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The ecology of alpine birds:
Linking breeding and migration



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**The ecology of alpine birds:
Linking breeding and migration**

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ABSTRACT

Mountains ecosystems are hotspots for biodiversity and endemism. At the same time, they are threatened by a rate of warming due to climate change that is more than double that in lowlands. This makes them one of the most vulnerable ecosystems worldwide and thus is of major conservation concern. To protect mountain species from extinction, a basic understanding of their ecology is needed, which is missing to a large extent due to the practical and logistical difficulties of carrying out research in these landscapes. Despite this, mountains offer an excellent study system by providing an elevation gradient and a multitude of habitats along this gradient, making it possible to study species' adaptations to changing environmental conditions. However, these habitats and their climates differ between tropical and temperate mountains. This thesis focuses on temperate mountains, which are highly seasonal, resulting in a high variability in resources across the year, driven by temperature and snow cover. In the first part, the focus is on larger scale patterns of morphological adaptation and species distribution along elevation gradients. The second part is an in-depth investigation into the breeding and migration ecology of a typical species of alpine grasslands, the Northern Wheatear *Oenanthe oenanthe*.

Previous literature on mountain ecology describes important patterns in species' biology and ecology. When looking at morphological traits, Bergmann's rule and Allen's rule have been supported by some studies that found larger bodies and shorter extremities in animals living at high elevations. An analysis of bird ringing data from the European Alps and adjacent regions did not support these rules, as even longer wings have been observed in individuals breeding at higher elevations, which is assumed to facilitate their performance when flying in thin air and windy conditions (Chapter 2).

The diversity of many taxa, including birds, decreases with elevation, with the tree-line as an ecological border between high and low diversity. In Chapter 3, it is shown that this border also divides species with narrow habitat niches from

species in the alpine zone that are more generalist, and thus exploit a wider range of environmental conditions.

In Chapter 4, the distribution of species in relation to microclimate is considered. Birds breeding in open alpine grasslands were found to select for specific microclimates, whereas the distribution of mountain forest species was more closely linked to climate at a larger scale or was independent of climate. Thus, when studying the distribution of alpine birds, microclimates need to be considered, as the thermal niche of birds breeding in generally colder landscapes may be defined at quite a small scale. Open alpine grassland birds find this by selecting warmer sites (e.g. by favouring sun exposed slopes), where snow melts earlier in the season and resources and nest sites become available earlier.

Our model species, the Northern Wheatear, occupies its breeding territories as soon as some areas are snow-free, but it is also limited in the timing of breeding due to its long-distance migration. In Chapter 5, this was evident when comparing an early spring with an average one, as birds arrived at the breeding grounds around the same time of the year, even though long stopovers before reaching the breeding area implied a certain flexibility in arrival timing. Birds needed to catch up with the green-up of the habitat by laying earlier. This resulted in a reduced breeding success in the early year. The same pattern was found in Chapter 6 when analysing the nest survival in this population across six consecutive breeding seasons. Across years, early clutches, and those at high elevations, had lower chances of survival than later ones. On the contrary, nestling mass was found to be higher in early clutches, which points towards a trade-off between breeding early and late in the season. This shows a certain flexibility in the timing of the breeding according to advancing spring conditions which are becoming more frequent with climate change. The Alpine population of the Northern Wheatear might be able to cope with these phenological changes by adjusting its migration schedule and the arrival-laying interval, assuming that its habitat, the open alpine

grassland, will remain despite the current and predicted upward moving tree-lines and land-use changes.

To conserve biodiversity in mountains and keep their ecological systems intact, we need to maintain their specific habitats. To protect the species in these habitats, we need to understand basic species ecology and patterns of species distribution. Here, we have contributed to the knowledge of what drives bird distributions across elevation gradients, and have investigated in detail the breeding ecology of a typical alpine songbird, and in particular we have incorporated the complexity of its annual cycle in our research by linking the breeding season and migration. On this basis, further studies could elaborate the drivers of productivity in alpine songbird populations by connecting the different measures of breeding success, timing of life-history events and survival estimates with environmental variables to ultimately develop management strategies for the conservation of alpine habitats.

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CHAPTER I – Introduction

The importance of mountains to global biodiversity

Mountains are created by plate tectonics and shaped by relief development, weathering and erosion, leading to highly intricate environmental heterogeneity, which ultimately provides the conditions for high biodiversity (Antonelli *et al.* 2018). Species diversity is generated through radiation, i.e. colonization of novel mountain habitats by populations (and thus exploitation of ‘vacant’ niches), by isolation through barriers, but also by providing bridges, i.e. when northerly distributed species follow their optimal niche to southern latitudes by using high elevation habitats as corridors (Perrigo *et al.* 2019; Rahbek *et al.* 2019). The global land surface defined as mountains differs from one definition to another, ranging from 2.64 % (Testolin *et al.* 2020) to 30.5 % (Körner *et al.* 2017). Definitions differ mostly due to different focuses, as the climatic and geomorphological point of view (Testolin *et al.* 2020) excludes habitats that are interesting from the ecological perspective, such as low elevation habitats which show characteristic alpine features that allow alpine species (i.e. species of open habitats above the tree-line) to occur there (Körner *et al.* 2017). This is true for many upland regions at northern latitudes in Europe, such as Scotland and Norway, that are inhabited by e.g. the Rock Ptarmigan *Lagopus mutus* that also occurs above the tree-line in the European Alps (Smith *et al.* 2013). All definitions, however, agree that mountains contain a disproportionately high biodiversity of terrestrial species, hosting an estimated one third (Martin *et al.* 2021) of the world’s terrestrial biodiversity and half of all global biodiversity hotspots (Körner *et al.* 2017; Myers *et al.* 2000), including hotspots of endemism (Noroozi *et al.* 2018). This thesis focusses on Holarctic (temperate) mountains, which are highly seasonal compared to mountains in the tropics. Nevertheless, tropical mountain habitats can also show strong seasonal (rainy and dry seasons) as well as diurnal (large difference between day and night conditions) patterns. Holarctic mountains host 324 bird species that are mountain specialists (at least 50% of the species’ breeding range in high

elevations of Holarctic mountains, Scridel *et al.* (2018)), such as the White-winged Snowfinch *Montifringilla nivalis* (Brambilla *et al.* 2020), the Alpine Accentor *Prunella collaris* (Figure 1) and the Alpine Chough *Pyrrhocorax graculus* (de Gabriel Hernando *et al.* 2021), but also 494 generalists (at least 50% of the species' breeding range in Holarctic mountains, Scridel *et al.* (2018)), such as the Northern Wheatear *Oenanthe oenanthe* (Bastianelli *et al.* 2017; Jähnig *et al.* 2018, 2020; Mermillon *et al.* 2021; Pearce-Higgins 2010; Sander *et al.* 2021), the Water Pipit (Bastianelli *et al.* 2017; Rauter *et al.* 2002) and the Ring Ouzel *Turdus torquatus* (Barras *et al.* 2021a, 2021b) (Figure 2). Mountain birds also include many long-distance migrants that are of special conservation concern (Boyle and Martin 2015; Inouye *et al.* 2000). Studying biodiversity in mountains is therefore of global importance for conservation.

Mountain habitats are comparatively far less impacted by anthropogenic disturbance and show lower rates of land-use change (Martin 2001) than lowland habitats. Apart from their role as refugia during past (non-anthropogenic) climate-driven species extinctions (Rahbek *et al.* 2019), they provide a current refuge not only for cold-adapted species, but also for lowland generalist species that have suffered recent population declines due to land-use change, including agricultural intensification and urbanisation (Scridel *et al.* 2018). In Europe, for many farmland birds such as the Ortolan Bunting *Emberiza hortolana* and Woodchat Shrike *Lanius senator*, these trends are currently leading to local extinction (BirdLife International 2021; Brambilla 2019), but some, such as the Tree Pipit *Anthus trivialis* and Whinchat *Saxicola rubetra*, may persist in alpine open grasslands when former lowland habitats have undergone land-use change, and are no longer suitable (Archaux 2007).

At the same time, mountains show a more than doubled rate of warming compared to the global average (Brunetti *et al.* 2009; Martin *et al.* 2021; Oyler *et al.* 2015; Wang *et al.* 2016). In mountain environments, this warming is followed by: 1. a phenological shift towards earlier springs across trophic levels, and

potentially prolonged summers (even though these changes are not well studied and general patterns are not yet understood) (Asam *et al.* 2018; Jabis *et al.* 2020; Migliavacca *et al.* 2008; Vitasse *et al.* 2021), 2. a higher number of extreme events, such as late snowfalls in spring (Martin and Wiebe 2004; Moreno *et al.* 2015), and 3. habitat shifts and an upslope advance of the tree-line, leading to a decreasing area and degeneration of open grasslands (Chamberlain *et al.* 2013; Ewing *et al.*; Lehtikoinen *et al.* 2018; Scridel *et al.* 2018; Smith *et al.* 2013), e.g. the projected loss of suitable habitat for the Rock Ptarmigan above the current tree-line in the Italian Alps is c. 30 % (until 2039) to 50 % (until 2099) (Ferrarini *et al.* 2017). The loss of alpine open habitats is additionally fuelled by human land-use change, such as their use for recreation (Caprio *et al.* 2011), alteration of grazing activities and afforestation (Herrando *et al.* 2016). Across taxa, alpine species are expected to decline or even become extinct due to range contractions and higher temperatures (Bender *et al.* 2019; Elsen and Tingley 2015; Pauli *et al.* 2012; Urban 2018), but population status and trends for alpine species are poorly known (Chamberlain *et al.* 2012), although this issue has been addressed recently for birds (Bani *et al.* 2019; Lehtikoinen *et al.* 2018). Some case studies on temperate alpine birds reflect that high elevation specialists and/or cold-adapted species such as the White-winged Snowfinch and ptarmigan spp (genus *Lagopus*), show a high sensitivity to warming, and severe future population declines are predicted for many alpine birds (Brambilla *et al.* 2020; Chamberlain *et al.* 2016b; de Gabriel Hernando *et al.* 2021; Scridel *et al.* 2021).



Figure 1. Alpine Accentor (juvenile) as an example of a mountain specialist. M. M. Sander, Val Troncea, 2021.



Figure 2. Ring Ouzel as an example of a mountain generalist. M. M. Sander, Val Troncea, 2021.

Adaptations to high elevations

To live at high elevations, animals need to cope with lower temperatures, higher precipitation, windier conditions, high solar radiation and lower air pressure, which result in a range of physiological and behavioural adaptations. Additionally, the high variability in all environmental conditions between and within years, and even on a daily basis, forces animals to react flexibly to changes, as e.g. temperature differences can be more than 40°C between day and night in the early season. Species therefore need to cope with extremely high and low temperatures, or dry and wet conditions, and within a short timeframe (MacDonald *et al.* 2013; Martin 2001; Martin and Wiebe 2004; Nagy and Grabherr 2009). This may result in the occurrence of more generalist species at higher elevations (Figure 2), i.e. above the tree-line, and alpine specialists breeding in the highest habitats (nival zone) (Mermillon *et al.* 2021) (Figure 1).

Physiological adaptations to low temperatures include larger bodies in populations at high elevations or high latitudes (Bergmann's rule), that have a lower surface-volume ratio and thus less heat loss compared to their conspecifics in warmer climates. However, results in former studies were highly inconsistent across species showing support for the Bergmann's rule, thus larger bodies in colder environments in some (Laiolo and Rolando 2008; Meiri and Dayan 2003; Yoccoz *et al.* 1998) and contradictory patterns in others (Bears *et al.* 2008; Freeman 2017; Lundblad and Conway 2019; Sander and Chamberlain 2020) (Table 1). In the latter studies, where Bergmann's rule was not supported and bodies were smaller in colder environments, it was argued that the larger bodies would also require more energy intake, which is not beneficial in highly seasonal and thus temporarily resource-limited habitats. These limitations may also generally reduce the growth of morphological traits (Bears *et al.* 2008). A further morphological adaptation to high elevations can be longer wings (for increased flight efficiency by reducing metabolic costs) in birds flying in conditions with lower air pressure and more wind (Bears *et al.* 2008; Lundblad and Conway 2019; Martin and Wiebe 2004; Sander and

Chamberlain 2020), but also here inconsistencies are found across species (Meiri and Dayan 2003), which might be again due to the growth limitations in resource-limited environments. Low air pressure furthermore requires adaptations to hypoxia, e.g. egg shell porosity in birds was found to be higher at higher elevations, probably as an adaptation to increase the rate of gas exchange under conditions of low atmospheric pressure (Nagy and Grabherr 2009).

The generally short breeding season in temperate mountains (approximately three months) and the harsh environmental conditions require adaptations in life-history traits to reproduce successfully. Across taxa, this seems to be achieved by low fecundity, but higher survival of adults and juveniles (Bastianelli *et al.* 2017; Camfield *et al.* 2010; Lu 2005; MacDonald *et al.* 2013; Martin *et al.* 2009; Yoccoz and Ims 1999) (Table 1). In birds, this results in usually only one clutch per season (Camfield *et al.* 2010; Martin and Wiebe, 2004). In a high elevation population of the ground-nesting Savannah Sparrow *Passerculus sandwichensis*, the breeding season was shorter and annually highly variable in duration which was related to the variability in environmental conditions, as the timing of snowmelt determined the start of nesting. To compensate for the reduced annual fecundity, the single clutch was larger, and the adult and juvenile return rates were higher than in lowland populations (Martin *et al.* 2009). Similar patterns have been found in alpine populations of the Horned Lark *Eremophila alpestris* (Camfield *et al.* 2010), Northern Wheatear and Water Pipit *Anthus spinoletta* (Bastianelli *et al.* 2017). However, different strategies may occur, as in Blackbirds *Turdus merula*, where smaller clutches have been observed in a high elevation subspecies, but these had larger eggs (Lu 2005), and in Water Pipits, where birds risk higher nest failures in early seasons by early clutch initiation, but in doing so they increase the possibility for renesting after failure, or of raising a second clutch after successful early nesting (Bollmann and Reyer 2001).

Behavioural adaptations include movements that can be seasonal, mid-seasonal (e.g. between first and second broods), but also daily (e.g. in early spring),

to avoid low temperatures, precipitation and snow cover (e.g. Ring Ouzel, Barras *et al.* (2021b)) (Table 1, Figure 2). The latter influences the availability of food resources in particular, whereas the first two require higher energy intake for thermoregulation in homeothermic animals. More regular movements are called migration. In temperate mountains, elevational migration is performed when animals move towards lower elevations in winter where snow cover is lower, and temperatures, and food abundance and availability are higher (Barçante *et al.* 2017; Boyle 2017; Inouye *et al.* 2000). Seasonal migration is another strategy to avoid food scarcity or unavailability, low temperatures and severe weather during winter in seasonal environments, and birds migrate short or long distances towards southern regions in autumn and northwards in spring (Hansson *et al.* 2014), which additionally determines the species' breeding phenology and success in high elevation habitats (e.g. Northern Wheatear, Sander *et al.* (2021)). Furthermore, some mammal species hibernate during winter (Inouye *et al.* 2000) or shift their activities below ground (Yoccoz and Ims 1999).

Table 1. Examples of adaptations of homeothermic vertebrate species to living and breeding at high elevations.

Category	Species	Adaptation	References
Physiology	Red-billed Chough <i>Pyrrhocorax pyrrhocorax</i> , Alpine Chough <i>Pyrrhocorax graculus</i>	Larger individuals, shorter extremities	Laiolo and Rolando 2008; Meiri and Dayan 2003
	Dark-eyed Junco <i>Junco hyemalis</i> , Yellow-eyed Junco <i>Junco phaeonotus</i> , Blackbird <i>Turdus merula</i>	Lower body mass, longer wings	Bears <i>et al.</i> 2008; Lundblad and Conway 2019
	Bank Vole <i>Myodes glareolus</i>	Higher body weight, larger males	Yoccoz <i>et al.</i> 1998
Life-history traits	Blackbird	Larger eggs, smaller clutches	Lu, 2005
	Savannah Sparrow <i>Passerculus sandwichensis</i> , Horned Lark <i>Eremophila alpestris</i> , Water Pipit <i>Anthus spinoletta</i> , Northern Wheatear <i>Oenanthe oenanthe</i>	shorter breeding seasons, fewer broods per season, larger clutches, and higher adult and juvenile survival	Bastianelli <i>et al.</i> 2017; Camfield <i>et al.</i> 2010; Martin <i>et al.</i> 2009
	Bank Vole, Snow Vole <i>Chionomys nivalis</i>	Smaller litter size, higher age at 1 st reproduction	Yoccoz and Ims, 1999
Behaviour	Ring Ouzel <i>Turdus torquatus</i> , Yellow-eyed Junco	Seasonal and daily movements to avoid harsh weather	Barras <i>et al.</i> 2021b; Lundblad and Conway 2019
	Citril Finch <i>Carduelis citrinella</i> , White-throated Dipper <i>Cinclus cinclus</i> , Grey Wagtail <i>Motacilla cinerea</i>	Elevational migration	Borras <i>et al.</i> 2010; Crowther <i>et al.</i> 2018; Klemp 2003
	Northern Wheatear	Selection for nest sites with beneficial microclimate, long-distance migration	Conder 1989; Jähnig <i>et al.</i> 2020; Sander <i>et al.</i> 2021
	Bank Vole, Snow Vole	Below ground activity during cold season	Yoccoz and Ims 1999; Yoccoz <i>et al.</i> 1998

Open alpine grassland habitats as a highly seasonal environment

As this study was carried out in temperate mountains, the European Alps, we focus here on the habitat distribution and characteristics and species occurring in the Western Italian Alps. Here, at lower elevations, in the sub-alpine zone, forests are dominated by the European Larch *Larix deciduas* interspersed with Norway Spruce *Picea abies*, Mountain Pine *Pinus uncinata* and Arolla Pine *P. cembra*. The tree-line is around 2,200 m a.s.l., but may vary locally due to pastoral activities or microclimates. This habitat (tree-line ecotone) is characterized by shrubby vegetation, formed by rhododendron *Rhododendron ferrugineum*, juniper *Juniperus nana* and single or patches of small larches, and to a lesser extent common bilberry *Vaccinium myrtillus* and bogberry *V. uliginosum*. Above the tree-line, in the middle-alpine belt, wide open grasslands are found, dominated by grasses (Gramineae, *Festuca* and *Nardus* spp.) that are influenced by grazing cattle. Open grasslands transform to rocky areas, the nival zone, around 2,700 m a.s.l. (Figure 3). Due to pastoral activities, and some natural drivers (in particular avalanches), open grassland habitats occur frequently below the tree-line, so that open grassland bird species can be found along a wide elevational gradient. The abandonment of pastoral activities, but also pressures from tourism, in particular skiing, has led to a decline and/or degradation of open habitats and their species across the Alps (Caprio *et al.* 2011; Chamberlain *et al.* 2016a, 2013; Jähnig *et al.* 2018; Oddi *et al.* 2021). Even though species diversity decreases with elevation, and is thus relatively low in open grasslands compared to the forest and ecotone, high elevation habitats are important for conservation as they are inhabited by species with declining population trends (Boyle and Martin 2015; Chamberlain *et al.* 2013). Typical open grassland birds in alpine habitats are the Northern Wheatear, Water Pipit and Black Redstart *Phoenicurus ochruros*, but territories of these species overlap to a large extent with species related to shrubby vegetation or small trees, such as the Whinchat, Rock Thrush *Monticola saxatilis*, Linnet *Carduelis cannabina*, Rock Bunting *Emberiza cia* and Ring Ouzel. On the border of

the scree dominated habitats, the occurrence of open grassland birds can overlap with birds of the nival zone, such as Alpine Accentor, Red-billed Chough, Alpine Chough and White-winged Snowfinch (Jähnig *et al.* 2020; Mermillon *et al.* 2021).

In open alpine grasslands, across trophic levels, the phenology of food resources is highly variable between years, and the point of time when they become available for animals is driven by the annual snowmelt in spring. In recent years, an advance in the date of snowmelt due to climate change has been recorded, which alters plant phenology, insect emergence, and thus effects higher trophic levels such as birds (Jabis *et al.* 2020). As long as the area is covered by snow, ground nesting birds have no access to food resources and/or nesting sites (Figure 4). An additional challenge is the assessment of the quality of the breeding territories by males that is limited by snow cover (Bollmann *et al.* 1997; MacDonald *et al.* 2016; Rauter *et al.* 2002) (Figure 5). Knowing which habitat characteristics are selected at certain times of the breeding season is therefore important in order to understand the distribution of open alpine grassland species and fine-scale species-habitat associations (Chamberlain *et al.* 2012; Jähnig *et al.* 2020; Sander *et al.* (under review)). The seasonality drives the emergence of insects and the accessibility and abundance of their larvae, which are important for feeding nestlings. The timing of snowmelt and subsequent emergence of insects is thus crucial for the timing of breeding and reproductive success of insectivorous bird species (Kristensen *et al.* 2015; Sander *et al.* 2021, (under review)) (Figure 6).



Figure 3. Cold snaps and late snowfall in alpine grasslands in early spring. M. M. Sander, Val Troncea, 2021.



Figure 4. Arrival of the Northern Wheatear at alpine breeding grounds (left: male, right: female). M. M. Sander, Val Troncea, 2021.



Figure 5. Establishment of territories by the Northern Wheatear in early spring. 1st year male. M. M. Sander, Val Troncea, 2021.



Figure 6. Emergence of prey species, such as butterfly larvae (Lepidoptera), for insectivorous birds varies inter-annually. D. Trense, Val Troncea, 2021.

Effects of global warming on migratory birds breeding in alpine habitats

In seasonal environments, the optimal exploitation of food resources by higher trophic levels requires the synchronization with lower levels, namely plant phenology and insect emergence (Kristensen *et al.* 2015; Kubelka *et al.* 2022). The need for synchronization is likely to be especially marked at high latitudes and high elevations given the relatively short breeding season. Recently, phenological shifts across taxa under climate change have been observed in alpine habitats (Vitasse *et al.* 2021). The degree of flexibility in the arrival of migratory birds at the breeding grounds thus influences the optimal exploitation of resources, but also sets the horizon for the ability to adapt breeding phenology to changing (advanced) springs (Both and Visser 2001; Both *et al.* 2010). In Afro-Palaeartic migrants, strong population declines have been noted, which in several cases have been linked to breeding phenology, in particular an overall advancement in spring phenology at the breeding grounds together with variations in weather at the wintering grounds (Haest *et al.* 2020; Saino *et al.* 2011). Indeed, an increasing mismatch between the arrival at the breeding grounds and the spring green-up has been noted in arctic shorebirds (Lameris *et al.* 2021; Saalfeld *et al.* 2019), but some species may adapt to the earlier onset of spring by speeding up their migration (Amélineau *et al.* 2021; Costa *et al.* 2021), or shortening their arrival-laying interval (lowland population of Northern Wheatears (Low *et al.* 2019), Pied Flycatchers *Ficedula hypoleuca* (Nicolau *et al.* 2021)). Phenological mismatches impact the fitness of migratory animals, but do not necessarily reduce species' fitness if a minimum of resources is still available to raise offspring (Corkery *et al.* 2019). In addition to potential phenological mismatches in seasonal environments, inclement weather events are likely to become more frequent with global warming, and may affect the breeding success directly by reducing hatching success and nestling survival during cold snaps, late snowfall and high precipitation (Figure 3), or indirectly by reducing the availability of arthropods for insectivorous species, and thus adult survival (Kluen *et al.* 2011; Martin and Wiebe 2004; Moreno *et al.* 2015).

The Northern Wheatear breeds in open alpine grasslands at the southern border of its breeding distribution (Jähnig *et al.* 2018, 2020; Mermillon *et al.* 2021; Pearce-Higgins 2010; Sander *et al.* 2021). This species is an insectivorous long-distance migrant that feeds its nestlings with larvae of Lepidoptera and Diptera (Oosten *et al.* 2014), and is thus highly dependent on the spring phenology and the emergence of these prey species (Figure 6). Whether mismatches between the arrival at the breeding grounds, clutch initiation and the advancement in spring green-up occur in alpine populations, and if there are negative effects on their reproductive success, has not been investigated so far (Sander *et al.* 2021) (Figure 7). In other migratory songbirds breeding at high elevations, effects of the variability in spring conditions (temperature, precipitation, storms) on breeding success and/or nestling growth have been inconsistent across species, which may show different strategies in coping with inclement weather in the early season and overall changes in spring conditions (MacDonald *et al.* 2013; de Zwaan *et al.* 2020, 2021). Further research is needed on the variation of migration schedules and breeding and/or life-history traits of alpine breeding long-distance migrants to adapt to the annual variability and the overall expected advancement of spring onset. It remains to be investigated whether these coping mechanisms are effective in maintaining population productivity in the future (Sander *et al.* 2021) (Figure 7).



Figure 7. Female Northern Wheatear tagged with a light-level geolocator and ringed with an individual colour combination. C. Fiedler, Val Troncea, 2021.

Aims of this thesis

With this thesis, the overarching aim is to discover more about the ecology of mountain bird species and so be in a better position to understand likely impacts of future environmental change. In the first part, a broader perspective is taken by considering mountain bird communities across a generally wide range of habitats (e.g. elevation gradients), describing physiological adaptations to living at high elevations and factors affecting mountain species' distributions. The second part presents the results of intensive studies on the ecology of a model alpine grassland species, the Northern Wheatear, considering detailed information on habitat selection, reproductive success, migration and phenology. These studies shall help to understand how birds might react and adapt to future land-use (such as abandonment of grazing activities, afforestation, recreational activities) and climate change, i.e. phenological shifts in spring progression and exceptional (more extreme) weather conditions.

In **Chapter 2**, we investigate the intra-specific adaptations in morphological traits of six resident and common songbird species occurring across a wide latitudinal and elevational range in Europe to understand the ability of species to adapt to potential changes in habitat distribution and climate.

The elevational distribution of birds breeding in mountain habitats according to their ecological niche is described in **Chapter 3** by using point-count and habitat data from different sites in the Western Italian Alps. In **Chapter 4**, we investigate the drivers of species distribution and the importance of the consideration of fine- and large-scale approaches. A particular importance is given to birds of open alpine grassland habitats, as these are especially vulnerable and show declining trends due to climate and land-use change. Most of the species inhabiting these habitats are migratory, which adds an additional challenge for their conservation. In our model species, the Northern Wheatear, the decline of open grassland breeding habitats and their long-distance migration add up to extremely difficult conditions to persist and adapt to climate and land-use change within their current alpine breeding range.

In **Chapter 5** and **6**, we therefore focus on linking the breeding ecology and the migration of the Northern Wheatear to investigate how an alpine population of a widely distributed long-distance migrant may adapt its phenology to environmental changes, and in doing so, if this may have effects on its reproductive success. No study to date has combined light-level geolocation, environmental data and nest monitoring of a migratory songbird breeding in European open alpine grasslands. Our study links data on breeding success with nesting habitat and annually variable environmental conditions from six consecutive breeding seasons, and explores the relationship between the migration schedule and wintering locations with breeding phenology for one year of tracking with light-level geolocation. In this way, we aim to obtain a complete picture of the species' life cycle. In **Chapter 5**, we address the following research questions: Where are the stopover and wintering sites of our population located? How and to what extent do

the between-year differences in local environmental conditions, arrival date and date of first nesting correlate with the breeding success in the population? In **Chapter 6**, we investigate in more detail the breeding success and question whether individual nest survival and nestling mass depend on an early or late start to breeding. Furthermore, we question whether and how environmental conditions influence these demographic parameters and the overall timing of breeding.

In **Chapter 7**, we discuss the overall implications of the results of the thesis in a broader context of environmental change and propose the next crucial research steps that are needed in alpine ornithology.

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CHAPTER II

Evidence for intra-specific phenotypic variation in songbirds along elevation gradients in central Europe

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ABSTRACT

Studying phenotypic variations along gradients may provide insights into mechanisms that drive species distributions, and thus can be useful indicators of environmental change. In mountains, the study of phenotypic variation along elevation gradients is of increasing relevance due to impacts of climate change. We analysed European ringing data to measure the direction of phenotypic variation along elevation gradients in six common, resident songbird species occurring along a wide elevational range. We modelled intra-specific change in wing length, body mass and their ratio with elevation and found a significant increase in wing length and a decrease in body mass at high elevations. The results of our exploratory analysis show the potential that continent-wide ringing databases offer to describe patterns of phenotypic variation along environmental gradients.

Keywords: Alps, Bergmann's Rule, body mass, wing length.

Running head: Phenotypic variation in Alpine birds

INTRODUCTION

Species with high variability in traits may more readily adapt to environmental changes (Lehikoinen *et al.* 2018). Phenotypic variation within species is shaped by the spatial and temporal differences of the habitats in which different populations live and includes differences in morphological traits such as wing length (Poblete *et al.* 2018). Studies of phenotypic variation in relation to the environment are important, as they may reveal fundamental drivers of variation within and between species. For example, Bergmann's Rule proposes that species of larger size tend to be found in colder climates (Bergmann 1847), a concept that has also been extended to variation within species, although support is not universal (Blackburn *et al.* 1999). Furthermore, studies of phenotypic variation may reveal sensitivity to environmental change. For example, recent studies have documented evidence that morphological changes in mountain birds (Delgado *et al.* 2019) and migratory passerines (Weeks *et al.* 2019) are correlated with climate change.

Along elevation gradients, numerous factors shape phenotypic adaptations. Variables that are causally related to elevation include ultraviolet radiation, oxygen levels, and (of particular relevance to phenotypic adaptation) temperature and air pressure. Bergmann's Rule is used to explain morphological differences across climate gradients, predominantly from warmer to colder environments (Meiri and Dayan 2003). There is some evidence for larger individuals (i.e. a higher body mass) with relatively shorter extremities, e.g. legs and wings, at high elevations (Laiolo and Rolando 2008, Meiri and Dayan 2003, Poblete *et al.* 2018). This may arise through selection for larger animals that have a lower surface area to volume ratio than smaller animals, so they radiate less body heat per unit of mass, in agreement with Bergmann's Rule. Conversely, a preponderance of smaller individuals (a combination of different length measurements and body mass) has been reported at higher elevations (Lundblad and Conway 2019), as have smaller individuals (body mass) with longer wings (Bears *et al.* 2008, Lu *et al.* 2009). The latter seems reasonable as smaller bodies require lower energy intake, which might

be a limiting factor in high elevation habitats with seasonally variable resource availability. For example, Freeman (2017) found little evidence for body size clines within tropical bird species, but where there were differences, they were inconsistent with Bergmann's Rule. Similarly, Boyce *et al.* (2019) found that body mass of Bornean mountain birds decreased with elevation whereas relative tarsus length increased. The authors argued that phenotypic adaptation is more likely to be driven by the foraging mode of high elevation species, rather than temperature (Boyce *et al.* 2019). In both of these studies, wing length was not related to elevation, even though other studies have argued that longer wings reduce the cost of flying at lower air pressure (Scott 2011) and may increase aerodynamic performance (Altshuler and Dudley 2006). Furthermore, flying in oxygen-thin environments requires physiological and morphological adaptations to enable the birds to cope with hypoxia and to reduce the metabolic cost of staying aloft (Barve *et al.* 2016, Scott 2011). A consensus on the association between phenotypic adaptations and elevation is therefore lacking, possibly because there have been few large-scale investigations on this topic.

We aimed to test whether there was a trend in intra-specific morphological variation in songbird species along elevation gradients. We analysed the variation in two phenotypic traits (wing length, body mass) and their ratio (i.e., wing length relative to body mass) in six different songbird species that occur along elevation gradients in the breeding and post-fledging period (spring and summer). We used ringing data retrieved from the EURING Data Bank (du Feu 2019), the coordinating organisation for European bird ringing schemes, and collected mainly in the Alps and their foothills.

METHODS

We selected species breeding along a continuous elevation gradient from 0 to >2000 m based on information in BirdLife International (2019), and from digital elevation maps available at www.ornitho.it. Furthermore, we selected species

which are classified as residents and/or facultative short-distance migrants (del Hoyo and Christie 2006, Glutz von Blotzheim and Bauer 1991), as long-distance migration itself shapes wing morphology (Fiedler 2005). We requested all available ringing data of birds captured and recaptured frequently (Fasano *et al.* 2018) in our prior defined Alpine landscape (44°N - 48°N, 4°E - 16°E, Switzerland, France, Italy, Austria, Germany, Slovenia) from the EURING database. These data included captures from outside the defined area (e.g. northern France, northern Germany, Sweden) if birds were then recovered inside this area (Fig. 1). Within the data set of all 14 species, we selected only adults that were first captures (to exclude pseudoreplication). Although we restricted our species to those that are mainly resident in the study region, we cannot exclude altitudinal migration during winter (Barcante *et al.* 2017, Boyle 2017, Hsiung *et al.* 2018). Furthermore, some of our species are known to disperse over short distances within their ranges, including some longer distance movements within Europe, e.g. Black Redstart *Phoenicurus ochruros*, Common Blackbird *Turdus merula* (del Hoyo and Christie 2006, Glutz von Blotzheim and Bauer 1991). We therefore excluded captures outside the period May to September to minimise the chances of including migrant individuals breeding at other elevations than those expected from the ringing location. After filtering the records following the above criteria, we selected those species for which we had sufficient records across the elevation gradient (10 % of all records per species had to be from locations above 1200 m.a.s.l.) and which had biometric data, i.e., wing length (as measured by the length of 3rd primary) and body mass. They were Common Blackbird, Eurasian Wren *Troglodytes troglodytes*, Coal Tit *Periparus ater*, Goldcrest *Regulus regulus*, Black Redstart, and Willow Tit *Poecile montanus*.

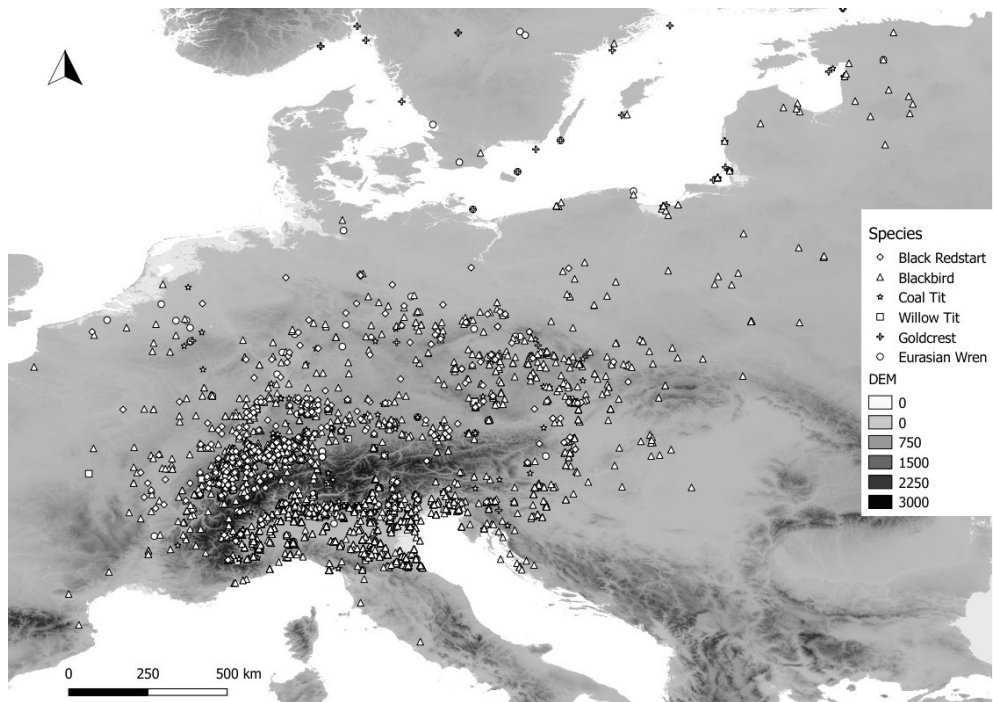


Figure 1. Locations of all first captures during breeding season (May – September) for each species. Origin of ringing data retrieved from EURING, entirely collected by the Swiss Ringing Scheme. Sample sizes of the whole dataset are given in Table S1.

Statistical Analyses

As wing length is allometrically correlated with body mass (i.e., individuals with longer wings also have higher body masses, Fig. S1) and both may be a proxy for body size, we calculated the ratio of wing length to the cubic root of body mass ($\text{wing length} / \sqrt[3]{\text{body mass}}$, henceforth wing:mass ratio) to analyse the differences in relative wing length between individuals breeding at low and high elevations. To allow direct comparison of effect sizes across species, we scaled all biometrics at the species level (z-score). To assess how wing length, body mass and wing:mass ratio varied as a function of elevation, we used linear mixed effect models, using the ‘lmer’ function in R 3.4.2 (R Core Team 2019), assuming normally distributed errors. The models included elevation as an explanatory variable, which we considered in two different ways in separate models: first, as a continuous

variable, and second as a categorical variable. Following the definition of mountain habitat for the Alps (Lehikoinen *et al.* 2018), we defined locations <1200 m.a.s.l. as low and >1200 m.a.s.l. as high elevations. Grouping the birds according to high and low elevations reflects the ecological context of this study, whereas showing the effect along a continuous gradient gives information about the distribution of our data.

Wing length, body mass and wing:mass ratio (all scaled) were analysed as response variables in three separate models in relation to elevation. We were interested in general trends with elevation across Alpine birds, hence we pooled all species for the analysis and set species as a random effect in all six models (i.e. three different response variables in relation to two different measures of elevation) to account for the fact that variation in scaled traits may be species-specific. However, we also ran the same models for each individual species (without the random term) to determine the extent to which individual species associations were consistent with the overall trends. There is evidence that biometrics of birds have changed over time in relation to increasing global temperatures due to climate change (Delgado *et al.* 2019, Weeks *et al.* 2019). To account for possible temporal trends over our time period of 36 years, we tested the effect year by including it as a fixed effect in the overall model and comparing AIC values for models with and without year. Additionally, we performed linear models for each species including year.

Analysis of model residuals did not show any violation of the model assumptions. We used Bayesian methods to obtain uncertainty estimates of the model parameters (Korner-Nievergelt *et al.* 2015) and therefore to account for the uncertainty of the model estimates and model predictions. Following Korner-Nievergelt *et al.* (2015), we used improper prior distributions, namely $p(\beta) \sim 1$, for the coefficients and $p(\sigma) \sim 1/\sigma$ for the variance parameters and furthermore obtained posterior distributions of the respective models by simulating 5000 values from the joint posterior distributions of each model's parameter, applying the

function 'sim' included in the package 'arm' (Gelman and Hill 2007). For the respective model estimates, we used the means of the simulated values from the joint posterior distributions of each model's parameter and the 2.5% and 97.5% quantiles as limits for the 95% credible intervals (CrI; Korner-Nievergelt *et al.* 2015). The effect of a variable was declared as significant if the corresponding 95% CrI did not include zero or if the 95% CrIs of the comparative groups (low and high elevation) did not overlap.

RESULTS

After selecting the six target species with sufficient sample sizes, the raw data from EURING contained 79,653 records, of which 30,426 were first captures and 12,805 fitted our time period of May to September. Of these, only 1,445 records contained biometrics (11% of all first captures during the breeding season; see Table S1 for sample sizes according to species), and, despite having considered data from a total of six countries, only data from the Swiss Ringing Scheme were usable. The records spanned a 36 year period (1982 – 2018, mean: 2010, 1st quartile: 2008, 3rd quartile: 2015), and presented an overall elevation gradient from 95 m.a.s.l. to 1,900 m.a.s.l. (mean: 962 m.a.s.l., 1st quartile: 462 m.a.s.l., 3rd quartile: 1,233 m.a.s.l.). The locations of first captures were widely distributed across Europe, but most records were located within or close to the Alps (Fig. 1; see Fig. S2 for heatmaps).

When considering the two elevation categories, there were $n = 908$ records for the low elevation group and $n = 534$ records for the high elevation group. In the overall model, the year had no significant effect on the biometrics and did not improve the model in terms of AIC, hence it was not considered further (Table S2). We additionally tested the effect of year on the wing:mass ratio in single-species models and found a positive effect in Coal Tit, indicating their wings increased in length relative to body mass over a period of 30 years (Fig. S3), but not in any other species, nor in the combined-species model.

We found a significant positive effect of elevation (continuous) on scaled wing length, which increased by 0.15 mm (95% CrI: 0.04 – 0.27) per 1000 m increase in elevation. Body mass was found to decrease significantly with elevation ($\beta = -0.11$, 95% CrI: -0.21 – -0.01). The wing:mass ratio also increased significantly with elevation ($\beta = 0.14$, 95% CrI: 0.09 – 0.20). When records were grouped into high and low elevation, the results were similar, with a positive effect on wing length ($\beta = 0.15$, 95% CrI: 95% CrI: 0.02 – 0.28) and wing:mass ratio ($\beta = 0.20$, 95% CrI: 0.12 – 0.28; Table 1, Fig. 2). In all models, much variation was unexplained, resulting in very low marginal R^2 -values (<0.1 , Table 1). High conditional R^2 -values were achieved only in models with wing:mass ratio, suggesting much variation was explained by differences between species (i.e., the random factor ‘species’ had a strong effect). For single-species models, parameter estimates were in general in accord with those of the combined-species model in terms of direction of effect. There was stronger support (i.e., a significant effect) for longer wings in Common Blackbird and Willow Tit, lower body masses in Coal Tit and increasing wing:mass ratio in Common Blackbird and Coal Tit, with increasing elevation. However, Willow Tit body mass showed the opposite trend to the overall model, significantly increasing with elevation (Table S3).

Table 1. Effect of elevation (continuous in $m \times 10^3$, and categorical) on the bird's scaled (z score) wing length, body mass and wing:mass ratio, modelled with linear mixed effect models (LMMs). The effect is significant if the 95% Credible interval (CrI) does not include zero. Significant effects of elevation are given in bold. $N = 1442$ in each case.

LMM	Intercept	Estimate (elevation)	Marginal R^2	Conditional R^2
Wing length ~ elevation (continuous) + (1 Species)	-0.157 (95% CrI: -0.292 – -0.022)	0.153 (95% CrI: 0.040 – 0.270)	0.007	0.010
Body mass ~ elevation (continuous) + (1 Species)	0.119 (95% CrI: 0.002 – 0.238)	-0.111 (95% CrI: -0.210 – 0.010)	0.004	0.005
Ratio ~ elevation (continuous) + (1 Species)	-0.23 (95% CrI: -1.44 – 1.01)	0.140 (95% CrI: 0.09 – 0.20)	0.002	0.930
Wing length ~ elevation (categorical) + (1 Species)	-0.061 (95% CrI: -0.405 – 0.002)	0.145 (95% CrI: 0.013 – 0.279)	0.005	0.008
Body mass ~ elevation (categorical) + (1 Species)	0.178 (95% CrI: -0.002 – 0.363)	-0.120 (95% CrI: -0.241 – 0.004)	0.004	0.005
Ratio ~ elevation (categorical) + (1 Species)	-0.171 (95% CrI: -1.38 – 1.060)	0.197 (95% CrI: 0.120 – 0.277)	0.004	0.930

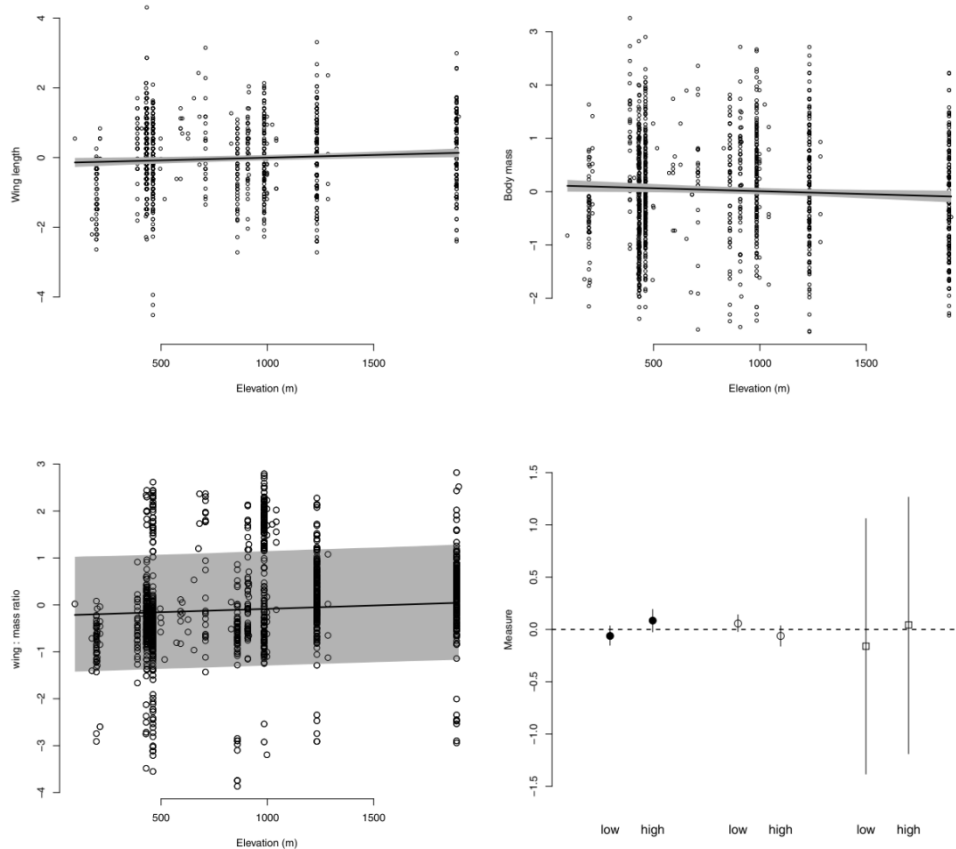


Figure 2. Intra-specific morphological variation of passerines along an elevation gradient. Plots show combined data of six species. Scaled measures wing length, body mass and wing:mass ratio along a continuous elevation gradient were analysed. Regressions are black solid lines and the corresponding 95% CrI are in grey, when the effect was significant. Right below: Differences in scaled measures wing length (filled circle), body mass (circle) and wing:mass ratio(square) between captures from low (<1,200 m.a.s.l.) and high (>1,200 m.a.s.l.) breeding grounds. Results of the appropriate LMMs are provided in Table 1.

DISCUSSION

Individuals breeding at high elevations were generally smaller and had longer wings. Wing:mass ratio increased with higher elevations; in other words, wing length increased relative to body size along the gradient, which was driven by both increases in wing length and decreases in body mass (Table 1, Fig. 2). These associations were, however, quite weak in terms of the variation explained by the models, and for body mass, in terms of the consistency of results at the species level.

Interestingly, our results do not provide much support for Bergmann's rule, which predicts shorter wings and larger bodies in colder (therefore higher elevation) environments (as shown by Laiolo and Rolando 2008, Meiri and Dayan 2003, Poblete *et al.* 2018). The combined-species model suggested a general decrease in body mass with elevation, although at the individual species level (Table S3), there was a single species, Willow Tit, that showed an increase in body mass. There was more consistency in associations between wing length and elevation, longer wings being evident in combined-species models and in most individual species (although only two were significant). Similar results have been found in individual species. For example, female Dark-eyed Juncos *Junco hyemalis* breeding at high elevations had longer wings and shorter tarsi (a measure of body size; Bears *et al.* 2008), and snowfinch *Montifringilla* species were smaller (in terms of body length, bill length, body mass, tarsus length) with longer wings and a higher ratio of wing length and body size at high elevation sites (Lu *et al.* 2009).

Along an elevation gradient, temperature (the variable hypothesized to explain Bergmann's Rule) might not be the only determining factor shaping bird morphology. Indeed, in tropical mountain systems, it has been shown to be of lower importance for trait variations along elevation gradients (Boyce *et al.* 2019, Freeman 2017); instead, flying in thin air (lower air pressure at high elevations) and the necessity to increase flight performance (due to stronger winds) might select for longer wings (Altshuler and Dudley 2006, Bears *et al.* 2008). The seasonality of

resource availability in higher elevation habitats, e.g., the later peak in insect abundance due to snow cover, hypoxia and climate severity (Bears *et al.* 2008) may further lead to an advantage of having a small body in order to reduce the amount of energy needed. It is possible that these factors selected for smaller body sizes in high elevation habitats, but there may also be direct effects that restrict the growth of morphological traits, such as body mass, during the individual's lifetime.

Although our results give some support to phenotypic adaptation to lower air pressure at higher elevations, it must be acknowledged that there are many potentially important drivers that vary along the gradient which were unable to take into account. For example, it is known that variation in wing morphology within species may be influenced by the degree of forest fragmentation (e.g., Fiedler 2005, Desrochers 2010) which could vary from more anthropogenically disturbed lowlands to mountain forests. Additionally, wing morphology may vary according to foraging habitat, as round-winged species have been shown to forage closer to the ground, whereas species with more pointed wings forage more commonly in trees (Marchetti *et al.* 1995). Furthermore, the influence of environmental factors such as forest cover and fragmentation may vary at large geographical scales. Our sample was derived from a relatively large area in order to maximize sample size. The availability of a larger sample of biometrics from ringed birds (see below) would also allow habitat and geographical influences (e.g. latitude) to be estimated.

Unfortunately, the data were not sufficient to account for sex and age. In addition to effects of environmental variables (see above), we assume that a large proportion of the unexplained variation in our models comes from morphological differences between males and females, as shown for songbirds in similar studies (Bears *et al.* 2008, Lu *et al.* 2009). Furthermore, our measure of body size (body mass) is likely to vary between individuals and may be sensitive to fine-scale seasonal and even diel variations that we were not able to take into account. Nevertheless, we would expect that body mass represents a reasonable,

approximate measure of body size. A better measure of body size would be one related to skeletal growth, such as relative tarsus length, which is likely to be less temporally variable (Bears *et al.* 2008), but which was not available on the EURING Data Bank. Another reason for the relatively weak effect of elevation on the morphological traits is that we used species occurring across the entire elevation gradient instead of comparing subspecies of low and high elevation. Additionally, due to the habitat requirements of the species we have chosen (mostly forest species), we do not have data from very high elevation habitats above the tree-line, where environmental cues may exert stronger pressures on the breeding and survival of birds (Lu 2005), in particular to cope with hypoxia (Barve *et al.* 2016), although within the studied region, possibly only Black Redstart would occur at these elevations in addition to lower elevation habitats.

This study has used a continental-scale database to analyse phenotypic variability in passerine species across elevation gradients. Whilst we find some intriguing results, notably individuals at higher elevations having lower body mass and relatively longer wings, we were restricted in the conclusions that we were able to draw due to data availability. To better understand phenotypic adaptations of birds to elevation, we highlight the importance of the collection of biometric ringing data, especially for high elevation populations, where data from breeding periods is lacking for many species. We suggest that ringers always record wing length (both 3rd primary and maximum wing length) and tarsus length, as well as body mass. Furthermore, the scientific potential of standardised bird ringing could be higher if we were able to improve the data transfer from national ringing schemes to the EURING Data Bank. Even though measurements are commonly taken within the standard protocols in all European ringing schemes, we only located usable data from the Swiss Ringing Scheme. Enhancing biometric data availability at the European scale would greatly enhance our ability to study species adaptations.

The current literature covers almost exclusively tropical mountain ecosystems, and comparative within-species studies in temperate regions are lacking, which might be an additional reason for the inconsistency in results. European-wide or even global ringing datasets have a huge potential to address questions regarding the phenotypic adaptations to different environments within the same species and their response to climate change (as there are indications for changes in morphology within recent decades (Fig. S3 and Delgado *et al.* 2019, Weeks *et al.* 2019). Further studies with larger biometric datasets (especially for high elevation populations of species) may even enable us to analyse differences in morphological variability between specialists and generalists, species of different habitat types (open grassland vs. forest), or differences in the degree of phenotypic plasticity between single species or subspecies (see Fig. S4 for visual comparison of the variability in traits between the study species, showing slightly higher variability in the data of Blackbirds and Coal Tits). Ultimately, we might be able to use phenotypic traits as predictors for the ability of a species to shift their range, and to assess whether they are more resilient and/or resistant to environmental changes.

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APPENDICES

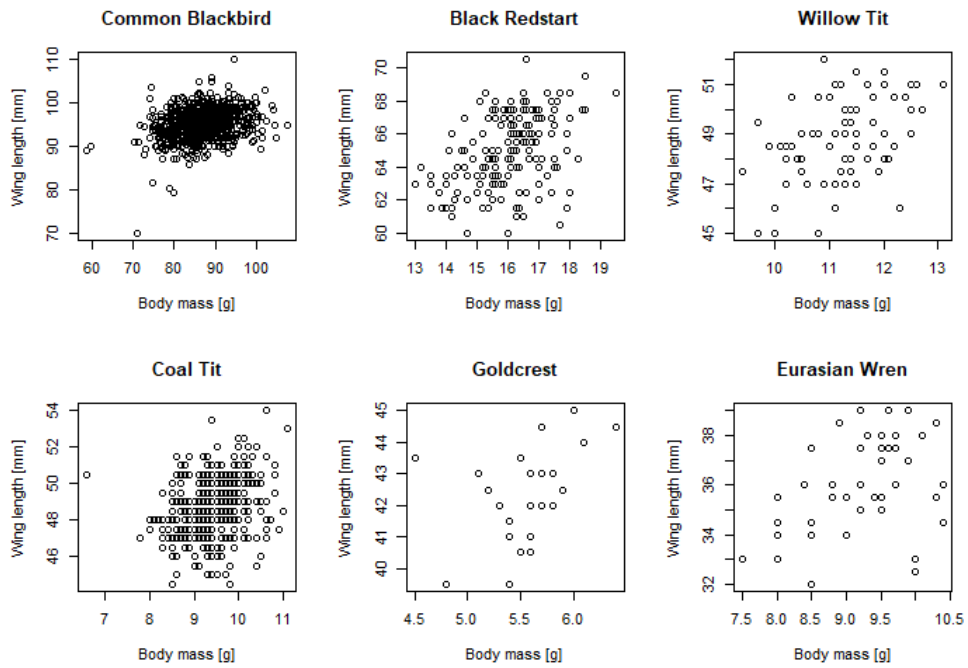


Figure S1. Associations between wing length and body mass for all six study species. The unscaled raw data are shown. Sample sizes for each species are given in Table S1.

Table S1. Sample sizes of each species included in the analysis (Number of records with biometrics). Number of records from birds captured above 1,200 m.a.s.l. are given in brackets. Ringing records were included if, for each individual (first capture during breeding season), location, date, wing length and body mass was available (% of records with biometrics).

Species	Total no. of records in Data bank	No. of adult first captures	No. of first captures during breeding season	No. of records with biometrics	% of records with biometrics
All species	79,653	30,426	12,805	1,442 (908)	11
Common Blackbird <i>Turdus merula</i>	53,811	20,039	8,844	739 (61)	8
Eurasian Wren <i>Troglodytes troglodytes</i>	8,285	3,195	485	50 (13)	10
Coal Tit <i>Periparus ater</i>	7,633	3,210	1,936	388 (364)	20
Goldcrest <i>Regulus regulus</i>	5,437	2,272	441	26 (21)	6
Black Redstart <i>Phoenicurus ochruros</i>	3,026	1,168	706	170 (15)	24
Willow Tit <i>Poecile montanus</i>	1,461	542	393	72 (62)	18

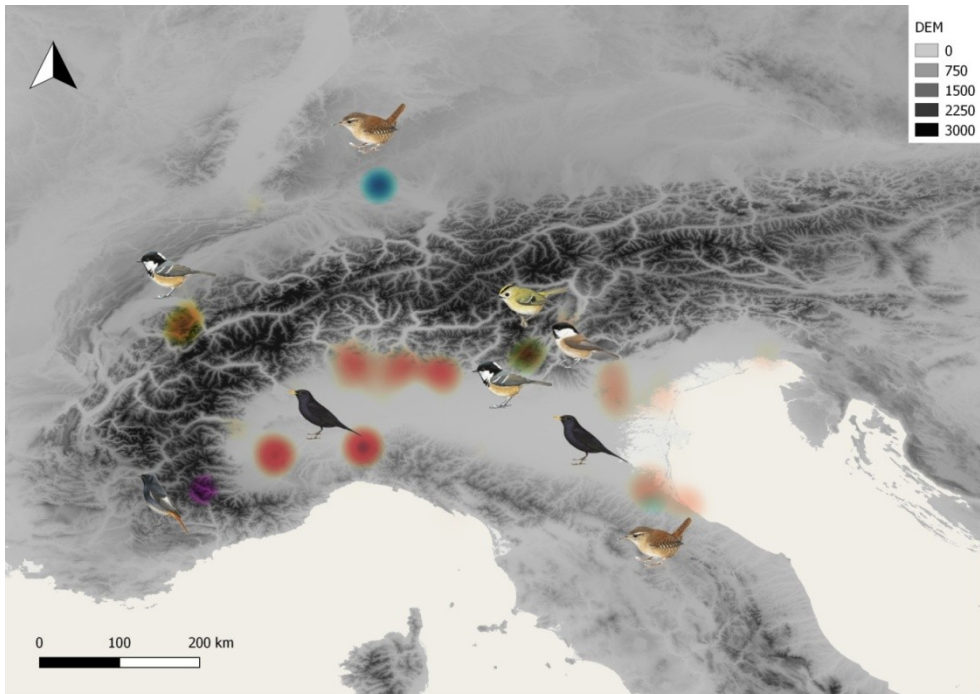


Figure S2. Species-specific heatmaps for locations of first captures (Common Blackbird: red, Eurasian Wren: blue, Coal Tit: orange, Goldcrest: green, Black Redstart: purple, Willow Tit: yellow). Origin of ringing data retrieved from EURING, entirely collected by the Swiss Ringing Scheme. Sample sizes of the dataset used in the analysis are given in Table S1 and their distribution across the whole area in Fig. 2 (main text).

Table S2. Effect of elevation (continuous in $\text{m} \times 10^3$) on the bird's scaled (z score) wing length and body mass as well as the wing:mass ratio between both, modelled with linear mixed effect models (LMMs, function 'lmer'), including year as fixed effect. The effect is significant if the 95% Credible interval (CrI) does not include zero. Significant effects are given in bold. ΔAIC is the difference between the model without year (that used in the main text) and the model including year as a fixed effect (that presented here). $N = 1442$.

LMM	Intercept	Estimate (elevation)	Estimate (year)	Marginal R^2	Conditional R^2	ΔAIC
Ratio ~ elevation + year + (1 Species)	-4.86 (95% CrI: -12.19 – 2.54)	0.136 (95% CrI: 0.080 – 0.190)	0.002 (95% CrI: -0.001 – 0.006)	0.002	0.930	0.5

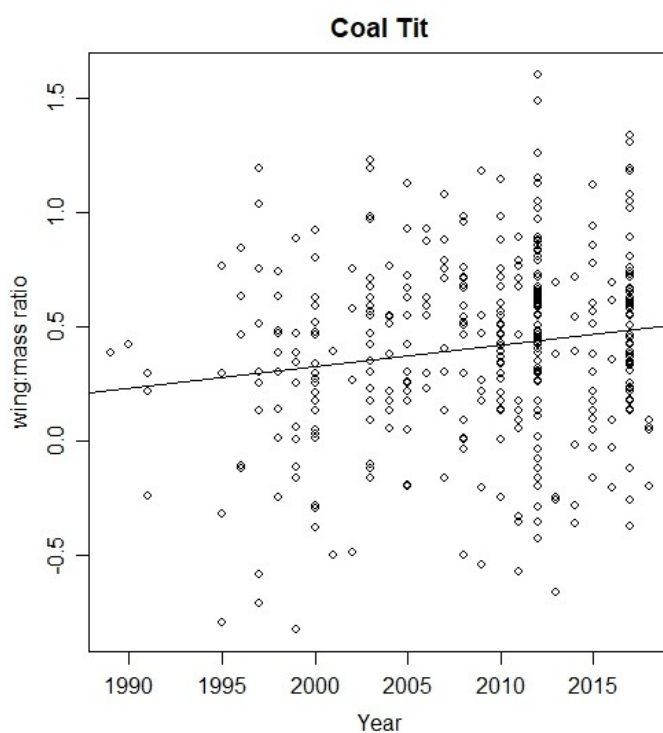


Figure S3. Significant effect of year on the scaled wing:mass ratio in Coal Tits ($y=0.009x -18.63$, $df = 385$, $P<0.01$) using a linear model (response variable: wing:mass ratio, explaining variable: year) with the function 'lm'.

Table S3. Single-species models for the effect of elevation (continuous in $\text{m} \times 10^3$) on the bird's scaled (z score) wing length and body mass as well as the wing:mass ratio (ratio), modelled with linear models (function 'lm').

Species	LM	Intercept $\pm$ se	Estimate (elevation) $\pm$ se	Sample size (No. of individuals)	P-value	R^2
Common Blackbird <i>Turdus merula</i>	Wing length ~ elevation	-0.173 $\pm$ 0.069	0.266 $\pm$ 0.091	734	0.004	0.010
	Body mass ~ elevation	0.037 $\pm$ 0.068	-0.031 $\pm$ 0.090	734	0.72	-0.001
	Ratio ~ elevation	-0.518 $\pm$ 0.030	0.120 $\pm$ 0.039	734	0.002	0.012
Eurasian Wren <i>Troglodytes troglodytes</i>	Wing length ~ elevation	-0.127 $\pm$ 0.263	0.152 $\pm$ 0.264	49	0.57	-0.014
	Body mass ~ elevation	0.068 $\pm$ 0.264	-0.081 $\pm$ 0.265	49	0.76	-0.019
	Ratio ~ elevation	-2.840 $\pm$ 0.116	0.100 $\pm$ 0.117	49	0.42	-0.007
Coal Tit <i>Periparus ater</i>	Wing length ~ elevation	0.008 $\pm$ 0.225	-0.007 $\pm$ 0.144	386	0.96	-0.003
	Body mass ~ elevation	1.380 $\pm$ 0.207	-0.904 $\pm$ 0.133	386	< 0.001	0.105

	Ratio ~ elevation	0.044 ± 0.089	0.238 ± 0.057	386	< 0.001	0.040
Goldcrest <i>Regulus regulus</i>	Wing length ~ elevation	-0.895 ± 1.131	0.700 ± 0.904	24	0.48	-0.017
	Body mass ~ elevation	-0.413 ± 0.978	0.421 ± 0.781	24	0.60	-0.030
	Ratio ~ elevation	0.560 ± 0.407	0.188 ± 0.325	24	0.57	-0.029
Black Redstart <i>Phoenicurus ochruros</i>	Wing length ~ elevation	-0.120 ± 0.226	0.146 ± 0.241	167	0.55	-0.004
	Body mass ~ elevation	0.053 ± 0.218	-0.026 ± 0.233	167	0.91	-0.006
	Ratio ~ elevation	-1.751 ± 0.099	0.070 ± 0.106	167	0.51	-0.003
Willow Tit <i>Poecile montanus</i>	Wing length ~ elevation	-1.228± 0.397	0.857± 0.266	71	0.002	0.12
	Body mass ~ elevation	-0.933± 0.409	0.651 ± 0.274	71	0.02	0.06
	Ratio ~ elevation	-0.516 ± 0.161	0.156 ± 0.107	71	0.15	0.015

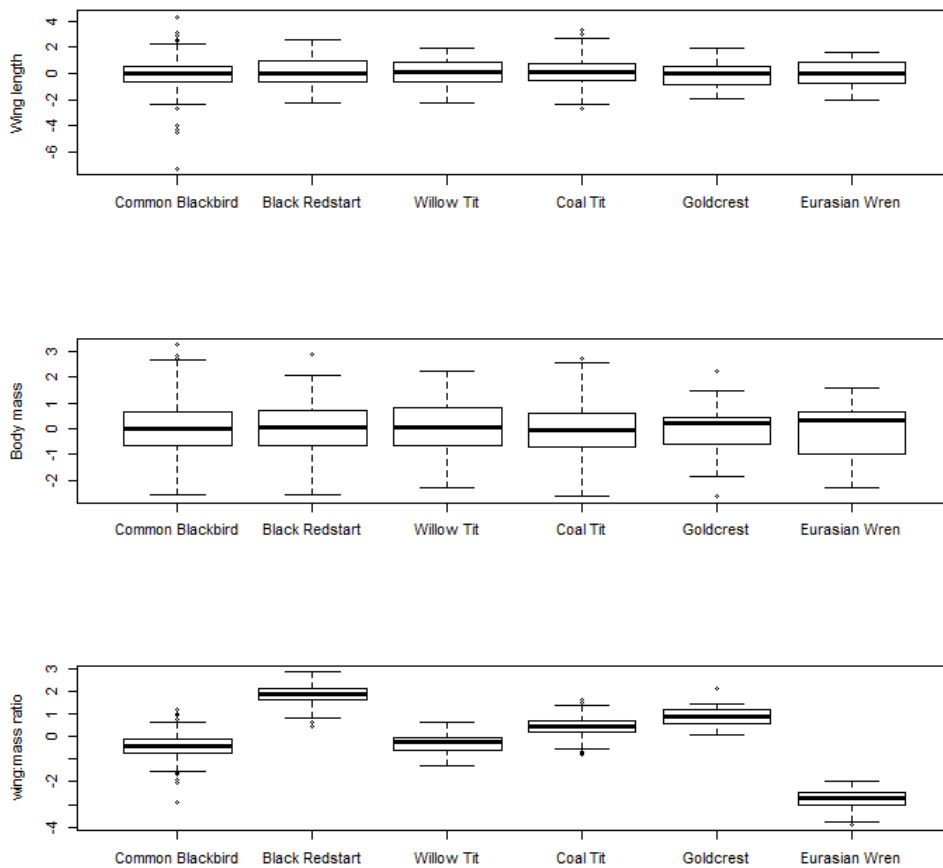


Figure S4. Boxplots show a similar variability in the scaled biometrics across the study species. All available data across all elevations included. Slightly higher variability seems to occur in Blackbirds and Coal Tits. Inter-species variability is highest in the wing:mass ratio.

CHAPTER III

Variations in niche breadth and position of alpine birds along elevation gradients in the European Alps

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ABSTRACT

Mountains support high biodiversity, often including endemic and vulnerable species, but they are also particularly sensitive to climate change. Whilst studies on mountain biodiversity at the species level are common, studies that consider whole assemblages are scarce. We assessed how an alpine bird assemblage varied in terms of ecological habitat niche by surveying birds and habitat at point count sites placed along elevational gradients (1,700–3,000m) in the Western Italian Alps. Niche breadth, as measured by habitat use, increased along the gradient, suggesting that being more generalist is an advantage in terms of survival at high elevation. Niche position also increased with elevation, which means that species occurring at higher elevations use habitats that are atypical with respect to the average species in the assemblage. Both niche breadth and position were negatively associated with habitat diversity, but these relationships were mainly driven by species occurring at elevations above 2,500m, suggesting that high alpine specialists show a different pattern from the other species of the assemblage. Our results therefore generally supported the idea that a wider niche breadth is useful in harsh environments, such as high mountains, enabling the exploitation of a wider range of resources. The broader niche of many high elevation species may therefore indicate some degree of resilience to environmental change, as long as key habitat types are maintained.

Keywords: Alpine specialists, Avian community, Mountains, Habitat niche

Running head: Bird habitat niche along elevation gradients

INTRODUCTION

Climate and land use changes are regarded as the major threats to global biodiversity (Travis 2003; Stephens *et al.* 2016). The interaction between these two threats can intensify their impacts on biodiversity. Species are thus constrained to adjust their spatial distribution according to their ecological niches in order to have the resources they need to survive (Bani *et al.* 2019). It therefore follows that species with a broader niche ('generalists') will be better placed to adapt to environmental changes (McKinney and Lockwood 1999). Indeed, there are many examples of generalists expanding their range in response to environmental changes, often accompanied by decreases in narrow-niche specialists (e.g. Warren *et al.* 2001; Clavel *et al.* 2011). Studying ecological niches is thus likely to give an insight into those species that may be more vulnerable to environmental change in the future.

Compared to other habitats, bird distribution and population dynamics in mountains are less well known, mainly because of the logistical constraints of working in this type of environment (Chamberlain *et al.* 2012). Mountains are subject to such pressures as climate change (Gobiet *et al.* 2014), land-use change (Laiolo *et al.* 2004) and human disturbance (Caprio *et al.* 2011; Brambilla *et al.* 2016). Mountain species are considered particularly vulnerable, since opportunities to shift their distributions towards the mountain tops in response to environmental changes are constrained by mountain orography – i.e. they effectively run out of space on the so-called 'escalator to extinction' (Freeman *et al.* 2018) – and dispersal to alternative suitable sites may be limited by low connectivity with other mountain ranges (Lehikoinen *et al.* 2018).

Many species have already shown shifts in their distributions in response to environmental changes, notably towards higher latitudes and elevations (Maggini *et al.* 2011; Reif and Flousek 2012; Bani *et al.* 2019). These effects could have considerable consequences for mountain biodiversity (Chamberlain *et al.* 2013, 2016), and it has been shown that birds of high elevations are already declining in

Europe (Lehikoinen *et al.* 2018). Given that habitat preference is one of the key ecological traits of any bird species (Reif *et al.* 2010), analysing how habitat niche breadth and niche position are associated with the distribution of species along environmental gradients is useful to understand and predict their future responses to environmental change. It may help to identify which species (perhaps those with narrower niches or that use less typical resources) may be negatively impacted by, and which species will be resilient to future environmental change, if environmental gradients are considered as a space-for-time substitution. This is the idea that drivers of spatial gradients of species assemblages also drive temporal changes in species composition (Hodkinson 2005; Blois *et al.* 2013). In the absence of long-term monitoring data, this approach can be useful to understand changes in the community.

Niche breadth and niche position are two complementary measures of specialisation. Niche position assesses how typical the resource use of a particular species is relative to all other species and the resources available. Thus, species with a distal niche position use less typical resources, i.e. are specialised compared to the community studied (Mac Nally 1989). Niche breadth measures the range of environmental conditions or habitat used by a species (Shugart and Patten 1972). As species that have a wide niche breadth show more tolerance to environmental conditions (Evans *et al.* 2011), they should be better adapted to higher elevations than species with a narrow niche breadth as conditions become harsher and less predictable (Körner 2003). Furthermore, if high elevation species are considered more generalist because of the environmental conditions, they should occupy a mean niche position relative to the whole assemblage. Moreover, if niche trends only reflect habitat along the elevational gradient (i.e. habitat use corresponds to habitat availability), we also expect a positive and linear relationship between niche breadth and habitat diversity (defined with a diversity index).

Studying a whole assemblage (i.e. a taxonomically related group of species that live in a defined area at the same time – Stroud *et al.* 2015) in terms of habitat selection can be useful to assess ecosystem health (Siriwardena *et al.* 2019). We

are unaware of any studies that have considered potential drivers of bird species distributions, including habitat and climate, along elevation gradients from an assemblage perspective in the Alps. Here, we take an assemblage approach to consider how habitat niche varies along elevation gradients in the Western European Alps at relatively high elevations (1,700–3,100m) using multi-species and multi-variate analyses. This study focuses on assessing the relationship (1) between niche (position and breadth) and elevation and (2) between niche (position and breadth) and habitat diversity.

METHODS

Study sites

Sites were located in the far north of Italy close to the French border in the Western Alps (Supplementary material, Appendix 1, Figure A1). The European Larch *Larix decidua* is the dominant species in the study area at lower elevations. The natural treeline is around 2,200–2,300m, although it is lower in many areas, owing to pastoral activities. Common Juniper *Juniperus communis* and Alpenrose *Rhododendron ferrugineum* are the main shrub species in the area. Above the treeline, alpine meadows and grasslands are found. At higher elevations (>2,700m), rocks and scree predominate (Chamberlain *et al.* 2016; Jähnig *et al.* 2018).

Point counts

A database of bird species present was compiled from two different bird surveys, the first carried out between 2010 and 2012 and the second in 2017. In the majority of cases, points were only surveyed in a single year. Point counts were carried out from mid-May to mid-July along elevation gradients on transects that were a minimum distance of 300m apart. On a single transect, each point was separated from another by at least 200m to ensure that two successive points did not overlap. All points were above 1,700m (minimum = 1,717m) and reached a maximum of 3,056m. The mean elevational range for each transect was 601m $\pm$

339m (mean $\pm$ SD; n = 39). At each point, for ten minutes, all birds heard or seen within 100m radius (estimated with a laser range finder) were recorded by the observer, and signs of potential breeding (e.g. singing, carrying nesting material or food for young, territorial disputes) were noted. Overflying birds were not included unless there was evidence that they were using the point count area, e.g. hunting Kestrels *Falco tinnunculus* or Skylarks *Alauda arvensis* in song flight. Transects were visited one to three times. Presence was assigned if a given species was detected on any visit, for the relatively small proportion of points that had more than one visit. Further details of the survey method are given in Chamberlain *et al.* (2013).

Both studies (i.e. 2010–2012 and 2017) adopted the same point count method, except that only the earlier survey included a five-minute settling period before the point count period started. Previous work (Chamberlain and Rolando 2014) and additional analyses (Supplementary material, Appendix 2, Table B1 and B2) have demonstrated that including a settling period makes very little difference to estimates of species occurrence. Observer effects were minimised since all observers were experienced in identifying alpine birds by sight and song, and the two surveys were not independent and were done in a consistent manner (one observer took part in both and led training days for all observers to standardise the recording methods).

Two data sets were created, one with all the species observed and another that included only observations of birds showing evidence of potential breeding (singing in >95% of cases). In total, 309 point counts were undertaken on 38 transects. During the first survey (2010–2012), 271 points were surveyed along 33 transects. In 2017, a total of 38 points were surveyed along five transects. On average, there were 8 ± 4 (mean $\pm$ SD) points per transect across the whole sample.

In order to carry out the multivariate analyses (CCA), points where no species were observed and where habitat descriptions were unavailable were removed from both datasets, since this type of analysis cannot include zeros or missing values. For the breeding data, 259 points were used, while for the complete data, 277 points were used.

Environmental data

Habitat was described within 100m radius of each point count location (all variables are summarised in Supplementary material, Appendix 1, Table A1). The percentage cover of each type of habitat was estimated by eye, including canopy (vegetation above head height), shrubs (woody vegetation below head height), grassland (without canopy), rock (unvegetated areas and screes), and snow (surface still covered by snow during the survey). Such estimates have proved to match those from remote-sensed land cover datasets closely (Chamberlain *et al.* 2013). The presence or absence of water, footpaths and dung was recorded. The number of mature trees (greater than c. 20cm in diameter at breast height) was recorded within a 50m radius (in forested areas, it was not possible to count trees at a greater distance). The elevation of each point (in metres) was recorded with a GPS in the field. Topographic data (slope and aspect) were extracted from a Digital Terrain Model of Northern Italy. Slope was measured in degrees. Both northing and easting were considered and were expressed as an index equal to $-\cos(x)$ where x is the aspect (north or east) in radians. A value of 1 indicates facing directly south (or east) and a value of -1 indicates facing directly north (or west).

Climate data were obtained from CHELSA (Climatologies at High Resolution for the Earth's Land Surface Areas) Climate (Karger *et al.* 2017). Data comprised monthly precipitation and temperature for the period 1979–2013 at a resolution of 30 arc sec. The mean monthly precipitation for the breeding season (May–July) was used. For temperatures, three variables were extracted: the minimum, maximum and mean monthly temperatures for the breeding season.

Data analysis

All analyses were carried out in R 4.0.0 (R Core Team 2020). Preliminary analyses showed that including rare species (present in less than 1% of points) often resulted in convergence problems; hence these species were removed from the dataset in subsequent analyses ($n = 9$ for complete data, $n = 5$ for breeding data).

We defined habitat niche (henceforth 'niche') as the environmental conditions present within 100m radius (i.e. the point count area) in which a given species was detected, which included measures of habitat, topography and climate. We assume therefore that a given species is using the habitat resources as expressed by our niche measures at any point where it was recorded. Following Reif *et al.* (2010) and Evans *et al.* (2011), niche position and breadth were calculated using Canonical Correspondence Analysis (CCA) with environmental data (habitat and climate) and presence data for each species. CCA was performed using the *cca* command in the *vegan* package (Oksanen *et al.* 2013). CCA is a weighted ordination method, thus rare species (species contacted only on a few point counts) have a low weight and do not have a great influence on the rotation ordination (species' weights are their frequencies, i.e. number of points where they were contacted). Elevation (which is highly correlated with habitat and climate variables) was not included as we were interested in explaining which environmental variables were the key drivers of assemblage change that may explain elevational trends. Using both habitat and climate variables to define the niche of each species was justified by the fact that models combining habitat and climate usually perform best when studying species distribution along elevational gradients (Acharya *et al.* 2011; Chamberlain *et al.* 2016). The niche breadth and niche position of each species were calculated from the first four axes of the CCA (those explaining the largest proportion of variability in bird community structure). Niche position was considered as the distance of the centroid of a species from that of the whole sampled mountain bird assemblage (= mean of the coordinates of all the species' centroids). Niche breadth was calculated as the standard deviation of each species' distribution across each axis identified by the CCA (species tolerance calculated with the *tolerance* function from the *vegan* package), providing estimates of niche breadth. The root-mean-squared standard deviations across the first four axes provided an overall estimate of niche breadth. To reduce the skew in their distribution and hence approximate normal distributions, niche position and niche breadth were log-transformed prior to analyses.

Habitat diversity was estimated at each point count with the percentage cover of each type of habitat, calculating the Shannon diversity index with the function *diversity* from the *vegan* package. Habitat diversity was estimated in elevation bands of 100m (e.g. 1,800-1,899m) by calculating the mean Shannon index of all point counts located in each band.

Niche breadth and position were modelled separately in relation to elevation, considering both linear and quadratic effects (i.e. two models per response variable). The niche breadth and position of each species (extracted from the CCA – see above) were related to the median elevation (centred and scaled) across all points at which each species was recorded. In the same way, the relationship between niche breadth of each species and the standard deviation of elevation (centred and scaled) was analysed in order to see if species with a greater elevational range also had a wider niche breadth, as expected. Niche breadth and niche position were then analysed in relation to habitat diversity along the elevation gradient. In order to account for the non-independence of species due to shared ancestry, we used a Phylogenetic Generalised Least Squared (PGLS) approach for the analysis of niche breadth and niche position. Closely related species are expected to have more similar traits because of their shared evolutionary history (functional traits are defined as any phenotypic characteristic, i.e. morphological, physiological, behavioural or reproductive, of an individual that can be assigned to a species; Kissling *et al.* 2018; Schneider *et al.* 2019), and hence tend to produce more similar residuals from least squares regression. PGLS provides estimates of this covariance and includes it in a statistical model (Symonds and Blomberg 2014). The PGLS approach was carried out in R using the *caper* package (Orme 2018) and the phylogeny of Jetz *et al.* (2012).

Outliers were first defined visually with a qq-plot (Mundry 2014) and then checked with the phylogenetic residuals. If outliers were detected (studentised residuals ≥ 3 ; Jones and Purvis 1997; Cooper and Purvis 2009), models were run again without these points. Both linear and quadratic models were fitted for each response variable, and their performance was assessed using Akaike's Information

Criterion (AIC). The model with the lowest AIC was presented in the Results, unless the difference in AIC (ΔAIC) was less than 2, in which case they were considered as equivalent (Burnham and Anderson 2010).

RESULTS

In total, 47 species were recorded, but only 34 showed signs of breeding (Table 1). There were 38 species recorded on at least 1% of the survey points (i.e. at least 3 records), 29 of which showed evidence of potential breeding. Models were run for both datasets (complete and breeding records) but, since the results were similar, only those for the complete dataset are presented here (Supplementary material, Appendix 2, Table B1 and B2 for the main results with the breeding dataset).

Table 1. Number of records of each species contacted during the surveys (Count, given as all records/breeding records). Species with fewer than three records were excluded from the analyses.

Code	Species		Count	Code	Species		Count
AA	Alpine Accentor	<i>Prunella collaris</i>	21/10	LI	Linnet	<i>Linaria cannabina</i>	10/4
AC	Yellow-billed Chough	<i>Pyrrhocorax graculus</i>	6/0	LW	Lesser Whitethroat	<i>Curruca curruca</i>	38/32
B	Eurasian Blackbird	<i>Turdus merula</i>	1/1	M	Mistle Thrush	<i>Turdus viscivorus</i>	45/23
BF	Eurasian Bullfinch	<i>Pyrrhula pyrrhula</i>	1/0	MN	White-winged Snowfinch	<i>Montifringilla nivalis</i>	3/0
BK	Black Grouse	<i>Lyrurus tetrix</i>	1/0	NC	Eurasian Nutcracker	<i>Nucifraga caryocatactes</i>	9/0
BT	Blue Tit	<i>Cyanistes caeruleus</i>	1/0	PM	Rock Ptarmigan	<i>Lagopus muta</i>	1/0
BX	Black Redstart	<i>Phoenicurus ochruros</i>	72/54	Q	Common Quail	<i>Coturnix coturnix</i>	1/1

C	Carrion Crow	<i>Corvus corone</i>	4/0	R	European Robin	<i>Erithacus rubecula</i>	29/29
CC	Common Chiffchaff	<i>Phylloscopus collybita</i>	44/43	RO	Rufous-tailed Rock-Thrush	<i>Monticola saxatilis</i>	3/0
CF	Citril Finch	<i>Carduelis citrinella</i>	2/1	RP	Rock Partridge	<i>Alectoris graeca</i>	4/0
CG	Red-billed Chough	<i>Pyrrhocorax pyrrhocorax</i>	1/0	RU	Rock Bunting	<i>Emberiza cia</i>	37/17
CH	Common Chaffinch	<i>Fringilla coelebs</i>	184/172	RZ	Ring Ouzel	<i>Turdus torquatus</i>	32/10
CI	Crested Tit	<i>Lophophanes cristatus</i>	11/4	S	Eurasian Skylark	<i>Alauda arvensis</i>	63/56
CK	Common Cuckoo	<i>Cuculus canorus</i>	19/16	SK	Eurasian Siskin	<i>Spinus spinus</i>	1/1
CR	Red Crossbill	<i>Loxia curvirostra</i>	30/0	ST	Song Thrush	<i>Turdus philomelos</i>	10/9
CT	Coal Tit	<i>Pariparus ater</i>	66/58	TC	Eurasian Treecreeper	<i>Certhia familiaris</i>	29/13
D	Dunnock	<i>Prunella modularis</i>	48/47	TP	Tree Pipit	<i>Anthus trivialis</i>	80/79
FF	Fieldfare	<i>Turdus pilaris</i>	4/2	W	Northern Wheatear	<i>Oenanthe oenanthe</i>	83/59
GC	Goldcrest	<i>Regulus regulus</i>	6/6	WC	Whinchat	<i>Saxicola rubetra</i>	10/7
GO	European Goldfinch	<i>Carduelis carduelis</i>	4/3	WI	Water Pipit	<i>Anthus spinoletta</i>	99/81
GS	Great Spotted Woodpecker	<i>Dendrocopos major</i>	20/4	WR	Eurasian Wren	<i>Troglodytes troglodytes</i>	69/69
GW	Garden Warbler	<i>Sylvia borin</i>	7/7	WT	Willow Tit	<i>Poecile montanus</i>	91/50
IW	Western Bonelli's Warbler	<i>Phylloscopus bonelli</i>	35/35	Y	Yellowhammer	<i>Emberiza citrinella</i>	13/9
J	Eurasian Jay	<i>Garrulus glandarius</i>	4/0				

Species-habitat associations

The first four axes of the CCA accounted for 76.5% of the variation in the data and represented the following gradients: (1) an elevation gradient from closed habitats (forest and shrubland) with light precipitation and relatively warm temperatures to open habitats (grasslands and rocks) with low temperatures and heavy precipitation (explaining 44.9% of the variation in the data); (2) from grassy and south-exposed slopes to rocky areas (14.9%); (3) from shrubby habitats to all other habitats (10.7%); (4) from steep slopes with heavy precipitation to less steep areas with dung indicating the presence of cattle (6.1%; Supplementary material, Appendix 3 Figures C1 and C2 for figures and Table C1 habitat scores on each axis).

Niche position and breadth along the elevation gradient

Niche position increased non-linearly with elevation (Fig. 1A; Supplementary material, Appendix 3, Table C2), while niche breadth showed no association with elevation. However, after removal of one detected outlier (White-winged Snowfinch *Montifringilla nivalis*), there was a positive association between niche breadth and elevation (Fig. 1B; Table C2). Niche position varied non-linearly but generally increased with the standard deviation of elevation (Fig. 2A, Table C2). Niche breadth was positively associated with the standard deviation of elevation in both linear and quadratic models (Fig. 2B) which performed equally ($\Delta AIC_c < 2$; Table C2). Although the Snowfinch was again identified as an influential outlier in the linear regression, its removal did not affect the outcome of the model (Table C2).

Niche position and breadth along the habitat diversity gradient

Niche position was negatively and linearly related to habitat diversity as measured by the Shannon index (Table C2). Niche breadth did not show any association with habitat diversity. However, an outlier (Snowfinch) was detected and removing this species resulted in a negative relationship between niche breadth and habitat diversity (Table C2). As previously, this trend was driven by two species (Alpine Accentor *Prunella collaris* and Yellow-billed Cough *Pyrhacorax graculus*), which

had above average niche breadth values in contrast to the Snowfinch that had a lower niche breadth value; Supplementary material, Appendix 3, Figure C4). When these were excluded, there was no longer evidence of a relationship between niche breadth and habitat diversity.

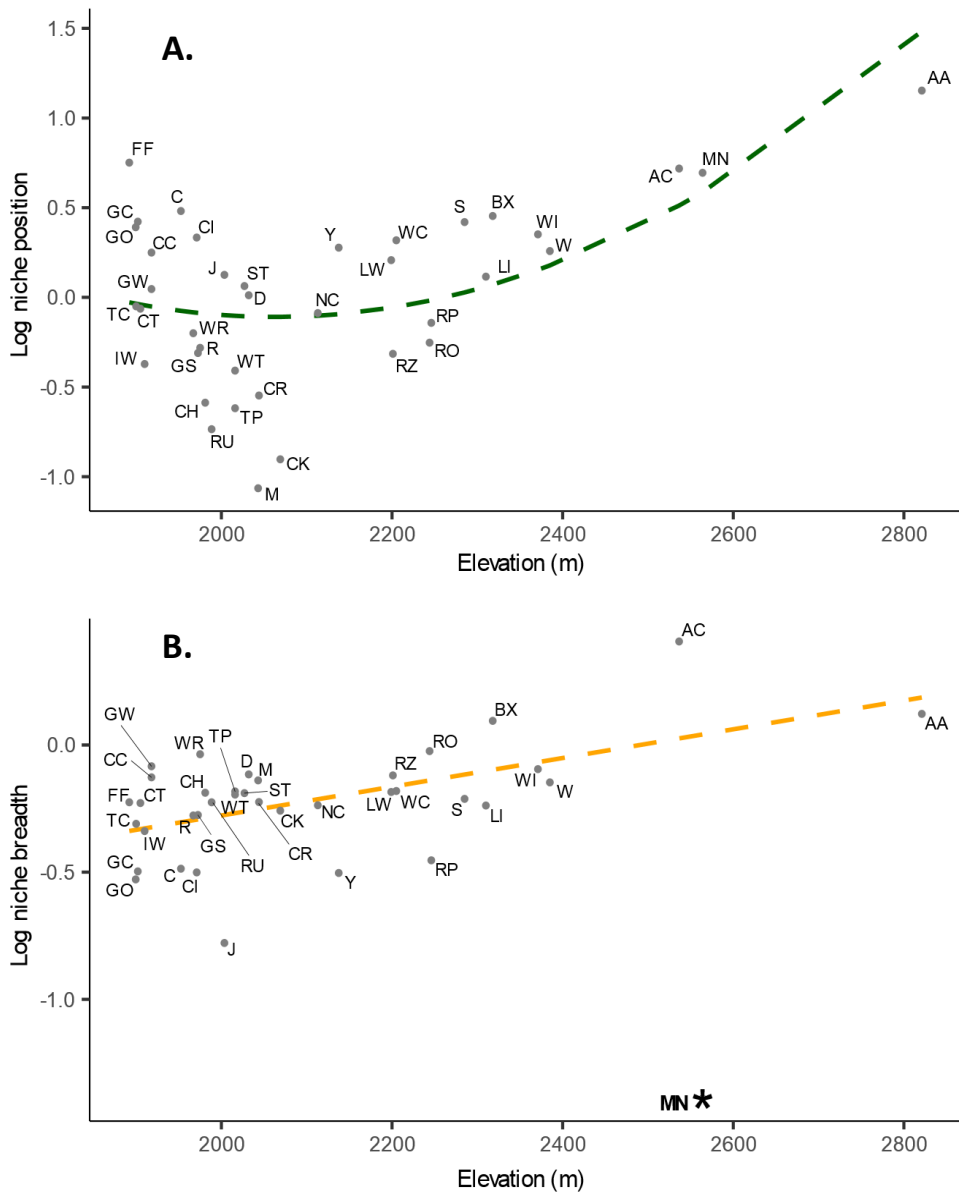


Figure 1. Niche position (A) and niche breadth (B) in relation to the median elevation of each species' range. The dashed lines are fitted from the models given in the Supplementary material, Appendix 3, Table C2. For niche breadth, the influential outlier is represented by a bold black star (Snowfinch MN). See Table 1 for species codes.

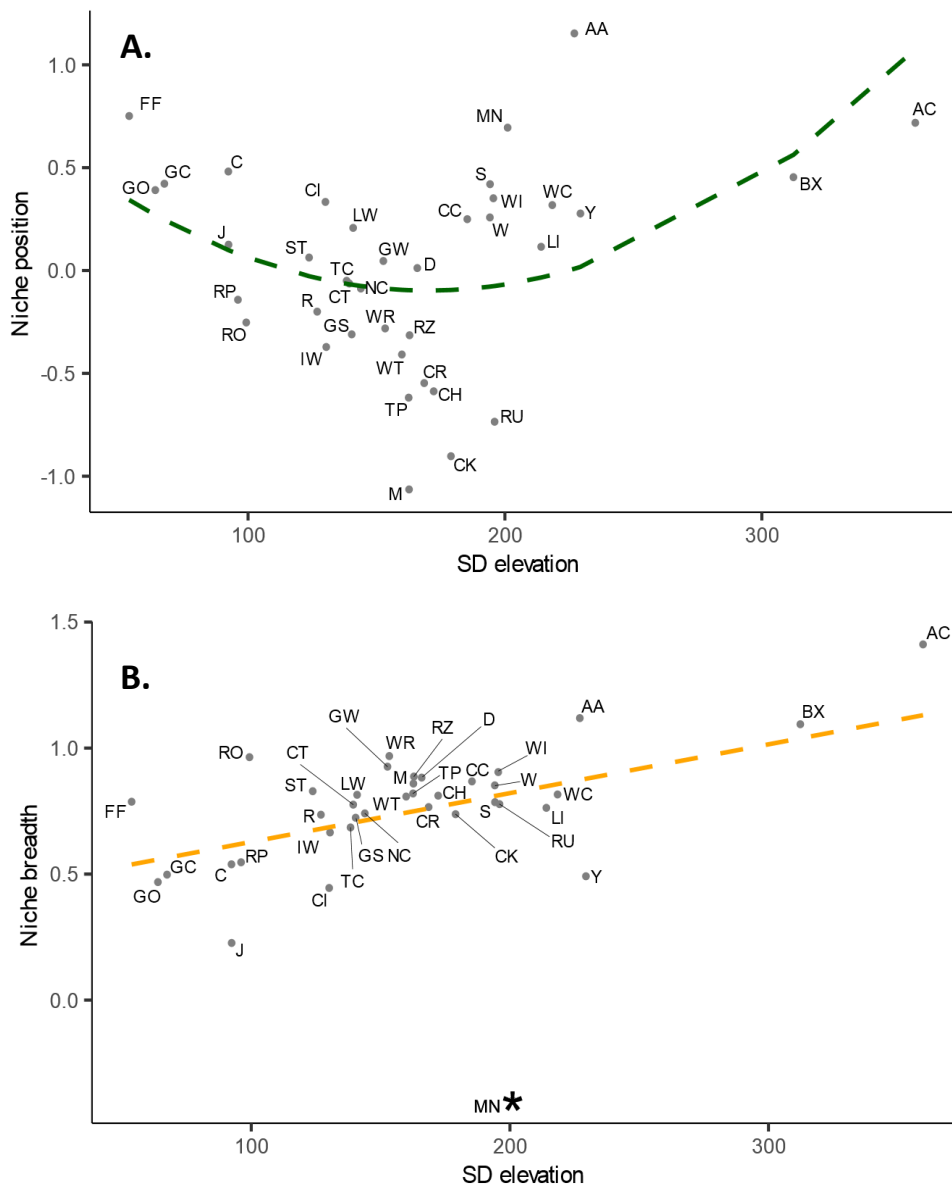


Figure 2. Standard deviation of elevation in relation to habitat niche position (A) and niche breadth (B). An influential outlier is represented by a bold black star (Snowfinch MN). The green line represents the prediction of the quadratic model (with all the species; Supplementary material, Appendix 3, Table C2). The orange line represents the prediction of the linear model (with all the species; Table C2). See Table 1 for species codes.

DISCUSSION

Niche position and breadth along the elevation gradient

Niche position increased with elevation, suggesting that compared to the rest of the community, species occurring at higher elevations are associated with atypical habitats, characterised by high precipitation, low temperatures, rock and grass. This result represents the turnover of species along the elevation gradient from forest species such as Chaffinch *Fringilla coelebs* and Tree Pipit *Anthus trivialis* to open habitat species such as Northern Wheatear *Oenanthe oenanthe* and finally high elevation species including Yellow-billed Cough, Snowfinch and Alpine Accentor. Similarly, García-Navas *et al.* (2020) showed that the alpine bird community (>2,000 m) constituted a group distinct from lower elevation species (from 500m to 2,000m) in terms of functional richness. However, they defined the treeline as the division between these two groups, whereas we found a continuum from forest species to open grassland species (from 1,700m to 2,500m), and then a more marked division for high elevation species (>2,500 m). This difference probably results from differences in methods. Firstly, we measured the habitat niche whereas García-Navas *et al.* (2020) measured the functional niche. Secondly, our study was at a much finer resolution (100m-radius point counts versus surveys in 1 x 1km squares). Thirdly, our gradient range was shorter (c. 1,700-3,000m versus c. 500-3,000m): hence for lower elevation species, we were able to quantify the niche only across a part of their potential elevation range (see below).

Niche breadth increased with increasing elevation, which supported our hypothesis that it is an advantage to be more generalist in a harsh environment, i.e. to be able to exploit a wider range of resources. Blondel and Farré (1988) found that specialisation by birds was more important in the early stages of ecological succession in open and semi-open forest than in mature forest. At first glance, the elevational gradient is similar to this ecological succession, with high-elevation open-habitat analogous to early stages and forests analogous to later stages at lower elevation. Thus, niche breadth should have decreased with elevation.

However, specialisation is only possible when environmental conditions are stable, and with increasing elevation the variability of some (particularly climatic) conditions increases. The elevation niche breadth hypothesis based on ecological succession as analogous to the habitat-elevation gradient is thus not supported. As in insects (Rasmann *et al.* 2014), a wider niche breadth is an advantage for birds at higher elevations. Furthermore, a narrower niche breadth at lower elevations could be explained by interspecific competition (Pigot *et al.* 2016). Indeed, more species live at low elevations and thus compete for the available resources. Due to competition between species, they have to narrow their niches (Fuller 2012b). Also, our finding of a broader niche at high elevations could result from a broader range of climate conditions, rather than a broad range of habitat structure, which means that high elevation species could be resilient to changes in climate conditions but not to changes in habitat structure.

For higher elevation species, the results indicate both a wide niche breadth and the use of less typical habitats (i.e. a distal niche position). These two results may at first sight seem contradictory but they arise because although high elevation species use a broad range of habitats, these habitats are atypical compared to the average species in the assemblage and are not used by the other species.

Niche breadth and position increased with increasing standard deviation of elevation, indicating as expected that species occupying a wider elevation range use a greater range of habitats that are more typical of the community as a whole. A notable exception to the expected pattern of niche breadth increasing with variation in elevation range was the Snowfinch. This species showed a fairly large range, but a narrow niche breadth, which indicates it exploits a limited range of resources even across its relatively large elevation range. Snowfinches were always found in open habitats characterised by the presence of rock and snow.

Niche position and breadth along the habitat diversity gradient

Niche position was negatively associated with habitat diversity. Niche breadth only showed an association with habitat diversity when species of high elevation (Alpine Accentor, Yellow-billed Chough, Snowfinch) were included in the model. Had habitat availability matched habitat use perfectly, then we would have seen a positive relationship between niche breadth and habitat diversity. Instead, the results imply that other factors also drive species distribution along this habitat diversity gradient. For example, when interspecific competition increases, species exploit a narrower range of resources, which usually corresponds to their optimal niche (i.e. they have a narrower niche breadth which is commonly defined as the realised niche; Fuller 2012b). There are fewer species of high elevations, thus interspecific competition between them is lower, allowing them to exploit a wider range of resources (although the Snowfinch was the exception to this pattern). Finally, there was little evidence for a gradient from low diversity habitat with 'generalist' species (broad niche breadth) to high diversity habitat 'specialist' species (narrow niche breadth). Instead, there was an indication of a threshold that separated high elevation species from the others (which could be induced by incomplete sampling along the elevation gradient). These species correspond to alpine specialists as defined by Thompson *et al.* (2012). Alpine specialists are confined to the alpine zone: i.e. the major part of the population breeds in this zone, while alpine generalists breed in mountains but can also breed at lower elevations in different habitats. This result suggests that mountain generalists and mountain specialists may not show the same pattern regarding the link between niche and habitat diversity. For example, Altamirano *et al.* (2020) demonstrated that the alpine bird community is distinct from species occurring at lower elevation (above treeline), and that the composition of this community is structured by habitat heterogeneity.

Implications for mountain bird conservation and caveats

The species with smaller niches at lower elevations tended to be forest species. Although this may reflect greater specialisation, these species are thought to be less threatened by climate change as upslope shifts in treelines are unlikely to result in a net loss of suitable habitats (or indeed suitable climates) (Chamberlain *et al.* 2013). Species with a wider niche breadth may adapt better to environmental change than species with a narrower niche breadth (e.g. Evans *et al.* 2011), since they can exploit a larger range of resources. Indeed, there is evidence that generalist bird species are adapting to climate change better than specialist species (Davey *et al.* 2012; Pearce-Higgins *et al.* 2015; Bowler *et al.* 2019). Given that we found that niche breadth increased with elevation, species at higher elevation should be fairly resilient to environmental change. This therefore suggests that high elevation species, including some currently relatively widespread grassland species likely to be negatively affected by future climate change, e.g. Water Pipit *Anthus spinoletta*, Northern Wheatear (Chamberlain *et al.* 2013) and Ring Ouzel *Turdus torquatus* (Beale *et al.* 2006; Barras *et al.* 2021), will have some capacity to adapt to environmental changes. However, the greatest impact of climate change on such species is likely to be the loss of suitable habitat caused by forest encroachment (García-Navas *et al.* 2020); hence such species may have some resilience but only within habitat of suitable structure. Nevertheless, alpine bird species that are not currently considered as threatened could be endangered in the near future because of the loss of suitable habitat, as predicted for Snowfinch, Alpine Accentor, Yellow-billed Chough and Wallcreeper *Tichodroma muraria* (de Gabriel Hernando *et al.* 2021). Furthermore, according to our results, these habitats are atypical and hence only associated with higher elevations that are under threat from upslope shifts in vegetation zones. Strategies to minimise gross changes in habitat (e.g. maintaining open grasslands) may therefore benefit these species, despite increases in temperature. In addition, some species occurring at the highest elevations did not seem to follow the general pattern. For example, among the three species occurring above 2,500m, the Snowfinch, a scarce species, had a

notably low niche breadth, suggesting that this high alpine specialist may indeed be particularly threatened (as per Scridel *et al.* 2018). Nevertheless, the two other species, the Alpine Accentor and Yellow-billed Chough, had particularly wide niche breadths suggesting that they could adapt more easily to future environmental changes. The Yellow-billed Chough is indeed known to be adaptable and able to exploit anthropogenic habitats even at high elevations (Vallino *et al.* 2019).

Our results could be slightly biased by some factors. Firstly, we were not able to account for the entire elevation range of each species since our gradient started at 1,700m. This could affect our results since we covered most of the likely range of high elevation species but not all the range of low elevation species. The niche breadth of lower elevation species could have been underestimated. It is thus important to stress that the results need to be interpreted in terms of species niches within high elevation habitats, approximately from close to the treeline and above, rather than the complete range of a given species. Nevertheless, the results are still valid for the area under investigation which is likely to be the most threatened by future climate change (e.g. Chamberlain *et al.* 2013; Barras *et al.* 2021).

Secondly, we did not account for detectability of species. Thus, we cannot know whether a species is rare because it has a low probability of detection or because it is indeed very scarce. That is particularly true for the Snowfinch which was rarely contacted during the surveys and seemed to be a specialist of high elevation habitats. Similarly, some species known to be present in the area were detected only rarely, or not at all. For example, the Boreal Owl *Aegolius funereus*, Black Grouse *Lyrurus tetrix* and Rock Ptarmigan *Lagopus muta* have lower detectability and are probably not suitably assessed by the point count method used. It would be interesting to get more data for these species in order to assess their influence on our analyses. Nevertheless, for the species that were included, we think that incorporation of detectability would not have greatly influenced the results. It seems reasonable to assume that for the assemblage sampled here (mostly passerines), detectability will be high for the breeding data set, as it almost

entirely involved singing birds, which have much higher detectability than observations only. The repeat analysis considering only singing birds arrived at the same conclusions as the entire data set, thus we do not feel that the results would change significantly if detectability was estimated more formally.

Thirdly, we had more point counts at lower elevations than at higher elevations which implies that the probability of observing high elevation species was lower because of unequal sampling effort across elevations. Thus, the study could be improved by a better distribution of point counts across the elevation gradient. The median elevation at which species occurred could be more accurately assessed had the abundance of each species been estimated. Indeed, bird distributions do not show symmetrical patterns along elevation gradients (Chamberlain *et al.* 2016), thus weighting presence by abundance would give a more precise median elevation for each species.

Finally, given that, in theory, a species can vary remarkably in its occupancy rate of identical patches in different landscape contexts (Fuller 2012a), more studies are needed in other regions of the Alps in order to corroborate our results and assess the transferability of our models. As Chamberlain *et al.* (2016) showed, species distribution is mainly driven by habitat and climate (and thus elevation), but much variation was still unexplained by their models, suggesting that other factors affected bird occurrence. Studying which factors (diet for example) can modulate bird occurrence along the elevation gradient could be the subject of further ecological studies on alpine birds. Furthermore, since niche space is multidimensional, it would also be useful to study the relationship between niche and elevation by using a broader niche definition including other factors, such as diet or foraging substrate, that indicate how species use the habitat, in contrast to our definition of niche that measured the available habitat.

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APPENDICES

Additional supporting information can be found in the online version of this article:

<https://bioone.org/journals/ardeola/volume-69/issue-1/arla.69.1.2022.ra3/Variations-in-Niche-Breadth-and-Position-of-Alpine-Birds-along/10.13157/arla.69.1.2022.ra3.full>

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CHAPTER IV

Microclimate affects the distribution of grassland birds, but not forest birds, in an alpine environment

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ABSTRACT

Predictions derived from species distribution models (SDMs) are strongly influenced by the spatial scale at which species and environmental data (e.g. climate) are gathered. SDMs of mountain birds usually build on large-scale temperature estimates. However, the topographic complexity of mountain areas could create microclimatic refuges which may alter species distributions at small spatial scales. To assess whether fine-scale data (temperature and/or topography) improve model performance when predicting species occurrence, we collected data on presence-absence of bird species, habitat and fine-scale temperature at survey points along an elevational gradient in the Alps (NW Italy). Large-scale temperature data, and both large- and fine-scale topography data, were extracted from online databases for each point. We compared species models (fine-scale vs large-scale) using an information-theoretic approach. Models including fine-scale temperature estimates performed better than corresponding large-scale models for all open habitat species, whereas most forest/ecotone species showed no difference between the two scales. Grassland birds such as Northern Wheatear *Oenanthe oenanthe* and Water Pipit *Anthus spinoletta* were positively associated with warmer microclimates. These results suggest that alpine grassland species are potentially more resistant to the impact of climate change than previously predicted, but that indirect effects of climate change such as habitat shifts (forest- and shrub encroachment at high elevations) pose a major threat. Therefore, active management of alpine grassland is needed to maintain open areas and to prevent potential habitat loss and fragmentation. SDMs based solely on large-scale temperatures for open habitat species in the Alps should be re-assessed.

Keywords: information-theoretic approach, mountains, species distribution models, temperature, topography.

INTRODUCTION

Species distribution models (henceforth SDMs) are a widely used tool in conservation (Guisan and Thuiller 2005; Rodríguez *et al.* 2007; Franklin 2013; Engler *et al.* 2017) for a range of taxa (Ongaro *et al.* 2018; Lewthwaite *et al.* 2018, Hof and Allen 2019). In the face of climate change, SDMs have become particularly important in predicting current and/or future distributions of species under different climate change scenarios (Avalos and Hernández 2015; Jackson *et al.* 2015; Lehikoinen and Virkkala 2016). These studies usually rely on macroclimate data, which describe climatic conditions at a relatively large scale (approximately one square kilometre or more; Zellweger *et al.* 2019) derived from national networks, weather stations or online databases (e.g. Worldclim; Hijmans *et al.* 2005).

However, mountain environments are often poorly represented by conventional climate station data, and uncertainty for interpolated climatic values is high (Hijmans *et al.* 2005). Furthermore, local temperature can vary substantially due to the topographic complexity in mountain areas (Scherrer and Körner 2010; Gunton *et al.* 2015), thus creating a mosaic of microclimatic conditions over small spatial scales. Depending on discipline, microclimates have been defined in various ways. In this study, we adopt the definition by Bramer *et al.* (2018) who defined microclimate as fine-scale climate variations at spatial resolutions of < 100m, which are influenced by fine-resolution biotic and abiotic variations (topography, soil type and vegetation). Topographic variables like aspect and slope can markedly alter microclimate by influencing the amount of incoming solar radiation between different exposed slopes. Between north and south exposed slopes, temperature can differ by approximately 1°C if slopes are gentle (<5° gradient) but can increase up to 5°C if slopes are steep (40° gradient; Gubler *et al.* 2011). Moreover, these differences could subsequently influence snow accumulation processes and thus the rate of snow melt in spring (Gubler *et al.* 2011).

There is mounting evidence of the importance of microclimate in influencing habitat selection. For example, Bramblings *Fringilla montifringilla* tend to rest in

higher densities in areas with warm microclimatic conditions (Zabala *et al.* 2012). In Mountain Chickadees *Poecile gambeli*, microclimates influence the selection of foraging sites (Wachob 1996). Microclimates can also act as thermal refuges, which enable individuals to persist despite unfavourable ambient conditions (Wilson *et al.* 2015). This has been shown in Northern Bobwhites *Colinus virginianus*, which mitigated thermal stress by seeking thermally-buffered microclimatic sites during hot days (Carroll *et al.* 2015). Furthermore, Northern Bobwhite nest site selection was proven to be influenced by microclimate: Individuals nested in cooler and moister microclimatic conditions compared to surrounding non-nesting locations (Tomecek *et al.* 2017; Carroll *et al.* 2018).

Only a few studies have investigated the role of microclimate within a mountain context. Frey *et al.* (2016) showed that fine-scale temperature metrics were strong predictors of bird distributions, with temperature effects being larger than vegetation effects on occupancy dynamics in mountain forests (but see Viterbi *et al.* 2013). In the Alps, the habitat of the alpine Rock Ptarmigan *Lagopus muta helvetica* is characterised by a wide variety of microclimates over small spatial scales with individuals choosing colder sites in summer (Visinoni *et al.* 2015).

Beside the direct impact on birds, microclimate also plays a crucial role in habitat selection in insects. It has been demonstrated that in *Parnassius apollo*, a mountain specialist butterfly, larval habitat selection is related to ambient temperature. Larvae selected warm microclimates when ambient temperatures fell below a threshold of 27°C, whereas cold microclimates were selected when this threshold was exceeded (Ashton *et al.* 2009). Microclimate can further influence oviposition (Stuhldreher *et al.* 2012), and the precise microclimatic conditions for thermoregulation are actively sought by montane species of the genus *Erebia* (Kleckova *et al.* 2014). In this respect, microclimate not only shapes the distributions of these butterfly species, but it will also indirectly influence bird species which rely on caterpillars as a food source for chick rearing.

Microclimate thus has the potential to influence many aspects of an organism's life cycle. It could help to buffer or to compound the effects of climate

change (Spasojevic *et al.* 2013). To assess the impact of climate change on current or future distributions of species it is crucial to gather climate data at the most appropriate scale in order to increase model accuracy (Barton *et al.* 2018; Randin *et al.* 2009). However, predictions for future geographic distributions of mountain birds under a range of climate change scenarios have thus far been based on models which have considered climate variables measured at large scales, usually ca. 1 km² (Chamberlain *et al.* 2013, 2016; Brambilla *et al.* 2016, 2017a). Given the potential for bird responses to microclimatic conditions in mountains (Frey *et al.* 2016; Visioni *et al.* 2014), it may be more appropriate to consider the role of climate measured at finer spatial resolutions in determining mountain bird distributions. This is particularly important given that environmental conditions in mountains typically change over very small spatial scales thanks to steep elevation gradients (Scherrer and Körner 2010; Gunton *et al.* 2015).

In this study, we investigated the role of microclimate for a range of Alpine ecotone and open habitat species. There were two specific aims. First, to evaluate if models including a microclimatic variable (in this case temperature) show better performance than models using large-scale climate estimates. This will inform future modelling studies, and should help to improve predictions of future impacts of climate change on Alpine birds where microclimatic effects are evident. Second, to assess if models including topographic variables (slope and aspect) in combination with climatic variables (fine and large scale) increase model performance. This will assess the extent to which topographic variables should be included in SDMs of alpine bird species. Based on previous studies, which showed that microclimate can influence bird distributions within mountain habitats (Frey *et al.* 2016; Visinoni *et al.* 2015), we hypothesise that models using fine-scale temperature estimates will show better model performance than models using large-scale temperature estimates.

METHODS

Study area and point selection

The study was carried out in Val Troncea Natural Park (44°57'28" N; 6°56'28" E) in the western Italian Alps. At lower elevations, the area is dominated by larch *Larix decidua*. The natural treeline is typically found at around 2,200 m a.s.l., but varies depending on local conditions. Typical shrub species are *Juniperus nana* (henceforth Juniper) and *Rhododendron ferrugineum* (henceforth Rhododendron) which rapidly encroached wide areas of grasslands after the decline of agro-pastoral activities. Grasslands are mainly dominated by *Festuca curvula*, *Carex sempervirens*, and *Trifolium alpinum*. Scree and rocky areas occur predominantly at higher elevations, above approximately 2,700 m a.s.l..

Point counts were carried out along an elevational gradient ranging from 1,750 m to 2,820 m encompassing forest, ecotone and open habitats. Point count locations coincided with the centroids of a pre-existing grid at a scale of approximately 100 x 100 m (there was some variation, due to access constraints for example; Probo *et al.* 2014) along the south-western facing slope of the valley. All points were spaced a minimum of 200 m apart.

Bird surveys

Point counts (n = 221) were carried out from mid-May to mid-July 2017 following the methods of Bibby *et al.* (2000), using a 10 minute count period. At each point count location, all individual birds seen or heard were recorded within a 100 m radius (estimated with the aid of a laser range finder). Point counts commenced 1-1.5 h after sunrise and continued until 1200 h. Surveys did not take place in excessively wet or windy conditions. Each point count location was visited once. Point counts were performed by a team of four field workers. Fieldwork was preceded by at least one day of training for each of the field workers in order to minimise potential observer bias.

Habitat data collection

At each point count location, habitat data were collected through the visual estimation of the percentage cover of canopy (i.e. vegetation above head height), the dominant shrub species, open grassland and bare rock (including scree and unvegetated areas) within a 100 m radius of the point's centre. The dominant shrub species were defined into four groups: Rhododendron, Juniper, bilberry (*Vaccinium myrtillus* and *V. gaultherioides*) and other (e.g. Green Alder *Alnus viridis*, Willow *Salix spp*, and also including young trees less than two meters in height, mostly European Larch *Larix decidua*). Furthermore, the number of mature trees (greater than c. 20 cm in diameter at breast height) within a 50 m radius of a point count location was counted. These estimates have been shown to correlate well with estimates of land cover derived from remote sensing and have been used as the basis of predictive models for several species considered here (Chamberlain *et al.* 2013, 2016; Jähnig *et al.* 2018).

Temperature measurements

At each point count location, temperature was measured with hygro buttons (Plug & TrackTM), using methods based on Frey *et al.* (2016). Each button was stuck on the bottom of a small plastic cup, which was attached upside down to a bamboo stick to protect the button against wind, direct sunlight and water. Mean button height was 40.89 cm (min = 28 cm, max = 47 cm). Hygro buttons were programmed to record temperature every 5 minutes. They were placed 24 hours before a point count commenced and were collected 24 hours after the point count ended, which resulted in a total recording time of 48 hours. At every hygro button location, button height, distance to slope, substrate and canopy presence/absence was recorded.

Statistical analysis

Temperature modelling

For each point count location, minimum, maximum and mean temperatures were derived over the 48 hour recording period. All temperature measurements were checked for collinearity by calculating Pearson's correlation coefficient. Mean temperature was strongly correlated with both minimum ($r = 0.80$) and maximum temperature ($r = 0.73$) over the recording period. Therefore, temperature modelling was undertaken with mean temperature values. The same procedure was repeated for night-time temperatures. Minimum, maximum and mean night-time temperatures were obtained for the time period between 23.00 pm and 03.00 am over the same recording period at each point. There was a strong positive correlation of mean night-time temperature between minimum ($r = 0.97$) and maximum night-time temperature ($r = 0.89$).

The objective of the first analysis was to model temperature in relation to date and elevation. This model was then used to predict a standardised temperature at each point count location, set at a fixed date, which was representative of the fine-scale temperature at that point controlling for seasonal effects. This procedure provided data which was analogous to the larger scale temperature data (see below). This standardised temperature was then used subsequently as a variable in species distribution models. Note that all subsequent modelling steps were performed separately for mean temperature and mean night-time temperature. However, models with night-time temperature were very similar to those using mean temperature, so we focus on the latter. Further details on night-time temperature models are given in the Electronic Supplementary Material (ESM) Table S1.

First, to investigate if temperature recording was influenced by characteristics of the hygrometry button's position, it was analysed using a generalised linear model in relation to button height, distance to slope, substrate underneath the button and canopy presence/absence, specifying a normal error distribution. None of the

variables showed a significant effect on mean temperature ($p > 0.05$), therefore they were not considered further in the analysis.

In the next modelling step, standardised temperature estimates were derived separately for open Alpine grassland and forest/ecotone habitat, i.e. models were used to estimate temperature for a given elevation whilst accounting for seasonal variation. Points were classified as Alpine grassland if there was no canopy within 100m radius of the point count centre (following Chamberlain *et al.* 2013). For open habitat points ($n = 93$), temperature was modelled in relation to date and elevation. Date was described as the number of days passed since the start of the field season, where day 1 = 27-May-2017. Canopy cover was added to the model structure for points located in forest and ecotone habitat ($n = 128$). In both cases, a normal distribution was specified. Prior to modelling, all variables were scaled and centred using the scale function in R version 3.5.2 (R Development Core Team 2018). Collinearity was assessed using Variance inflation factors (VIFs), calculated using the 'corvif' function (package 'AED', Zuur *et al.* 2009), and by considering Spearman correlations between continuous variables. All variables had VIF < 3 , and no pair of variables showed a correlation > 0.7 , indicating low levels of inter-correlation. These models were used to derive a standardised temperature for each point, based on the elevation at that point, the canopy cover (for forest/ecotone habitat) and for a date fixed at 15th June.

Species distribution models

Birds detected within a 100-m radius of a point count location were used to analyse species distribution (presence/absence of individual species). Bird species were considered in the modelling process if they were present on at least 15 % of the points; below this threshold model performance is consistently poor (Chamberlain *et al.* 2013) (Table 1).

The commonest species were modelled in relation to four different variable sets: (i) habitat (HABITAT), (ii) habitat + temperature (TEMP), (iii) habitat + topography (TOPO), (iv) habitat + temperature + topography (COMB; Table 2).

Temperature and topographic variables were used at two different scales (large-scale/fine-scale). Fine-scale temperature estimates were derived from the temperature modelling approach described above, whereas large-scale temperature data for each point were extracted from the Worldclim database (Hijmans *et al.* 2005) by calculating the average temperature within a 1000 m radius of the point count centre. Topographic variables (aspect and slope) were derived from a Digital Elevation Model (DEM) at a spatial resolution of 10 metres. Aspect was transformed as $x = -1 * \cos[\phi(\pi/180)]$, where ϕ is measured in degrees. Values ranged from 1 where solar insolation was higher (south-facing slopes) to -1 (north-facing slopes) where it was lower.

The mean aspect (transformed values) and slope was calculated within a 100 m (fine-scale) and a 1000 m (large-scale) radius of the point count centre for the analysis. Habitat variables were kept at a constant scale in the models (as the objective was to test scale effects in temperature and topography). Habitat models of Lesser Whitethroat *Sylvia curruca* and Dunnock *Prunella modularis* were tested for non-linear relationships with Rhododendron and Juniper cover as suggested by previous work (Jähnig *et al.* 2018). Habitat models with and without quadratic terms for shrub species cover were compared using AIC. Lesser Whitethroat models showed lower AIC values for the habitat model without quadratic terms. Therefore these were omitted in further modelling steps. The addition of the quadratic term for Rhododendron cover reduced the AIC of the habitat model for Dunnock by $\Delta AIC > 2$, hence it was included in the next modelling steps.

The occurrence probability of each species was modelled in relation to the different variable sets using a binomial logistic regression, after controlling for potential collinearity (as above). In the case of open habitat species, we found high VIFs for the variables rock and grass cover. After the removal of rock cover, all VIFs were below the threshold of three. As a result, rock cover was removed from all models for open habitat species. The correlation between rock and grass cover occurred because of the landscape characteristics above the treeline, where alpine

grassland is often interspersed with rocks. As those two habitat characteristics are not separable, we used grass cover as proxy to describe this kind of habitat.

Data were analysed using an information theoretic approach with the MuMIn package in R (Bartón 2013). This entailed deriving full models for each variable set at each scale (except habitat which was kept constant in all models) using generalised linear models (R package lme4; Bates *et al.* 2015). This approach served two goals. First, model-averaged parameter estimates were derived for all combinations of variables in each full model set in order to identify variables that were most closely associated with bird distribution. p -values derived from the model-averaged parameter estimates and their SEs were considered to represent significant effects when $p < 0.05$. Second, the Akaike information criterion corrected for small sample size (AICc) was determined for each individual model and was used to assess model performance for different variable combinations at different scales in the full model. In this way it was possible to assess which combination of the four different variable sets produced the best models, and at which scale.

At each scale, the residuals for all full models were extracted and tested for spatial autocorrelation using Moran's I (Moran 1950). Significant spatial autocorrelation was found for models of Eurasian Skylark *Alauda arvensis*, Tree Pipit *Anthus trivialis* and Water Pipit. For these species, spatial effects were incorporated by modelling their distributions using Generalized Additive Models (GAMs) from the mgcv package (Wood 2011) by fitting smoothed terms for latitude and longitude in the model, following Wood (2017). However, for Skylark, these models failed to converge, so a GLM was used (as for the other species). Interpretation of the Skylark model outputs therefore needs some caution, although the level of spatial autocorrelation for the best model was not especially high (12%).

Table 1. Variables considered in the analysis, and the scale at which they were measured.

Parameter	Scale	Description
Canopy	fine	Percentage cover of canopy (above head height) within a radius of 100 m of the point count centre
Rod	fine	Percentage cover of Rhododendron within a radius of 100 m of the point count centre
Jun	fine	Percentage cover of Juniper within a radius of 100 m of the point count centre
Vac	fine	Percentage cover of bilberry within a radius of 100 m of the point count centre
Oth	fine	Percentage cover of shrubs different from Juniper, Rhododendron and bilberry within a radius of 100 m of the point count centre
Grass	fine	Percentage cover of grass within a radius of 100 m of the point count centre
Rock	fine	Percentage cover of rock within a radius of 100 m of the point count centre
Trees	fine	Number of mature (greater than ca. 20 cm in diameter) trees within a radius of 50 m of the point count centre
Temp	fine	Modelled fine-scale standardised average temperature of the point count centre
Temp	large	Large-scale average temperature within 1000 m of the point count centre extracted from WorldClim.
Aspect	fine	The average direction a slope is facing within a 100 m radius of the point count centre transformed as $x = -1 \cdot \cos[\phi(\pi/180)]$, where ϕ is measured in degrees.
Aspect	large	The average direction a slope is facing within a 1000 m radius of the point count centre transformed as $x = -1 \cdot \cos[\phi(\pi/180)]$, where ϕ is measured in degrees.
Slope	fine	The average inclination of the surface within a 100 m radius of the point counts centre measured in degrees.
Slope	large	The average inclination of the surface within a 1000 m radius of the point counts centre measured in degrees.

Table 2. Variable combinations for each model set. Model sets for TEMP, TOPO and COMB were considered at two different scales (fine and large) and included temperature, slope and aspect at their matching scale. The variables Rock and Trees were omitted from the habitat model for open habitat species (Northern Wheatear, Water Pipit and Skylark).

Full models	Parameter
HABITAT	Rod + Jun + Vac + Oth + Grass + (Rock) + (Trees)
TEMP	Rod + Jun + Vac + Oth * Grass + (Rock) + (Trees) + Temp
TOPO	Rod + Jun + Vac + Oth * Grass + (Rock) + (Trees) + Slope + Aspect
COMB	Rod + Jun + Vac + Oth * Grass + (Rock) + (Trees) + Temp + Slope + Aspect

RESULTS

In total, 862 individuals of 40 species were recorded in 221 point counts over an elevational range of 1750 – 2800 m a.s.l. There were seven species that were recorded on at least 15% of the points within forest and ecotone habitat: Dunnock, Lesser Whitethroat, Chaffinch *Fringilla coelebs*, Mistle Thrush *Turdus viscivorus*, Coal Tit *Parus ater*, Rock Bunting *Emberiza cia*, Tree Pipit and three species within open habitat: Eurasian Skylark, Water Pipit and Northern Wheatear.

The best model to predict Rock Bunting occurrence was always the null model for each model set at each scale, with no model-averaged parameter estimates being significant. Therefore, this species was not considered further in the analysis.

Forest and ecotone species

Habitat variables such as trees and shrubs were the variables most commonly associated with species occurrence within the HABITAT model for forest and ecotone species. In general, the results of the HABITAT models were in line with previous findings by Jähnig *et al.* (2018). Juniper showed a positive relationship with Coal Tit, Dunnock and Lesser Whitethroat, but was negatively related to Tree Pipit presence. Rhododendron was positively associated with Mistle Thrush and Lesser Whitethroat presence, whereas it showed a non-linear relationship with Dunnock presence. The number of mature trees showed a positive relationship with forest species (Chaffinch, Mistle Thrush and Coal Tit). Habitat associations among the species remained mostly constant in TEMP, TOPO and COMB models (for full details see ESM Table S2, S4).

Each variable set at each scale performed equally well for Lesser Whitethroat, Mistle Thrush and Coal Tit (Table 3). (Note that full details of all models are given in ESM Table S3). Large-scale temperature and topographic variables were included in the best performing model for Dunnock, temperature being negatively associated with Dunnock presence (Table 4, Fig. 1). In contrast, large-scale temperature showed a positive relationship with Chaffinch presence in models including only large-scale temperature (Table 4, Fig. 1), or in models including a combination of

large-scale temperature and topographic variables. In both species, large-scale model sets performed better than their fine-scale equivalents. Large-scale models for TOPO and COMB were the best performing models for Tree Pipit, whose presence was more closely associated with large-scale topographic variables such as aspect, for which it showed a strong negative relationship indicating a preference for westerly over southerly slopes (Fig. 2). Beside Tree Pipit, only Mistle Thrush showed a negative association with aspect. No other species showed any association with slope or aspect. Furthermore, Tree Pipit was the only species that showed better model performance ($\Delta AICc \leq 2$) for the large-scale TOPO model compared to all fine-scale models and the large-scale TEMP model. All other species showed better (Chaffinch) or equal model performance of TEMP models compared to TOPO models at both scales.

Table 3. ΔAIC_c value for each model set at each scale for all species. A ΔAIC_c value of zero indicates the best performing model. Note that in some cases, the best performing models were identical in different model sets, hence a value of zero can appear more than once for a given species. Original AIC_c values are listed in ESM Table S3.

	HABITAT	TEMP		TOPO		COMB	
Species	fine-scale	fine-scale	large-scale	fine-scale	large-scale	fine-scale	large-scale
<i>Prunella modularis</i>	3.9	2.7	0.8	3.9	3.9	2.7	0
<i>Sylvia curruca</i>	0	0	0	0	0	0	0
<i>Parus ater</i>	1.4	1.4	0	1.4	1.4	1.4	0
<i>Turdus viscivorus</i>	1.2	1.2	1.2	0	1.2	0	1.2
<i>Fringilla coelebs</i>	13.9	6.3	0	13.1	12.9	6.3	0
<i>Anthus trivialis</i>	10	8.5	10	9.8	0	8.4	0
<i>Oenanthe oenanthe</i>	7.7	3.5	7.7	5.8	6.5	0	6.5
<i>Anthus spinoletta</i>	4.6	0.9	4.6	3.2	4.6	0	4.6
<i>Alauda arvensis</i>	6.0	0.9	2.7	2.3	4.8	0	2.7

Table 4. Significant model averaged parameters of the best model for each species. The model type, scale (large or fine), estimate, standard error (SE), test value (z) and *p*-value are given for each parameter. Note that species where there was more than one model in the best model set (i.e. $\Delta AIC_c < 2$) are marked with *. In these cases, the model with the lowest AIC_c is presented, but competing models are shown in ESM, Table S3, along with full details for all species.

Species	Model	Scale	Parameter	Estimate	SE	z	p
<i>Prunella modularis</i>	COMB	large	Rod	1.285	0.618	2.068	0.038
			Jun	0.818	0.308	2.632	0.008
			Oth	0.580	0.270	2.126	0.033
			Temp	- 0.886	0.406	2.163	0.030
<i>Sylvia curruca</i> *	TEMP	fine	Rod	1.029	0.265	3.835	≤ 0.001
			Jun	0.624	0.265	2.332	0.019
			Rock	- 1.174	0.467	2.487	0.012
<i>Parus ater</i> *	COMB	large	Jun	0.677	0.333	2.017	0.043
			Oth	0.657	0.277	2.351	0.018
			Grass	0.938	0.434	2.145	0.031
			Trees	1.126	0.303	3.678	≤ 0.001
<i>Turdus viscivorus</i> *	TOPO	fine	Vac	- 1.700	0.823	2.049	0.040
			Aspect	- 0.644	0.316	2.017	0.043

<i>Fringilla coelebs</i>	TEMP	large	Trees	2.453	0.809	3.004	0.002
			Temp	1.500	0.462	3.218	0.001
<i>Anthus trivialis</i>	TOPO	large	Jun	– 1.187	0.399	2.939	0.003
			Aspect	– 2.614	0.644	4.022	≤ 0.001
<i>Oenanthe oenanthe</i>	COMB	fine	Temp	0.736	0.305	2.386	0.017
			Aspect	0.622	0.288	2.133	0.032
<i>Anthus spinoletta</i>	COMB	fine	Temp	1.336	0.577	2.281	0.022
<i>Alauda arvensis</i>	COMB	fine	Jun	0.616	0.282	2.158	0.030
			Grass	1.010	0.436	2.289	0.022
			Temp	– 0.896	0.447	1.980	0.047

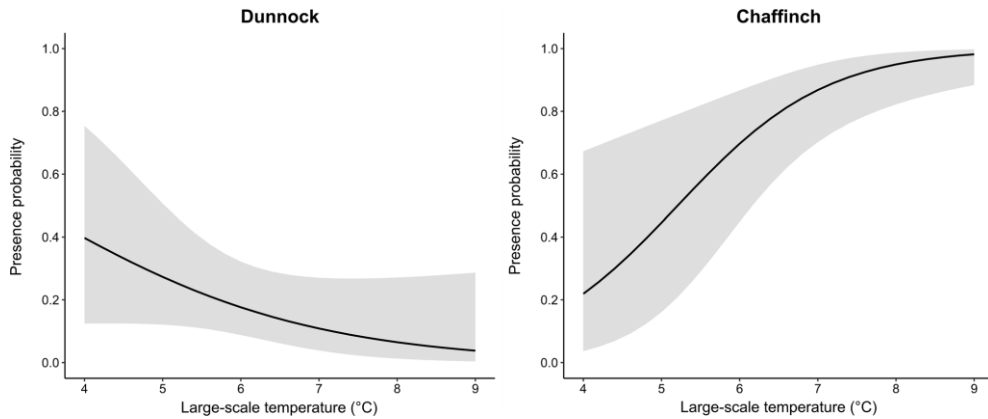


Figure 1. Relationship between large-scale temperature and the probability of occurrence of Dunnock and Chaffinch based on the large-scale COMB model. Shading indicates the 95% confidence interval.

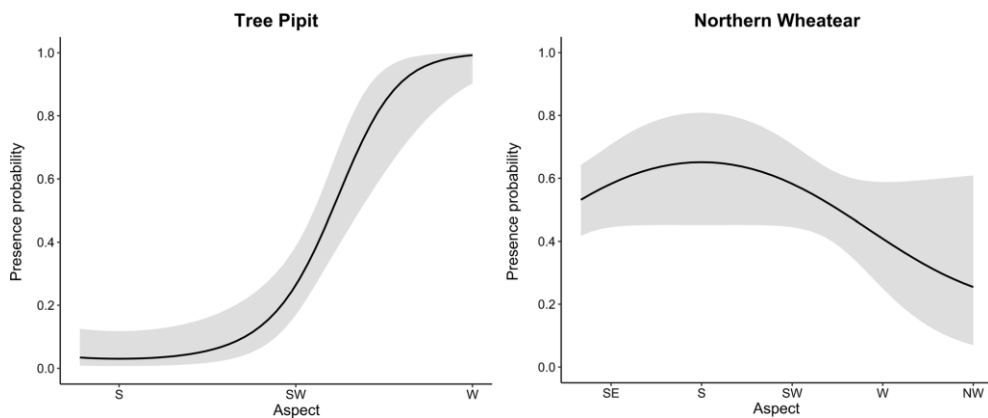


Figure 2. Relationship between aspect and the probability of occurrence for Tree Pipit and Northern Wheatear for the large-scale TOPO and the fine-scale COMB model, respectively. Note that aspect was modelled as an index from 1 (south-facing) to -1 (north facing), but here we present the axis as the equivalent cardinal direction for ease of interpretation. Shading indicates the 95% confidence interval.

Open habitat species

The HABITAT model for each open species did not show any habitat associations among the recorded variables. However, all fine-scale models (TEMP, TOPO and COMB) showed a positive association between grass cover and Skylark presence while Juniper cover was only positively associated in the TEMP and COMP models.

Models including fine-scale temperature and topography performed best ($\Delta AIC_c \leq 2$) for Northern Wheatear. The best performing models of Skylark and Water Pipit included both fine-scale TEMP and COMB models. Fine-scale temperature was positively associated with Water Pipit and Northern Wheatear presence, whereas Eurasian Skylark presence was negatively associated (Table 4, Fig. 3).

At a fine scale, TEMP models showed better model performance than TOPO models for Northern Wheatear and Water Pipit, whereas on a large scale, model sets for TEMP and TOPO were overlapping (Northern Wheatear, Water Pipit). The large-scale TOPO model showed equal model performance compared to the large-scale TEMP model for Skylark, but AIC_c was still higher compared to fine-scale COMB. In addition, aspect showed a positive relationship with Northern Wheatear (Fig.2, fine-scale COMB model) and Skylark presence (large-scale TOPO model) while slope was positively related to Skylark presence in the fine-scale TOPO model.

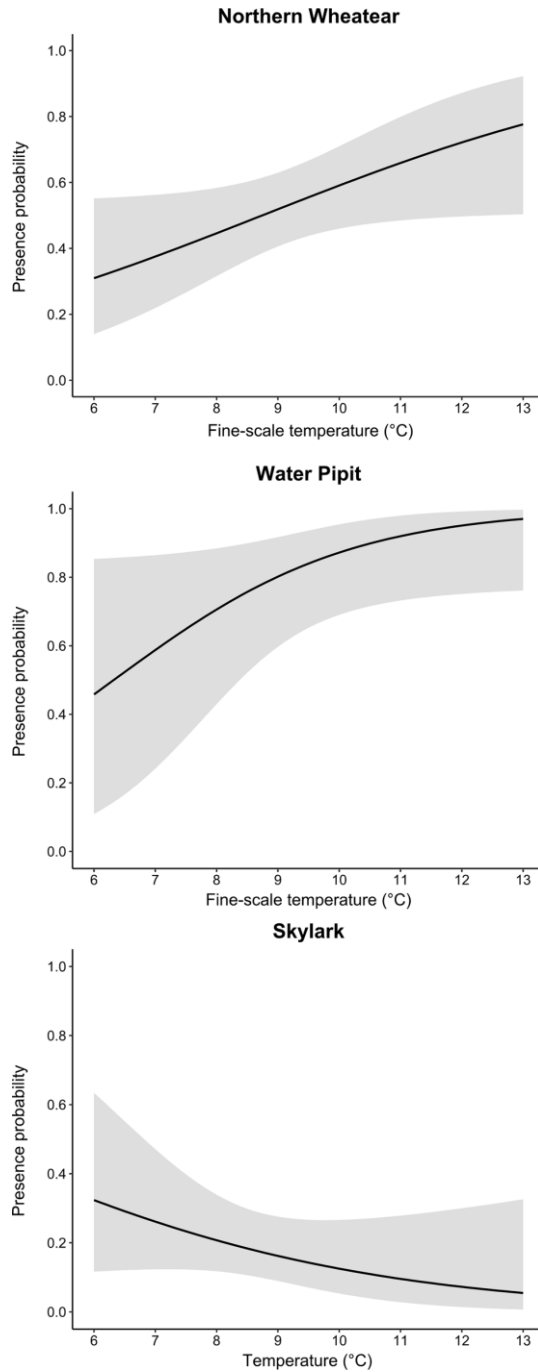


Figure 3. Relationship between fine-scale temperature and probability of occurrence for open habitat species for the fine-scale COMB model. Shading indicates the 95% confidence interval.

DISCUSSION

Models including fine-scale temperature estimates (TEMP, COMB) showed better model performance ($\Delta AIC_c < 2$) than corresponding large-scale models for all three open habitat species. Northern Wheatear and Water Pipit were both positively associated with warm microclimates while Skylark presence was negatively associated with fine-scale temperature. These results contrast with previous findings from the same region of the Alps (Chamberlain *et al.* 2013, 2016), where model predictions were based on large-scale climatic variables. In these studies, SDMs (based on temperature change and assuming no change in habitat) suggested that under warmer conditions, Skylark and Northern Wheatear would show an increase in their distribution whereas Water Pipit distribution would decrease. Therefore, for Water Pipit and Skylark distributions, our findings suggest opposite associations between fine-scale and large-scale temperature.

Differences in model predictions at different spatial scales have been reported for a range of studies, and thus identifying the appropriate scale represents a major problem when forecasting suitable habitat in order to inform conservation planning (Elith and Leathwick 2009; Randin *et al.* 2009; Franklin *et al.* 2013; Logan *et al.* 2013; Scridel *et al.* 2018). To improve SDMs, it is therefore necessary to carefully select predictors (e.g. temperature variables) and their spatial resolution. In the case of microclimate, local topography could create areas with suitable climatic conditions under which it would still be possible for a species to persist under the impact of climate change. Through the use of large-scale climate data, these areas might not be recognised by SDMs (Austin *et al.* 2011). Besides affecting the future distribution of a species, microclimate can also influence many other aspects of a species' life cycle.

There is evidence that microclimate can be important in influencing habitat selection in mountain birds which may explain our findings. For example, it has been shown that Horned Larks *Eremophila alpestris* adjusted the amount of incubation time in response to microclimatic conditions (Camfield and Martin 2009)

by spending less time on the nest as temperatures in the nest surrounding increased, which may imply energy savings in warmer microclimates. Furthermore, microclimate and aspect strongly influenced nestling survival in Water Pipits (Rauter *et al.* 2002). Nests which were located at ENE-facing slopes (temperature maximum in the morning) had more fledglings than those on WSW-facing slopes (temperature maximum in the afternoon). In contrast, foraging habitat selection by alpine White-winged Snowfinches *Montifringilla nivalis*, a high altitude specialist, was influenced by solar radiation (Brambilla *et al.* 2017b). Snowfinches preferred to forage at colder sites (low solar radiation) throughout the season. These studies illustrate that behaviour, foraging habitat selection and choice of nest sites could be driven by microclimatic conditions thereby affecting bird species distributions. Therefore, we would strongly recommend considering microclimate as a predictor in future SDMs for open habitat Alpine species.

In contrast to the open habitat species considered, forest and ecotone species showed no association with fine-scale temperature. One possible reason might be the buffering effect of vegetation. Körner *et al.* (2007) showed that temperature can vary strongly between forest and open alpine grassland along the elevation gradient with intermediate values at the treeline ecotone. Furthermore, canopies can buffer the diurnal amplitude of air temperature in the forest (Chen *et al.* 1999).

For two species (Dunnock and Chaffinch) large-scale models including temperature (TEMP, COMB) performed better than fine-scale models. The probability of occurrence of Chaffinch was positively associated with large-scale temperature, whereas the probability of Dunnock presence was negatively affected. A future increase in temperature could therefore affect the distribution of Chaffinches by expanding its range towards higher elevations. In contrast, the distribution of Dunnocks might be severely limited. Bani *et al.* (2019) demonstrated that Dunnock distribution experienced a lower range contraction along the elevational gradient during the last 35 years, but a simple dispersal into higher elevations as a response to environmental change might not be possible because

it's preferred nesting habitat in our study area, *Rhododendron*, has a slow rate of colonisation to the extent that treeline shifts towards higher elevations are likely to be more rapid than upwards shifts in this species (Komac *et al.* 2016).

The mismatch between temperature and available future habitat can also affect open habitat species considered in this study. Due to increasing temperatures, shifts in major habitat types (i.e. forest and shrub encroachment; Harsch *et al.* 2009) may lead to habitat fragmentation and/or loss of open alpine grassland at higher elevations. This process might even be exacerbated by the abandonment of pastoral activities which formerly have maintained the forest limit at lower elevations than would be possible under climatic constraints only (Gehrig-Fasel *et al.* 2007).

We have considered the associations between bird species distributions and temperature estimated at different scales. In doing so, one of our goals was to compare our results with previous work that has focussed on temperature as a likely driver of species distributions. There seems little doubt that temperature has a direct effect on the distribution and behaviour of organisms along elevation gradients. Nevertheless, we must acknowledge that there are potentially other important climate variables that vary along the gradient, including light intensity, humidity, wind speed and precipitation that may affect bird species distributions and their invertebrate prey (e.g. Hodkinson 2005; Tingley *et al.* 2012) which would be worth considering in future research.

Topography

For the majority of species, COMB models performed equally well in comparison with TEMP models at both spatial scales. Combining temperature with topographic variables increased model performance only for Northern Wheatear at a fine scale, whose occurrence was more closely related with south-facing slopes. At a large scale, the probability of Tree Pipit presence was higher on westerly slopes. However, general topographic variables were rarely associated with species occurrence. The influence of aspect on the occurrence of some species could be

explained by its effect on snow melt patterns during spring. Thermal differences among slopes with different exposition, which are caused by the amount of received solar radiation, could lead to an early snow melt on south-exposed slopes whereas north-exposed slopes might stay snow covered for a longer period (Keller *et al.* 2005). These early snow free areas could potentially benefit Northern Wheatears by making suitable nesting sites available earlier. Furthermore, it has been shown that differences in temperature among slopes can influence plant species diversity in temperate mountains (Winkler *et al.* 2016) with south-exposed slopes favouring a higher degree of species richness and diversity which may in turn influence insect availability. However, a potential caveat of this study might be that not all aspect directions were equally represented as we were tight to the south-western facing side of our study area due to frequent snow and rock avalanches and large inaccessible areas on the north-easting facing side of Val Troncea Natural Park (ESM Figure S1). Therefore, aspect varied only from 123 to 311 degrees, which might limit the transferability of our results. To complement our findings, further research is needed to fully understand how bird species distribution might be influenced by topographic variables in mountain areas of different exposition.

Conservation implications

Previous studies from the Italian Alps have indicated that increasing temperatures could have detrimental effects for certain Alpine species in the future (Chamberlain *et al.* 2013), with some species being potentially impacted by both temperature and habitat shifts (Water Pipit), while for others, loss of habitat due to forest and shrub encroachment will likely be more important (Northern Wheatear, Skylark). Indeed, Water Pipit in particular has shown declines at their lower elevation range margin in some areas that are apparently consistent with these predictions (e.g. Ebenhöf 2003; Bani *et al.* 2019). However, our results have shown that species such as Water Pipit and Northern Wheatear are positively associated with warm microclimates which could indicate that both species are potentially more resistant

to the impact of a warming climate than previously emphasised by large-scale temperature modelling (e.g. Chamberlain *et al.* 2013). As a consequence, our results imply that changes in habitat in the form of advancing treelines and the encroachment of formerly open areas by shrubs and trees (Gehrig-Fasel *et al.* 2007, Leonelli *et al.* 2011) are currently the major threat to those Alpine species, rather than direct effects of temperature. Therefore, it becomes particularly important to actively manage open areas within mountain environments. This could be achieved by targeted grazing techniques such as mineral mix supplements (Pittarello *et al.* 2016) or temporary night camp areas (Tocco *et al.* 2013). Both techniques lead to the mechanical damage of shrubs (including saplings) and eventually result in a reduction of shrub cover (Probo *et al.* 2013, 2014).

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APPENDICES

Additional supporting information can be found in the online version of this article:
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CHAPTER V

Early breeding conditions followed by reduced breeding success despite timely arrival in an alpine migratory songbird

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ABSTRACT

Timing reproduction to coincide with optimal environmental conditions is key for many organisms living in seasonal habitats. Advance in the onset of spring is a particular challenge to migratory birds that must time their arrival without knowing the conditions on the breeding grounds. This is amplified at high elevations where resource availability, which is linked to snowmelt and vegetation development, shows much annual variation. With the aim of exploring the effects of variability in the onset of local resource availability on reproduction, we compared key life history events in an Alpine population of the Northern Wheatear (*Oenanthe oenanthe*) between years of contrasting timing of snowmelt.

Based on remote sensed images, we identified 2020 as an exceptionally early snowmelt and green-up year compared to the preceding year and the long-term average. Individuals tracked with light-level geolocators arrived well before the snowmelt in 2020 and clutch initiation dates across the population were earlier in 2020 compared to 2019. However, observations from a citizen science database and nest monitoring data showed that the arrival-breeding interval was shorter in 2020, thus the advance in timing lagged behind the environmental conditions. While hatching success was similar in both years, fledging success was significantly reduced in 2020.

A trophic mismatch in early 2020 could be a possible explanation for the reduced reproductive success, but alternative explanations cannot be excluded. Our results show that, despite the timely arrival at the breeding grounds and a contraction of the arrival-breeding interval, Wheatears were not able to advance breeding activities in synchrony with environmental conditions in 2020. Earlier reproductive seasons are expected to become more frequent in the future. We show that the negative effects of changing seasons in Alpine migratory birds might be similar to birds breeding at high latitudes, despite their shorter migratory distance.

Running title: Timing of reproduction in an Alpine migratory songbird

Keywords: arrival, laying, interval, light-level geolocation, alpine, citizen science, remote sensing

INTRODUCTION

Alpine habitats are highly seasonal and are characterized by a relatively short reproductive period compared to the lowlands at similar latitudes (Lisovski *et al.* 2017; Nagy and Grabherr 2009). However, the onset of the reproductive season depends on the timing of snow melt that can be highly variable between years, requiring a level of phenotypic flexibility in organisms to respond accordingly (Jabis *et al.* 2020; Martin and Wiebe 2004). Timely arrival at the breeding site is crucial (Møller *et al.* 2010), and the entire annual schedule of migrants is meticulously tuned and adapted to spring phenology (La Sorte and Graham 2020), in particular resource availability during offspring rearing (Doiron *et al.* 2015). Years with relatively extreme conditions, especially in early spring, can have severe consequences for migrants (Shipley *et al.* 2020). Late arrival can result in a mismatch between the energetic demands of the migrants and their reproductive effort, and local food abundance, with subsequent negative effects on offspring growth (Doiron *et al.* 2015), survival (Post and Forchhammer 2007), annual productivity (Visser *et al.* 2006), recruitment in following years (Reed *et al.* 2013) and thus population size (Both *et al.* 2010). Extreme weather events, cold snaps, shorter days and colder nights at the beginning of early snow melt years can pose additional challenges and may also reduce the reproductive success of alpine birds (Bründl *et al.* 2020; MacDonald *et al.* 2013; Martin *et al.* 2017; Moreno *et al.* 2015; Shipley *et al.* 2020).

Understanding the fitness consequences and the phenotypic constraints of migratory animals during years with early breeding conditions has become a focal issue, since climate warming results in the advancement of spring conditions worldwide (Parmesan and Yohe 2003) which can have negative consequences for biodiversity when these changes result in phenological mismatches (Visser & Gienapp 2019). The phenological shifts seem especially fast in highly seasonal environments, including Alpine habitats (Oyler *et al.* 2015). Long-distance migrants have also experienced strong population declines over recent decades (Sanderson

et al. 2006; Vickery *et al.* 2014). Furthermore, trophic mismatches appear to be most prominent in long-distance migrants that breed at high latitudes of the northern hemisphere and depend on highly seasonal food resources (Both *et al.* 2010; Doiron *et al.* 2015). In contrast, shorter distance migrants seem to have higher flexibility in adjusting their arrival dates, and long-term studies have shown that bird populations that match the pace of changing climate and underlying resources can even have positive population trajectories (Koleček *et al.* 2020).

The Northern Wheatear (*Oenanthe oenanthe*, henceforth wheatear) has one of the largest breeding distributions amongst migratory songbirds (Conder, 1989; Dunn *et al.* 2020), but the non-breeding distribution is confined to northern sub-Saharan Africa (Bairlein *et al.* 2012; Cramp 1988; Schmaljohann *et al.* 2012). Thus, migratory distance in wheatears can vary between 3.000 and almost 15.000 km (Bairlein *et al.* 2012; Förschler and Bairlein 2011). European Alpine breeding wheatears have amongst the shortest migratory distance from breeding to wintering grounds (approx. 3.500 km) relative to other wheatear populations. However, the high-elevation breeding sites are similar to those of northerly breeding populations, being characterised by strong seasonal climate and food resources, and the duration of snow cover and the short season limits the reproductive period and requires accurate timing of life-history events (de Zwaan *et al.* 2020, 2019). The European Alps have experienced marked phenological changes over recent decades, including earlier springs (Migliavacca *et al.* 2008) and prolonged snow free periods (Asam *et al.* 2018), with potential consequences for high elevation species (e.g. Resano-Mayor *et al.* 2019).

Despite wider population declines in Europe (Pan-European Common Bird Monitoring Scheme, 1980-2009, Vickery *et al.* 2014), wheatear population trends in the Alps seem stable (Lehikoinen *et al.* 2018). This in part may be due to the shorter migratory distances of Alpine breeding birds that allow a greater flexibility to adjust the timing in synchrony with environmental conditions. Whilst the wheatear is classed as a long-distance migrant, the relatively short journey for

those in southern Europe may mean these populations can cope better with environmental fluctuations, as has been proposed for short-distance migrants (Alerstam and Högstedt 1980). Alpine breeding individuals may have always arrived in advance or stayed at nearby stopovers to monitor environmental conditions and occupy their breeding sites as soon as conditions permit (de Zwaan *et al.* 2019), thereby buffering effects of recent earlier springs in the Alps. Effects of climate change on alpine species' demography through phenological changes seem highly likely (Scridel *et al.* 2018), although it is as yet unknown how earlier snow melt and spring green-up affect the timing and success of alpine breeding birds.

It is important to study biodiversity responses in climatically extreme years as they can serve as templates for likely future conditions (McGuire *et al.* 2020). A late snowmelt in 2019 and an exceptionally early snowmelt in 2020 across the European Alps provided a natural experiment that allowed us to explore how Alpine breeding wheatears' reproduction is affected in years when the season is advanced. Our primary objective was therefore to understand how wheatear arrival varied in relation to snowmelt (in other words, is there evidence that they are able to arrive on the breeding grounds when conditions are right for the onset of breeding in years with widely different snowmelt dates), and thus determine whether this might have had any consequences for reproductive success. A secondary aim was to describe the migration of this species to and from the wintering grounds, adding tracks and more detailed locations to previously published data (Schmaljohann *et al.* 2016). There is a lack of detailed information on mountain bird ecology compared to other habitats, especially outside the breeding season (e.g. Boyle and Martin 2015). It is thus important to study the whole annual cycle of mountain species to better understand how they may respond to environmental change. We thus provide an important baseline for understanding migration and how this relates to breeding season ecology, in our population of wheatears.

We used light-level geolocators to track wheatears across their annual migration and thus define their arrival at the breeding grounds, and collected detailed information on individual breeding activity and success as well as environmental conditions during the reproductive season. In addition, we used citizen science data on wheatear observations in order to quantify estimated arrival and transition dates of wheatears in the wider area of our study site, and potential longer term trends. Environmental conditions were measured both in the field and using remote sensed images in order to quantify seasonal vegetation development (i.e. spring green-up, the seasonal development of new vegetation growth). By combining the citizen science observations and remote sensing data, we aimed to put the data from our study into a wider spatio-temporal context. We predicted that the relatively short migration distance of Alpine breeding wheatears would lead to early arrival at the breeding grounds, allowing reproduction in synchrony with environmental conditions, even in the exceptionally early year of 2020. We thus predicted that individual plasticity in arrival would result in no effect of the variation in conditions from year to year on fitness.

METHODS

Study area

Data on environmental conditions, breeding phenology and breeding success were collected in 2019 and 2020 during the breeding season, from May to August, in Parco Naturale Val Tronca, 44°57'28"N, 6°56'28"E, Western Alps, Piedmont, Italy (Figure 1a). The elevation of the study area varied from 1,560 m a.s.l. to 2,700 m a.s.l. and was located on a south-eastern slope. The landscape structure is characterised by forests (predominantly larch *Larix decidua*) with shrubby patches at lower elevations, and larches interspersed with open grasslands at around 2,200 m a.s.l., followed by rocky areas, above the treeline. The valley is used seasonally as pasture, and grazing cows influence the distribution and availability of potential open grassland habitat across all elevations (Jähnig *et al.* 2018).

Environmental conditions

To investigate the longer-term trends in the annual date of snowmelt (“the snow free date”), we used the remotely sensed MODIS (MOD10A1.006) Terra Snow Cover Daily Global 500m dataset with recordings starting in 2000 (Hall *et al.* 2016). Daily values for all pixels (N = 68) within the study area were extracted from Google Earth Engine (Gorelick *et al.* 2017) via the R package *rgee* (Aybar 2020). For each pixel and each year, we identified the snow free date as the first date without snow that was followed by at least 60 days (approximately two months) of snow free conditions, ignoring potential snow free periods within the winter.

To derive higher-resolution snow free dates for the actual nest sites in the study area during 2019 and 2020, we used the remotely sensed Sentinel-2 MSI MultiSpectral Instrument Level-2A dataset with a spatial resolution of 10 m (Drusch *et al.* 2012). On the Google Earth Engine Server, we first selected all images taken in 2019 and 2020 intersecting at least one of the nest sites. Next, we masked cloud pixels using the Sentinel-2 Cloud Probability layer with the standard probability threshold of 60. We then calculated the normalised differenced snow index (NDSI, Band 8 & 4) and the normalised vegetation index (NDVI, Band 3 & 11). For each nest site and each image, we extracted the mean NDSI and NDVI values of all pixels within a 10 m radius (N = 2-4) around the nest. For each nest site and for both years, we fitted a smooth line (loess fit with span = 0.2 from the R package *stats*) to the NDVI and NDSI values over the day of the year, and extracted the day when the model fit fell below 0.1 NDSI (less than 10% of snow cover was defined as the snow free date) and exceeded 80% of the NDVI annual amplitude (the defined threshold when the peak in spring green-up was reached).

In the field, snow cover and grass height, as proxies for the spring green-up were monitored throughout the two breeding seasons (see Supplementary Table S1 for details and sample sizes). Data were collected using a standardised protocol for territory mapping. In summary, we defined four sectors above the treeline (total area: 161 ha) that were characterized by open grassland habitat, variation in

elevation (~ 700 m) and a high density of wheatear territories. We defined a route (~ 6 km in each sector) along which we defined habitat survey points separated by a distance of 200 m (6-8 points each sector, 30 in total). Territory mapping and habitat point surveys were conducted over five visits between 27th May and 21st July 2019. Positions of singing males were recorded with a GPS device during the period between sunrise and 12 am and during suitable weather conditions. Following the protocol introduced by Südbeck and Weick (2005), territories were confirmed when a singing male or other territorial behaviour was recorded during at least two visits at the same point. Habitat parameters were recorded at each of these points (covering an area of 200x200 m at habitat survey points and a 100 m radius around territory points) at each of the five visits and were all included in analyses to track changes in environmental conditions across the season. The territory mapping as well as the habitat point survey was repeated in 2020 over 5 visits between 14th May and 6th July.

Light level geolocation

Males and females were trapped either at their nest during chick feeding or with spring traps (using mealworm bait) when the nest location was unknown, not yet established, or chicks had fledged. In 2019, 35 adults were tagged, using 15 (8 males, 7 females) light-level geolocators manufactured by Migrate Technology Ltd. (Intigeo P65, light stalk, 0.8 g, fitted with a leg-loop harness (Rappole and Tripton 1991) and 20 (10 males, 10 females) geolocators manufactured by the Swiss Ornithological Institute (SOI, SOI-PAM, light stalk, recording pressure, 1.1 g). Device weights were on average 4.1% of the individuals' body mass (2.8-5.2 %, see Supplementary Table S2). All captured individuals were marked with three plastic colour rings and a metal ring of the Italian bird ringing scheme. As a control for the effect of geocator devices on return rates, an additional 16 individuals were ringed, but were not fitted with a geocator. All animal handling and protocols were carried out in accordance with relevant guidelines and regulations under licenses issued by Istituto Superiore per la Protezione e la Ricerca Ambientale

(ISPRA, protocol no. 27303, no. 2463) and Città di Torino (license no. 56.1433/2019, no. 197.4765/2019).

Light-intensity data were recorded at 5 minute intervals and analysed using a threshold method (Lisovski *et al.* 2020a). Sunrise and sunset events (twilight events) were identified on log-transformed light data and a threshold of 1 log lux, using the R package TwGeos (Lisovski *et al.* 2015).

Twilight events recorded at the known deployment site during periods after deployment and before recapture were used for calibration, i.e. to estimate the error distribution of twilight events and the individual reference sun elevation angle (position of the sun when twilight events were detected). For recordings from Migrate Technology Ltd. tags, migratory movements were identified as sudden and directed changes of consecutive sunrise or sunset events (for details, see the “invMovement” method description in Lisovski *et al.* 2020b). Stationary periods with a minimum of two consecutive twilight events were then identified as periods surrounded by migratory movements. For data recordings from Swiss Ornithological Institute tags, we used the additional air pressure measurements to identify movement periods with a change in a pressure threshold of 4 (change in the altitudinal position of the bird), using the method implemented and described in the R package PAMLR (Dhanjal-Adams 2019).

For the final track estimation, we used a Bayesian approach from the R Package SGAT (Wotherspoon *et al.* 2016) allowing the incorporation of twilight events, their error distribution (gamma density distribution), the information on periods of movement and residency, a spatial probability mask and expected flight speed distribution (gamma distribution with shape = 2.2 and rate = 0.08).

The method provides the most likely paths with credible intervals derived via Markov Chain Monte Carlo (MCMC) simulations. The applied *groupedThresholdModel* provides a single location estimate for stationary periods as well as one location estimate for each twilight during movement. A spatial mask was applied for the estimate of stationary locations, restricting positions to be

estimated on land. During the MCMC simulation, the first and last site of residency (in case the logger was still recording light on return from the wintering grounds) were fixed to the deployment site.

We first ran a *modifiedGamma* model (relaxed assumptions) for 1000 iterations to initiate the model, before tuning the model with final assumptions/priors with three runs, each containing 300 iterations. Finally, the model was run for 2000 iterations to ensure convergence. Median location estimates and 95% CrI were calculated using the entire final MCMC chain (i.e. each location estimate was based on 2000 estimates from within the MCMC chains). Locations from the most likely track were used for plotting.

Arrival Dates

We used three different approaches to estimate the timing of departure and arrival at the breeding grounds in 2020 from the geolocator data. First, we used the dates from the above-described analysis of the stationary periods (first day at breeding ground after last northward migration stopover site, Supplementary Table S3). Second, we performed a separate analysis on the defined twilight times to estimate the probability that each sunrise and sunset time were recorded within the larger area around the breeding site (radius = 250 km). To this end, we used the calibrated individual gamma distribution of the twilight error and simulated 500 locations for each twilight time. The resulting locations reflect the expected precision of the location estimates (see Lisovski *et al.* 2018). The probability was then defined as the percentage of location estimates per twilight falling into the defined radius around the breeding site. A symmetrical Gaussian curve was then fitted to the probabilities over time, and departure and arrival were calculated as the dates when the curve fell respectively below or exceeded a probability of 0.5 (as well as the 0.025 and 0.975 probability to report the 95% confidence intervals). The idea behind the third approach emerged while inspecting the light recordings. During the sunrise periods at the beginning and the end of the recordings, thus at the breeding site, we discovered a time delay in the daily maximum light values.

This was caused by the south-eastern slope of the breeding area and the fact that the direct sunlight was blocked by the mountain ridge in the east (Figure 1a). To make use of this pattern in the identification of the exact arrival and departure time at the breeding site, we applied an additional calibration with a higher light intensity threshold (9 log lux), slightly below the maximum light values that the tags can resolve (11 log lux), resulting in a gamma distribution of the delayed maximum light intensities. Due to the changes in the position of the sun, the delay was expected to change over the course of the year, thus we estimated the gamma distribution parameters for autumn and spring separately. Next, we calculated the probability that the daily timing of the maximum light intensity during sunrise would belong to the derived gamma distribution (the first half of the light recordings were compared to the autumn gamma distribution and the second half to the spring gamma distribution). A symmetrical Gaussian curve was then fitted to the probabilities over time, and departure and arrival was calculated as the date when the curve fell respectively below or exceeded a probability of 0.5 (as well as the 0.025 and 0.975 probability to report the 95% confidence intervals).

To estimate the general migration transition of wheatears migrating northwards from African wintering ranges into the regions of Piedmont and Aosta Valley, and thus elaborate a proxy for the arrival in the wider area of the breeding site in the Western Alps in 2019 and 2020, we additionally used citizen science data of wheatear sightings during spring submitted via the ornitho.it platform. The data includes the number of all observations of wheatears per day in the period March-May. We furthermore used data from the years 2010-2020 to describe changes over a longer period, being aware of the bias in the data that might include not only local breeding wheatears, but also individuals migrating further north. It is not possible to formally account for observer effort in the ornitho.it data, as observers often submit occasional observations of specific species. However, based on both the total number of observations of any species submitted in each year (2019: $n = 151.799$, 2020: $n = 168.180$) and the number of individual wheatear observations

(2019: n = 101, 2020: n = 93), there appears to be negligible differences between years, hence we consider the data appropriate to indicate the general temporal migration patterns in the larger area of the study site.

Breeding phenology and success

From the fourth week of May until the first week of August (2019, 2020), we searched for wheatear nests in all four sectors as well as adjacent accessible areas, including open grassland sites at lower elevations (pastures). Each identified nest was marked with bamboo sticks at a distance of at least 5 metres, and consecutively monitored until the chicks fledged or the nest failed.

Depending on the stage (e.g., longer breaks during incubation when date of hatching could be estimated from date of laying the last egg, following Conder 1989), the status of the nests was recorded on average every five days. In 2020, at each visit, habitat parameters at the nest were recorded. We were able to record the exact dates for building, laying, hatching and fledging for some nests in 2019 and 2020, and subsequently estimate the duration of each stage for our population (see for details Supplementary Table S4). We used the average of these individual durations of each stage (Supplementary Table S4) to estimate breeding phenology dates for nests where direct observation was not possible in all their stages (back or forward in time from a known breeding phenology date). If the number of eggs laid was unknown, we assumed a clutch size of five eggs, which is the average number within our population (nests reaching the stage of incubation and no. of eggs known, 2019: 36, 2020: 22), to estimate the lay date. Breeding phenology dates were calculated only for stages reached by the individual nest, e.g. we did not estimate a fledge date if the nest failed before. The arrival-breeding interval (A-B interval) was estimated by calculating the difference between the median arrival date and lay date, providing two estimates of A-B interval for 2020 (using geolocation and citizen science observations).

To estimate and compare the breeding success of the population between the two consecutive years 2019 and 2020, we considered three different measures:

a) the hatching success rate (eggs that hatched), b) the fledging success rate (hatchlings that fledged), and c) the nest success rate (successful nests/all nest attempts). Measures a and b allowed us to separate the breeding success into two states of a nest, i.e. nests during incubation and nests during chick rearing, by considering the success rates of individual eggs and hatchlings estimated as probabilities of reaching the next state (“period” hatching and fledging). We excluded nests where number of eggs or chicks was unknown or incomplete. For the vast majority of the nests, we could not determine whether this was a first attempt or a replacement of a failed attempt due to predation, abandonment or hatching failure. Thus, we included all nests monitored in our analyses, except for the nests known to be replacements.

We applied a general linear mixed model with binomial errors to quantify the success rate of hatching and fledging (a, b) of each egg laid within the population, with the fixed effects “year” (2019, 2020) and “period” (hatching, fledging), adding “nest id” as a random effect (using the function `glmer` from package `lme4` (Bates *et al.* 2007)). To quantify the nest success rate (c), we applied a generalized linear model with the fixed effect “year” (using the function `glm` from package `stats`). Model assumptions were tested by deriving residual plots and checking for overdispersion (function `dispersion_glmer` from package `blmeco` (Korner-Nievergelt *et al.* 2019)). Conclusions from test statistics were based on the credibility intervals from the model predictions calculated using the function `sim` from package `arm` (Gelman and Hill 2007), and by drawing 2000 random samples from the posterior distribution of the model parameters to obtain their 95% credible intervals from these simulations. An effect was considered significant if the credible interval of the model estimate did not include zero (Korner-Nievergelt *et al.* 2015).

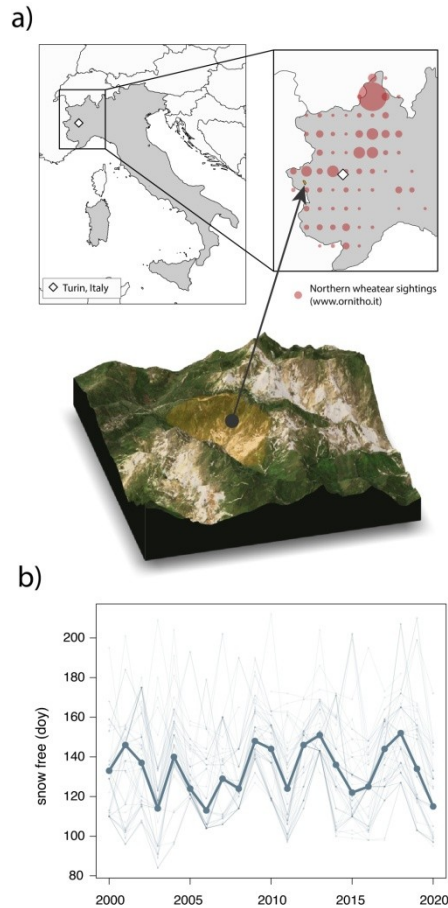


Figure 1. a) Location of the study area, Parco Naturale Val Troncea in the Western Alps in Piedmont, Italy (yellow shaded south-eastern slope in topographical map), and the locations of wheatear sightings between March to May submitted to the ornitho.it database (red circle size corresponds to the number of sightings within a 0.25 degree grid cell). b) The day of the year, from 2000 to 2020, after which the study area was generally snow free in spring for at least 60 days. The fine lines represent the snow free dates for all MODIS satellite image pixels within the study area and the thick line connects the annual median values across pixels. Map data from Natural Earth (naturalearthdata.com), Landsat 5 and topographic model was downloaded from mapbox (www.mapbox.com).

RESULTS

Environmental conditions

The time series of the snow free date within the study area (Figure 1a) from 2000 to 2020 showed high interannual variation, but no significant trend over time ($t_{1191}=1.88$, $p=0.059$, 0.20 days/year; -0.002 - 0.419 95%CI) (Figure 1b). In 2019, the median snow free date was close to the long-term average, whereas the snow free date in 2020 was the earliest for over a decade (Figure 1b). On average and at the finer scale around the detected wheatear nests, the area was snow free more than three weeks earlier in 2020 (median = 130 day; 40th to 60th quantile 125 – 143) compared to 2019 (155; 148 – 164) (Figure 2a). Similarly, vegetation growth reached the 80% threshold 17 days earlier in 2020 (162; 156-167) compared to 2019 (181, 178-184), and was strongly correlated with snow free dates ($R^2 = 0.43$, $p < 0.001$, $t_{254} = 7.68$) (Table 1). Snow cover and vegetation height data from direct observations in the field matched remote sensed images (Figure 2a, date of snowmelt and 80%-ndvi amplitude).

Migration schedule and arrival dates

In 2020, we retrieved 11 geolocators, of which 9 contained sufficient data for further analyses (6 Migrate Technology, 3 SOI, of 5 males and 4 females). Fourteen tagged individuals were resighted ($n = 35$, return rate: 40 %) of which 13 were recaptured. Two individuals lost the device. Nine adults of the control group were resighted ($n = 16$, return rate: 56 %). The frequency of return rate between tagged and control groups was not significant (Fisher exact test, $P = 0.126$). Six tags recorded light levels for the full annual cycle. One tag stopped recording after arrival at the main wintering site (24EA). Two tags stopped recording during spring migration (24DK, 24EP). In total, we derived arrival dates at the breeding site from six tracked individuals in 2020 (Figure 2b, Table 1, see for details Supplementary Figures S1a-c, Tables S5).

Geolocation data reveals that in 2020 the arrival period at the breeding site for the six tagged individuals ranged from 13th April to 6th May 2020 (Figure 2b, Supplementary Table S5, Figure S1b). The three males (BT795, BT800, BT801) were on average 13 days earlier than the three females (Figure 2b, Supplementary Table S6). Interannual variation in the timing of spring arrival/transition in the larger region of the study area (citizen science observations of wheatears) was high over the last ten years ($R^2 < 0.001$), with an average arrival in 2019 (median doy = 119) and a rather late arrival in 2020 (median doy = 130) (Figure 2b, Table 1, Supplementary Figure S2). For 2020, observation dates differed from the geolocator arrival dates by twelve days, with earlier arrivals of tagged birds (median doy = 118, Table 1).

Individual tracks revealed, compared to further stopovers in the same year, relatively long stopovers (approx. 20-30 days) before crossing the Sahara desert in autumn and shorter stopovers (approx. 5-10 days) just before reaching the wintering sites (Figure 3, see for details Supplementary Table S3, Figures S1a,S1c). Spring migration appeared to be faster, with fewer and shorter stopovers (approx. 5-10 days) (Figure 3, Supplementary Table S3, Figures S1a-c) until the coast of the Mediterranean Sea and Sardinia was reached. Here, most (4 out of 6) wheatears stopped again for a longer period (approx. 15-20 days, Figure 3, Supplementary Table S3, Figure S1a). With larger sample sizes, it will be possible to link data on migration routes, stopovers and arrival times more strongly to the breeding season, so we will have a much better idea of how non-breeding and breeding seasons are linked.

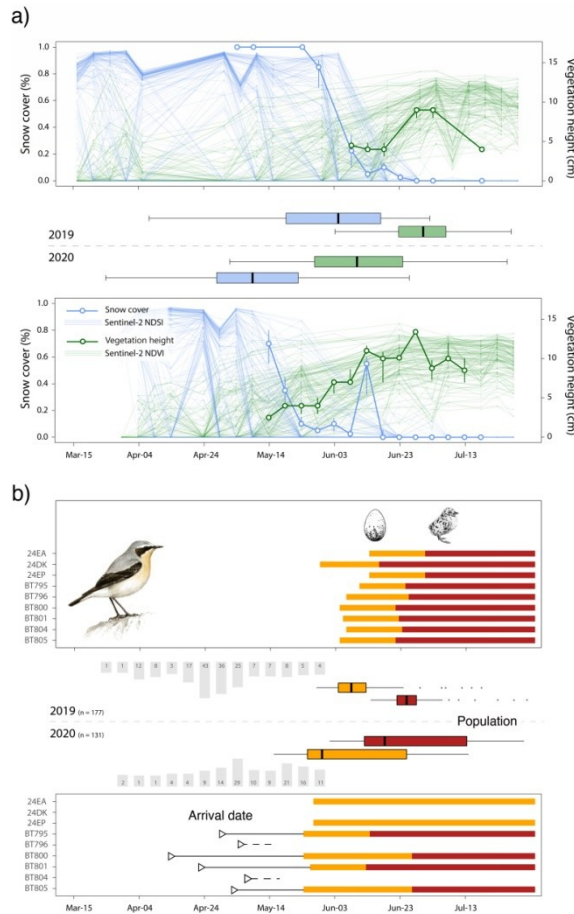


Figure 2. Arrival and lay dates at the Alpine breeding ground in relation to the spring green-up. a) Snow cover and vegetation height data derived from territory, habitat (2019 & 2020) and nest monitoring (2020) (thick lines). Measures for the green-up derived from Sentinel-2 data (thin lines). Day of year when snow cover was less than 10% of the maximum and NDVI reached 80 % of the amplitude are shown in boxplots. b) Barplots (grey) show the no. of observations from ornitho.it in Piedmont and Aosta Valley from March to May. Triangles show arrival dates of the tagged individuals (n = 6, 2020). Rectangles represent lay (orange) and hatch (red) dates of 9 tagged individuals (2019 & 2020), whereas the orange and red boxplots show the distribution of lay and hatch date across the whole population and season (nest monitoring 2019: n = 73, 2020: n = 48).

Table 1. Snow free and green-up date, arrival date (median date from geolocation/median date of citizen science observations), median lay date, difference in days (A-B interval), median hatch date and sample sizes for the breeding success models (no. of eggs, no. of hatchlings, no. of nests monitored). Median dates for tagged individuals are given for each year (Tags), as well as two-sample tests for comparing dates of tagged birds with population (Test). Arrival dates for each tagged individual are given in Supplementary Table S5. All dates in day of year.

Year	Snow free/ Green-up	Arrival date	Lay date	A-B Interval	Hatch date	Eggs in nests	Hatchlings in nests	No. nests monitored
2019	155/181	---/119	158 (range: 147-198)	--/39	175 (range: 164-214)	206 in 36	176 in 37	74
Tags		---	163 (range: 146-163)	--/44	180 (range: 171-180)	---	---	---
Test		---	P = 0.32, W = 232	--	P = 0.32, W = 192	---	---	---
2020	130/162	118/130	150 (range: 135-195)	32/20	167 (range: 152-212)	150 in 32	149 in 32	53
Tags		118 (range: 112-126)	147 (range: 144-147)	29/17	164 (163, 164)	---	---	---
Test		P = 0.009, t = -3.73	P = 0.48, W = 188	--	P = 0.76, W = 130	---	---	---

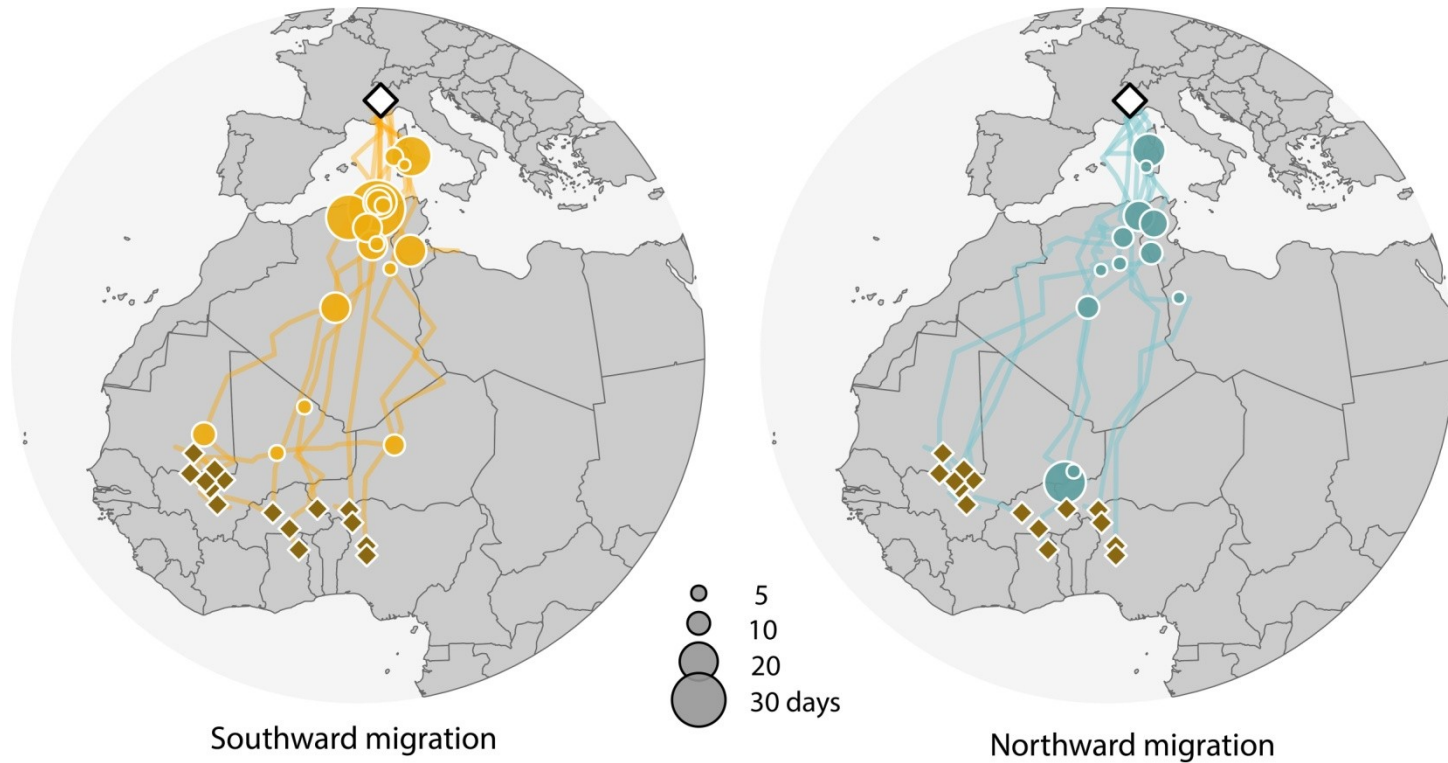


Figure 3. Most likely migration route estimates of individual Alpine breeding Northern wheatears. The breeding location is marked with a white diamond, stopover sites (>2 days) with an orange and blue circle, and wintering grounds with a brown diamond. Some individuals changed location and had more than one wintering ground. Southward migration tracks include 9, and northward migration tracks 6, individuals. Map data downloaded from Natural Earth (naturalearthdata.com).

Breeding phenology and success

In 2019, we monitored 74 nests, of which 27 failed. In 2020, 53 nests were monitored, of which 23 failed. Nest failure was caused mainly by predation (23 nests in 2019, 15 in 2020), but also by nest abandonment or hatching failure (4 and 7, respectively). The cause of failure could not be identified in all cases (2 and 1, respectively). The first and last lay dates in 2019 were 28th May and July 18th, and in 2020 May 15th and July 14th. The number of monitored nests is assumed to be representative of this population, as they were located over an elevational gradient of 680 metres which encompassed most of the elevation range of the species in the local area (attempts at higher or lower elevations are rare). According to results of the territory mapping (spanning an area of 1.15 km²), the study area holds 60 breeding pairs per km² and includes a range of different habitats (mountain grassland, grazed shrubland, scree).

In 2020, for five nests out of all 53 attempts, we had enough information to distinguish replacements from first attempts (identified by colour ringed adults). For 2019, only one out of 75 nests could be identified as a replacement nest. For the lay date and the interval between arrival and breeding (arrival-breeding interval) estimates, we therefore excluded the replacement nests.

Lay dates in 2020 were eight days earlier on average, although there was much variation, compared to 2019 (Figure 2b; median day 2019: 158, range: 147-198, n = 73; median day 2020: 150, range: 135-195; N = 48). However, due to later arrival in 2020 (citizen science observations), the arrival-breeding interval was shorter in the early year of 2020 (20 days) than in 2019 (39 days) (Figure 2b, Table 1). The median hatch date was eight days earlier in 2020 (median day: 167) than in 2019 (median day: 175), but in 2020, we observed greater variability in hatch dates (range: 152-212) than in 2019 (range: 164-214). The difference in days between the peak of the green-up (NDVI 80% of amplitude) and hatching was similar in both years (difference in median dates: - 6 days in 2019, + 5 days in 2020), but in 2020, hatching was five days behind the peak (Table 1, Figure 2b). Breeding phenology

dates of tagged individuals did not differ from those of the studied population, but sample sizes were low due to nest failures in 2020 (Table 1).

The success rates (a, b) were lower in 2020 than in 2019. Even though the difference in hatching success between years was negligible, the probability that a hatchling would fledge differed significantly and was lower in 2020 (Figure 4, see for sample size and model output Supplementary Table S7). The nest success model (c) showed a non-significant lower success rate in 2020 (Figure 4, Supplementary Table S7).

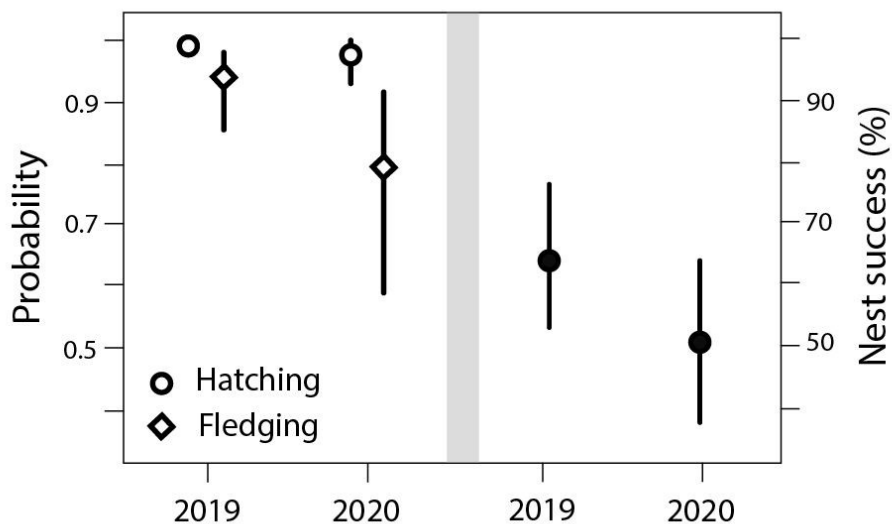


Figure 4. Left: Year effect on the probability of hatching (a) and fledging (b) ($\beta = -1.4$, 95 % CrI: -2.870 – -0.018, $P = 0.05$). Hatching probability: 99% (0.98 – 1.00) in 2019 and 98 % (0.93 – 0.99) in 2020. Fledging probability: 94 % (0.85 – 0.98) in 2019 and 80 % (0.59 – 0.92) in 2020, $\beta = 2.38$, 95 % CrI: 1.754 – 2.996, $P < 0.001$, $N = 683$. Right: Year effect on nest success (c): 65 % (0.54 – 0.76) in 2019 and 51 % (0.38 – 0.64) in 2020, $\beta = -0.139$ (0.314 – 0.040), $P = 0.12$, $N = 126$.

DISCUSSION

In long-distance migratory birds, phenological asynchronies are mainly attributed to the inability to advance spring arrival at the breeding grounds in synchrony with temporal shifts in resource availability (Mayor *et al.* 2017; Møller *et al.* 2008; Reed *et al.* 2013; Saino *et al.* 2011). While a growing number of studies have provided evidence for such asynchronies, reports on the impacts on fitness are less frequent (Visser *et al.* 2012). Despite having only two years of detailed data, we show that there was a significantly lower reproductive success in an exceptionally early spring, compared to an average year, in a bird population with a relatively short migration distance. Based on that and on previous findings, we predicted that wheatears breeding in the European Alps would arrive before the conditions became suitable for breeding and would therefore cope with an early spring by advancing their clutch initiation date. While our predictions regarding the arrival seem true (time buffer before laying), and clutch initiation was earlier in 2020 compared to the later spring in 2019, the advancement and thus the adjustment in the arrival-breeding interval was only about 8 days compared to the three weeks of the advancement in environmental conditions (Figure 2b).

Seasonal dynamics in the European Alps are changing; over recent decades, the snow cover period has become shorter resulting in an increase in primary productivity during the summer (Asam *et al.* 2018), and while we could not find a strong trend in the snow free dates within the very low resolution remote sensing data (MODIS NDSI) of the study area in the Western Alps in Piedmont, we found high interannual variations (Figure 1b), with an average year in 2019 and a very early snow free date in 2020. Direct observations and high-resolution remote sensing data (Sentinel-2) allowed a more detailed quantification of the differences between the two years, showing that snowmelt, crucial for clutch initiation (Liebezeit *et al.* 2014), and green-up of the vegetation, a proxy for food availability (Marcelino *et al.* 2020; Pettorelli *et al.* 2006), occurred about three weeks earlier in 2020 (Figure 2a). These yearly differences set the scene to compare key

phenological events, such as arrival, clutch initiation, date of hatching and fledging, as well as breeding success as a measure of individual and overall population fitness.

Sightings of Northern Wheatears arriving in and passing through the Piedmont and Aosta valley during spring migration did not show a significant advance over the last decade (Supplementary Figure S2). However, individuals migrating through the area can come from various wintering sites in Africa and can vary even more strongly in their breeding destinations. Population-specific migration schedules, such as the later transition of northerly populations (Maggini *et al.* 2013), and potential trends may thus be hidden in the sightings dataset. In fact, wheatears from Greenland (*O. o. leucorhoa*) have advanced their migration within the last three decades (Desaever and Bairlein, 2020) and previous studies on a northern lowland population of the wheatear have shown a continuous trend towards earlier arrival at breeding sites (Low *et al.* 2019). Constant effort trapping data of wheatears stopping-over on islands in the Mediterranean Sea has revealed a weak, but not significant, trend towards earlier passage during spring migration within the last 18 years (Maggini *et al.* 2020). The tracked individuals in this study provided exact arrival dates for 2020, showing that the studied population might arrive earlier than the major migration flow of wheatears in the region (Figure 2b), including birds of northerly populations (Maggini *et al.* 2013). This might be also true for 2019. However, citizen science data enabled us to compare the overall timing of arrival and transition of wheatears in the Western Alps for both years, showing that birds were recorded about ten days later in 2020, which implies a further shortening of the arrival-breeding interval in 2020. There are known biases associated with citizen science data (e.g. Callaghan *et al.* 2017), including variations in spatial and temporal survey effort. In 2020, restrictions on people's movement were imposed in March in Italy as a measure against the Covid-19 pandemic. However, there was no evidence that this had an impact on sampling effort – indeed, the total number of observations submitted to ornitho.it was slightly higher

in 2020 (2019: $n = 151.799$, 2020: $n = 168.180$), and there was a negligible difference in the number of wheatear observations (2019: $n = 101$, 2020: $n = 93$). We cannot control for differences in spatial coverage, but most wheatears arrive first in lowlands and are detected commonly on agricultural fields, i.e. close to human populations and therefore potential observers. Furthermore, many contributors to ornito.it are park rangers who were allowed to carry out their normal field activities during the pandemic (E. Caprio, pers. comm.). We do not thus think there would be any effect of the fact that people could not travel far (i.e. into the mountains) in 2020 on the relative arrival dates estimated from citizen science data in the two years.

During spring migration, the tracked individuals stayed for relatively long periods at stopover sites in the Mediterranean region before making the final leg of their migration and arriving some weeks ahead of breeding (Figure 2b, 3). This finding is in line with tracking studies of the Swedish lowland population (Arlt *et al.* 2015). It has been suggested that these longer stopovers after the Sahara crossing are used to assess the environmental conditions in Europe and could therefore be used to buffer interannual variation in the timing of spring. Similar patterns were found in migratory Horned Larks (*Eremophila alpestris*) that performed long stopovers before reaching their high elevation breeding grounds (de Zwaan *et al.* 2019). In addition to a general adjustment in the arrival time, wheatears can adjust the arrival-breeding interval according to their arrival dates and spring progression (Low *et al.* 2019), strongly suggesting that, to some extent, wheatears are able to match their migration and breeding activities with local conditions and seasonally limited resources (Arlt and Pärt 2017).

While hatching success was similar between the two years, the probability that a hatchling fledged, i.e. became independent, was significantly lower in the early year of 2020, leading to a reduced reproductive output in the population (Figure 4). While this might point towards phenological asynchrony, since the differences occurred during the most resource-demanding period and the peak in

NDVI was missed by about a week, we can only speculate about the underlying mechanisms of hatchling mortality. To identify food shortages, data on chick growth and prey abundance (Barras *et al.* 2021) are necessary. However, phenological asynchronies may also have indirect effects. In our population, most nest failures were caused by predation. Increased begging behaviour due to food shortage could make nests more obvious to predators (Leech and Leonard 1997). Furthermore, due to cold snaps, predators may have higher energy demands in early spring years, leading to greater predator activity and higher nest failure rate. Potentially colder days and even cold-snaps including snow and frost during the early season are more likely to occur in earlier years. This in general could negatively affect fitness via lower adult survival (Both 2010) and reduced reproductive success (Bründl *et al.* 2020; Klueen *et al.* 2011; Moreno *et al.* 2015), even if migrants match the advanced spring conditions. We observed a generally higher variability in breeding phenology in the early spring of 2020, which was found also in McGuire *et al.* (2020), and a delayed hatching. Clutches experiencing a rainy season or severe weather events, such as snow storms, have a prolonged incubation period, exposing the nest to predators for a longer period at the same time, and generally higher failure rates (due to abandonment, hatch failure and predation) than clutches in a dry season (Higot *et al.* 2020; Klueen *et al.* 2011; Marcelino *et al.* 2020; Rauter *et al.* 2002). Further explanations for variations in breeding success in alpine birds include annual variations in temperature, where success is lower in years with lower mean temperatures (Mingozzi *et al.* 2021), but also variations in weather-dependent resources (Barras *et al.* 2021) and local predation risk (Rauter *et al.* 2002).

Here, we have shown that breeding success was reduced in wheatears breeding in the European Alps in an exceptionally early year and despite timely arrival. We expected that the timely arrival, before the conditions allow the onset of breeding, would buffer the effects of early springs. However, the adjustment via shortening the arrival-breeding interval might not be flexible enough, as birds seem

to be unable to advance egg laying sufficiently and thus may need to arrive even earlier to have the same arrival-breeding interval as in average years. The arrival-breeding interval is needed for recovering after migration, territory choice and defence, and mating (Kristensen *et al.* 2015; Nicolau *et al.* 2021). A shortening of this interval could be driving the observed lower fledging success. Arriving even earlier is limited by a trade-off between achieving good territories and matching the hatch date with the peak availability of resources on the one side, and a higher risk of potentially lowered survival for adults (Both 2010) on the other. Similar limits in timing have been found in long-distance migrant Pied Flycatchers (*Ficedula hypoleuca*), which do not seem to be able to advance arrival at breeding sites to the same extent as the advance of spring, but they lay eggs earlier (Both and Visser 2001). Nevertheless, the advance in lay dates still seems insufficient to track the advance of spring, which might be the result of the inflexibility in their migration onset, that is triggered by day length rather than temperature (Both and Visser 2001), as well as migration speed (Schmaljohann and Both 2017; Fraser *et al.* 2013). Within the same species, flexible adjustment to earlier springs seemed to be realised by shortening the arrival-breeding interval (Nicolau *et al.* 2021). McDermott and DeGroot (2017) analysed data on 17 migratory species, and found a positive relationship between earlier arrival at the breeding grounds and earlier breeding in four species, whereas in six species, the arrival-breeding interval shortened in warmer springs, as occurred in our Alpine wheatear population in 2020 (Figure 2b).

Although we cannot definitively identify the factors that drive the annual variations in breeding success, we can speculate that the reduced success in 2020 could potentially be related to environmental constraints (i.e. harsh weather conditions in early spring and cold snaps), to the mismatched peak in food resources, or to the shorter arrival-breeding interval, or a combination of these. Disentangling these effects will be an important challenge for ongoing and future long-term studies that combine phenological data, breeding performance, chick

growth and predation, as earlier reproductive seasons are expected to become more frequent in the future, and climate change effects are known to be especially severe at high latitudes and elevations.

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APPENDICES

Table S1. Sample sizes for habitat mapping and for the habitat variables grass height and snow cover. N does not correspond to the sum of sample sizes of the mapping category included, as some measurements are missing due to constraints in the field.

Year	N habitat	N territory	N nest	N grass height	N snow cover
2019	196	190	0	153	196
2020	158	189	163	337	488

Snow cover data for 2019 were derived from the habitat point survey. For grass height in 2019, we used the measurements from the territory mapping, as these represented the habitats actually used. Territory mapping and habitat point surveys were conducted in both years equally, but in 2020, we additionally mapped grass height at nest sites. Therefore, for the habitat variable grass height in 2020, we included data from both territory mapping and nest monitoring. Snow cover data in 2020 included measurements of all three habitat mapping categories (habitat point survey, territory mapping, nest monitoring), as snow cover was estimated consistently in all mappings over time.

Table S2. List of all colour ringed and tagged individuals in 2019 and 2020, with ring number (ID), tag ID, body mass, device weight and percentage of tag weight to bird's body mass.

Year	ID	body mass (g)	device weight (g)	Tag ID 2019. 2020	% of bird mass
2019	LW59553	21.3	1.1	24CO	5.2
2019	LM71002	24.9	1.1	24CP	4.4
2019	LW59555	21.8	1.0	24CQ	4.6
2019	LM81491	24.2	1.1	24CR	4.5
2019	LM81494	24	1.0	24CS	4.2
2019	LW59575	24.6	1.1	24CT	4.5
2019	LW59551	25.8	1.2	24DG	4.7
2019	LW59546	22.3	1.1	24DH	4.9
2019	LW59548	22.8	1.1	24DI	4.8

2019	LW59547	22.6	0.8	24DJ	3.5
2019	LW59549	23.7	1.0	24DK	4.2
2019	LW59545	20.7	1.0	24DL	4.8
2019	LW59544	25.3	1.1	24DY	4.3
2019	LW59550	23	1.0	24DZ	4.3
2019	LW59569	21.1	1.1	24EA	5.2
2019	LW59552	25.3	1.1	24EB	4.3
2019	LW59541	22.2	1.0	24EM	4.5
2019	LW59556	22.3	1.1	24EN	4.9
2019	LM81492	23.6	1.1	24EO	4.7
2019	LW59578	22.9	1.1	24EP	4.8
2019	LM81484	24.3	0.9	BT793	3.7
2019	LM81485	24	0.8	BT794	3.3
2019	LM81425	23	0.8	BT795	3.5
2019	LM81472	22.8	0.8	BT796	3.5
2019	LM81452	22.9	0.8	BT797	3.5
2019	LM81428	22.6	0.8	BT798	3.5
2019	LM81415	24.5	0.8	BT799	3.3
2019	LM81430	25.8	0.9	BT800	3.5
2019	LM81414	24.7	0.8	BT801	3.2
2019	LM81429	24.8	0.7	BT802	2.8
2019	LM81460	22.4	0.8	BT803	3.6
2019	LM81490	22.3	0.8	BT804	3.6
2019	LM81431	23.8	0.8	BT805	3.4
2019	LM81459	23.3	0.8	BT806	3.4
2019	LM81471	25.4	0.8	BT807	3.1
2019	LM81495	22.2	NA	control 2019	NA
2019	LM81493	22.1	NA	control 2019	NA
2019	LM71001	23.7	NA	control 2019	NA
2019	LM71003	24.4	NA	control 2019	NA
2019	LM71012	21.2	NA	control 2019	NA
2019	LM71014	21.8	NA	control 2019	NA
2019	LM71016	23.5	NA	control 2019	NA
2019	LM71032	21.3	NA	control 2019	NA
2019	LM71026	21.7	NA	control 2019	NA
2019	LM71035	22.3	NA	control 2019	NA
2019	LW59554	27	NA	control 2019	NA
2019	LM71046	22.9	NA	control 2019	NA

2019	LM71047	22.3	NA	control 2019	NA
2019	LM71013	22.5	NA	control 2019	NA
2019	LM71015	21.2	NA	control 2019	NA
2019	LM71027	22.8	NA	control 2019	NA
2020	LM71088	25.5	1.1	24SR	4.3
2020	LM71072	24.7	1.1	24ST	4.5
2020	LM71079	22.6	1.1	24SU	4.9
2020	LM71086	24.7	1.0	24SV	4.0
2020	LM71086	26	1.0	24SV	3.8
2020	LM71062	22.6	1.1	24TJ	4.9
2020	LY67271	24.6	1.1	24TK	4.5
2020	LY67213	NA	1.1	24TL	NA
2020	LY67214	22.3	1.1	24VS	4.9
2020	LM71100	22.1	1.1	24VT	5.0
2020	LM71100	22.5	1.1	24VT	4.9
2020	LY67210	23.3	1.1	24WS	4.7
2020	LY67219	20.9	1.1	24WV	5.3
2020	LY67241	23.9	1.0	24WX	4.2
2020	LM71078	24	1.2	24XS	5.0
2020	LY67215	30.2	1.1	24XW	3.6
2020	LY67230	24.8	0.8	BX620	3.2
2020	LM71011	22.3	0.7	BX621	3.1
2020	LY67268	22.2	0.7	BX622	3.2
2020	LY67287	25.6	0.7	BX623	2.7
2020	LY67272	24.5	0.7	BX624	2.9
2020	LY67276	24.7	0.8	BX625	3.2
2020	LY67275	22.6	0.6	BX626	2.7
2020	LY67273	24.1	0.7	BX627	2.9
2020	LY67277	24.3	0.8	BX628	3.3
2020	LY67231	21.3	0.8	BX629	3.8
2020	LY67270	22.3	0.7	BX630	3.1
2020	LY67266	19.8	0.7	BX631	3.5
2020	LY67288	25.8	0.8	BX632	3.1
2020	LY67267	23.8	0.7	BX633	2.9
2020	LY67269	21.9	0.7	BX634	3.2
2020	LY67225	20.8	0.7	BX635	3.4
2020	LM71054	25.6	0.8	BY646	3.1
2020	LM71061	25.1	0.8	BY647	3.2

2020	LM71087	23.3	0.8	BY649	3.4
2020	LY67240	21.5	0.8	BY650	3.7
2020	LM71023	28.1	0.8	BY651	2.8
2020	LM71025	22.9	0.8	BY653	3.5
2020	LW59481	24.3	0.7	BY655	2.9
2020	LM71058	22.1	0.7	BY657	3.2
2020	LM71024	28.7	0.8	BY658	2.8
2020	LM71052	24	0.8	BY660	3.3
2020	LW59555	22	1.1	collected 24CQ. tagged 24VZ	5.0
2020	LW59547	24	0.7	collected 24DJ. tagged BY654	2.9
2020	LW59549	23.9	1.1	collected 24DK. control 2020	4.6
2020	LW59569	23.7	0.8	collected 24EA. tagged BY656	3.4
2020	LW59578	23.4	1.1	collected 24EP	4.7
2020	LM81425	22.8	1	collected BT795. tagged 24WS	4.4
2020	LM81472	20.9	0.8	collected BT796. control 2020	3.8
2020	LM81430	25.2	0.8	collected BT800. tagged BY6559	3.2
2020	LM81414	24.9	1.1	collected BT801. tagged 24TJ	4.4
2020	LM81490	24.9	0.8	collected BT804. control 2020	3.2
2020	LM81431	32	0.8	collected BT805. tagged BY648	2.5
2020	LM81431	27.3	0.8	collected BT805. tagged BY648	2.9
2020	LM71001	24.6	1.0	control 2019. tagged 24WT	4.1
2020	LM81493	NA	1.1	control 2019. tagged 24SS	NA
2020	LY67245	22.6	NA	control 2020	NA
2020	LY67328	24.9	NA	control 2020	NA
2020	LY67242	22.8	NA	control 2020	NA
2020	LY67274	21.9	NA	control 2020	NA
2020	LM81494	22.7	NA	lost 24CS. control 2020	NA
2020	LM81452	27.2	0.8	lost BT797. tagged BY652	2.9

Table S3. Dates (Start, End) and durations (Days) at breeding site (State 0), autumn stopover (State 1), spring stopover (State 3), and wintering sites (State 2), derived from geolocation for all nine tagged birds, retrieved in 2020.

Bird	Start	End	Days	Site	State
24EA	2019-07-21 19:44:00	2019-09-13 18:24:00	54	1	0
24EA	2019-09-18 18:09:00	2019-09-19 05:05:00	0	2	1
24EA	2019-09-21 05:10:00	2019-10-16 05:20:00	25	3	1
24EA	2019-10-17 05:30:00	2019-10-18 05:25:00	1	4	1
24EA	2019-10-23 05:35:00	2019-10-26 05:45:00	3	5	2
24EA	2019-10-27 05:30:00	2019-10-29 05:30:00	2	6	2
24DK	2019-07-21 19:44:00	2019-09-05 04:30:00	45	1	0
24DK	2019-09-08 04:45:00	2019-09-09 04:50:00	1	2	1
24DK	2019-09-10 04:50:00	2019-09-16 04:55:00	6	3	1
24EP	2019-07-21 19:34:00	2019-08-30 18:24:00	40	1	0
24EP	2019-08-31 18:19:00	2019-09-02 18:19:00	2	2	1
24EP	2019-09-03 18:24:00	2019-09-11 04:55:00	7	3	1
24EP	2019-09-12 04:50:00	2019-09-12 17:53:00	1	4	1
24EP	2019-09-16 04:55:00	2019-10-02 05:00:00	16	5	1
24EP	2019-10-06 05:10:00	2019-10-08 05:10:00	2	6	1
BT795	2019-08-17 19:07:22	2019-09-07 18:22:25	21	1	0
BT795	2019-09-10 04:33:16	2019-09-13 04:37:21	3	2	1
BT795	2019-09-14 18:02:26	2019-09-18 17:52:42	4	3	1
BT795	2019-09-22 05:06:38	2019-10-01 05:01:28	9	4	1
BT795	2019-10-04 18:11:12	2019-10-10 05:39:10	5	5	1
BT795	2019-10-13 05:54:10	2020-04-08 18:56:34	179	6	2
BT795	2020-04-15 04:37:46	2020-04-24 04:27:49	9	7	3
BT795	2020-04-26 18:49:16	2020-05-20 03:21:36	23	8	0
BT796	2019-09-01 18:31:20	2019-09-04 18:29:21	3	1	0
BT796	2019-09-06 04:32:47	2019-09-13 18:09:05	8	2	0
BT796	2019-09-15 04:41:22	2019-09-17 04:48:33	2	3	0
BT796	2019-09-21 05:12:40	2019-10-05 05:04:28	14	4	1
BT796	2019-10-08 05:27:36	2019-10-13 05:28:41	5	5	1
BT796	2019-10-14 17:51:35	2020-03-08 18:25:03	146	6	2
BT796	2020-03-10 05:47:39	2020-03-14 18:14:33	5	7	3
BT796	2020-03-16 05:45:22	2020-04-07 18:27:32	23	8	3
BT796	2020-04-09 18:25:14	2020-04-19 18:23:26	10	9	3

BT796	2020-04-22 18:39:23	2020-04-26 04:42:20	3	10	3
BT796	2020-05-06 19:07:42	2020-05-25 03:19:29	18	11	0
BT800	2019-08-26 18:41:19	2019-09-08 04:42:21	12	1	0
BT800	2019-09-09 18:02:40	2019-09-21 05:02:31	11	2	1
BT800	2019-09-22 17:58:27	2019-10-07 17:56:33	15	3	1
BT800	2019-10-11 06:03:15	2019-10-22 06:22:41	11	4	1
BT800	2019-10-23 18:13:47	2019-12-22 06:33:38	60	5	2
BT800	2019-12-23 18:33:30	2020-01-03 18:12:01	11	6	2
BT800	2020-01-05 07:01:13	2020-03-21 19:08:16	77	7	2
BT800	2020-03-25 05:04:08	2020-04-04 04:58:29	10	8	3
BT800	2020-04-05 18:14:03	2020-04-22 18:38:27	17	9	3
BT800	2020-04-24 03:57:53	2020-05-20 03:22:22	26	10	0
BT801	2019-08-24 18:46:23	2019-09-12 18:17:21	19	1	0
BT801	2019-09-14 04:43:13	2019-10-16 17:31:45	33	2	1
BT801	2019-10-18 05:16:43	2019-12-16 05:35:07	59	3	2
BT801	2019-12-17 17:43:01	2020-04-02 18:22:54	107	4	2
BT801	2020-04-06 18:02:56	2020-04-10 04:35:04	3	5	3
BT801	2020-04-12 04:48:50	2020-04-16 18:33:00	5	6	3
BT801	2020-04-19 18:39:47	2020-04-20 18:31:34	1	7	3
BT801	2020-04-24 03:59:44	2020-05-02 03:59:47	8	8	0
BT801	2020-05-04 03:44:32	2020-05-16 03:23:28	12	9	0
BT804	2019-08-26 18:46:19	2019-09-04 18:31:21	9	1	0
BT804	2019-09-06 04:41:19	2019-09-23 04:54:25	17	2	1
BT804	2019-09-24 17:52:18	2019-10-09 05:14:30	14	3	1
BT804	2019-10-11 05:11:49	2019-10-16 05:29:32	5	4	1
BT804	2019-10-19 05:47:47	2019-12-02 18:06:51	45	5	2
BT804	2019-12-05 06:28:32	2019-12-24 18:29:39	20	6	2
BT804	2019-12-26 18:36:59	2020-03-14 06:15:21	78	7	2
BT804	2020-03-15 19:02:25	2020-04-17 19:08:26	33	8	2
BT804	2020-04-21 04:19:44	2020-05-04 18:45:22	14	9	3
BT804	2020-05-08 19:09:26	2020-05-29 03:12:46	20	10	0
BT805	2019-08-22 04:26:02	2019-08-25 18:47:04	4	1	0
BT805	2019-08-27 04:28:22	2019-09-09 17:57:34	14	2	0
BT805	2019-09-11 04:37:30	2019-10-02 17:22:40	22	3	1
BT805	2019-10-07 17:49:25	2019-11-08 05:09:30	31	4	2
BT805	2019-11-09 17:27:24	2020-04-10 05:10:10	152	5	2
BT805	2020-04-11 18:05:40	2020-04-12 18:09:22	1	6	3
BT805	2020-04-14 04:43:18	2020-04-29 04:18:43	15	7	3

BT805	2020-04-30 18:42:18	2020-05-04 04:05:16	3	8	3
BT805	2020-05-07 03:44:01	2020-05-10 19:10:41	4	9	0
BT805	2020-05-12 03:38:13	2020-05-24 03:19:05	12	10	0

Table S4. Estimates of breeding phenology parameters. Average durations were from nests monitored in 2019, where exact lay, hatch and fledge dates were known. Average clutch size was derived from nests of 2019 and 2020.

No. of days building (n = 18)	No. of days incubating (n = 7)	No. of days feeding (n = 35)	Clutch size (n = 58)
4	13	15	5

We defined the different periods of building, laying, breeding and feeding as follows:

Duration of building: 1st day of transporting material to nest hole – laying of first egg

Duration of laying: laying of 1st egg – laying of last egg

Duration of incubation: day of laying the last egg – day before hatching

Duration of feeding: day of hatching – day of fledging

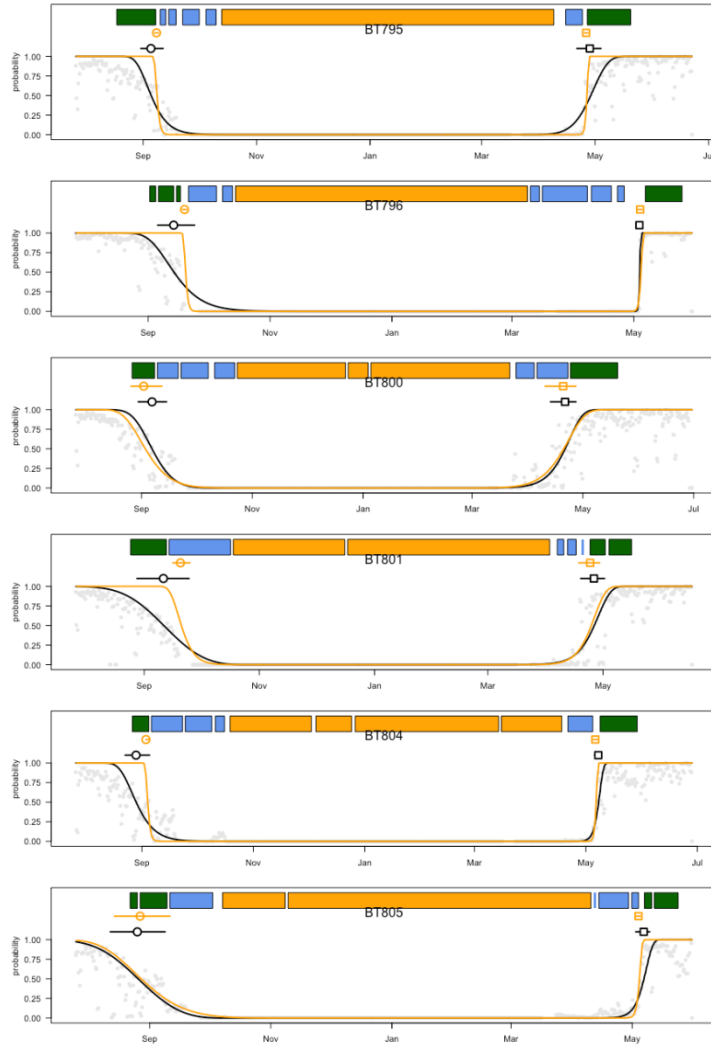


Figure S1a. Probabilities of the presence of six tagged individuals in the breeding range estimated by three approaches. “geolocation”: Green bars represent the duration spent at the breeding location (state 0), blue are durations at stopovers (state 1 and 3), and orange at wintering locations (state 2) (dates and durations provided in Table S3). “sensitivity analysis”: black lines and boxplots. “shadow”: orange lines and boxplots (circle = departure date, square = arrival date, values provided in Table S5).

Table S5. Arrival dates estimated by the methods “geolocation”, “sensitivity analysis” and “shadow”. For analysis, dates of method “shadow” were used (grey shaded).

ID	Depart ure geoloca tion	Depart ure prob. 0.2 sensitiv ity	Depart ure prob. 0.5 sensitiv ity	Depart ure prob. 0.8 sensitiv ity	Depart ure prob. 0.2 shadow	Depart ure prob. 0.5 shadow	Depart ure prob. 0.8 shadow	Arrival prob. 0.2 sensitiv ity	Arrival prob. 0.5 sensitiv ity	Arrival prob. 0.8 sensitiv ity	Arrival prob. 0.2 shadow	Arrival prob. 0.5 shadow	Arrival prob. 0.8 shadow	Arrival geoloca tion
BT795	2019-09-08	2019-08-28	2019-09-04	2019-09-15	2019-09-06	2019-09-07	2019-09-08	2020-05-07	2020-04-28	2020-04-16	2020-04-29	2020-04-28	2020-04-26	2020-04-26
BT796	2019-09-21	2019-09-01	2019-09-13	2019-09-30	2019-09-19	2019-09-20	2019-09-22	2020-05-04	2020-05-03	2020-05-03	2020-05-05	2020-05-04	2020-05-03	2020-05-06
BT800	2019-09-09	2019-08-25	2019-09-05	2019-09-18	2019-08-31	2019-09-08	2019-09-21	2020-04-30	2020-04-21	2020-04-08	2020-04-14	2020-04-13	2020-04-12	2020-04-24
BT801	2019-09-13	2019-08-19	2019-09-08	2019-09-28	2019-09-06	2019-09-09	2019-09-14	2020-05-02	2020-04-25	2020-04-14	2020-04-28	2020-04-22	2020-04-13	2020-04-24
BT804	2019-09-06	2019-08-18	2019-08-27	2019-09-09	2019-09-02	2019-09-03	2019-09-04	2020-05-10	2020-05-07	2020-05-04	2020-05-07	2020-05-06	2020-05-04	2020-05-08
BT805	2019-09-10	2019-08-04	2019-08-24	2019-09-14	2019-09-06	2019-09-07	2019-09-09	2020-05-10	2020-05-06	2020-04-29	2020-05-03	2020-05-02	2020-05-01	2020-05-05
24EA	2019-09-14	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
24DK	2019-09-05	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
24EP	2019-08-31	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

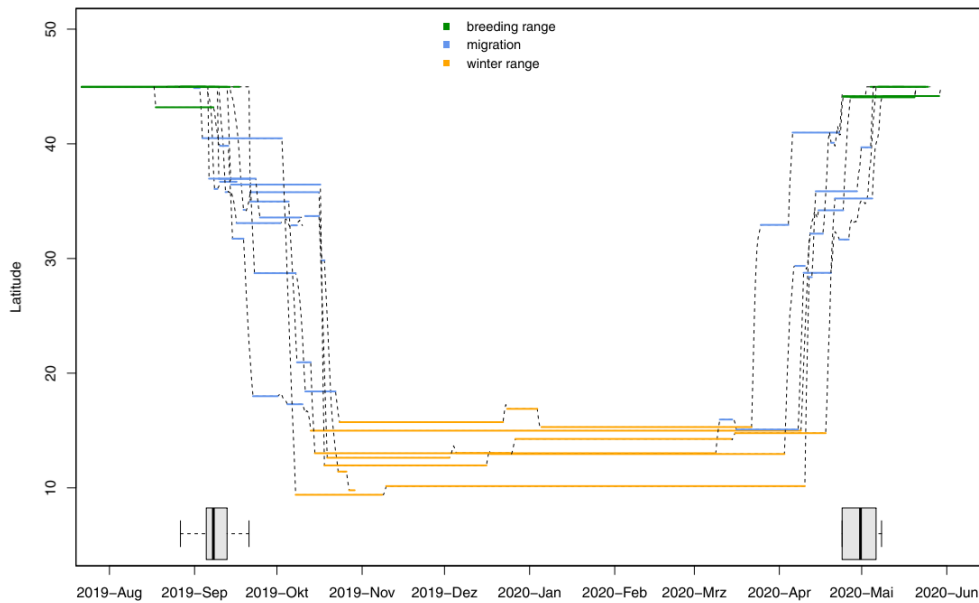


Figure S1b. Organisation of the annual cycle in Alpine breeding Northern Wheatears. Positions of the 9 tagged individuals (Latitude) with date; shown as coloured line with breeding range (green), stopover (blue) and winter range (orange). Dashed lines represent movements between sites. Sample sizes differ throughout the year as 3 tags stopped recording before arriving at the breeding grounds the following year (see Table S3, S5). Departure and arrival dates at breeding site from geolocation (method “shadow”) from 6 individuals (boxplots).

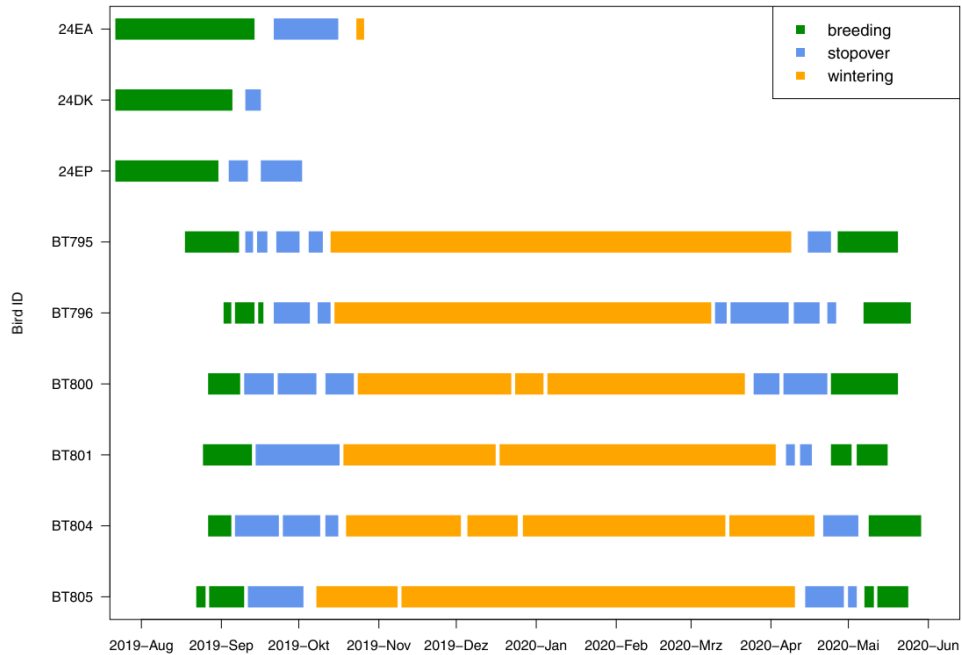


Figure S1c. Organisation of the annual cycle for 9 Alpine breeding Northern Wheatears. Duration of stay in breeding range (green), at stopover sites (blue) and in wintering range (orange). 6 Tags recorded light levels from departure from breeding grounds in autumn until arrival at breeding grounds in spring. 1 Tag recorded only until the bird reached the wintering range (24EA). 2 Tags stopped recording during the first (24DK) and second (24EP) stopover. Values provided in Table S3.

Table S6. Phenology dates (day of year) for the tagged individuals. Arrival date (AD), lay date (LD), and hatch date (HD) for both years.

Bird	AD 2019 (doy)	LD 2019 (doy)	HD 2019 (doy)	AD 2020 (doy)	LD 2020 (doy)	HD 2020 (doy)
24EA♀	-	13.06.2019 (163)	30.06.2019 (180)	-	27.05.2020 (147)	Nest abandoned
24DK♂	-	29.05.2019 (148)	16.06.2019 (166)	-	-	-
24EP♂	-	13.06.2019 (163)	30.06.2019 (180)	-	27.05.2020 (147)	Nest abandoned
BT795♂	-	27.05.2020 (146)	24.06.2019 (174)	28.04.2020 (118)	27.05.2020 (147)	13.06.2020 (164)
BT796♀	-	06.06.2019 (156)	25.06.2019 (175)	04.05.2020 (124)	-	-
BT800♂	-	04.06.2019 (154)	21.06.2019 (171)	13.04.2020 (103)	24.05.2020 (144)	Nest abandoned
BT801♂	-	05.06.2019 (155)	22.06.2019 (172)	22.04.2020 (112)	26.05.2020 (146)	12.06.2020 (163)
BT804♀	-	06.06.2019 (156)	23.06.2019 (173)	06.05.2020 (126)	-	-
BT805♀	-	04.06.2019 (154)	21.06.2019 (171)	02.05.2020 (122)	24.05.2020 (144)	Nest abandoned

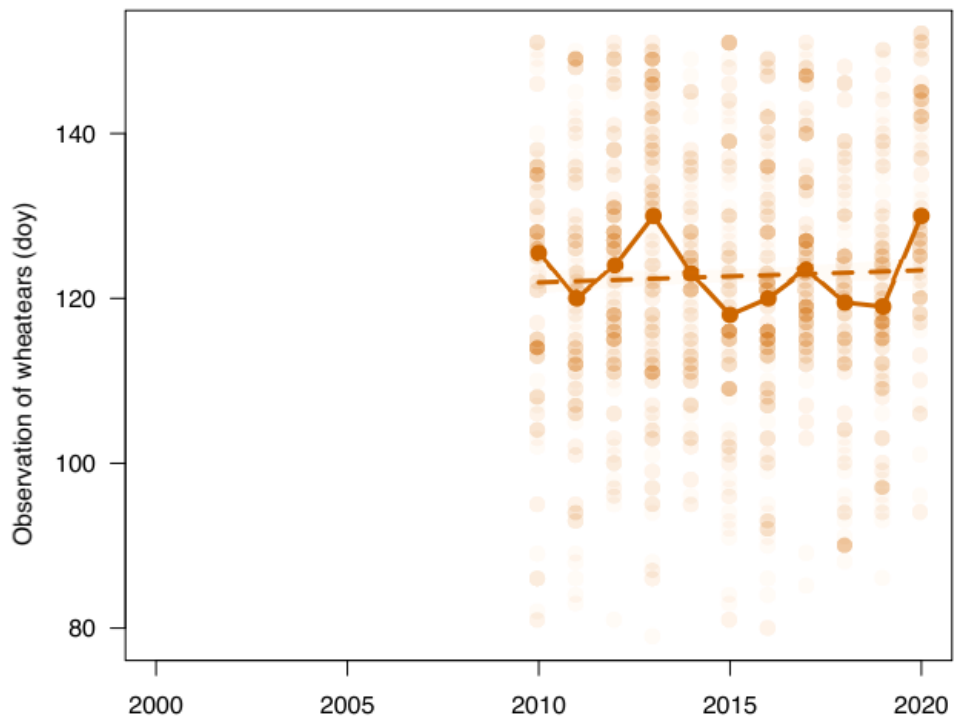


Figure S2. Median day of year (doy) of observations of wheatears for every year from 2010-2020 (dots, ornitho.it). Raw data is shown as transparent dots. The dashed line is the linear regression of $\text{doy} \sim \text{year}$. The trend is not significant (DF = 1732, $P = 0.21$, $R^2 = 0.0003$).

Table S7. Effect of year (2019/2020) and period (hatching (“period h”) and fledging) on success (GLMM). The sample size (N = 681) derives from total no. of eggs (for period hatching) and hatchlings (for period fledging) (see also table S5b). The year effect on the nest success (at the nest level, N = 127) was modelled using a GLM. Estimates were significant if bold: $P < 0.0001$, or * $P = 0.05$, and if 95 % credible intervals (Crl) of the model outputs did not include zero. Success rates for each combination (year*period) were derived from model estimates back-transformed with function *plogis* (R package stats).

	Intercept (Crl)	Year 2020 (Crl)	Period h (Crl)	N	DF Residuals	Null Dev	Random effect (nest id)	P (year)
Success ~ year + period + (1 nest id)	2.830 (1.708 – 3.843)	-1.441* (-2.870 – -0.018)	2.38 (1.754 – 2.996)	681	679	438.7	70	0.05
	2019*hatching	2020*hatching	2019*fledging	2020*fledging				
Success rate	0.99 (0.98 – 1.00)	0.98 (0.93 – 0.99)	0.94 (0.85 – 0.98)	0.80 (0.59 – 0.92)				
	Intercept (Crl)	Year 2020 (Crl)		N	Res Dev	Null Dev		P (year)
Nest success ~ year	0.649 (0.540 – 0.762)	-0.139 (- 0.314 – 0.040)		127	30.1	30.7		0.12
	2019	2020						
Success rate	0.65 (0.54 – 0.76)	0.51 (0.38 – 0.64)						

CHAPTER VI

Reproductive trade-offs for early breeders at high elevations in a long-distance migrant, the Northern Wheatear *Oenanthe oenanthe*

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ABSTRACT

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 annually variable spring conditions at the breeding sites in order to maximize nest survival probabilities and reproductive output. We analysed nest survival and nestling mass in relation to lay date and within-season habitat conditions in an Alpine population of the migratory Northern Wheatear *Oenanthe oenanthe* collected over six consecutive breeding seasons in the Italian Western Alps. This open grassland species showed the lowest nest survival 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 nest survival might be limited indirectly by severe weather conditions in the early season, leading to higher nest failure rates through higher predation risk. On the contrary, 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 in the early season. This trade-off may thus allow the Wheatear to maximize fitness under highly variable 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.

Running head: Trade-off in migratory alpine songbirds

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

INTRODUCTION

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 (Kristensen *et al.* 2015; Martin and Wiebe 2004). Additionally, the timing of spring progression shows a very high variability between years, and alpine animals need to adapt to annual changes in plant phenology and weather conditions (Martin and Wiebe 2004). Across the globe and across taxonomic groups, global warming results in the advancement of spring conditions (Thackeray *et al.* 2016), resulting in earlier snowmelt and green-up dates (Parmesan and Yohe 2003). 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 and Saracco 2021). Thus, understanding the drivers and consequences of global warming for species inhabiting these fragile habitats is crucial for effective conservation (Boyle and Martin 2015; Chamberlain *et al.* 2013; Lehikoinen *et al.* 2018).

Birds have different strategies to adapt to environmental cues by adjusting lay date, delaying the start of incubation once eggs have been laid, adjusting clutch size or the interval inbetween laying of eggs, or by adjusting the incubation time itself via nest attentiveness by the female (Higgot *et al.* 2020). There is typically a trade-off between early or late breeding. Generally, individuals breeding early in the season have a higher fitness by matching the time of chick rearing with the food peak (Both 2010; Perrins 1970). Nevertheless, choosing the right timing for laying, which needs to be done well in advance of the hatching event and the estimated food peak, is not trivial: Nest failure can be caused directly by environmental constraints, such as late snowfall, higher precipitation, low

temperatures and more variable weather (Martin *et al.* 2017). In addition, females could be prevented from laying due to low food abundance when their own survival is at risk (Both 2010; MacDonald *et al.* 2013; Perrins 1970). Breeding too early at high elevations, where breeding conditions are particularly challenging, may therefore have severe consequences for the reproductive output of the individual (MacDonald *et al.* 2016). Despite these direct environmental factors limiting breeding success, predation is assumed to be the most common cause for nest failure in songbirds (Martin 1995; Martin and Briskie 2009), and for alpine and ground nesting birds like 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), as a delay in hatching exposes nests to predators for longer, and/or the higher demand for food increases begging behavior (Leech and Leonard 1997), the number of nest visits by the adult and/or longer food search times (Rauter and Reyer 1997), thus increasing the likelihood of detection by a predator. Furthermore, indirect variation in predation risk across the season might occur when alternative prey species, such as voles, become active above ground and more abundant in summer compared to the spring (Hille and Rödel 2014; Yoccoz *et al.* 1998).

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 (Bründl *et al.* 2020; Fossøy *et al.* 2015, Hoover and Schelsky 2020; Klueen *et al.* 2011; Nicolau *et al.* 2021; Shipley *et al.* 2020). 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 (Amélineau *et al.* 2021; Lamarre *et al.* 2021; Low *et al.* 2019; Sander *et al.* 2021). In some long-distance migrant songbirds, the timing of breeding

events shows a high flexibility (Le Vaillant *et al.* 2021), lay dates being adapted by adjusting the arrival-laying interval, which 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 likely possible to estimate environmental conditions (de Zwaan *et al.* 2019), or to even periodically visit the breeding habitat and temporarily defend territories (Barras *et al.* 2021a).

In the Nearctic, global warming and extreme weather events have been found to affect the phenology and reproductive success of migratory species breeding at high elevations that showed later lay dates in colder springs or following cold snaps, but that generally had higher reproductive success when breeding early (de Zwaan *et al.* 2021, 2020, 2019; Martin *et al.* 2017, 2009). Comparable studies investigating these effects on Palaearctic long-distance migrants are lacking. 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 an open grassland species that breeds mostly above the treeline in Southern Europe, migrating c. 3500 km to its wintering grounds in sub-Saharan Africa (Bairlein *et al.* 2012; Conder 1989; Sander *et al.* 2021). This represents a system that is threatened in two ways: species of open grassland habitats are especially vulnerable to global warming (Bani *et al.* 2019; Chamberlain *et al.* 2013; Ferrarini *et al.* 2017; Scridel *et al.* 2018); and, long-distance migrants are showing the strongest population declines among all bird species (Kirby *et al.* 2008; Sanderson *et al.* 2006; Vickery *et al.* 2014), for which phenological mismatch is likely to be a key driver (Both *et al.* 2010; Saino *et al.* 2011). We collected nest and habitat data over six consecutive breeding seasons in high elevation open grassland. It is crucial to assess both nest survival and raising fledglings to

independence (related to nestling mass) when studying breeding productivity, as overall breeding success and thus population productivity cannot be estimated by only one of these parameters (Streby *et al.* 2014).

In the present study, we assessed whether nest survival and nestling mass were related to an early or late start of breeding, and if there was a relationship with local environmental conditions, in particular those related to snowmelt and spring green-up. 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 alpine open grassland species in our study area, nesting in rock crevices or holes covered by dwarf shrubs (*Juniperus nana*, *Rhododendron ferrugineum*, henceforth juniper and rhododendron) and soil, and usually (98%, $n = 97$) has only one brood per season with on average 5 eggs ($n = 108$). Its presence at the high elevation breeding grounds (most commonly from 1900 to 2800 m.a.s.l., on south-eastern slopes) is restricted to the snow-free period, and spans from mid-late May (arrival) to the beginning of September (post-breeding moult).

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 m a.s.l. to 2700 m a.s.l.. The landscape structure of the valley is characterised 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 a.s.l., followed by grassland interspersed with rocky areas above the treeline. Across all

elevations, grazing cows influence the distribution and availability of potential open grassland habitat (but see former studies carried out in the same area; Jähnig *et al.* 2020, 2018; Masoero *et al.* 2016; Sander *et al.* 2021).

Nest monitoring and nestling ringing

We monitored nests that were found throughout the whole breeding season. Nests were mostly found by observing males showing territorial and mating behavior in likely breeding habitat, females building or returning to the nest for incubation, or feeding adults. We knew very few female and male identities for the replacement broods or second attempts, and therefore we could not account for adult identity in our 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 failures (Sander *et al.* 2021). We estimated lay and hatch dates from nestling age (Low *et al.* 2019) and known mean duration of incubation within our population, if not observed directly (see for details 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 age of 6 to 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). We assume 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. Magrath 1991; Streby *et al.* 2014; Tinbergen and Boerlijst 1990).

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 by using the method described in Sander *et al.* (2021): Higher-resolution snow free dates for the actual nest sites in the study area from 2016 to 2021 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). We first selected all images taken in the years 2016 to 2021 (Google Earth Engine Server) intersecting at least one of the nest sites. We masked cloud pixels using the Sentinel-2 Cloud Probability layer with a probability threshold of 60. The normalised differenced snow index (NDSI, Band 8 & 4) and the normalised 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, we fitted a smooth line (loess fit with span = 0.2 from the R package stats) to the NDVI and NDSI values over the day of the year, and extracted the day when the line fell below 0.1 NDSI (snowmelt) and exceeded 80% of the NDVI annual amplitude (green-up). 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 addition to the remote sensing data of the environment, temporally variable habitat features, 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 for details in Sander *et al.* 2021). Habitat measurements that were closest to the individual point of 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 height 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 five minutes 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 2020). As we aimed to understand ecological relationships, we used the confirmatory modeling approach, i.e. model selection was based on predictive model checking (and comparing 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, we used the Bayesian approach by using improper prior distributions, namely $p(\beta) \propto 1$ for the coefficients, and $p(\sigma) \propto \frac{1}{\sigma}$ for the variance parameters. 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 and Hill 2007)).

Breeding success was expressed as nest survival probability, and was quantified by using daily failure rates (DFR, Mayfield 1975) estimated from general linear mixed models (Aebischer 1999). We built a binary response variable for DFR with the number of exposure days (no. of days from the date a nest was found until the date it failed, which is the median between the last visit and the penultimate visit), subtracting 1 for nest failures, as the denominator, and nest failure or success (respectively 1 or 0) as the numerator. Under this method, DFRs were corrected for the variable duration of monitoring of individual nests. Total nest survival probability was then calculated for each year by $1-(DFR \wedge 32 \text{ days})$, as in our population the combined laying, incubation and nestling periods span about 32 days (Sander *et al.* 2021).

DFR was analysed in relation to environmental and phenological factors. The explanatory variables considered 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 (that varied between the years of study), we performed different models for the study periods 2016-2021, 2019-2021, 2020-2021 and 2019 (see Table 1), seeking for the inclusion of as many of the above mentioned variables as possible. When sample size did not allow the inclusion of all variables, we tested the effects on DFR in univariate models beforehand and included only those with significant effects. The possibility of including the random term year (at least three levels) dictated whether we used binomial mixed models or binomial models.

Table 1. Availability of phenological and environmental data throughout the study period 2016 to 2021 (grey), and sample sizes (representing the no. of nests for which the type of data was recorded).

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

For the study period 2016 to 2021, we modeled DFR 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. We included the random term year (6 levels) to account for between-year variation in overall nest survival not captured by the fixed effects. We additionally tested for the effect of the difference between snowmelt (for the respective year) and lay date (for each nest) and between green-up and hatch date in univariate binomial models (function *glm* (logit link)), as there was collinearity when these variables were included in the full model.

In the years 2019 to 2021, grass cover was also recorded and included in the models for this subset. Here, we fitted a binomial mixed model, 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 random term (3 levels). In 2020 and 2021, we additionally recorded grass height at lay date (scaled), and included this habitat feature in a binomial model, but without including year as a random term (only two levels). Due to constraints in the field or nest failure prior to the nestling period, in many cases we did not have sufficient data to include all variables. Therefore, we decided to exclude grass cover and lay date from the analysis of the two-years subsample to understand whether grass height had an effect on nest survival. To control for the previously identified differences along the elevational gradient and between years, we kept these two variables. In 2019, we used temperature data loggers 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 higher when including the whole nest period, results are shown only for the whole nest period. As a former study on our population (Sander *et al.* 2021) highlighted 2020 as an exceptional year in terms of spring phenology and breeding success, we checked the influence of this year 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.

Nestling mass was modeled with linear models, using the function *lm*, due to the normal distribution of the response variable, and explanatory variables were included according to data availability for the different year subsets (Table 1). First, we checked for differences between years by modeling nestling mass in a separate

linear model including age and year as fixed effects. For the study period 2016 to 2021, nestling mass (scaled due to the size dependence of body mass) was modeled by fitting linear models with lay date (scaled within years), elevation (scaled), age of nestlings (in days, as quadratic and linear term) and number of nestlings (per nest) as explanatory variables. Model selection was performed by comparing AICs of models with different combinations of these variables. For the data collected in the years 2019 to 2021, we included grass cover in the models, for the data of 2020 and 2021 we included grass height, and for data of 2019 we included mean day and night temperatures. Due to the low sample size of 30 nests (Table 1), we excluded all other variables except age in this data set. We additionally modeled the relationship between hatch date (doy, response variable) and these temperatures (explanatory variables) in linear models.

RESULTS

Spring phenology and nest survival probabilities

We found a high variability in nest survival probability across years (ranging from 23 to 53 %) which might be driven by the between-year variability in snowmelt (ranging from 25th April in 2016 to 9th June in 2018) and green-up (Fig. 1 A). Although there were only six 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 about one month earlier than in 2018). In early 2020, lay dates in our population were advanced by one week, compared to the latest year 2018, and were highly variable (Fig. 1 B, median: 30th May, 1st quartile: 25th May, 3rd quartile: 26th June). We observed the highest survival in 2018 when lay date (median: 6th June, 1st quartile: 2nd June, 3rd quartile: 13th June) co-occurred with snowmelt, and hatch dates (median: 22th June) were before the peak in vegetation (green-up: 19th July). This pattern was found also in 2017 and 2019 (Fig. 1 A, B). On the contrary, we observed the lowest nest survival in the early years 2016, 2020 and 2021 when snowmelt was well before the lay

dates (Fig. 1 A). Across the study period of six years, median lay dates did not vary as much as snowmelt and green-up (Fig. 1 B).

There were 93 failed nests between 2016 and 2021, of which the cause of failure was determined in 88 nests: 6 failed during building (6 %), 33 during laying and incubation (38%) and 46 (52%) in the nestling period. 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. 2).

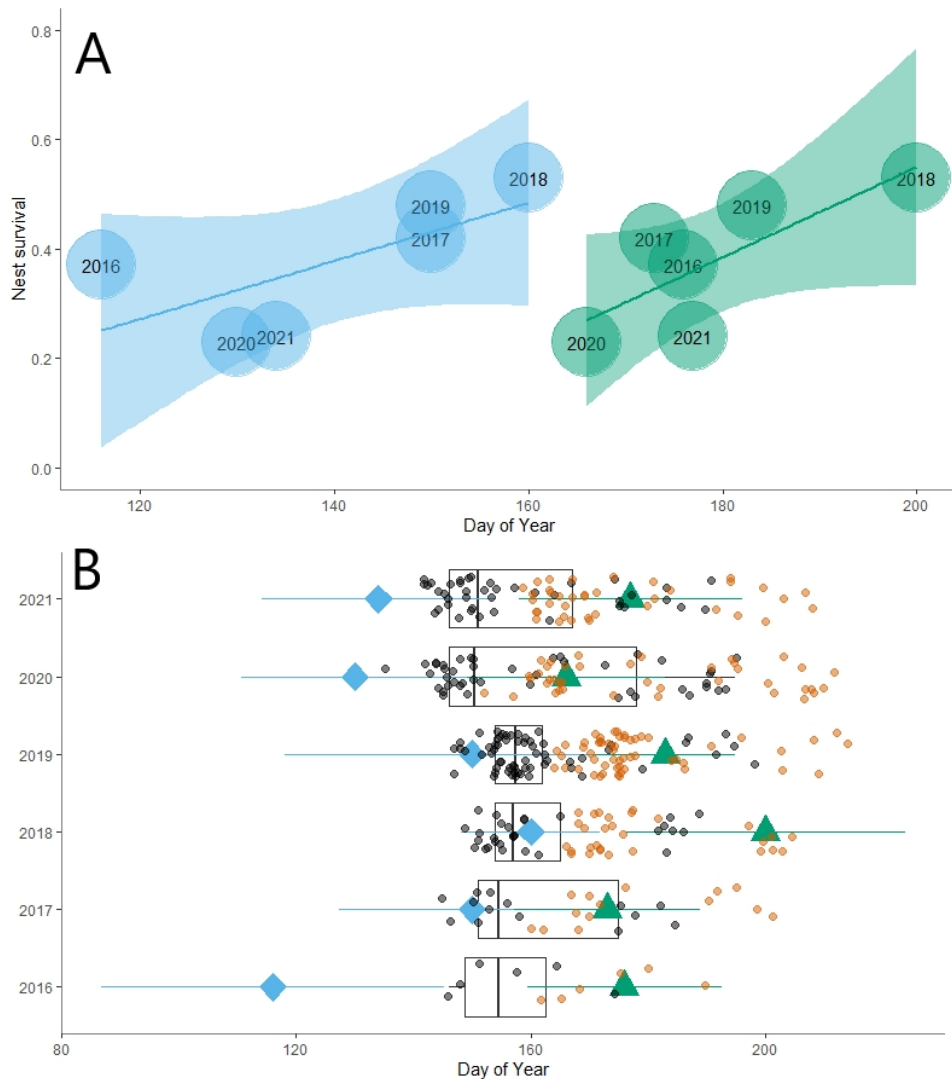


Figure 1. A) Relation between nest survival probabilities and median snowmelt (blue, $\beta=0.005 \pm 0.003$, $P=0.12$, $R^2=0.4$) and green-up (green, $\beta=0.008 \pm 0.003$, $P=0.07$, $R^2=0.5$) for each year ($N = 6$). Linear regressions and confidence intervals drawn with the function *geom_smooth (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.

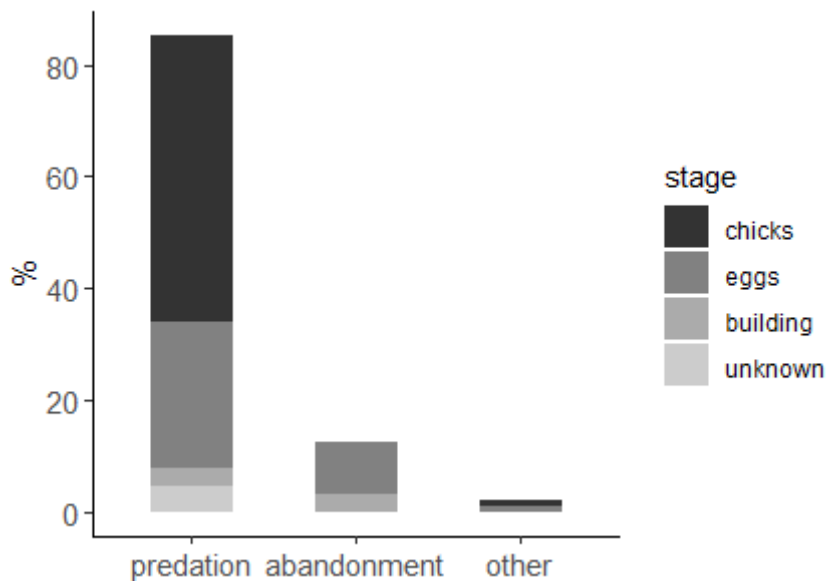


Figure 2. Failure cause and stage at failure for all failed nests ($N = 88$) monitored during 2016 to 2021.

Daily failure rate

Lay and hatch dates were correlated, so we selected lay date as the measure for breeding phenology in all models. There was no evidence of collinearity (using function *vif*, variance inflation factor) in any model for DFR and nestling mass. We therefore included breeding parameters as well as habitat parameters in all analyses. 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 we did not include any interactions in the selected models, although it should be noted that hatch dates were later at high elevations (Fig. S1). Furthermore, the difference between snowmelt and lay date did not have any effect on DFR or 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. We therefore did not include this variable 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 relatively earlier in the season) and an increase in DFR with elevation. The effect sizes for both variables were similar (Fig. 3 A-B, Table 2). In the reduced data sets from years when grass cover and/or grass height was recorded (Table 1, 2), there was a significant negative relationship between DFR and grass cover (Fig. 3 C, Table 2), and between DFR and grass height (Fig. 3 D, 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 random term (although we acknowledge that caution is needed in interpreting mixed models with relatively few levels for a given random factor; Harrison *et al.* 2018). It should be also noted that in Figure 3 D the y-axis is scaled differently due to the subset of 2020-2021 that had higher DFR than in all other years (see also Fig. 1 A). Models including mean temperature at the specific nest location during incubation (2019) did not show any effect of day ($\beta_{\text{day}} = -0.020 \pm 0.124$, $P_{\text{day}} = 0.87$) or night temperature ($\beta_{\text{night}} = -0.006 \pm 0.159$, $P_{\text{night}} = 0.97$) on DFR, either in univariate or in combined models.

Table 2. Effects of lay date (scaled within year) and habitat variables (scaled) on nest survival (daily failure probability). For the study period 2016-2021 and 2019-2021 we used GLMM, and 2020-2021 GLM. The degrees of freedom (Df) differ between models due to data availability (see Table 1). Estimates were significant if bold: $P < 0.05$, and if 95 % credible intervals (CrI) of the model estimates did not include zero. Null deviance and residual deviance on Df respectively is shown.

Selected models for nest survival	estimates (95 % CrI)	Df	P
2016-2021			
Intercept	-3.689 (-4.024 - -3.360)	191	<0.001
Lay date	-0.391 (-0.695 - -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- -3.466)	123	<0.001
Lay date	-0.223 (-0.648 - 0.216)		0.298
Elevation	0.266 (-0.098 - 0.619)		0.140
Grass cover at hatch date	-0.436 (-0.864 - -0.016)		0.042
Year (random effect, 3 levels)	variance: 0.193, sd: 0.439		
2020-2021			
Intercept	-3.088 (-3.489 - -2.661)	40	<0.001
Elevation	0.292 (0.012 - 0.580)		0.041
Grass height at lay date	-0.611 (-1.076 - -0.132)		0.009

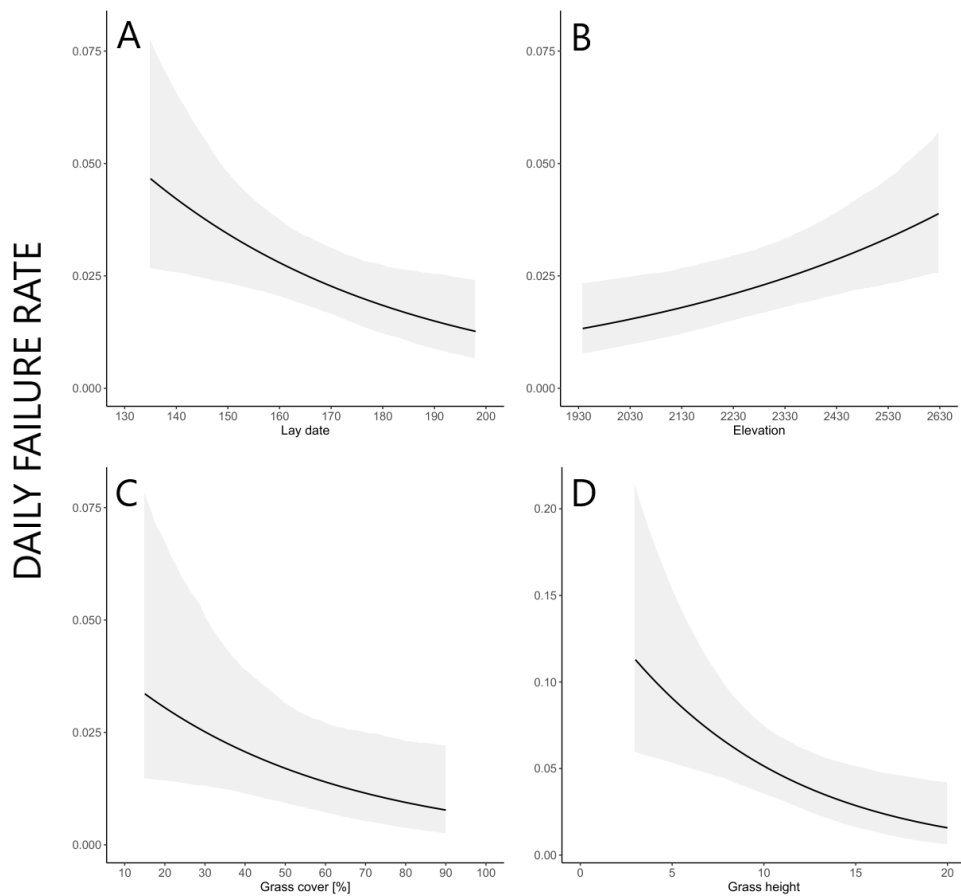


Figure 3. Variations in Daily failure rate (DFR) with A) lay date (doy) and B) elevation (m a.s.l.) for the study period 2016-2021, C) grass cover for data of 2019-2021, modeled with GLMMs, and D) grass height (cm) modeled with GLM for data of 2020-2021 (note that the y-axis is scaled differently). Lines represent the fitted values and grey shaded areas the 95% CrI of the models given in Table 2.

Nestling mass

Nestling mass 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 nestling mass. Age, but not number of nestlings, was included in all consecutive models. Nestling mass did not vary between years in a linear model with year and age as fixed effects (Fig. S3) and was thus not included in consecutive models.

Although hatch date was positively influenced by elevation (see above), showing later hatching at higher elevations, the variance inflation factor (function *vif*) did not show any collinearity ($\text{vif} < 2$). Therefore, we kept both variables 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 nestling mass. Thus, the results presented for 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. 4 A, Table 3), whereas elevation had no significant effect (Fig. 4 B, Table 3).

For the subset of 2019, there was no significant effect of temperature during the incubation period during the day ($\beta_{\text{dayT}} = -0.016 \pm 0.048$, $P = 0.74$) or night ($\beta_{\text{nightT}} = -0.030 \pm 0.059$, $P = 0.62$) on nestling mass, but there was a significant effect of age ($\beta_{\text{day}} = 0.338 \pm 0.125$, $\beta_{\text{night}} = 0.334 \pm 0.122$). Although 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 later 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 $\pm$ sd, $\leq 2,300$ m a.s.l. ($n = 7$):

13.7 $\pm$ 2.4, > 2,300 (n = 10): 13.4 $\pm$ 3.1, > 2,400 (n = 8): 12.1 $\pm$ 3.3) that is especially obvious early in season (Fig. S2).

Table 3. Effects of hatch date (doy, scaled), elevation (scaled) and age on nestling mass (LM). Estimates were significant if bold: $P < 0.05$, and if 95 % credible intervals (Crl) of the model estimates did not include zero.

Selected model for nestling mass (scaled)	Estimates (95 % Crl)	$\pm se$	R^2	Df	P
Intercept	-2.345 (-2.998 - -1.718)	0.321	0.36	106	<0.001
Hatch date	-0.112 (-0.312 - -0.005)	0.077			0.043
Elevation	0.109 (-0.036 - 0.260)	0.075			0.142
Age	0.282 (0.209 - 0.355)	0.038			<0.001

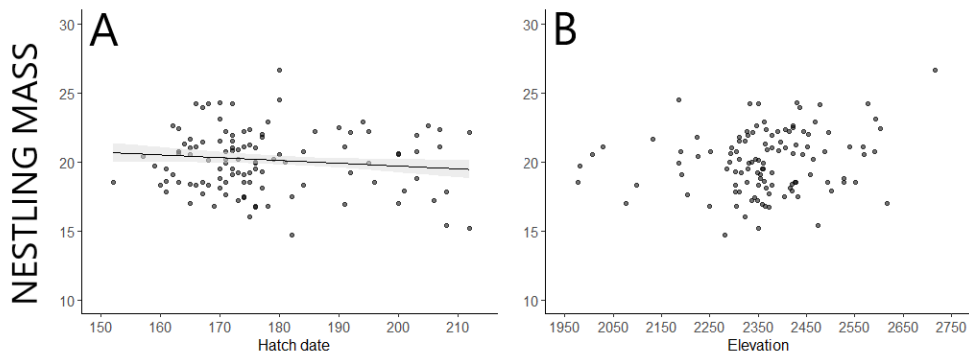


Figure 4. Variations in nestling mass (g) with A) hatch date (doy) and B) elevation (m a.s.l.) modeled with a linear model for the study period 2016-2021. Line represents the fitted values (when age is scaled) and grey shaded areas the 95% Crl of the unscaled model estimate given in Table 3.

DISCUSSION

Between-year differences in nest survival were high, ranging from survival probabilities of 23 (2020) to 53% (2018). The main cause of failure was predation. Across our study period of six years, nest survival was highest for late breeders, both in actual and relative terms (i.e. respectively raw and scaled dates), at lower elevations, and at nest locations with higher grass height and cover. Nestling mass was found to decrease with hatch date, showing that relatively late breeders are at a disadvantage in terms of nestling quality and hence probably in their fitness (Magrath 1991; Streby *et al.* 2014; Tinbergen and Boerlijst 1990).

Breeding timing and nest survival

Overall, we did not find any trends in lay dates across our six study years, but there was a high inter-annual 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 early years (2016, 2020, 2021) had a lower nest survival than the late years (2017, 2018, 2019). Our findings are thus in contrast to other lowland studies of the Wheatear (Arlt and Pärt 2017; Low *et al.* 2019) and of other species (e.g. Pied Flycatcher *Ficedula hypoleuca* (Le Vaillant *et al.* 2021; Nicolau *et al.* 2021), Prothonotary Warblers *Protonotaria citrea* (Hoover and Schelsky 2020)), that seem to be able 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.* 2021), 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.* 2021)) and longer seasons (Rock Sparrow *Petronia petronia* (Mingozzi *et al.* 2021)), whilst 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 and Pärt 2017)).

In long-distance migrating 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 through increased predation risk (e.g. Higgot *et al.* 2020; Klueen *et al.* 2011; Marcelino *et al.* 2020; Rauter *et al.* 2002). This seems to be especially the case for the higher elevation nests within our study site that were subject to lower temperatures in the early season and which had higher failure rates at this time, in common with Horned Larks in British Columbia (MacDonald *et al.* 2016).

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 to a more favourable microhabitat with a higher food abundance, but also to better nest (and adult foraging activity) concealment (see study on nest survival in Savannah Sparrows *Passerculus sandwichensis* and American Pipits *Anthus rubescens* (MacDonald *et al.* 2016)). Vegetation growth, and thus insect abundance, is limited by temperature: While 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 could find high elevation nest locations that provided higher food abundance by having a higher grass cover and height, and that showed a higher nest survival, compensating for potential negative effects of elevation on nest survival (Table 2, model 2019-2021).

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). In early 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 is lower (Leech and Leonard 1997; Rauter and 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 in the early season (MacDonald *et al.* 2016). Common predators that have been recorded above the treeline in our study region include the red fox *Vulpes vulpes* and the stoat *Mustela erminea* (Jähniq 2018; Masoero *et al.* 2016; Patriarca and Debenardi 1997). 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 to sibling species in lowlands, and that population dynamics are non-cyclic (Yoccoz *et al.* 1998; Yoccoz and 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 and Rödel 2014)), when above ground food resources become more available. The increase in above ground activity and abundance of voles increases their detectability for 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.

Nestling mass

We found nestling mass to be 6 % lower in relatively late broods (Fig. 4 A, Table 3), showing that these were in poorer condition compared to nestlings in the early 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 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.* 2021, 2020)) 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 nestling mass due to a trophic mismatch. 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 not able 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 in early 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 in the early season in our population.

Synthesis

Our population of Wheatears apparently shows a trade-off between having a higher nestling mass, and thus having fledglings in better condition (Magrath 1991,

Tinbergen and Boerlijst 1990) in early clutches, and the increased risk of nest failure at the same time. Both mechanisms may play an important role in our population: Environmental constraints in early seasons (and early springs) increase nest failure probabilities when laying early, but the potential trophic mismatch when breeding late can lead to fledglings in poorer condition.

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 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), resulting in lower nest survival in early years and, within season, higher failure rates in the early season. Second, although our population migrates a relatively short distance compared to 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 in arrival dates (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 inter-annual variability and the general trend of advancing spring onset.

To some extent, the trade-off between higher predation rates and better quality fledglings in the early season 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 make as our study period is too short to estimate a long-term trend for this population. Nevertheless, variations in nest survival and nestling mass within and across years with different spring green-

up patterns may disrupt this trade-off and thus have population consequences. Years with advanced springs (2016, 2020, 2021) showed a lower overall nest survival probability. Advanced springs might increase the probability of nest failure during the early season (unpredictability of weather and overall harsher conditions in the early season), 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 global warming, leading to more nest failures and in lower reproductive success by producing replacement (late) broods with nestlings in poorer condition (Martin *et al.* 2017). Alternatively, the trade-off may actually facilitate adaptation to climate change as low nest survival could be compensated by heavier nestlings in the early season, and thus higher fledgling survival probabilities may buffer negative effects of low nest survival on reproductive output.

Migratory birds breeding in seasonal environments need to breed early in the season to maximize the nestling mass by matching the nestling 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 achieve the production of fledglings in optimal condition, they need to time their migration schedule, and most importantly their arrival at the breeding grounds, according to local environmental conditions, which might be enabled by longer stopovers close to the breeding grounds (de Zwaan *et al.* 2021; Sander *et al.* 2021). With this study we show that there are constraints limiting nest survival in early springs and in the early season, but 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 global warming.

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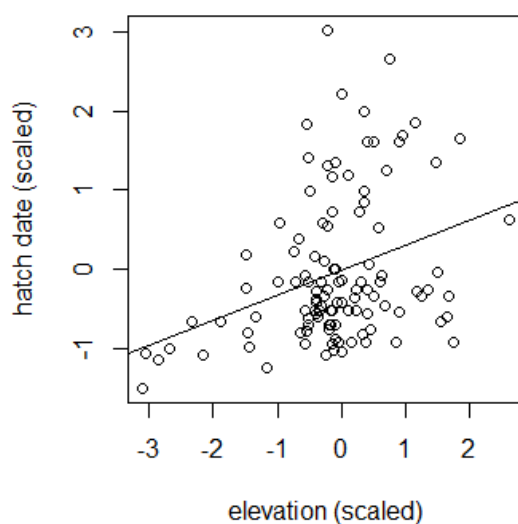
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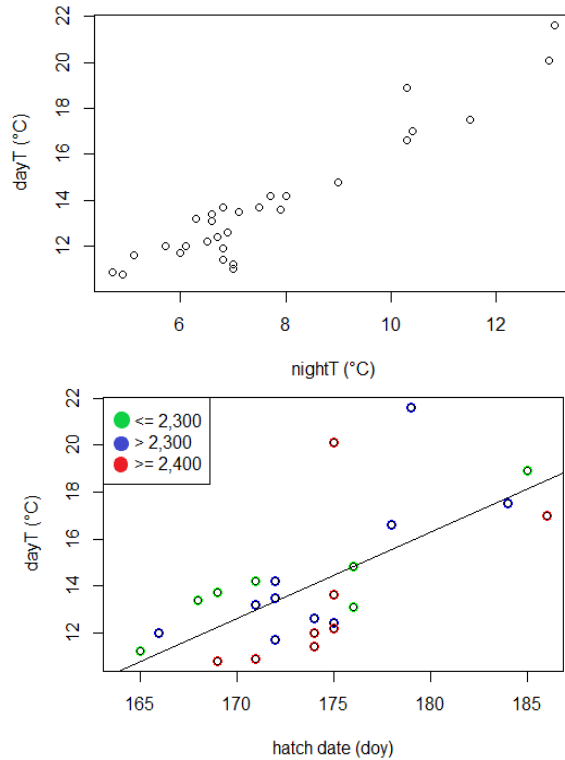
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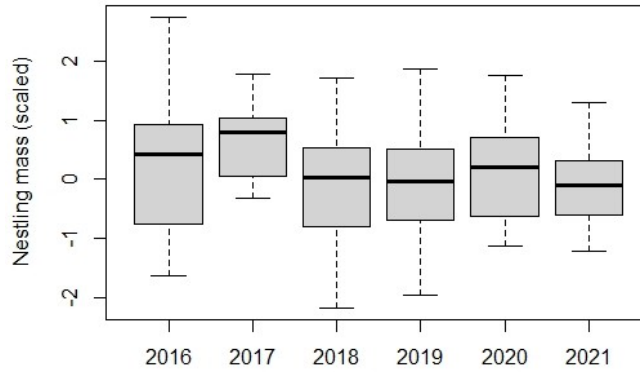
APPENDICES



S1. Linear relationship between hatch date 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 ($N = 179$).



S2. 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): $\leq 2,300$ m a.s.l., 3rd quartile (red): $\geq 2,400$ m a.s.l., median (blue): 2,350 m a.s.l.).



S3. Nestling mass (scaled) across the study period 2016 to 2021. Univariate linear model did not show any significant variation with year and age as fixed effects: $\beta_{\text{year}} = 0.023 \pm 0.054$, $P = 0.68$, $df = 106$. Boxplots show the median, the 1st and 3rd quartile, and whiskers represent the minimum and maximum.



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

CHAPTER VII – General Discussion

Discussion

The aim of this thesis was to contribute to the scarce knowledge on mountain bird ecology, and bird distribution and its drivers, with a special focus on open alpine grasslands, which are among the most vulnerable of all mountain habitats. By selecting a model species that is widely distributed, migratory and classified as a Holarctic mountain generalist, we were able to make predictions of how migratory songbirds breeding in highly seasonal alpine grasslands are reacting to weather and environmental variability within and across seasons. We presented for the first time how a Holarctic alpine breeding long-distance migrant schedules its migration and breeding season, and what influences its reproductive success.

Phenotypic plasticity is assumed to be a good predictor of resilience to environmental change, as high plasticity facilitates range shifts or adaptation to changing conditions. In Chapter 2 (Sander and Chamberlain 2020) we investigated whether resident songbirds breeding across a wide elevational range (95 to 1,900 m a.s.l.) show intra-specific variations in morphological traits across the elevation gradient by describing the phenotypic plasticity within species and thus their potential resilience to global change. By analyzing ringing data collected by the European ringing data bank EURING (du Feu *et al.* 2009), we found that across the six common species considered, wing length increased with elevation, whereas body mass decreased. As this result contradicts both Bergmann's rule (larger individuals in colder environments) and Allen's rule (shorter limbs in colder environments) we concluded that variables other than temperature may explain the variation in traits. Higher elevations require a range of physiological adaptations, as flying in conditions with higher wind speeds and lower air pressure may select for individuals with better flight performance and thus longer wings. Lower body masses may be beneficial when resources are scarce and highly seasonal, and energy intake is thus limited. However, other factors leading to the selection of smaller bodies, such as limited growth during the individual's life due

to food scarcity, cannot be excluded. Trends were similar in all six species, but the degree of variation differed, leading to the assumption that some species may be morphologically more plastic than others. Studying the trait variation within and across species along environmental gradients can be used to understand potential reactions to future global changes, and thus highlights the importance of European-wide or even global collections of bird data, such as ringing (morphology and reproductive timing, as collected by EURING and SPI-Birds (Culina *et al.* 2021) or movement data banks (spatial and temporal organization of the annual cycle through tracking technologies, such as MOVEBANK (Fiedler and Davidson 2012)). Here, we showed that species inhabiting similar habitats across a wide elevation gradient may be able to do so due to their phenotypic plasticity.

Changes in biodiversity and species distribution in mountain systems are studied mostly on single species, and the knowledge of the distribution patterns and its drivers of whole species assemblages in Holarctic mountains is rather scarce. In Chapter 3 (Mermillon *et al.* 2021), we moved from studying single-species adaptations to high elevations to characteristics of species assemblages across an elevational gradient. We showed with data from bird and habitat surveys collected in the Western Italian Alps (1,700 to 3,000 m a.s.l.) that the niche breadth increased with elevation, indicating the occurrence of more generalist species at high elevations, above the tree-line. At the same time, these habitats were more atypical compared to the whole assemblage (distinct niche position of birds occurring at high elevations). Generalists may have a greater ability to adapt to a range of environmental conditions and their seasonality, which is required for living and breeding at high elevation habitats. They show wider niches than species occurring at lower elevations. Here, species' niches are narrowed additionally due to inter-specific competition (higher species diversity at low elevations). Generalists are using a broader range of habitats, but they are using also more atypical habitats that are not used by other species (such as open alpine grasslands). We concluded that with future global warming, these high elevation generalists might be fairly

resilient to rising temperatures, as they can occur also at lower elevations as long as suitable (open) habitat is available. However, the availability of open habitats, i.e. grasslands, is the limiting factor for these species, as this habitat is declining due to the upward moving tree-line facilitated by rising temperatures and land-use change. Despite their narrower niche, species occurring at lower elevations (forest species) are unlikely to show negative population trends in future as their suitable habitat is increasing.

In Chapter 4 (Jähnig *et al.* 2020), we identified the relationships of bird species distribution along the elevational gradient with fine- and large-scale environmental variables (i.e. temperature and habitat), to make implications for future sampling designs for studies conducted in mountain systems when investigating effects of climate change. For most ecotone and forest species, models using fine- or large-scale temperature performed equally well, but grassland species distribution was clearly better described by fine-scale instead of large-scale temperature, and showed even reverse results with previous large-scale studies in two species, the Water Pipit and the Skylark *Alauda arvensis*. In the Skylark, fine-scale temperature models showed negative associations between the species' distribution and higher temperatures, whereas previous studies using large-scale climatic variables suggested that, under warming conditions, this species would have an increased distribution (Chamberlain *et al.* 2016a, 2013). For Water Pipits, a decrease in the distribution with increasing large-scale temperature was predicted (Chamberlain *et al.* 2016a, 2013), but in the present study, positive relationships of species distribution with increasing fine-scale temperature have been found. Also, the distribution of the Northern Wheatear was positively related to higher fine-scale temperature. It should be noted that this study has a rather explorative character, and predictions of species distributions would benefit from monitoring fine-scale temperature for longer than only two days at each sampling point (to account for high temporal variability), which should be visited more than once within the season (to potentially account for potential spatial shifts of species

within the area across the season). Furthermore, recording of the species in its habitat should include the specific behaviours within microclimates, such as the selection of foraging sites. Despite this, our results suggest that at least these two mountain generalist species may be resilient to direct effects of future global warming within their suitable breeding habitat when considering the temperatures at a finer scale as they might select warmer microclimates within overall colder breeding areas. This suggests, in accordance with the previous Chapter 3, that the main threats will be indirect effects of rising temperatures as such as the changing breeding habitat as a consequence of the upslope shift in tree-lines and the loss of open alpine grasslands. Therefore, to assess the vulnerability to future climate and land-use change for alpine species, studies should include fine-scale measurements of temperature and habitat, e.g. vegetation cover (Ceresa *et al.* 2020).

Whether high alpine birds will be able to occur in their current habitats under changing environmental and land-use conditions is not fully explained by bird and habitat observation surveys only. It is crucial to combine this information with knowledge on basic ecology, such as measures of population productivity, to investigate what effects environmental changes could have on future population trends (Chamberlain *et al.* 2012). To address this issue, we focused on the breeding phenology and success of a mountain generalist breeding in open alpine grasslands, the Northern Wheatear, under variable environmental conditions (within and between years), and linked this to the species' long-distance migration, i.e. the arrival at high elevation breeding grounds (Chapter 5, Sander *et al.* 2021, and 6, Sander *et al.* (under review)). Intensive field work has been conducted in an alpine population of this species, including territory mapping (two seasons), nest monitoring (six seasons) (Table A1), chick ringing (six seasons), trapping and ringing adults (three seasons) (Table A2), tagging adults with light-level geolocators (two seasons) (Table A3), habitat monitoring of the study area (fine-scale habitat, two seasons) and each single nest location (fine-scale habitat, six seasons), and resighting of colour-ringed individuals throughout the season, and in particular for

fledgelings/juveniles for 30 days post-fledging (three seasons) (Table A1). To describe spring arrival patterns of this population we used geolocation data (high precision from six individuals) and citizen science observations in the larger area of Piemonte and Aosta. Snowmelt and green-up patterns were described by using remote sensing data of the study area (large-scale habitat, six seasons).

As our alpine population has a rather short migration distance compared to lowland but high latitude populations (Bairlein *et al.* 2012; Conder 1989; Sander *et al.* 2021; Schmaljohann *et al.* 2016), and might be able to assess local environmental conditions better before arriving at the breeding grounds, we assumed a certain flexibility in the species' arrival and clutch initiation dates. According to this, we expected a high resilience towards the annual variability in timing of snowmelt and spring green-up. In fact, arrival dates (as derived from geolocation and citizen science data) did not show high variation between two very different years, but birds had a time buffer of different lengths before breeding (arrival-laying interval). This interval was shortened in the early spring in 2020, but lay dates did not advance by the same magnitude as the snowmelt and spring green-up. Breeding success, and in particular fledging success, was significantly lower in the year with early spring onset. We concluded that the species, despite its timely arrival at the breeding grounds, was not tracking the advance in spring onset. The high nest failure in the early year was hypothesized to be related to the negative effect of a shortened arrival-laying interval, environmental constraints in the early (environmentally unpredictable) season and a potential phenological mismatch with the peak in insect food resources (inferred from the peak in NDVI) during the nestling rearing period by starting laying too late (Chapter 5, Sander *et al.* 2021).

We studied the breeding success in more detail by including nest monitoring, chick ringing and habitat data from previous years, and relating measures of reproductive success, nest survival probability (Mayfield method) and nestling mass (as a measure of reproductive output), to changing environmental

conditions across the breeding season. We assessed whether an early or late start of breeding influenced the nest survival probability and nestling mass, and if these were further connected to breeding phenology, elevation, temperature at the nest site, and spring green-up (fine-scale: grass height and cover, large-scale: remote sensing images of NDVI and NDSI). Furthermore, we investigated whether reproductive success differed between years with different spring phenologies. Across the six years, we found differences in nest survival, which was highest in years with late spring onset, and lowest in years with early spring onset. Within seasons, early laying had a negative effect on nest survival, but was beneficial for nestling mass, and thus the predicted survival of the fledglings. Nests in high elevations had a higher failure probability, but this effect was weaker than the timing of nesting (lay date). In general, nests with 'greener' surroundings (higher grass cover and grass height) had a higher nest survival, but no such effect was found for nestling mass. As the timing of laying seemed to have the highest impact on both nest survival and nestling mass, but in opposite directions, we assumed a trade-off between early and late nesting. Early nesting increased the possibility of having fledglings in better condition, but incurred higher failure rates due to harsh environmental conditions and a higher predation risk, whereas later nesting reduced the risk of failure, but may lead to a mismatch with the peak in food abundance during the nestling rearing period (Chapter 6, Sander *et al.* (under review)).

The Northern Wheatear might therefore have a certain resilience to variable environmental conditions and the advance in the onset of spring conditions by adjusting/shortening the arrival-laying interval, thus advancing the lay dates, and choosing 'greener' nest locations at lower elevations. However, long-term population trends of open alpine grassland songbirds might become negative as years with early springs showed lower reproductive success within our model species and our short time window already, and these are likely to become more frequent due to global warming. Additionally, the abandonment of grazing

activities in the Alps, habitat degradation by recreational activities, and the upward moving tree-line lead to a decrease of suitable habitat for open alpine grassland species (Bani *et al.* 2019; Chamberlain *et al.* 2013), so that despite the assumed ability of the Northern Wheatear, and other migratory open grassland species, to adapt to advancing and more variable springs, a decline of the alpine populations is likely under current and predicted environmental conditions.

Studies on our alpine Northern Wheatear population, in addition to the findings on phenotypic variation (Chapter 2), niche patterns (Chapter 3) and species distribution (Chapter 4) across elevation gradients, show that mountain generalists have the potential to adapt to direct effects of climate change by showing a certain tolerance for warmer temperatures and high within- and between-year variability in spring conditions. Nevertheless, the potential for adaptation to climate change in terms of migration and breeding phenology (as suggested by long stop-overs before reaching the breeding site and shortening of the arrival-laying interval in early springs), seems to be limited, as shown by our data on breeding success. Studies on mountain specialists have shown that climate change has already led to significant population declines, e.g. of White-winged Snowfinch (Brambilla *et al.* 2020; de Gabriel Hernando *et al.* 2021) and Rock Ptarmigan (Scridel *et al.* 2021).

Although many aspects of climate change effects on the demography of alpine birds are yet to be resolved, we have shown that, generally, the biggest threat to open alpine grassland birds is habitat loss and degradation, which are also indirectly affected by anthropogenic climate and land-use change. Alpine species have no potential for adaptation to these habitat changes as they are strongly linked to the open character of the habitat. This main conclusion highlights the necessity for action and management strategies to protect open habitats in alpine environments.

Future perspectives

Within the years of this project, we collected far more data than we were able to publish here (Appendices, Table A1-3), and we plan to continue the work on our model species that combines two challenging aspects of its biology: Breeding at high elevations and in a threatened habitat, open alpine grassland (Bani *et al.* 2019; Chamberlain *et al.* 2013), and the Afro-Palaeartic long-distance migration which may be negatively impacted by phenological and trophic shifts on the one hand (Kubelka *et al.* 2022), and the use of increasingly degraded non-breeding regions on the other (Kirby *et al.* 2008).

Productivity: Post-fledging survival

We collected capture-mark-resighting data in three consecutive seasons to investigate environmental (habitat data) and biotic effects (timing of breeding, adult body condition) on adult and fledging survival after the fledging event (Table A1, A2). Few studies have included post-fledging survival data in the estimation of species' productivity and resilience to environmental change. In a long-distance migrant, the Willow Flycatcher *Empidonax traillii*, the highest mortality (estimated from annual apparent survival through colour banding) for adults was found during migration, but juvenile mortality was not considered (Paxton *et al.* 2017). Juvenile post-fledging survival studies are scarce, but they add important information to the productivity of a population (Cox *et al.* 2014; Evans *et al.* 2020; Rushing *et al.* 2017). These data collected within our alpine population of the Northern Wheatear may help to sharpen future predictions of population trends of open alpine grassland birds under changing climatic conditions.

Seasonal habitat use

To understand what type of habitat this species selects at different points of time during the season after arriving in the high elevation breeding area, we conducted detailed territory mapping in two seasons (Table A1). Results of this analysis will

show which habitat features are important to maintain for the protection of open alpine grassland populations under climate and land-use change, and thus this study will give directions for the management of current grazing and recreational activities in the Western Alps where threat levels were highest compared to other Alpine regions (Chamberlain *et al.* 2016b).

Linking breeding with non-breeding seasons

In total, we retrieved 21 light-level geolocators that contained enough data for the analysis of the migration routes, locations of wintering grounds and stopovers, and the overall migration timing (2020: 9, 2021: 12, Table A3). Hence, the explorative analysis on the migration patterns published in Chapter 5 (Sander *et al.* 2021) will be enlarged by more tracks and individuals from an additional year of tracking, nest monitoring and annual survival of adults and juveniles (colour ringed population), and combined with large-scale environmental data from remote sensing data (including environmental tracking throughout the non-breeding periods) and local fine-scale breeding habitat measurements (Table A1-3). With this, we will be able to enrich our predictions of the species' ability to adapt to global changes, which were mainly based on the breeding range, by data from the whole annual cycle and habitats used during stopover and at the wintering grounds. Combining breeding ecology with the migration schedule is crucial to understand impacts of changing environmental conditions on Afro-Palaearctic long-distance migrants, and how these may shift their annual cycles accordingly (Briedis *et al.* 2020; Morrison *et al.* 2013; Sanderson *et al.* 2006; Vickery *et al.* 2014). Recent developments in the tracking technologies, such as ICARUS tags (www.icarus.mpg.de), set the scene for high-resolution movement studies in the breeding range as well as during non-breeding seasons, and thus will enrich our understanding of the full annual cycle of migratory species (McKinnon and Love 2018).

Predation

In Chapter 6 (Sander *et al.* (under review)), we identified and discussed nest predation as a main driver of the breeding success of ground-nesting birds in open alpine grassland, but the spatial and temporal relationships between predator abundance and their prey species, including the vole community, have never been investigated in open alpine grasslands in Holarctic mountains. In these systems, there is a lack of knowledge on basic ecological patterns across trophic levels. Explorative studies on predation have been carried out within our study area before, i.e. an experimental study on nest survival in relation to tree-line proximity by using fake nests (Masoero *et al.* 2016), and single camera traps at nest entrances to identify predators (Jähnig 2018). We are unaware of any study investigating relationships across trophic levels, i.e. on alternative prey abundance. Our study area and system provides a suitable infrastructure to collect data on the spatial and temporal abundance of small mammal species, such as the bank and snow vole, which is assumed to be tightly linked to the nest predation of ground-nesting songbirds in open grasslands, such as the Water Pipit, Skylark and Northern Wheatear. By setting up transects with ink or Sherman traps, such studies could be carried out additionally to the nest monitoring of songbirds during the breeding season to identify peaks of prey abundance, and relate these to the nest and post-fledging survival. Predator species and their abundance could be identified by setting up camera traps along those transects.

Trophic links: Birds and invertebrate food resources

In Arctic systems, studies on links between migratory birds and the temporal and spatially variable availability of their invertebrate food point towards an increasing trophic mismatch, leading to decreasing trends in population productivity with increasing global warming and advancing springs (Lameris *et al.* 2021; Nolet *et al.* 2020; Saalfeld *et al.* 2019). Whether such direct relationships are also true for migratory birds breeding in mountain grasslands has not been investigated yet.

Thus, in future studies, invertebrate abundance (e.g. with pitfall (ground invertebrates), sticky and Malaise traps (aerial invertebrates)) should be investigated across the breeding season to measure the direct effects of its availability on reproductive output of higher trophic levels such as birds, and thus the vulnerability of these to global warming and phenological shifts.

Demographic modelling

Integrated population models of a Swedish population of Wheatears breeding in open farmland showed the effect of habitat characteristics (driven by different land use practices) on population growth rates, and pointed towards the necessity of converting low quality to high quality habitats to prevent farmland (open grassland) birds from further declining (Paquet *et al.* 2018). By developing a full-annual-cycle, integrated, population model for Alpine nesting Northern Wheatears, we will be able to better predict impacts of environmental change. More broadly, this is required for migratory species in general for which spatially and temporal complex mechanisms are shaping population dynamics (Rushing *et al.* 2017).

Combining diverse elements from previous studies with future projects on productivity and survival (see “Productivity: Post-fledging survival”, “Predation”, “Trophic links: Birds and invertebrate food resources”, Chapter 5 and 6), distribution (see “Seasonal habitat use”, Chapter 5) and phenology (see “Linking breeding with non-breeding seasons”, Chapter 5 and 6) has great potential in understanding what drives the overall alpine population of a migratory open grassland songbird.

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APPENDICES

Table A1. Data collected in the period of this PhD in the Northern Wheatear population in Parco Naturale Val Troncea.

Study period	Nest monitoring	Resighting (post-fledging)	Territory mapping	Remote sensing	Temperature loggers	Light-level Geolocators
2019 to 2021	176	c. 30 days	--	+	--	--
2019 & 2020	--	--	369	--	--	86
2019	--	--	--	--	30	--

Table A2. Ringing data of the Northern Wheatear collected in three breeding seasons (2019-2021). All birds were ringed with metal rings received from the Italian Ringing scheme (ISPRA), all adults and most of the chicks were additionally ringed with a unique colour ring combination (three rings).

Category	Type	2019	2020	2021	Total	Total Category
chicks	colour	125	88	76	289	328
chicks	metal	38	0	1	39	
juveniles	colour	0	13	5	18	18
adults	colour, tags	35	51	0	86	157
adults	colour, control	16	7	48	71	
recaptures		0	19	18		37
first ringed		214	140	112		466

Table A3. Number of individuals tagged with light-level geolocators and retrieved/resighted in the period 2019 to 2021. Values represent birds that were tagged in 2019 and were resighted in 2020, and birds tagged in 2020 which were resighted in 2021. Tags used: P65B1-11-NOT, P65B2-7-DIP-NOT (0.6-0.8 g, light stalk, migrate technology ltd.) and SOI-GDL 2 (1.0-1.1 g, light stalk, Swiss Ornithological Institute).

Year	Type	tagged	retrieved	resighted	% retrieved	% resighted
2019	SOI-GDL 2	20	5	6	25	30
	P65B1-11-NOT	15	6	8	40	53
	P65B2-7-DIP-NOT	0	0	0		
	total	35	11	14	31	40
2020	SOI-GDL 2	20	2	3	10	15
	P65B1-11-NOT	15	11	15	35	48
	P65B2-7-DIP-NOT	16				
	total	51	13	18	25	35
2019&2020		86	24	32	28	37

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