrease in DFR with lay date (i.e. greater probability of failure earlier in the season) and an increase in DFR with elevation. The effect sizes for both variables were similar (Fig. 3a,b, Table 2). In the reduced datasets from years when grass cover and/or grass height was recorded (Tables 1 and 2), there was a significant negative relationship between DFR and grass cover (Fig. 3c, Table 2), and between DFR and grass height (Fig. 3d, Table 2). The model on the subset 2019–2021 including year as a fixed effect caused model fitting problems, but year nonetheless had a significant effect. We therefore decided to include year as a random term. It should be also noted that in Figure 3d the *y*-axis is scaled differently due to the subset of 2020–2021, which had higher DFR than in all other years (see also Fig. 1a). Models including mean temperature at the specific nest location during incubation (2019) did not show any effect of day ($\beta_{day} = -0.020 \pm 0.124$, $P_{day} = 0.87$) or night temperature ($\beta_{night} = -0.006 \pm 0.159$, $P_{night} = 0.97$) on DFR, either in univariate or in combined models.

Mean nestling mass

Mean nestling mass (see Table S1 for sample sizes of each year) was significantly affected by the age of the nestlings ($\beta = 0.28 \pm 0.04$, $P < 0.001$) in a combined linear model with age (linear) and number of nestlings as explanatory variables. The number of nestlings per nest ($\beta = 0.01 \pm 0.07$, $P = 0.9$) did not influence mean nestling mass. Age, but not number of nestlings, was included in all consecutive models. Mean nestling mass did not vary between years in a linear model with year and age as fixed effects (Supporting Information Fig. S2), and thus year was not included in consecutive models.

Although hatch date was positively influenced by elevation (Supporting Information Fig. S3), showing later hatching at higher elevations, the variance inflation factor (function *vif*) did not show any collinearity (*vif* < 2). Therefore, both variables were kept in the models. Including grass cover (subset 2019–2021) and grass height (subset 2020–2021) did not improve the fit of the respective models and did not show any significant influence on mean nestling mass. Thus, the results presented for mean nestling mass derived from the model on the whole data sample (2016–2021), and included the variables hatch date, elevation and age. In this model, mass increased significantly with nestling age and decreased significantly with hatch date, meaning that relatively late nests had lighter nestlings, with a decrease in average body mass of 6% (1.2 g where the population mean is 20.6 g) across the study period of 60 days (Fig. 4a, Table 3), whereas elevation had no significant effect (Fig. 4b, Table 3).

For the subset of 2019, there was no significant effect of temperature during the incubation period during the day ($\beta_{dayT} = -0.016 \pm 0.048$, $P = 0.74$) or night ($\beta_{nightT} = -0.030 \pm 0.059$, $P = 0.62$) on mean nestling mass, but there was a significant effect of age ($\beta_{day} = 0.338 \pm 0.125$, $P = 0.016$, $\beta_{night} = 0.334 \pm 0.122$, $P = 0.015$). Although mean nestling mass was not affected by temperature directly, we found a significant relationship between hatch date (doy) and temperature, showing that eggs that hatched relatively late experienced higher average daytime temperatures (2.6 °C increase per week), and a difference in average day temperature of 1 °C between nest locations at the lowest and highest elevations (median ± sd, ≤ 2300 m asl ($n = 7$): 13.7 ± 2.4, > 2300 m ($n = 10$): 13.4 ± 3.1, > 2400 m ($n = 8$): 12.1 ± 3.3) that is especially obvious early in the season (Supporting Information Fig. S4).
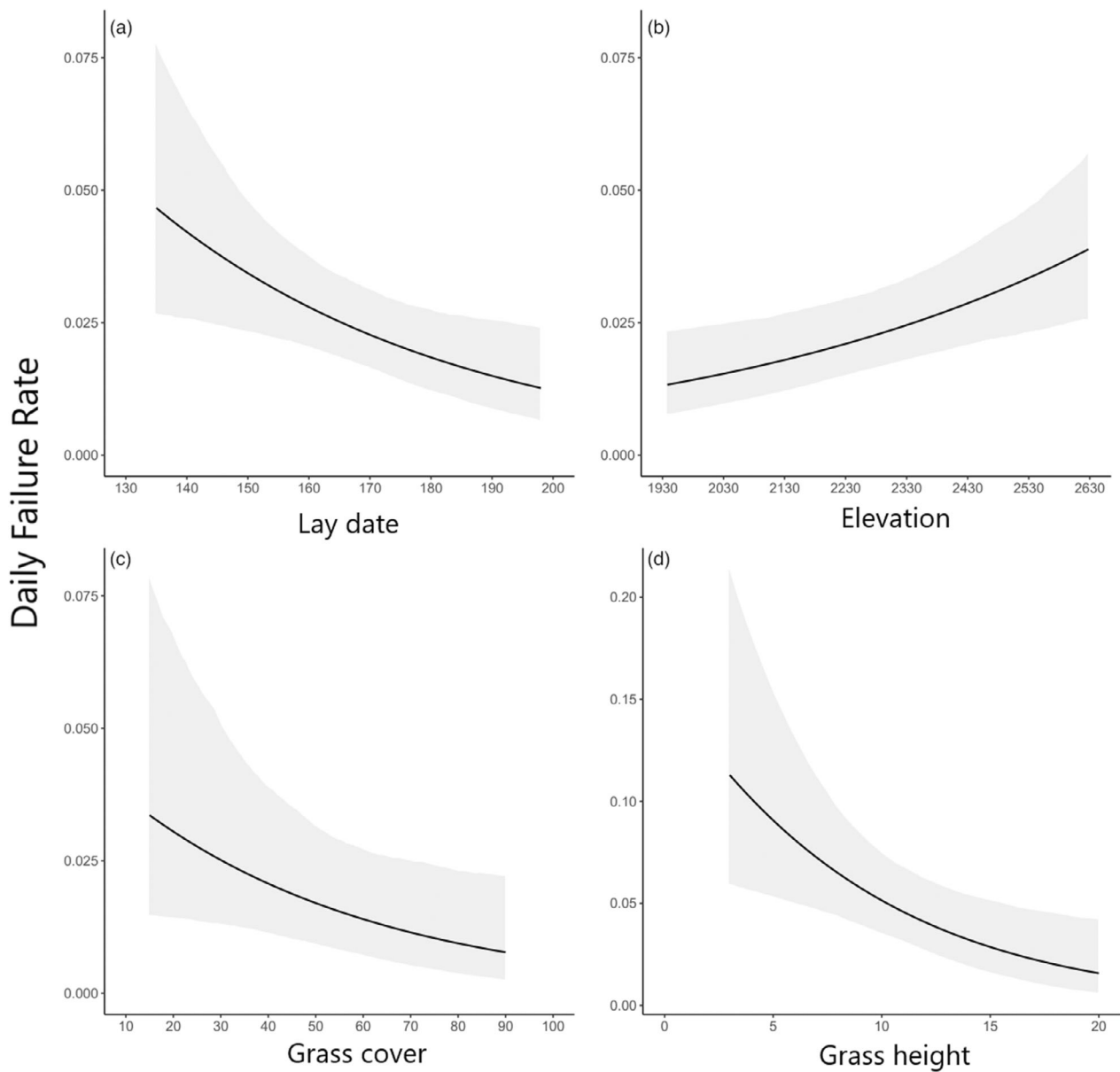
Figure 3. Variations in daily failure rate (DFR) with (a) lay date (doy) and (b) elevation (m asl) for the study period 2016–2021, (c) grass cover (%) for data of 2019–2021, modelled with GLMMs, and (d) grass height (cm) modelled with a GLM for data of 2020–2021 (note that the *y*-axis is scaled differently). Lines represent the fitted values. Grey-shaded areas represent the 95% credible intervals (CrI) of the models given in Table 2.

DISCUSSION

In this study, we show that the two different measures of reproductive success in an Alpine population of Wheatears, nest survival probability and mean nestling mass, differed in their response to timing of breeding. In contrast, a similar study on a lowland population of the same species showed a

decline in all reproductive measures as the season progressed (Öberg *et al.* 2014). Across our study period of 6 years, nest survival probability was highest for late breeders (using within-year scaled lay dates) and in years with later spring onset, at lower elevations, and at nest locations with higher grass height and cover. Conversely, mean nestling mass was found to decrease with hatch date,

Table 2. Effects of lay date (scaled within years) and habitat variables (scaled) on daily failure rate (DFR).

Selected models for DFR	Estimates (95% CrI)	df	P
2016–2021			
Intercept	**−3.689 (−4.024 to −3.360)**	191	**< 0.001**
Lay date	**−0.391 (−0.695 to −0.080)**		**0.014**
Elevation	**0.362 (0.050–0.611)**		**0.005**
Year (random effect, 6 levels)	Variance: 0.038, sd = ± 0.194		
2019–2021			
Intercept	**−4.106 (−4.749 to −3.466)**	123	**< 0.001**
Lay date	−0.223 (−0.648 to 0.216)		0.298
Elevation	0.266 (−0.098 to 0.619)		0.140
Grass cover at hatch date	**−0.436 (−0.864 to −0.016)**		**0.042**
Year (random effect, 3 levels)	Variance: 0.193, sd = ± 0.439		
2020–2021			
Intercept	**−3.088 (−3.489 to −2.661)**	40	**< 0.001**
Elevation	**0.292 (0.012–0.580)**		**0.041**
Grass height at lay date	**−0.611 (−1.076 to −0.132)**		**0.009**

For the study periods 2016–2021 and 2019–2021 we used a generalized linear mixed model (GLMM), and 2020–2021 generalized linear model (GLM). The degrees of freedom (df) differ between models due to data availability (see Table 1). Estimates are given in bold if significant ($P < 0.05$) and if 95% credible intervals (CrI) of the model estimates did not include zero. Null deviance and residual deviance on df respectively are shown.
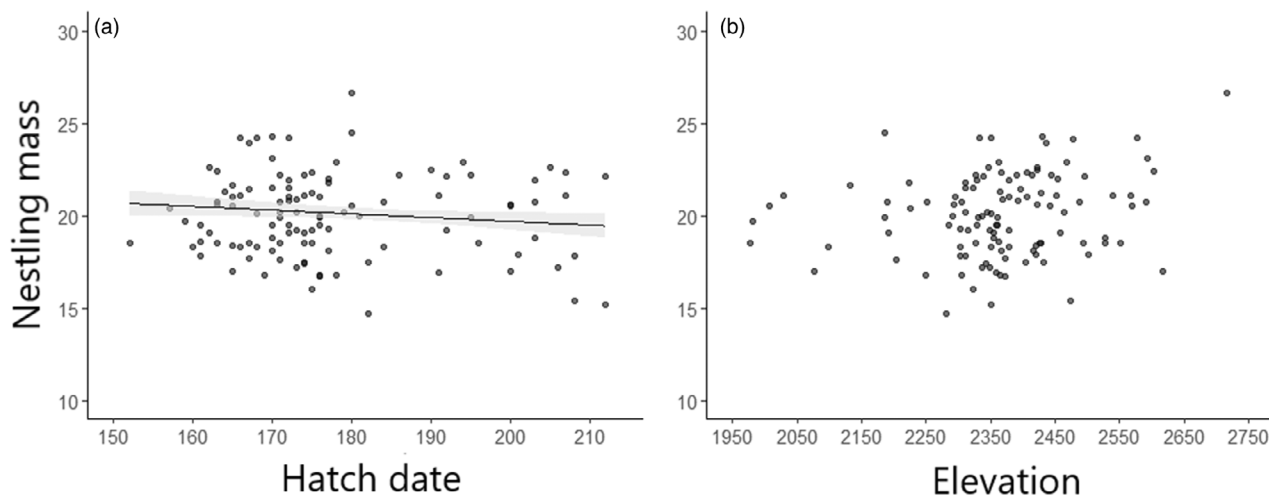
Figure 4. Variations in mean nestling mass (g) with (a) hatch date (doy) and (b) elevation (m asl) modelled with a linear model for the study period 2016–2021.The line represents the fitted values (when age is scaled). Grey-shaded areas represent the 95% CrI of the model estimate given in Table 3.

Table 3. Effects of hatch date (doy, scaled within year), elevation (scaled) and age on mean nestling mass (LM).

Selected model for mean nestling mass (scaled)	Estimates (95% CrI)	± se	R^2	df	P
Intercept	**−2.345 (−2.998 to −1.718)**	0.321	0.36	106	**< 0.001**
Hatch date	**−0.112 (−0.312 to −0.005)**	0.077			**0.043**
Elevation	0.109 (−0.036 to 0.260)	0.075			0.142
Age	**0.282 (0.209–0.355)**	0.038			**< 0.001**

Estimates are given in bold if significant ($P < 0.05$) and if 95% credible intervals (CrI) of the model estimates did not include zero.

showing that relatively late breeders are probably at a disadvantage in terms of nestling quality and hence probably in their fitness (Tinbergen & Boerlijst 1990, Magrath 1991, Streby *et al.* 2014).

Overall, we did not find any trends in lay dates across our six study years, but there was a high interannual variability that seemed to be dependent in part on the annual snowmelt and green-up. The flexibility to adjust to annually variable snowmelt and green-up dates seemed to be limited, resulting in a wide annual variation in breeding success in our population, where the years of early breeding (2016, 2020, 2021) had a lower nest survival than years of late breeding (2017, 2018, 2019). Our findings are thus in contrast to other lowland studies of the Wheatear (Arlt & Pärt 2017, Low *et al.* 2019) and of other species (European Pied Flycatcher *Ficedula hypoleuca* (Le Vaillant *et al.* 2021, Nicolau *et al.* 2021) and Prothonotary Warbler *Protonotaria citrea* (Hoover & Schelsky 2020)), which seem to adjust the arrival–laying interval without significant negative impacts on fecundity. For arctic-alpine species, there seems to be a range of different responses to early or late seasons. Some species have shown no advancement in lay dates over time, e.g. Horned Lark (de Zwaan *et al.* 2022) and White-winged Snowfinch *Montifringilla nivalis* (Schano *et al.* 2021), in the latter case despite an advance in snowmelt. Some species benefit from earlier springs (Horned Lark; de Zwaan *et al.* 2022) and longer seasons (alpine population of the Rock Sparrow *Petronia petronia*; Mingozzi *et al.* 2021), whereas others show lower fledging success in years with an early onset of breeding (Snow Bunting *Plectrophenax nivalis*; Fossøy *et al.* 2015), or the fitness advantage of early breeding has been reduced over time (Wheatear; Arlt & Pärt 2017).

In long-distance migrant species, a generally higher breeding success for early breeders might derive from matching the peak in food abundance (Both *et al.* 2010). However, for the Wheatears breeding in our high-elevation study site, early breeding also carries the risk of low temperatures and severe weather conditions, which may indirectly lead to high failure probability in early springs and early in the season through increased predation risk (e.g. Rauter *et al.* 2002, Kluen *et al.* 2011, Higgot *et al.* 2020, Marcelino *et al.* 2020). This seems to be especially the case for the higher elevation nests within our study site that were subject to lower temperatures early in the season and which had higher failure rates at this time, in common with Horned Larks in British Columbia (MacDonald *et al.* 2016). Despite previous studies on birds in alpine systems providing evidence of the relationship between environmental conditions and predation risk (Rauter *et al.* 2002), interactions with indirect effects of weather are complex and remain to be analysed in future studies.

Vegetation characteristics seem to be a further factor that might influence Wheatear nest success and hence explain higher early failures. Nest locations having a higher grass cover and height had a lower failure rate, which might be linked both to better concealment of the nest (and to better adult foraging activity) from predators (as in Savannah Sparrow *Passerculus sandwichensis* and Buff-bellied Pipit *Anthus rubescens*; MacDonald *et al.* 2016), but also to a more favourable microhabitat with a higher invertebrate food abundance. Vegetation growth, and thus insect abundance, is limited by temperature. Whereas early in the breeding season, low temperatures limit food resources, high elevations become richer later in the season when low-elevation grasslands are already becoming depleted. However, even at high elevations, nest locations can be selected so that microhabitat and climatic features facilitate successful breeding (Jähnig *et al.* 2020). Hence, we found high-elevation nest locations that had a higher grass cover and height, and that showed a higher nest survival, compensating for potential negative effects of elevation on nest survival, e.g. by providing higher food abundance and nest concealment (Table 2, model 2019–21).

We cannot tease apart the effects of environmental constraints and those of more complex mechanisms including predator–prey interactions. Predation is the main reason for nest failure in our study area (Fig. 2). Early in the spring, feeding adults might be more detectable to potential predators, due both to lower vegetation cover and an increase in foraging activity and nest visits, and additionally nests are exposed to predators longer due to delays in hatching when temperature and nest attentiveness are lower (Leech & Leonard 1997, Rauter & Reyer 1997). Predators may face a higher pressure to acquire resources, too (harsh weather and reproductive costs leading to higher energy expenditure), and thus may be more active in searching for prey early in the season (MacDonald *et al.* 2016). Common predators that

have been recorded above the tree line in our study region include the red fox *Vulpes vulpes* and the stoat *Mustela erminea* (Patriarca & Debenardi 1997, Masoero *et al.* 2016, Jähnig 2018). For these species, voles are important prey (Yoccoz *et al.* 1998) in addition to ground-nesting birds. The alpine vole community consists mainly of common *Microtus arvalis*, bank *Clethrionomys glareolus* and snow voles *Chionomys nivalis*, and studies on these reflect that between-year fluctuations in survival and reproduction are fairly stable compared with sibling species in lowlands, and that population dynamics are non-cyclical (Yoccoz *et al.* 1998, Yoccoz & Ims 1999). We therefore do not assume that our observed differences in annual nest survival are due to between-year changes in vole abundance. Instead, the within-year decrease in Wheatear nest failure might be connected to the increasing abundance of voles with the progression of the season, which in turn may affect predation rate. Vole abundance is linked to snow cover and temperatures and is lower early in the season. Reproduction in spring leads to an increase in the population that reaches its peak between June (Western Alps, I. Melcore pers. comm.) and late July (subalpine forest, Austria; Hille & Rödel 2014), when above-ground food resources become more available. The increase in above-ground activity and abundance of voles increases their detectability to predators (Yoccoz *et al.* 1998) and may thus provide an abundance of prey that leads to lower predation rates for ground-nesting birds. Future studies should investigate in more detail predator–prey species interactions, i.e. predator and prey species abundance in alpine grasslands, and how predation risk changes with the between-year variability in environmental conditions.

We found mean nestling mass to be 6% lower in relatively late broods (Fig. 4a, Table 3), showing that these were in poorer condition compared with nestlings early in the season and subsequently might show a lower fledging survival (Streby *et al.* 2014). We did not find any effect of temperature on nest survival or mean nestling mass, but we measured higher temperatures at nests that were established later. Thus, we can state that nestlings of later clutches experienced higher temperatures. Nevertheless, and contrasting with previous studies on other species in arctic-alpine habitats (Snow Buntings (Fossøy *et al.* 2015), Savannah Sparrow and Dark-eyed Junco *Junco hyemalis* (de Zwaan *et al.* 2020, 2022)) that suggested a negative effect of low temperatures, our Wheatear nestlings from later clutches were significantly lighter than earlier ones. One possible explanation might be that late broods missed the peak in food abundance and thus we might find limitations of mean nestling mass due to a trophic mismatch (Doiron *et al.* 2015). This was discussed in a previous study on our population in relation to fledging success, which was significantly lower in a year with considerably advanced spring conditions when birds were presumably unable to adjust to the earlier season (Sander *et al.* 2021). de Zwaan *et al.* (2020) suggested that the larger nestlings in Horned Larks when temperatures were lower (which is usually the case early in the season) were due to the thermo-regulatory benefit of larger bodies, but that these adaptations could not be applied across species. However, this might be another explanation for the larger nestlings early in the season in our population. Ultimately, late broods are often replacements that typically have nestlings in poorer condition (Martin *et al.* 2017). As a generalist, the Wheatear might be able to use the most abundant prey species across the breeding season, and is thus potentially more resilient to climate change-related phenological shifts in the emergence of invertebrates than more specialized mountain birds. However, little is known about the key prey species for mountain populations of Wheatears and indeed other mountain passerines, or the extent to which these prey show seasonal peaks in availability. This should be a priority for investigation in future studies to understand better whether trophic mismatches influence timing of breeding and seasonal variation in reproductive success.

Our Wheatear population faces two major challenges. First, the alpine habitat with its strong seasonality and short breeding season forces birds to time their reproduction according to the annual snowmelt and spring green-up, where the onset of vegetation growth, and thus temperature, determines the availability of food resources. Following these constraints, we found rather stable lay dates and thus assume a low degree of flexibility in timing of breeding. In early springs, lay dates were slightly advanced, but did not track the advancement in spring onset (see also Sander *et al.* 2021), which might be one explanation for lower nest survival in early years and, within season, higher failure rates early in the season. Secondly, although

our population migrates a relatively short distance compared with more northerly populations, the arrival at the alpine breeding grounds needs to be timed accurately in relation to local environmental conditions, and a certain flexibility in their migration schedule is required (e.g. by adjusting stopover durations). A previous study on our population compared arrival dates of geolocator-tagged birds in two very different years in terms of spring onset, showing low variation (Sander *et al.* 2021). Further analyses on more individuals and additional years will improve the predictions of how Wheatears may alter their migration schedule according to interannual variability and the general trend of advancing spring onset.

Advanced springs might increase the probability of nest failure early in the season (unpredictability of weather and overall harsher conditions) and also lead to a delay in the breeding schedule. This in turn may result in higher asynchrony between rearing nestlings and the peak in food abundance, namely, a trophic mismatch (Both *et al.* 2010, Saino *et al.* 2011, Sander *et al.* 2021). Furthermore, we expect more frequent severe weather events (cold snaps, late snowfalls) with increasing climate change, leading to more nest failures and lower reproductive success. Both mechanisms may play an important role in our population; environmental constraints early in the season (and in early springs) increase nest failure probabilities indirectly when laying early, but a potential trophic mismatch when breeding late can lead to fledglings in poorer condition.

Synthesis

Migratory birds breeding in seasonal environments need to breed in timely fashion in the season to maximize nestling mass by synchronizing the rearing period with the peak in food abundance, despite a higher risk of predation or failure due to unfavourable weather and low food abundance for the adults. To do so, migrants in these environments need to time their migration schedule according to local environmental conditions at the breeding grounds. This might be realized by longer stopovers close to the breeding grounds, allowing better prediction of the conditions at the breeding site (de Zwaan *et al.* 2022, Sander *et al.* 2021). To some extent, the trade-off between early and late breeding may enable the Wheatear to maximize its fitness under variable spring conditions. So far,

implications for the species' adaptation to future climate change are hard to draw, as our study period is too short to estimate a long-term trend for this population. Nevertheless, variations in nest survival probability and mean nestling mass within and across years with different spring green-up patterns may disrupt this trade-off and thus have population consequences, as years with advanced springs showed a lower overall nest survival probability. Alternatively, the trade-off may actually facilitate adaptation to climate change, as low nest survival could be compensated for by heavier nestlings early in the season, and thus higher fledgling survival probabilities may buffer negative effects of low nest survival on reproductive output. With this study, we have shown that there are constraints limiting nest survival in early springs and early in the season. However, whether they adjust their migration schedule according to annual differences in spring green-up, and how this will impact the reproductive output in high-elevation populations, needs to be investigated further to understand their capability to adapt to recent and future climate change.

AUTHOR CONTRIBUTIONS

Martha Maria Sander: Conceptualization (lead); formal analysis (lead); investigation (equal); methodology (equal); project administration (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Susanne Jähnig:** Conceptualization (supporting); formal analysis (supporting); investigation (equal); methodology (equal); project administration (equal). **Simeon Lisovski:** Formal analysis (supporting); methodology (supporting); writing – review and editing (equal). **Camille Mermillon:** Investigation (supporting); methodology (supporting);

writing – review and editing (supporting). **Riccardo Alba:** Formal analysis (supporting); investigation (supporting); methodology (supporting); writing – review and editing (supporting). **Domenico Rosselli:** Project administration (supporting); writing – review and editing (supporting). **Daniel Edward Chamberlain:** Conceptualization (supporting); formal analysis (supporting); investigation (supporting); project administration (equal); supervision (lead); writing – original draft (supporting); writing – review and editing (equal).

CONFLICT OF INTEREST

The authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership, or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

ETHICAL NOTE

None.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Number of failed nests out of all nests monitored across the study period 2016 to 2021, and cause of failure. Weather means nest destruction by e.g. soil eruption after events of rainfall. Sample size for mean nestling mass represents the number of nests for which ringing data of nestlings was available.

Figure S1. Nestling mass (scaled) across the study period 2016 to 2021 (*n* given in Table S1). Univariate linear model did not show any significant variation with year and age as fixed effects: $\beta_{year} = 0.023 \pm 0.054$, $P = 0.68$, df = 106. Boxplots show the median, the 1st and 3rd quartile, and whiskers represent the minimum and maximum.

Figure S2. Linear relationship between hatch date (scaled within year) and elevation with regression line ($\beta = 0.283 \pm 0.066$, $P < 0.001$, $R^2 = 0.09$), and raw data points for all nests monitored in the years 2016 to 2021, where hatch date was available ($n = 179$).

Figure S3. Linear relationships between (left) average daytime and nighttime temperature during the egg period, and (right) mean day temperature and hatch date ($\beta = 0.369 \pm 0.084$, $R^2 = 0.43$, $P = 0.0002$, $n = 23$), shown across three different elevations (1st quartile (green): ≤ 2300 m asl, 3rd quartile (red): ≥ 2400 m asl, median (blue): 2350 m asl).

Figure S4. Male Northern Wheatear *Oenanthe oenanthe* perching in open alpine grassland territory, Western Italian Alps, Parco Naturale Val Troncea, 2019.