Assessing the response of mountain birds to rapid environmental change: conservation ecology of the Alpine Ring Ouzel (*Turdus torquatus alpestris*)

Inauguraldissertation
der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern

vorgelegt von

Arnaud G. Barras

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Leiter der Arbeit:
Prof. Dr. R. Arlettaz
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SUMMARY

Mountain ecosystems are exposed to increasing threats globally, of which changes in land-use and climate are commonly regarded as the most serious. In this context of rapid environmental change, it is of fundamental importance to assess the current and future responses of high-elevation organisms. There is in fact an urgent need to understand the ecological and demographic mechanisms underlying mountain species' distributions and population trends for proper conservation planning. Here, we focused on the Ring Ouzel *Turdus torquatus*, an emblematic thrush species of upland and mountainous regions of Europe. The main goal of this PhD thesis was to improve our knowledge of the ecology and demography of the *alpestris* subspecies, i.e. the Alpine Ring Ouzel, to identify possible drivers of negative trends in central Europe and envision possible conservation action. We first looked at functional ecological relationships, such as patterns of habitat selection and resource acquisition during the breeding season in the Swiss Alps, and how these relate to environmental variables. In a next step, we focused on demographic aspects and described the structure and dynamics of two focal populations in the western European Alps. We then examined behavioural and movement patterns across the annual cycle using tracking devices. Lastly, we relied on the initially accrued knowledge of species' ecological requirements to parameterize a country-wide, fine-scale habitat suitability model. The latter was used to delineate key areas for the Ring Ouzel and evaluate its vulnerability to environmental change based on various scenarios.

Our results demonstrate specific foraging preferences for soft and moist soils within a short and sparse grass sward, conditions that rapidly vanish from the breeding grounds as the season advances. This underlines strong temporal constraints on breeding, most probably driven by the brief time window of availability of the main prey, earthworms, as corroborated by the observed reduction in provisioning activity and efficiency in dry and warm weather contexts. Variations in weather conditions had, however, no clear impact on fitness parameters. Still, the narrow time window available for reproduction in the Alps may explain the apparent slower life-history strategy of Alpine populations when compared to Northern populations. Retrieved tracking data evidenced flexible seasonal and day-to-day movements but a year-round reliance on high-elevation regions, with winter quarters located in mountain ranges of Spain and Morocco. Finally, we reveal the more prominent role of climate compared to land-use in predictive models of species distribution and abundance. Indeed, climate shifts are expected to override the potential impact of land-use change in the coming decades, such as land abandonment and farming intensification. This highlights the vulnerability of the species to climate disruption, despite the strategies evolved to cope with environmental changes, in particular weather variation. Altogether, our findings unfortunately suggest limited leeway for implementing adaptive conservation strategies capable of fully mitigating the impacts of environmental change on Alpine Ring Ouzels. Nonetheless, recommendations for habitat management are framed while our predictive models constructed on fine-grained ecological information enable spatial prioritization of conservation programmes. These recommendations will not only help to conserve Alpine Ring Ouzels but also to maintain a rich biodiversity in Alpine treeline ecotones into the future.

GENERAL INTRODUCTION

Mountain ecosystems under threat

Pressures on biodiversity have increased unabated in the last century (Sala *et al.* 2000; Butchart *et al.* 2010). Anthropogenic impacts such as resource overexploitation, pollution, invasive species, land-use change and climate shifts are commonly listed as the main threats to biodiversity conservation worldwide (Butchart *et al.* 2010), and are responsible for what is now defined as the sixth mass extinction (Ceballos, Ehrlich & Dirzo 2017). These drivers are acting at a global scale but vary spatially in intensity, with mountain regions commonly perceived as the remnants of pristine ecosystems, spared from the effects of global change (Hamilton & McMillan 2004; Rodríguez-Rodríguez & Bomhard 2012). Indeed, the remoteness, harshness, and inherent risks of these areas have contained human populations to lower densities in the mountains (Kollmair *et al.* 2005; Rodríguez-Rodríguez & Bomhard 2012), hindering their intensive exploitation. Even in densely populated regions like central Europe, traditional low-intensity farming systems have persisted at higher elevations up to today (McCracken & Huband 2005; Plieninger, Hoechtl & Spek 2006). Mountains thereby still harbour a rich biodiversity, including numerous endemic species (Steinbauer *et al.* 2016), and are found in half of all global biodiversity hotspots (Mittermeier *et al.* 2011) while covering *sensu* Kapos *et al.* (2000) only about a quarter of the total land surface. Mountains also provide numerous and crucial ecosystem goods and services, the most obvious being freshwater supply (EEA 2010; Egan & Price 2017).

However, mountain regions are at risk, now standing 'in the firing line of human exploitation and climate change' (Malakoff & Sugden 2019). The continuous human-induced increase in the atmospheric concentrations of greenhouse gases in the last 300 years (IPCC 2014) is causing a global climate disruption (Pimm 2009), unfolding its effects even in the most remote areas. The pace of warming is in fact more rapid in mountainous compared to lowland areas (Nogués-Bravo *et al.* 2007; Pepin *et al.* 2015), with, for example, an increase of ca. 2°C in the European Alps over the 20th century (Auer *et al.* 2007), more than double the global average (IPCC 2014). Yet, effects other than warming are manifest, such as multidirectional changes in precipitation amount and seasonality, together with more extreme weather events like droughts (Beniston 2003; Gobiet *et al.* 2014). Snow cover duration, a fundamental component of mountain ecosystems (Beniston 2003; Wipf & Rixen 2010), has generally decreased following reduced snowfalls and an earlier snowmelt (Gobiet *et al.* 2014;

Klein *et al.* 2016). Because of the strong adaptations of high-elevation taxa to local conditions induced by steep environmental gradients (Martin & Wiebe 2004; Cheviron & Brumfield 2012), climate change is expected to have a profound impact on mountain ecosystems in the future.

Nonetheless, changes in land-use are considered by many as a more serious and immediate driver of habitat and biodiversity loss in mountains than climate change (Spehn & Körner 2005; Chamberlain *et al.* 2016b; Tasser, Leitinger & Tappeiner 2017). In addition, the interplay between these two drivers may considerably complicate the interpretation and predictions of their impact on high-elevation species (Chamberlain *et al.* 2013; Guo, Lenoir & Bonebrake 2018; Peters *et al.* 2019). Management of forests and grasslands has shaped landscapes in numerous mountainous regions globally, in the European Alps since centuries or even millennia (Schwörer *et al.* 2015; Mollet *et al.* 2018). These traditional extensive land-use systems are associated with an exceptionally rich biodiversity (McCracken & Huband 2005) but are jeopardized by a dichotomous trend toward either abandonment followed by progressive forest encroachment (MacDonald *et al.* 2000; Laiolo *et al.* 2004) or farming intensification to increase fodder productivity (Andrey *et al.* 2014; Gillet *et al.* 2016). Both processes are ultimately leading to a functional and compositional homogenization of ecological communities (Gossner *et al.* 2016; García-Navas *et al.* 2020). Apart from agricultural management, the use of mountain areas is also intensifying through the development of outdoor recreational activities (e.g. skiing, ski touring, mountain biking, hiking) and their associated infrastructure, which represent an additional threat for ecosystems already under pressure (Arlettaz *et al.* 2007; Rixen & Rolando 2013; Arlettaz *et al.* 2015).

Environmental change and mountain birds

While the threats on mountain ecosystems are manifold, we still know relatively little about how high-elevation wildlife is impacted by those drivers (EEA 2010). This holds true for the alpine avifauna (Chamberlain *et al.* 2012; Scridel *et al.* 2018), even though birds, as a widespread, conspicuous and diverse taxonomic group, are among the most studied organisms. Along with their dominant position in food chains and high mobility, these characteristics make them good ecological indicators (Gregory & van Strien 2010) and there is compelling evidence that they respond rapidly to environmental change (Järvinen & Väisänen 1979; Stephens *et al.* 2016). In addition, bird species distributions are generally well correlated with climatic conditions (Stephens *et al.* 2016), especially so for mountain specialists, which are confined to small elevational belts (Brambilla *et al.* 2019; Jähnig *et al.* 2020). Therefore, birds have been repeatedly used as models to forecast the effects of increasing ambient temperatures on wildlife (Huntley *et al.* 2008). Most projections describe northward and upward range shifts, ultimately leading to range contraction and increased extinction risks for mountain species (La Sorte & Jetz 2010). While evidence of such elevational shifts is growing (Tingley *et al.* 2009; Chen *et al.* 2011; Maggini *et al.* 2011), there are still major discrepancies between predictions and observations (Lenoir *et al.* 2010), and inconsistent patterns across mountain bird species and populations are common (Scridel *et al.* 2018). This may result from logistical difficulties to monitor mountain birds (Chamberlain *et al.* 2012), and hence to detect relatively small elevational shifts compared to latitudinal shifts (Pearce-Higgins & Green 2014). Yet, superimposed on climatic conditions, there is a number of other potentially confounding factors that determine species distribution ranges (La Sorte & Jetz 2010; Chamberlain *et al.* 2012; Pearce-Higgins & Green 2014; Guo, Lenoir & Bonebrake 2018).

Besides the necessity to improve the monitoring of mountain bird populations (Lehikoinen *et al.* 2019), there is thus the equally important task of better describing the ecological and demographic mechanisms underlying species distribution ranges (Chamberlain *et al.* 2012). For instance, fine-scale species-habitat associations remain largely unexplored, despite their importance in highly heterogenous mountain ecosystems (Braunisch *et al.* 2014; Resano-Mayor *et al.* 2019). Likewise, the effects of local weather conditions on the breeding ecology are poorly known (Martin *et al.* 2017), mainly because long-term demographic studies on mountain birds are still rare (Chamberlain *et al.* 2012). Overall, this clearly limits our understanding of how environmental change affects population trends (Sæther, Sutherland & Engen 2004; Pearce-Higgins *et al.* 2011). In addition, further studies on the various adaptations to high-elevation living are required (Martin & Wiebe 2004; Scridel *et al.* 2018), in particular to investigate whether plasticity in behaviour (Beever *et al.* 2017) or life-history traits (Boyle, Sandercock & Martin 2016; de Zwaan *et al.* 2019) constitute important strategies for coping with rapid environmental fluctuations. By incorporating information gathered from intensive empirical field-based studies, we would be able to improve the accuracy and resolution of predictive models of species distribution and abundance (Chamberlain *et al.* 2016a). This might represent the crux of the matter, given the growing importance of spatial modelling in the planning of conservation strategies (Pearce-Higgins *et al.* 2011) and the need for fine-scale guidance for efficient habitat management (Braunisch, Patthey & Arlettaz 2011; Braunisch, Patthey & Arlettaz 2016).

The Ring Ouzel

The Ring Ouzel *Turdus torquatus* is an emblematic representative of mountain bird species showing contrasting population trajectories across their range, and for which the relative contribution of climate and land-use changes in these trends are debated. The species is a sturdy thrush breeding almost exclusively in mountainous and upland regions of Europe (95% of the range; Keller *et al.* 2020). Three subspecies are distinguished: *T. t. torquatus* (or Northern Ring Ouzel) in the British Isles and Fennoscandia, *T. t. alpestris* (or Alpine Ring Ouzel) further south, mainly in the Pyrenees, Alps, Carpathians and Balkans, and *T. t. amicorum* in the east, in the Caucasus and Turkey (Glutz von Blotzheim & Bauer 1988; Keller *et al.* 2020). The Alpine Ring Ouzel is closely associated with semi-open subalpine forests, having a core distribution at the treeline ecotone (von dem Bussche *et al.* 2008) where it nests in coniferous trees and raising generally a single brood per season (Glutz von Blotzheim & Bauer 1988). This contrasts with the breeding habitat of the Northern subspecies in the British Isles, where Ring Ouzels are essentially ground nesting in steep open landscapes of heather moorland (Burfield 2002), commonly raising two broods a year (Sim *et al.* 2011). Across its range, the species lays clutches of 3–5 eggs (rarely 2–6), incubated for 12–14 days and nestlings fledge after 11–15 days (Glutz von Blotzheim & Bauer 1988; Burfield 2002). It feeds on ground- or soil-dwelling invertebrates during the breeding season, showing a clear preference for earthworms (Burfield 2002), then shifts to a berry diet during the autumn and winter seasons (Glutz von Blotzheim & Bauer 1988). The Ring Ouzel is a short-distance migrant whose populations from central and northern Europe are assumed to overwinter mainly in the Atlas Mountains of Morocco and Algeria (Glutz von Blotzheim & Bauer 1988; Sim *et al.* 2015).

At the European level, the Ring Ouzel distribution range has shrunk to some degree in the last decades (Keller *et al.* 2020), albeit not to the point of necessitating a change in its global status of 'least concern' (BirdLife International 2021). It is regionally or nationally red-listed, however, following negative population trends in the UK (Eaton *et al.* 2015), southern Germany (Bauer *et al.* 2016) and Switzerland (Keller *et al.* 2010b). The steepest decline of any population has been noted in the UK since the early 20th century (Sim *et al.* 2010; Wotton *et al.* 2016), where detailed investigations have aimed at understanding the causes of this population crash (summarized in Sim *et al.* 2010). Although no obvious driver could be identified, research highlighted the potential detrimental effects of both climate change (Beale *et al.* 2006; Sim *et al.* 2013) and land-use/cover alterations (Burfield 2002; Buchanan *et al.* 2003; Sim *et al.* 2007), acting both during and outside the breeding season (Ryall & Briggs

2006; Sim *et al.* 2011). In Switzerland, the species has decreased by ca. 36% in the last 30 years (Fig. 1a), mostly at lower elevations (Jura and northern Alps; Fig. 1b), resulting in a mean upward range shift of 84 m (Fig. 1c; Knaus *et al.* 2018), a pattern shared by other Ring Ouzel populations across the range (Sim *et al.* 2007; Anger *et al.* 2020; Fumy & Fartmann in press). The estimated 50,000–75,000 Swiss breeding pairs constitute ca. 15% of the European breeding population (Knaus *et al.* 2018; Keller *et al.* 2020) and confer a significant international responsibility on Switzerland for its conservation (Keller *et al.* 2010a). Given these figures, the Ring Ouzel is now one out of seven bird species of highest conservation concern and belongs to the 50 priority species for the development of specific management strategies in Switzerland (Keller *et al.* 2010a). Yet, the factors driving this decline are still unclear and so far, only a handful of studies have looked at the ecological requirements of central European populations (von dem Bussche *et al.* 2008; Schirutschke & Kalko 2010; Ciach & Mrowiec 2013; Anger *et al.* 2020; Pertl 2020; Fumy & Fartmann in press), which represents a serious impediment to the development of conservation action plans.

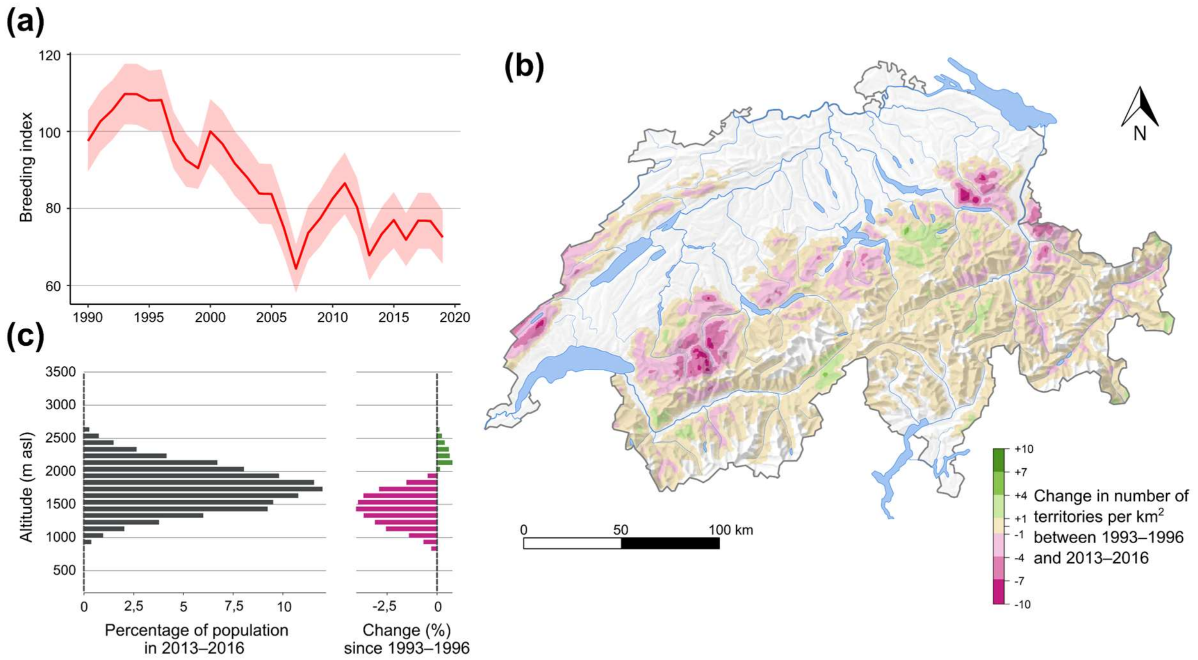

Figure 1 Population trends of the Ring Ouzel in Switzerland in the last decades. (a) Annual breeding index over the 1990–2019 period; (b) Absolute modelled change in the number of breeding pairs per 1-km^2 square between the two Atlas periods (1993–96 & 2013–16); (c) Percentage of the population in 2013–16 and percent change since 1993–96 for each 100-m elevational band. Figures adapted from Knaus *et al.* (2018) and Knaus *et al.* (2020).

Scope of the thesis

The main aim of this PhD thesis was to improve knowledge of the Alpine Ring Ouzel's ecology and demography, in order to identify the main factors determining its distribution and abundance, and ultimately population trends, with the idea to frame management recommendations. We first examined functional ecological relationships, such as species-habitat associations and patterns of resource acquisition during the breeding season. In a next step, we focused on demographic aspects, seeking to obtain a detailed picture of population structure and dynamics. Interpretation of those population parameters called for a broadening of the perspective to the annual cycle, with year-round movement data collected to that end. Finally, we integrated the information accrued during these initial research steps into a country-wide habitat suitability model of high resolution, so as to delineate key areas for the Ring Ouzel and better assess its vulnerability in the face of global change. Our ultimate goal was to bridge specific knowledge gaps identified by Spaar *et al.* (2012) for Ring Ouzel conservation, as well as to deliver spatially explicit recommendations for habitat management, hence paving the way for a conservation action plan at national level.

Overview of the thesis

In *Chapter 1*, we endeavour to identify crucial ecological requirements of the Alpine Ring Ouzel during the breeding season, focusing on the selection of foraging grounds by provisioning parents. To this purpose, we radiotracked individuals over two breeding seasons in a single, densely populated study area, investigating spatiotemporal patterns of habitat selection by comparing used to available sites at fine spatial scales. We further evaluated the transferability of these results by collecting data over a wider geographical area in the inner Alps. This initial approach describes the optimal foraging habitat profile and how its availability changes as the season progresses, thus providing key information for possible targeted habitat management measures.

Chapter 2 focuses on the nestling diet and provisioning behaviour of Ring Ouzel parents, and how their characteristics are influenced by prevailing weather conditions and season advancement. Video monitoring of several nests in the same core study area as in *Chapter 1* was used to identify prey items delivered by parents, as well as to quantify prey biomass and provisioning rates. This chapter highlights how weather variables play an important role in the breeding biology of the species, most likely through pronounced impacts on prey availability. These findings offer a mechanistic appraisal of the potential effects of climate change on the Ring Ouzel and thus enable a better assessment of species' future vulnerability.

In *Chapter 3*, we describe the demography and dynamics of two populations of Alpine Ring Ouzels in the French Vercors and in the Swiss Alps, aiming to determine demographic and ecological mechanisms underpinning contrasting population trends. This study also tests whether some of the important climatic factors identified in the two previous chapters correlate with demographic rates. Combining data on population size, breeding success and capture-mark-recapture, we estimate various population parameters (i.e. survival, productivity and immigration) using integrated population models. Results of this study reveal substantial variation in the demographic characteristics of Ring Ouzel populations across their range, providing essential information to interpret local population dynamics.

Chapter 4 concentrates on the movement and behavioural patterns of Ring Ouzels throughout the annual cycle. Using various tracking devices attached to birds breeding in the Swiss Alps, we recorded their movements over a year. This enabled us to describe their migration timing and routes, non-breeding quarters and year-round elevational movements. In comparison to the previous chapters, this study provides a broader perspective on the inherent threats to the species by covering periods outside the breeding season. At the same time, our results unravel complex and flexible movements which shed light into possible coping strategies of the Ring Ouzel to environmental change.

In *Chapter 5*, we present a modelling framework that — by integrating findings from the previous chapters — intends to deliver accurate and Swiss-wide projections of habitat suitability for the Ring Ouzel. As response variables, we rely on occurrence and abundance data from citizen science and standardized monitoring schemes. We then parameterize this model with important ecological relationships identified in this thesis or previously reported in the literature, in order to predict fine-scale occurrence probability and density. Our two main objectives are *i)* to pinpoint current density hotspots and species strongholds, *ii)* to evaluate the effects of realistic scenarios of climate and land-use change on species distribution and abundance for two different time horizons. We therefore provide a tool to delineate key areas for conservation interventions at a meaningful scale, as well as to better assess Ring Ouzel vulnerability in the face of global change.

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Chapter 1

The importance of seasonal environmental factors in the foraging habitat selection of Alpine Ring Ouzels (Turdus torquatus alpestris)

The importance of seasonal environmental factors in the foraging habitat selection of Alpine Ring Ouzels *Turdus torquatus alpestris*

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ABSTRACT

Species inhabiting mountain ecosystems are expected to be particularly vulnerable to environmental change, yet information on their basic ecology is often lacking. Knowledge from field-based empirical studies remains essential to refine our understanding of the impact of current habitat alterations and for the consequential development of meaningful conservation management strategies. This study focuses on a poorly investigated and vulnerable mountain bird species in Europe, the Ring Ouzel *Turdus torquatus*. Our aim was to identify the species' key ecological requirements during the crucial period of nestling provisioning in the context of environmental change. We radiotracked and observed Alpine Ring Ouzels in a high-density population, investigating their pattern of foraging habitat selection in 2015 & 2017, and evaluated the transferability of these results over a wider geographic range across the SW Swiss Alps. Foraging birds selected, consistently in space and time, short grass swards (< 10 cm) with interspersed patches of accessible and penetrable soils, at intermediate moisture levels (around 40–65% volumetric water content). In Alpine ecosystems, this microhabitat configuration is typically widespread during the spring snowmelt, but extremely seasonal, with a rapid decrease in its availability over the course of the breeding season. This underlines the high vulnerability of the Ring Ouzel to environmental change: an earlier snowmelt could generate a temporal mismatch between the peak of the breeding effort and optimal foraging conditions; however, abandoning grazing activities on semi-wooded Alpine pastures may further decrease foraging habitat suitability through taller and denser grass swards, and subsequent woody vegetation encroachment. This study provides a mechanistic appraisal of the challenges Ring Ouzels will face in the future, as well as initial guidelines for targeted habitat management within treeline ecotones.

Keywords: alpine birds, conservation, seasonality, snowmelt, soil conditions, treeline

INTRODUCTION

There is growing awareness that mountain ecosystems are facing steadily increasing threats. Those most commonly identified across mountain ranges are climate change (La Sorte & Jetz 2010; Scridel *et al.* 2018), changes in land-use, in particular farming practices (Laiolo *et al.* 2004; Guo, Lenoir & Bonebrake 2018), and the increase in anthropogenic disturbance (Rolando *et al.* 2007; Arlettaz *et al.* 2015). Nevertheless, there is still a paucity of research on how species of higher elevations will be affected. Contrary to the European lowland and forest avifauna, knowledge on the basic ecology and demography of alpine bird species is still lacking (Chamberlain *et al.* 2012; Lehikoinen *et al.* 2019). This precludes both predictions about their response to environmental change and framing management recommendations (Chamberlain *et al.* 2012).

Predictions of future distributions under different scenarios of climate change exist for most European bird species nowadays (e.g. Huntley *et al.* 2008), even combined with land-use change for specific regions (e.g. Maggini *et al.* 2014). These predictions mostly result from species distribution models that rely on coarse-grained environmental data, and therefore do not capture small-scale functional species-habitat associations (Braunisch *et al.* 2014; Brambilla *et al.* 2018). This is potentially problematic in alpine ecosystems where coarse-grained predictions are mainly driven by the steep macroclimatic gradient, whereas a very complex topography leading to a high diversity of microclimates and microhabitats may buffer general trends (Beniston 2003; Chamberlain *et al.* 2016; Brambilla *et al.* 2018). The harsh environment and remoteness of high elevation ecosystems have hampered fine-grained empirical studies in the past (Chamberlain *et al.* 2012), although such studies represent an absolute prerequisite for meaningful predictions of future distributions (Chamberlain *et al.* 2016; Jähnig *et al.* 2018), and ought to serve as the basis for conservation management at the local scale (Morris *et al.* 2001; Arlettaz *et al.* 2012). In addition to high spatial resolution, information should also be collected at a fine temporal resolution, such that seasonal patterns of habitat selection can be assessed (Brambilla *et al.* 2017; Resano-Mayor *et al.* 2019). This is of paramount importance in highly seasonal environments like temperate mountain ecosystems where birds are expected to be particularly vulnerable to changes in vegetation phenology (Inouye *et al.* 2000) but where very few asynchronies have actually been documented (Scridel *et al.* 2018).

The Ring Ouzel *Turdus torquatus* is a good example of an alpine species for which information on small-scale ecological requirements is still largely lacking across its breeding range. UK uplands represent the exception, as the sharp decline of the subspecies *T. t. torquatus* in the last 50 years and its status of high conservation concern (Wotton, Langston & Gregory 2002) have prompted some studies on its autecology and population dynamics (e.g. Burfield 2002; Beale *et al.* 2006; Sim *et al.* 2013; Sim *et al.* 2015). In central and southern Europe, where the subspecies *T. t. alpestris* breeds in a rather different habitat, in semi-open coniferous forests at the treeline, studies on its ecology are scarce (von dem Bussche *et al.* 2008; Ciach & Mrowiec 2013). Over the whole distribution range, the current population trend appears stable (BirdLife International 2018), but the well-monitored population in Switzerland, which represents around 15% of the European population (Knaus *et al.* 2018), has decreased by 36% over the period 1990–2018 (Swiss Ornithological Institute 2019). It is hence red-listed in the country, and is one of the seven bird species with the highest priority for the development of a recovery programme (Keller *et al.* 2010). In addition, its vulnerability index calculated from different large-scale scenarios of land-use and climate change is one of the highest across all Swiss breeding birds (Maggini *et al.* 2014). Nonetheless, while factors determining habitat selection at the territory and landscape scale in the Alps have been identified to some extent (von dem Bussche *et al.* 2008), information about the key drivers of local-scale habitat selection during the breeding period is still lacking. Only high-resolution studies may allow the underlying ecological mechanism of the observed decline to be deciphered (Morris *et al.* 2001). In this way, the vulnerability of the species can be better assessed in order to frame recommendations for future conservation.

One of the main determinants of habitat use during the reproduction period is the selection of feeding grounds, i.e. the foraging habitat selection. Parents must indeed supply large quantities of food to chicks for optimal somatic growth, representing a true energy bottleneck in the species' life cycle. Feeding grounds providing high prey availability represent therefore a *sine qua non* for successful reproduction (Naef-Daenzer, Naef-Daenzer & Nager 2000). For ground-foraging insectivorous birds, prey accessibility is often limited by ground vegetation structure (Atkinson, Buckingham & Morris 2004; Schaub *et al.* 2010), whereas soil conditions have a large influence on both abundance and accessibility of soil-dwelling invertebrates (Peach *et al.* 2004; Gilroy *et al.* 2008). Extensive research on the Ring Ouzel in the UK has shown that both adults (Burfield 2002) and fledglings (Sim *et al.* 2013) indeed favour foraging grounds with high soil pH and short grass swards within a heather-grass mosaic. Moreover, it has been hypothesized that soil conditions, such as soil moisture (Beale *et al.* 2006) and soil penetrability (Burfield 2002), could also play a key role, as they are known to influence the abundance and activity of earthworms (Oligochaeta; Edwards & Bohlen 1996), the staple food of Ring Ouzel nestlings (Glutz von Blotzheim & Bauer 1988; Burfield 2002; Sim *et al.* 2015).

Using radiotracking and direct visual observations, we investigated how fine-scale habitat characteristics influence the foraging habitat selection by Ring Ouzels during the nestling provisioning period in the European Alps. For this purpose, we focused on the selection of foraging grounds within the home-range (hereafter home-range scale) and on the resource acquisition within a foraging site (hereafter site scale), which correspond to the third and fourth orders of selection respectively, following the definition of Johnson (1980). Our aim was to identify key drivers of foraging microhabitat selection, and to characterize their seasonality so as to detect changes in the availability of suitable foraging habitat, all this in the perspective of future environmental change.

MATERIALS AND METHODS

Study area

The study was conducted in the central Swiss Alps, in the canton of Valais. This region is characterized by a continental climate, with warm and dry summers, and cold and wet winters. The site where radiotracking took place (46.33 N, 7.43 E), hereafter referred to as Serin, encompassed 205 ha, ranging from 1700–2200 m above sea level (asl), at the interface between the subalpine and the alpine belts. The zone is used for summer pasturing, with the continuous presence of cattle between mid-June and mid-September, which is a widespread traditional farming practice at these elevations in the Swiss Alps (Schulz, Lauber & Herzog 2018). Extensive pasturing results in a habitat mosaic consisting of open grasslands interspersed with isolated or groups of coniferous trees (predominantly larches *Larix decidua* and spruce *Picea abies*). The configuration of these semi-wooded pastures is particularly attractive for breeding Ring Ouzels (von dem Bussche *et al.* 2008), and the average density at the study area estimated from standardized monitoring is 40.7 territories/km^2 (see *Chapter 3*), which is among the highest observed in the country (Knaus *et al.* 2018).

Foraging locations sampling

Ring Ouzels (n = 41) were captured using mistnets and equipped with radio-transmitters (PD-2P; Holohil Systems Ltd., Carp, Canada; 3.0–3.7g — corresponding to 3.0–3.7% of the species mean body mass — life span 3–4 months) between mid-April and mid-May: 11 males and 10 females in 2015, and 10 males and 10 females in 2017. The permit for bird capturing was delivered by the Swiss Federal Office for the Environment (F044-0799) and authorisation for radiotracking by the Swiss Federal Food Safety and Veterinary Office. The radiotags were mounted with a leg-loop harness (loop span 76 mm, diameter 0.6 mm) made out of stretch-nylon tubes, following the method of Rappole and Tipton (1991). We tracked the birds during the whole breeding period (mid-April to the end of June) with the 'homing-in' technique, i.e. obtaining a series of repeated bearings using a radio-receiver (Australis 26k, Lawnton, Australia) coupled with a three-element hand-held Yagi antenna to approach and visually locate an individual. Each radiotagged individual was located at least twice a week to monitor its breeding status and, if possible, find its nest. From the first observations of adults provisioning chicks (2015: May 16th; 2017: May 24th), we started to track breeding adults more intensively (every 1–3 days per individual) until fledging of the brood occurred. Once a radiotracked bird was visually located, it was carefully approached (at 30–50 m distance), taking care not to influence its behaviour. From that moment, the exact spot of the first observed successful prey capture event was recorded with binoculars and marked with a labelled flag as soon as the bird had left the area. We referred to this visually evidenced prey capture as a 'foraging location'. To avoid, as far as possible, spatio-temporal correlation between the foraging locations, i.e. to achieve data independency, we left a time span of at least 30 min between two recordings from the same individual. This was enough to ensure that the bird had been provisioning nestlings in the meantime and had therefore started a new foraging bout. In 2017, several radiotagged individuals were particularly shy and showed increased flight-initiation distances, so that it was particularly difficult to obtain foraging locations for those birds. To increase our sample size, we therefore also recorded foraging locations of provisioning parents randomly encountered during radiotracking sessions. We are confident that this did not introduce any detection bias in our analysis, as all habitat types and sectors of the study area were visited regularly during the radiotracking sessions.

In 2016, 16 areas situated outside the main study area of Serin were visited once or twice along a predefined transect (1.5–3 km) during the reproductive season (May 15th –June 27th) to collect additional foraging locations from untagged provisioning individuals. These data, spanning from 1650 to 2200 m asl, served for external model evaluation on a wider area across the Swiss Alps with different climatic conditions (Fig. 1).

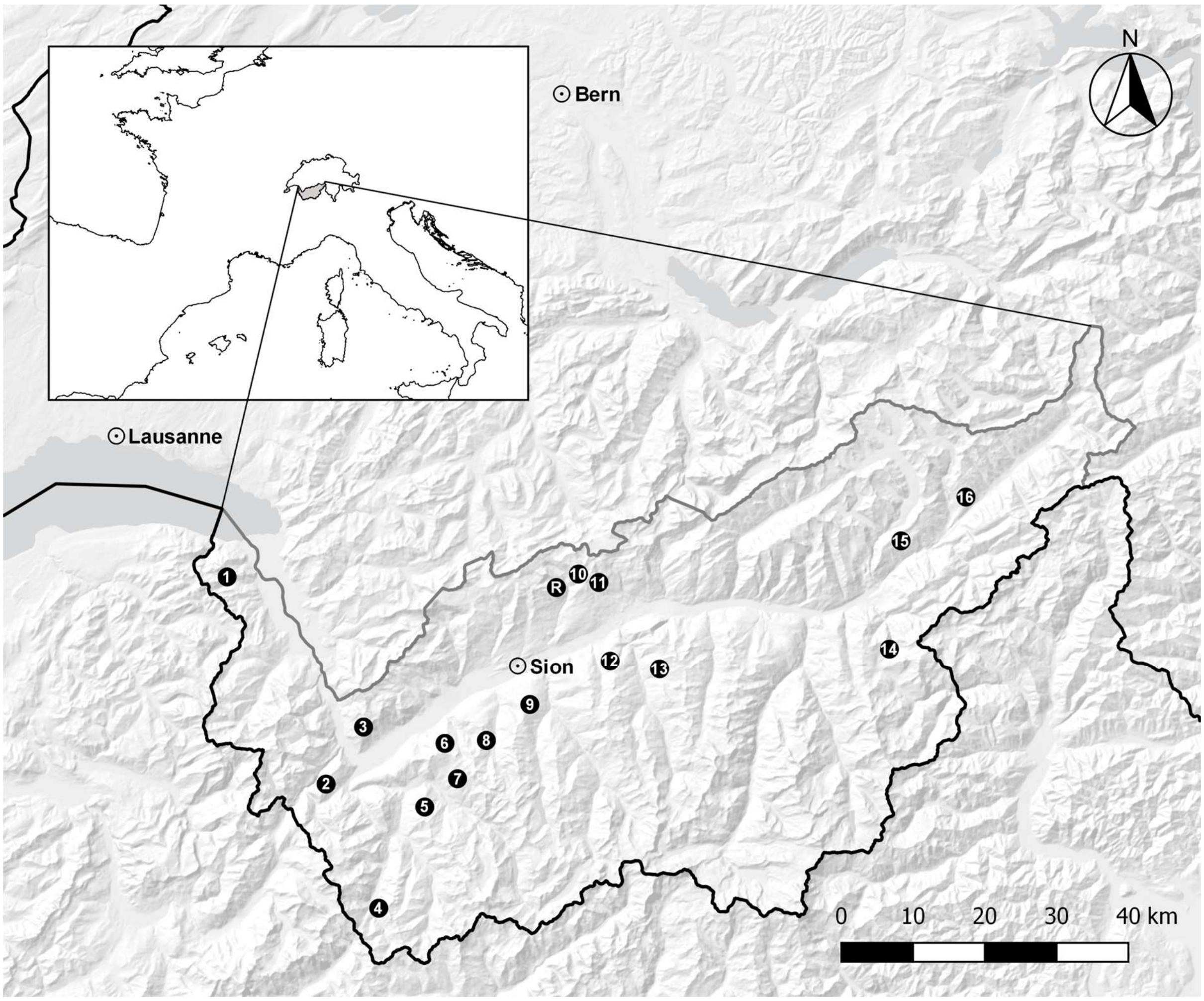

Figure 1 Map of the study region (Valais, Switzerland; shaded in the inset). The area where the radiotracking took place is symbolized with the letter R, and those for the collection of data for model evaluation are numbered from 1 to 16.

Habitat measurements

The habitat selection pattern was assessed by comparing the characteristics of the habitat at actual foraging locations with neighbouring locations, which were assumed to represent less suitable habitat because they were apparently not used for foraging. For that purpose, we randomly selected two pseudo-absences (PA) in the surroundings of a foraging location following a standard procedure. A random bearing (α: 0–359°) was generated, which defined the direction from the actual foraging location in which two PA locations were placed, the first one at a random distance between 5 and 14 m, and the second between 15 and 50 m. The former range (5–14 m) was chosen so as to investigate habitat selection at the foraging site scale. In effect, these distances from an actual location are within the range of a hopping bird, as typically observed during a single foraging bout (Burfield 2002; own pers. obs.). In contrast, the latter range (15–50 m) is more likely to express foraging habitat selection at the wider scale of the home-range, as the chosen distance is within the typical range of a Ring Ouzel flying from one part of its home-range to another (Burfield 2002). The PA locations were generated instantly after each recorded foraging location, so that the habitat measurements could occur during the same or the next day, and hence accurately reflect the environmental conditions encountered by a foraging bird. This represents a fundamental aspect of the sampling design, as several habitat variables showed strong temporal variations due to the high seasonality of the ecosystem at these elevations, in particular as regards snow cover.

Measurements of predefined habitat variables were taken in the same way at foraging and PA locations and restricted to a plot of 1-m radius around each location, so as to describe the microhabitat. Habitat variables were classified into four main categories: ground cover, topography, vegetation height and soil conditions (Table 1). Ground cover consisted of eight classes: brown grass (dry, i.e. dead annual herbaceous plants from the previous year), green grass (new annual living plants), accessible ground (cover of bare ground and leaf/needle litter combined; hereafter AG cover), mineral (gravel and rocks), dead wood (lying trunks and branches), snow, woody plants (shrubs and bushes below head height) and mosses. Topographic variables included slope inclination and aspect (as northness and eastness — see Table 1), both measured with a compass, and distance to the nearest snow patch if present within a radius of 50 m. Herbaceous vegetation height was measured for the brown and green grass swards separately. Two soil condition variables were also considered. Soil penetrability was measured with a penetrometer (EL 29-3729, ELE International, Loveland, USA), a device that indicates the force (kg/cm^2) needed to insert a metal tip into the soil to a depth of 6.35 mm, with high values thus indicating low soil penetrability. For soil moisture, we measured the volumetric water content (VWC) of the soil, calculated from its conductivity using a specific dual probe with two 51-mm rods (SM150, Delta-T, Cambridge, UK). For each soil variable, three measurements were taken within 10 cm of the centre of the plot, i.e. where prey capture occurred, with their means retained for subsequent analyses.

Statistical analyses

We assessed foraging habitat selection as a function of habitat variables measured at foraging vs. PA locations, using hierarchical logistic regression, which corresponds to a generalized linear mixed-effects model (GLMM) with a binomial error distribution and a logit link function. The habitat variables were included as fixed effects. Non-independence of the data coming from the same stratum (a triplet consisting of a given actual foraging location and its two associated PA locations), or the same individual, was accounted for with nested random effects (Gillies *et al.* 2006), i.e. stratum nested within individual, as several foraging locations per individual had been recorded. Data from untagged and therefore unidentified individuals were given unique factor values. All analyses were performed using the software R 3.5.1 (R Development Core Team 2018) and logistic models were fitted using the *glmer* function in the R-package 'lme4' (Bates *et al.* 2015).

Prior to model selection, several variables were transformed: marginal ground cover variables (> 90% of zero values) were not considered in the analysis, and those with more than 70% of zero values were transformed to binary presence/absence (1/0) variables. The other ground cover variables were arcsine-square-root transformed, and vegetation height variables log-transformed. Moreover, all variables were standardized to visualize and compare the effect size directly from the coefficient estimates. We also tested the addition of squared terms to variables for which we hypothesized a hump-shaped relationship in relation to occurrence probability: soil moisture, soil penetrability, AG and green grass cover. Finally, to avoid collinearity, we checked for Pearson's correlation coefficients between the variables, retaining only those with $|r| < 0.7$, and we carefully checked that all variables had variance inflation factors (VIF) < 3 in all fitted models.

To characterize each order of selection separately, we fitted two different sets of models. First, foraging locations were compared to PA in the closer range (5–14 m) and, second, to PA in the wider range (15–50 m). For each analysis, we adopted a model selection approach in two steps. First, for each of the four categories of variables, we generated a list of candidate models from all possible variable combinations and ranked them based on the Akaike Information Criterion with correction for small samples (AICc) using the function *dredge* of the package 'MuMIn' (Bartoń 2018). We defined the set of best-supported models as those within ΔAICc < 2 from the first-ranked one, after the exclusion of models with uninformative parameters, i.e. models that contained additional parameters compared to better-ranked models, but that have a higher AICc value (Arnold 2010). We then retained all variables appearing in at least one model of this set. In a second step, retained variables from every category were combined into a single model. The interaction term between AG cover and height of green grass was added to this model, to check for the potentially higher importance of AG cover within high ground vegetation. We then carried out the same model selection procedure as above to identify the set of best-supported models within ΔAICc < 2. The AICc weight (w_i) of each possible candidate model was calculated, and variable importance was assessed by summing the w_i of all the models where it appeared following Burnham and Anderson (2002). To evaluate the performance of the best-ranked model, we calculated R-squared with the function *r.squaredGLMM* from the package 'MuMIn', as well as the area under the receiver operating curve (AUC) using a five-fold cross-validation. Finally, we assessed model spatial transferability by calculating the AUC on the evaluation data collected in 2016. Plots of occurrence probability against a given habitat variable were based on the best-ranked model, while setting all other retained variables to their empirical mean. 95% credible intervals around the regression line were drawn from the 2.5% and 97.5% quantiles of the posterior distribution, obtained with 10,000 simulations with the package 'arm' (Gelman & Su 2018).

Table 1 Habitat variables measured at each foraging and pseudo-absence (PA) plot. Mean ± sd values are displayed for each group, except for woody plants and moss cover, which were transformed into binary factors as they contained > 70% of zero values, with resulting 0/1 counts shown here. Variables in brackets were removed from the analysis as they contained too many NAs or zero values (> 90%).

	Habitat variables	Unit	Foraging	PA (5–14m)	PA (15–50m)
Ground cover					
1	Brown grass	%	12.7 ± 14.0	12.2 ± 16.4	10.6 ± 12.4
2	Green grass	%	44.6 ± 28.3	50.3 ± 30.5	57.3 ± 30.7
3	Accessible ground	%	32.4 ± 25.6	25.2 ± 25.7	20.7 ± 23.9
4	Mineral	%	2.4 ± 4.2	3.6 ± 8.0	3.3 ± 8.2
5	Dead wood	%	3.2 ± 5.3	3.4 ± 6.8	3.0 ± 7.3
6	(Snow)	%	0.9 ± 5.1	1.1 ± 7.2	0.8 ± 8.1
7	Woody plants	0/1	155/53	165/42	164/44
8	Moss	0/1	159/49	167/41	172/36
Topography					
9	Slope	°	18.2 ± 8.9	18.4 ± 9.6	18.2 ± 9.9
10	Northness	cos(aspect[a])	0.5 ± 0.6	0.4 ± 0.6	0.2 ± 0.7
11	Eastness	sin(aspect[a])	0.4 ± 0.5	0.5 ± 0.5	0.4 ± 0.5
12	(Distance to snow if < 50 m)	m	10.6 ± 17.2	10.4 ± 13.4	14.3 ± 17.1
Vegetation height					
13	Brown grass height	cm	2.5 ± 1.6	2.7 ± 2.0	3.1 ± 3.2
14	Green grass height	cm	5.9 ± 3.3	7.9 ± 4.8	8.9 ± 5.7
Soil conditions					
15	Soil moisture	VWC[b]	49.9 ± 12.3	41.9 ± 14.3	41.1 ± 14.4
16	Soil penetrability	kg/cm^2	0.9 ± 0.5	1.2 ± 0.7	1.3 ± 0.6

[a] Expressed in radians
[b] Volumetric water content

Finally, we investigated the seasonal pattern of the best predictors of foraging habitat selection, i.e. those for which a significant relationship was detected in at least one of the two orders of selection. We built linear mixed-effects models with each key predictor as a response variable, using *lmer* from package 'lme4' (Bates *et al.* 2015). When necessary, we transformed the response variable to meet a normal distribution and checked model assumptions looking at standard residual plots (residuals vs. fitted values, QQ-plot of the residuals). As explanatory variables, we included date and year of sampling, as well as plot type, which was either foraging or PA (PAs of both distance ranges were grouped together). In addition, interaction terms between date and year, and date and plot type, were included in all models as fixed effects, and individual identity and stratum as nested random effects; 95% credible intervals were again drawn from simulations.

RESULTS

In total, we collected 137 foraging locations from 19 radiotagged individuals in 2015, and 71 locations from nine tagged and several untagged individuals in 2017 (ratio 26/45). For 13 radiotagged individuals, we could not record any foraging locations, as we either lost the signal, they did not breed, or the brood failed early on. For model evaluation over a wider range, we collected 53 foraging locations from untagged individuals across 16 different areas (1–11 locations per area). Out of the measured habitat variables, only AG cover and green grass cover were strongly correlated ($r = -0.75$). We excluded the latter, as the mean cover percentage was the highest across all plots, and removing it relaxed the unit-sum constraint of ground cover variables. All variables in our models had a VIF < 3.

Foraging habitat selection at the site scale

A final set of 4 models (ΔAICc < 2) was obtained for the analysis of habitat selection at the scale of the foraging site. The best-ranked model explained a relatively low proportion of variance $R^2 = 0.19$, with an AUC ± sd from the cross-validation equal to 0.70 ± 0.07. Performance based on the evaluation dataset was also fairly low (AUC = 0.64). All variables showed consistent coefficient estimates in the four different models, and hence their respective effects were considered to be well represented by the first-ranked model (Table 2). AG cover had a positive effect on occurrence probability ($\beta \pm \text{se} = 0.24 \pm 0.11$, $P = 0.03$), but the quadratic term was retained as well, suggesting a hump-shaped relationship (Fig. 2), despite not being significant ($\beta \pm \text{se} = -0.17 \pm 0.11$, $P = 0.12$). For soil moisture, the presence of an optimum was clear (linear: $\beta \pm$ se = 0.65 ± 0.12, $P < 0.001$; quadratic: -0.33 ± 0.12, $P < 0.01$) with a peak in occurrence probability at 64% VWC (Fig. 2), whereas soil penetrability had a negative effect ($\beta \pm$ se = -0.34 ± 0.13, $P < 0.01$), i.e. birds avoided impenetrable soils. These two soil condition variables were ranked as the most important (Table 2). A negative relationship with green grass height was highlighted only in the third-ranked model (Supplementary Materials, Table S1) and had the lowest variable importance overall (Table 2).

Table 2 Variables retained in the set of best models within ΔAICc < 2, in the analysis of foraging habitat selection at the site and the home-range scale, respectively. Coefficient estimates, *Z*- and *P*-values are from the best-ranked model in each analysis, whereas importance of the variable (from 0 to 1) is the sum of Akaike weights from the models where it appears out of all model combinations.

	Variable	Estimate ± se	*Z*-value	*P*-value	Importance
Site scale					
	AG cover	0.24 ± 0.11	2.14	0.033	0.85
	AG cover^2	-0.17 ± 0.11	-1.55	0.121	0.51
	Soil penetrability	-0.34 ± 0.13	-2.67	0.008	0.96
	Soil moisture	0.65 ± 0.12	5.24	< 0.001	1.00
	Soil moisture^2	-0.33 ± 0.12	-2.77	0.006	0.95
	GG height	–	–	–	0.51
Home-range scale					
	AG cover	0.22 ± 0.13	1.70	0.089	0.94
	AG cover^2	-0.27 ± 0.12	-2.19	0.028	0.69
	Soil penetrability	-0.64 ± 0.15	-4.41	< 0.001	1.00
	Soil moisture	0.49 ± 0.14	3.62	< 0.001	1.00
	Soil moisture^2	-0.42 ± 0.12	-3.44	< 0.001	1.00
	GG Height	-0.37 ± 0.15	-2.49	0.013	0.91
	Mineral cover	-0.21 ± 0.13	-1.55	0.122	0.49
	Northness	0.21 ± 0.12	1.76	0.078	0.63
	GG height x AG cover	–	–	–	0.36

AG cover: accessible ground cover; GG height: green grass height; ^{2}: quadratic term of a variable; x: interaction between two variables

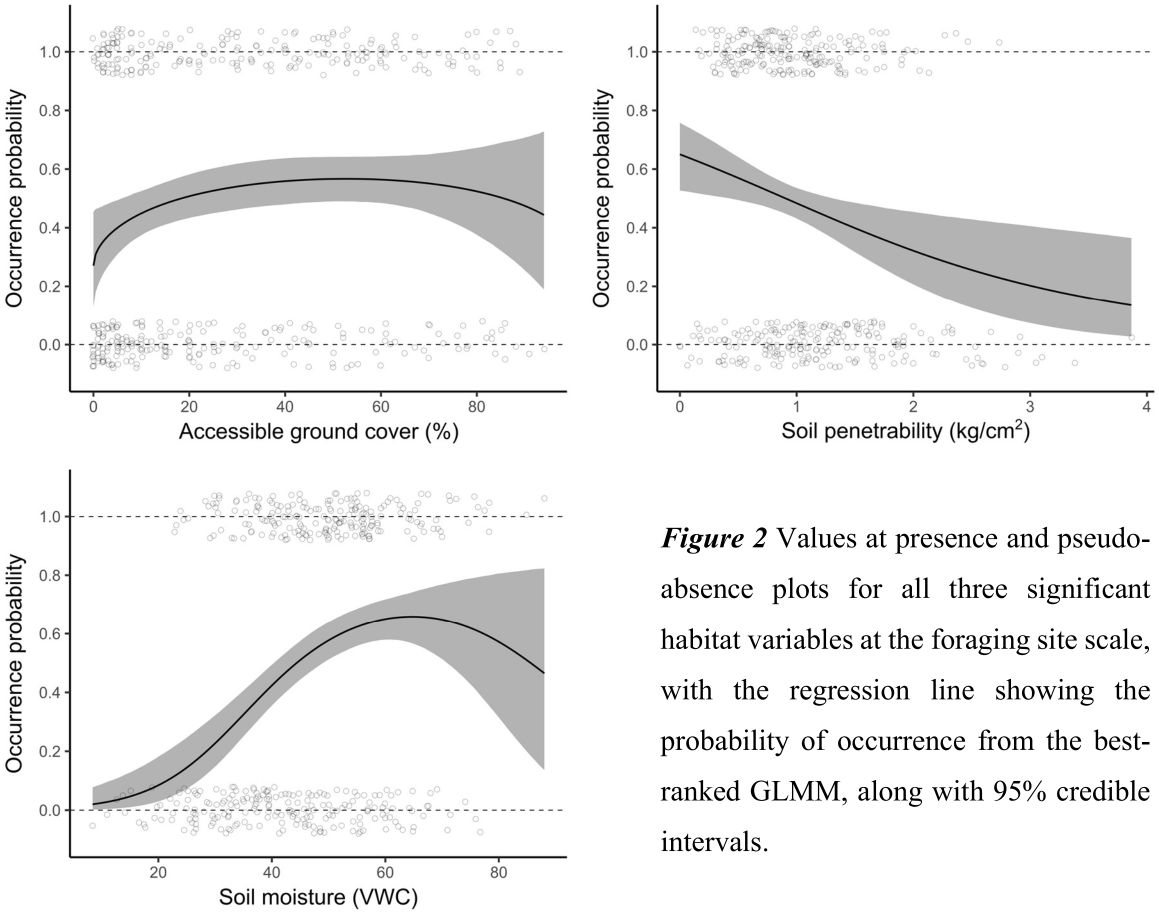

Figure 2 Values at presence and pseudo-absence plots for all three significant habitat variables at the foraging site scale, with the regression line showing the probability of occurrence from the best-ranked GLMM, along with 95% credible intervals.

Foraging habitat selection at the home-range scale

The analysis of foraging habitat selection at the home-range scale yielded a final set of four models. The best-supported model showed a higher performance than the site scale model for all three evaluation metrics considered: $R^2 = 0.33$, cross-validation AUC ± sd = 0.77 ± 0.10 and evaluation dataset AUC = 0.69. All variables showed consistent coefficient estimates in the four models, so that we again considered the first-ranked model to be representative of the set (Table 2). Again, soil moisture (linear: β ± se = 0.49 ± 0.14, $P < 0.001$; quadratic: -0.42 ± 0.12, $P < 0.001$) and penetrability (β ± se = -0.64 ± 0.15, $P < 0.001$) were the most important predictors (Table 2), with, in addition, a potential optimal range of moisture around a peak at 41% VWC (Fig. 3), i.e. somewhat lower than at the foraging site scale. At this order of selection, green grass height (β ± se = -0.37 ± 0.15, $P = 0.01$) was much more important than at the site scale (0.91; Table 2), with a clear selection for short grass swards (Fig. 3). The hump-shaped relationship with AG cover (linear: β ± se = 0.22 ± 0.13, $P = 0.09$; quadratic: β ± se = -0.27 ± 0.12, $P = 0.03$) was more supported than at site scale (Fig. 3; Supplementary Materials, Table S1). Finally, we detected a positive effect of northness (β ± se = 0.21 ± 0.12, $P = 0.08$), indicating a selection for north-facing slopes, and a negative effect of mineral cover (β ± se = -0.21 ± 0.13, $P = 0.12$), although those variables were not significant and ranked among the last in importance (Table 2).

Seasonality of key habitat variables

Models of seasonality were fitted only for the key habitat predictors retained in the dual foraging habitat selection analysis, namely, AG cover, green grass height, soil moisture and soil penetrability. The type of plot had a significant effect in all four models (Table 3), which means that the difference between foraging and PA plots was consistent throughout the breeding season for all four habitat variables (Fig. 4). The significant effect of date indicated a clear seasonal change in AG cover (β ± se = -0.15 ± 0.08, $P = 0.05$) and soil moisture (β ± se = -0.35 ± 0.07, $P < 0.001$), both decreasing, whereas grass height (β ± se = 0.44 ± 0.07, $P < 0.001$) progressively increased (Table 3; Fig. 4). For soil penetrability, the effect of date was positive but marginally significant (β ± se = 0.12 ± 0.07, $P = 0.07$). Furthermore, an effect of year on AG cover, soil moisture and soil penetrability was evident, with different intercepts in different years (Table 3), indicating a varying spring phenology. Only for soil moisture did the slope of the regression line differ significantly between 2015 and 2017, as indicated by the interaction between year and date (β ± se = 0.35 ± 0.12, $P < 0.01$; Table 3). Finally, the interaction between the type of plot and date was never significant ($P > 0.25$ for all variables), which indicates a similar seasonal pattern in both actual foraging and PA plots.

Table 3 Summary table of the coefficient estimates ± se from the linear mixed-effect models fitted for each of the four key habitat predictors. Explanatory variables are type of plot (presence/pseudo-absence), year (2015/2017) and date, as well as their interaction terms.

	Response variable			
	Soil moisture	Soil penetrability	Green grass height	AG cover
Presence	0.59 ± 0.06 ***	-0.49 ± 0.07 ***	-0.46 ± 0.06***	0.42 ± 0.06***
Date	-0.35 ± 0.07 ***	0.12 ± 0.07 ·	0.44 ± 0.07***	-0.15 ± 0.08*
Year 2017	0.30 ± 0.14 *	0.42 ± 0.13 **	-0.31 ± 0.19	0.46 ± 0.17**
Date x Year 2017	0.35 ± 0.12 **	-0.15 ± 0.12	0.16 ± 0.13	-0.17 ± 0.13
Date x Presence	-0.07 ± 0.06	-0.03 ± 0.07	-0.03 ± 0.06	0.01 ± 0.06

Level of significance is indicated with symbols: · $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

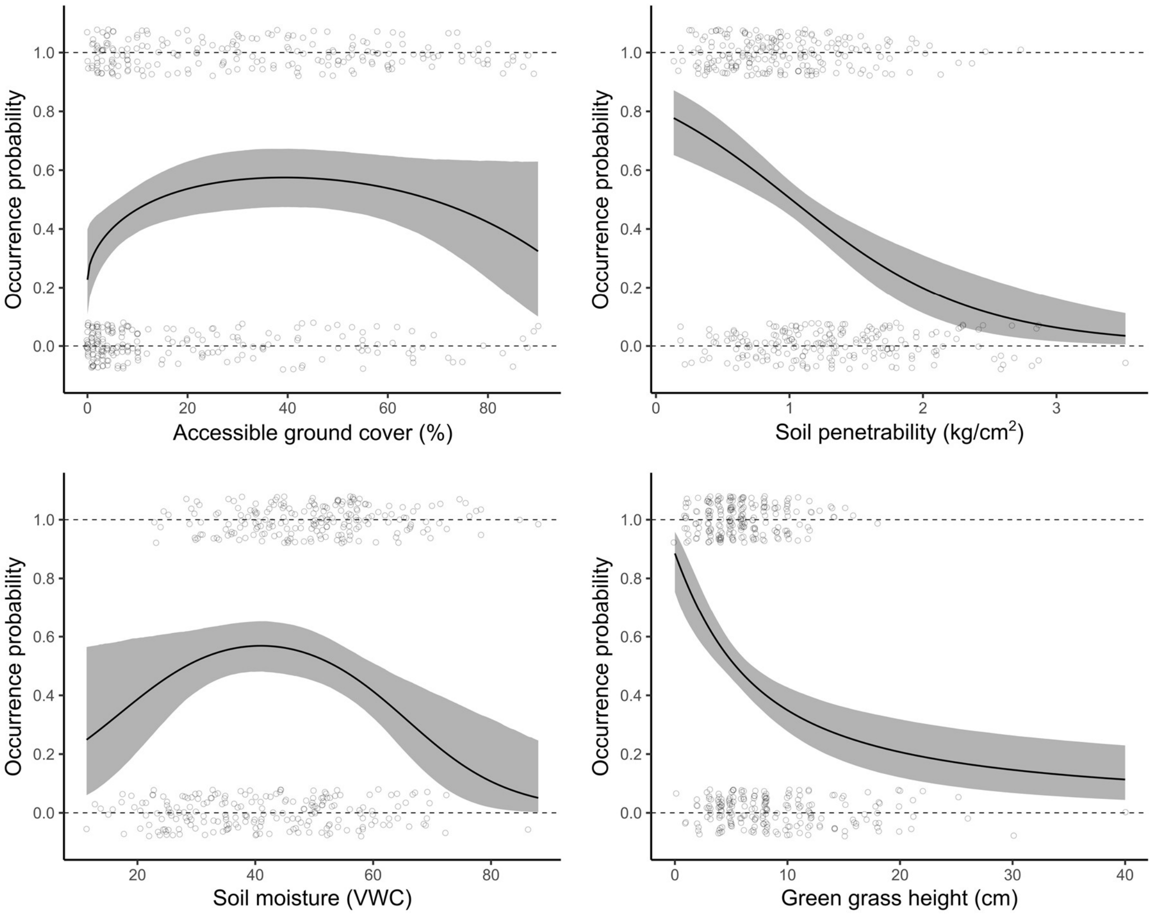

Figure 3 Values at presence and pseudo-absence plots for all four significant habitat variables at the home-range scale, with the regression line showing the probability of occurrence from the best-ranked GLMM, along with 95% credible intervals.

DISCUSSION

The present study delivers new insights into the fine-grained species-habitat associations of Alpine Ring Ouzel parents during the energetically critical period of nestling provisioning. It sheds light, in particular, on the challenges this emblematic passerine of treeline ecosystems is likely going to face in an era of rapid environmental change. Birds preferentially foraged in sites with intermediate soil moisture, high soil penetrability and short ground vegetation interspersed with accessible ground. Our models further emphasize the sheer spatio-temporal variability in these key variables, highlighting in particular the need to finely match reproductive effort with the narrow time window of optimal foraging conditions.

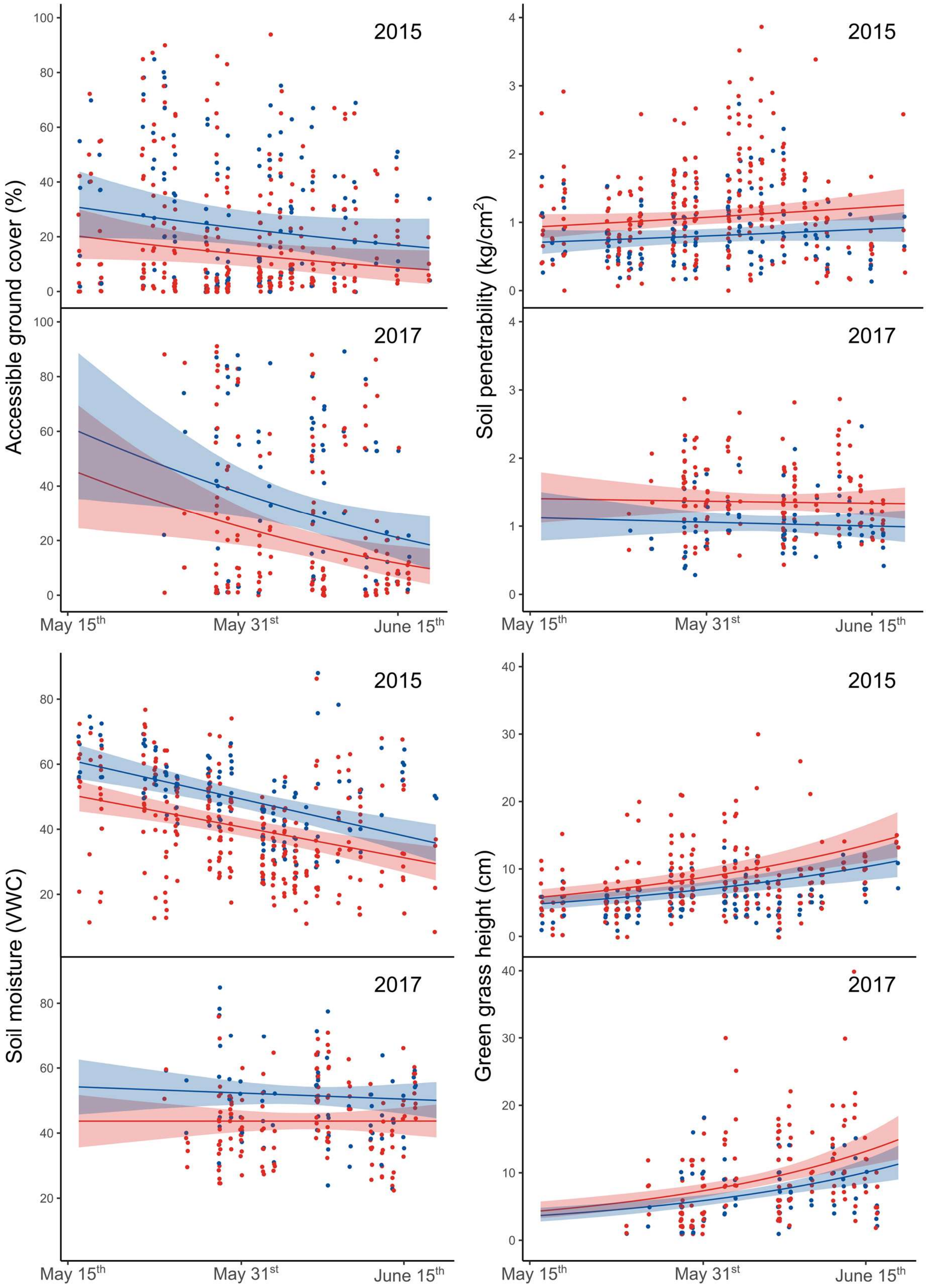

Figure 4 Relationship between each of the four key predictors and date during two different breeding seasons (2015 and 2017) at foraging (in blue) and pseudo-absence plots (in red) from the respective fitted linear-mixed models, along with 95% credible intervals.

When comparing the two different orders of habitat selection considered here (Johnson 1980), the model of habitat selection at the foraging site scale was unsurprisingly less accurate than at the home-range scale. An increasing predictive difficulty towards higher orders of selection, i.e. finer scales, is common in studies of habitat use (Fattebert *et al.* 2018) and can be explained by the fact that PA plots that are randomly selected in the close surroundings of the foraging plot are more likely to present habitat characteristics similar to those of the foraging plot itself. Indeed, we cannot rule out that our PA plots, although reflecting true absences at the very time of a given foraging observation, might have been visited by the same bird earlier or later on for foraging. Therefore, the metrics considered for evaluating model predictive performance, which assume no false negatives (i.e. false absences), are usually underrated (e.g. maximum AUC < 1). In addition, as regional evaluation data were collected in a different year (2016) to radiotracking data (2015 and 2017) due to logistic constraints, inter-annual variability in snowmelt phenology may also have influenced the predictive performance of our models. When taking these limitations into account, as well as the fine scale of our analysis (1-m radius), the overall performance of our models from the cross-validation and on the regional evaluation dataset can be deemed to be fairly good. Therefore, we consider that the significant selection patterns evidenced here are temporally consistent and can be generalized to the western central Alps, which harbour a significant fraction (ca. 20%) of the Swiss Alps, if not beyond to the entire Alpine massif.

Soil conditions and ground vegetation cover and structure were the most important predictors of foraging habitat selection in our study. Those parameters have been repeatedly highlighted as crucial for several ground-foraging bird species (Atkinson, Buckingham & Morris 2004; Gilroy *et al.* 2008; Schaub *et al.* 2010). Most of those studies have shown that these relationships are driven by prey availability, i.e. prey abundance modified by its accessibility. In the case of the Ring Ouzel, prey accessibility is probably driven by both soil penetrability, as prey is extirpated from the upper soil layers via beak probing, and opportunities for terrestrial foraging, which chiefly depends on ground vegetation structure. Even if we did not collect data on invertebrate prey abundance and distribution across our study area, food availability most likely explains the pattern we observed, especially because we restricted our foraging locations to ascertained prey captures.

The two soil condition variables measured here, moisture and penetrability, were the most important predictors of foraging occurrence at both scales considered (site and home-range), with birds selecting soft soils with intermediate moisture levels. Soil moisture is indeed known to strongly influence the biomass and activity of some soil invertebrates, notably earthworms (Edwards & Bohlen 1996; Peach *et al.* 2004). Most species of terrestrial earthworms favour a clear optimum of soil moisture and go either deeper into the soil in response to drought or emerge on the soil surface following heavy rainfall (Edwards & Bohlen 1996). Earthworms have been identified as a main component of the diet of Ring Ouzel chicks across the species' breeding range (Glutz von Blotzheim & Bauer 1988; Burfield 2002), which seems to be corroborated in our study area (ca. 90% of the biomass provisioned by parents; see *Chapter* 2). The avoidance of dry and very moist soils by Ring Ouzels may hence result from reduced earthworm availability under these conditions. This is further supported by a clear avoidance of impenetrable soils that are probably suited neither for earthworms nor for beak probing (Peach *et al.* 2004; Gilroy *et al.* 2008).

The selection for intermediate levels of accessible ground, as provided here by patches of bare soil surfaces and vegetation litter, underlines the importance of small-scale substrate heterogeneity in the foraging microhabitat. Similar requirements were evidenced for a variety of ground-foraging, insectivorous farmland birds (Atkinson, Buckingham & Morris 2004; Schaub *et al.* 2010; Arlettaz *et al.* 2012), but also for some alpine specialists such as the White-winged Snowfinch *Montifringilla nivalis* (Brambilla *et al.* 2017; Resano-Mayor *et al.* 2019). The preference for a heterogeneous microhabitat mosaic has already been demonstrated for foraging Ring Ouzels in the UK (Burfield 2002; Sim *et al.* 2013). The likely mechanism at play is that dense grass swards host a greater abundance of above- and belowground invertebrates (Atkinson, Buckingham & Morris 2004), including earthworms (Edwards & Bohlen 1996), and that walking birds profit from the interspersed open-ground patches enhancing prey detectability and accessibility (Schaub *et al.* 2010). Yet, the strong selection for short grass swards evidenced in this and other studies on the Ring Ouzel (Burfield 2002; Sim *et al.* 2013) indicates that prey accessibility may be traded-off against prey abundance during foraging. Interestingly, the importance of vegetation height was only clearly detected at the larger home-range scale, suggesting that, in the hierarchical process of selection, birds first elect to forage at sites with predominantly short grass, while suitable prey extraction sites are secondarily chosen within the grassy matrix.

Three out of the four key habitat variables driving Ring Ouzel foraging dramatically changed with season: soil moisture and AG cover gradually decreased, whereas ground vegetation height increased. At treeline elevation in the Alps (ca. 1800–2300 m asl), the depth and temporal duration of the snow cover constitute the main environmental drivers (Beniston

2003). In addition to its insulation property in winter, which is appreciated by overwintering Alpine wildlife (Arlettaz *et al.* 2015), the snowpack plays another crucial ecological role in spring, when its melt provides much of the water supply in subalpine and alpine ecosystems (Beniston 2003; Klein *et al.* 2016). First, the water supply resulting from snow, mirrored in our measurements of 2015, showed a progressive seasonal decrease in both average soil moisture and penetrability, while snow was almost fully melted at the study site when the first broods hatched. In 2017, despite a similar snowmelt phenology, both soil condition variables were much more constant across the season, probably as a result of regular precipitation and/or reduced soil desiccation during the entire breeding season. Second, the snowmelt also triggers the onset of the annual vegetation cycle (Inouye *et al.* 2000), thus defining the timing of vegetation growth. Ring Ouzels essentially foraged in very short grass swards, with 90% of the selected foraging sites offering ground vegetation shorter than 10 cm. According to our seasonality model, the mean green grass height in PA plots had already exceeded this value on June 5th and 8th, in 2015 and 2017, respectively. This points to a fairly brief period with suitable foraging conditions and is supported by our own field observations: parents left the breeding grounds towards higher elevations as soon as the brood had fledged, most probably to track suitable feeding grounds. However, we could not collect foraging information after this abrupt change in their whereabouts, as tagged birds became highly mobile and some rapidly left the study area.

Altogether, it appears that highly seasonal variables drive the foraging microhabitat selection of Ring Ouzels in the Alps. As a consequence, the availability of optimal foraging habitat progressively decreases across the period of nestling provisioning, resulting in a restricted time window with suitable conditions for breeding. High elevation specialists are adapted to such extreme environments (Martin & Wiebe 2004), but global environmental change, in particular climate change, represents a new challenge for matching the reproductive period with optimal environmental conditions. Climatic changes are particularly marked in the spring in the Alps, with higher solar radiation and ambient temperatures causing an earlier snowmelt (Klein *et al.* 2016), thereby potentially affecting the breeding success of alpine birds (Martin & Wiebe 2004). In the case of the Ring Ouzel, there is a risk of phenological mismatch due to a possible discordance between the spring peak in prey availability and the timing of breeding, as already predicted for other temperate mountain birds such as the American Robin *Turdus migratorius* (Inouye *et al.* 2000), another species of thrush. However, it is as yet unknown to which extent the Ring Ouzel may adapt to such changes by either advancing its breeding phenology or moving to higher elevations. We can expect that the migration schedule of the species, as a short-distance migrant, could be shifted so as to arrive earlier in the Alps. Moreover, an elevational shift of the breeding population has been observed in Switzerland in the last decades (Knaus *et al.* 2018). This process may nonetheless be limited by the growth of trees, in which most Alpine Ring Ouzels build their nests (Glutz von Blotzheim & Bauer 1988), and, higher up, by the formation of suitable soils, which is a very slow process at high elevations (Chamberlain *et al.* 2012).

Nevertheless, if, as suggested by our results, prey accessibility is vital, adaptive habitat management may to some extent buffer these detrimental effects if not compensate for them (see Braunisch *et al.* 2014; Brambilla *et al.* 2018). Initial measures should consist of maintaining a variegated habitat mosaic, which would be beneficial not only for the Ring Ouzel (von dem Bussche *et al.* 2008), but also for other emblematic species of the Alpine treeline (Jähnig *et al.* 2018), notably the Black Grouse *Lyrurus tetrix* (Patthey *et al.* 2012; Braunisch, Patthey & Arlettaz 2016). In effect, habitat heterogeneity guarantees the retention of suitable foraging sites, which probably explains the close association observed between the Ring Ouzel and the highly diverse and finely structured habitat matrix of the treeline ecotone in the Alps. In this respect, traditional extensive grazing practices, still widespread today in the Alps (Laiolo *et al.* 2004; Schulz, Lauber & Herzog 2018), are expected to benefit this species as well as other ground-foraging birds, notably by reducing the grass sward height and by increasing the availability of patches of bare ground through livestock trampling (Pittarello *et al.* 2016). Traditional pasturing would also limit the risk of encroachment by the woody vegetation of these valuable semi-open wooded grasslands (Laiolo *et al.* 2004; Schulz, Lauber & Herzog 2018). Another risk of habitat degradation stems from the progressive intensification of grasslands through slurry application, which results in a more homogeneous grass sward growing high and dense earlier in the season (Andrey *et al.* 2014). Finally, the development of ski infrastructure could also represent an additional threat, as the use of artificial snow and snow-grooming machines have wide-ranging negative effects on soil characteristics (Rixen, Haeberli & Stoeckli 2004) and their biodiversity (Rolando *et al.* 2007). All this points to a high vulnerability of the Ring Ouzel to the prevailing scenarios of climate and land-use change, which may act either singly or synergistically. In this context, the extent to which suitable alpine breeding habitat can be maintained via management, e.g. targeted grazing, needs further investigations which should optimally consider the potential evolution of agricultural practices and be carried out in controlled experimental setups. Additionally, whether other sympatric species with similar ecological requirements benefit from such practices should be evaluated, as habitat management recommendations formulated here may have far-reaching positive effects for the biodiversity of treeline ecosystems.

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SUPPLEMENTARY MATERIALS

Table S1 Set of best-ranked models from the model selection process within ΔAICc < 2, at the site and home-range scale, respectively.

#	Model	df	AICc	ΔAICc	weight
	Site scale				
1	AGC + AGC^2 + SMoist + SMoist^2+ SPen	8	529.79	0.00	0.37
2	AGC + SMoist + SMoist^2+ SPen	7	530.13	0.34	0.31
3	SMoist + SMoist^2 + SPen + GrGH	7	531.38	1.59	0.17
4	SMoist + SMoist^2 + SPen	6	531.70	1.91	0.14
	Home-range scale				
1	AGC + AGC^2 + SMoist + SMoist^2+ SPen + GrGH + MinCov + North	11	482.67	0.00	0.35
2	AGC + AGC^2 + SMoist + SMoist^2 + SPen+ GrGH + North	10	483.03	0.36	0.29
3	AGC + AGC^2 + SMoist + SMoist^2 + SPen + GrGH	9	483.63	0.96	0.22
4	AGC + SMoist + SMoist^2 + SPen + GrGH + MinCov + North + GrGH x AGC	11	484.62	1.95	0.13

AGC: accessible ground cover; SMoist: soil moisture; SPen: soil penetrability; GrGH: green grass height; MinCov: mineral cover; North: northness; ^{2}: quadratic term; x: interaction

Chapter 2

Nestling diet and parental food provisioning in a declining mountain passerine reveal high sensitivity to climate change

Nestling diet and parental food provisioning in a declining mountain passerine reveal high sensitivity to climate change

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ABSTRACT

Mountain ecosystems naturally experience strong seasonal weather variations leading to a brief peak in food availability that constrains bird reproduction. Climate change accentuates both the intra- and interannual weather variability, which in turn can reduce the predictability of food resources and hence impact population demography. Yet, relatively little is known about the influence of environmental factors on the breeding ecology of mountain birds. Here, we quantified the nestling diet and provisioning behaviour of the Alpine Ring Ouzel (*Turdus torquatus alpestris),* an emblematic and declining thrush species typical of central European treeline ecotones, and relate these parameters to local weather conditions. Nests were monitored with camcorders to assess prey provisioning frequency and identify items delivered by parents to nestlings, as well as to estimate prey biomass. Our results indicate the prominence of earthworms (Lumbricidae) in the nestling diet, both in terms of abundance (80%) and biomass (90%). Elevated ambient temperatures negatively impacted both prey provisioning rates and biomass delivered to chicks by parents, while rainfall had a positive effect on the delivered biomass. The mean prey item biomass decreased throughout the breeding season, as did the proportion of earthworms in nestlings' diet. These findings highlight the key role played by local weather in parental provisioning behaviour, probably reflecting the low availability of the staple food source, earthworms, in warm and dry weather contexts. In particular, they underpin how climate alterations, notably increasing ambient temperatures and changing precipitation regimes, could impact mountain birds. Although effects on reproductive performance and population dynamics still ought to be studied, these results further our understanding of the ecological mechanisms potentially at play in the decline of wildlife inhabiting high-elevation, climate-sensitive ecosystems.

Keywords: earthworms, nest monitoring, Ring Ouzel, temperature, treeline, weather conditions

INTRODUCTION

In highly seasonal environments such as mountain ecosystems, the reproductive period of animals is short because of the particularly narrow time window with suitable climatic conditions and subsequent brief peak in food availability (Pearce-Higgins 2010; McKinnon *et al.* 2012; Boyle, Sandercock & Martin 2016). Invertivorous mountain species also face rapid fluctuations in prey availability triggered by sudden weather variation (Martin *et al.* 2017), which often result in fairly unpredictable food resources in space and time (Rauter, Brodmann & Reyer 2000). High-elevation species have therefore evolved sophisticated behavioural and eco-physiological adaptations to cope with these highly stochastic environmental conditions (Martin & Wiebe 2004; Arlettaz *et al.* 2015) and to match their reproductive effort with peaks in food supplies. Yet, the advancing spring phenology and increasing frequency of extreme weather events, particularly acute in alpine regions (Gobiet *et al.* 2014), represent an additional challenge for high-elevation wildlife (Martin *et al.* 2017; Scridel *et al.* 2018; de Zwaan *et al.* 2020).

For birds, the relationships between weather conditions and prey availability, which is prey abundance modified by its accessibility (Schaub *et al.* 2010; Douglas & Pearce-Higgins 2014), have been extensively documented. For example, movements of belowground invertebrates are ruled by weather-dependent soil conditions that are of prime importance for ground-foraging invertivorous species (Edwards & Bohlen 1996; Peach *et al.* 2004; Martay & Pearce-Higgins 2020). Similarly, rainfall and low ambient temperatures reduce the activity of many aboveground insects, resulting in temporarily low prey availability (Siikamäki 1996; Winkler, Luo & Rakhimberdiev 2013; Perez *et al.* 2016; Schöll & Hille 2020). As a crucial driver of breeding success, seasonal prey availability is key for population persistence of short-lived species (Siikamäki 1996; Naef-Daenzer, Naef-Daenzer & Nager 2000; Pearce-Higgins *et al.* 2010), so that weather conditions generally have a strong influence on bird population dynamics (Sæther, Sutherland & Engen 2004). In effect, weather-mediated food availability can impact nestling growth rates, fledging success, and also post-fledging survival (Geiser, Arlettaz & Schaub 2008; McKinnon *et al.* 2012; Martin *et al.* 2017; de Zwaan *et al.* 2019; Schöll & Hille 2020). The combination of background climate alterations and increased occurrences of extreme weather events may thus profoundly affect passerines breeding at high elevations (Pearce-Higgins 2010; Martin *et al.* 2017). This risk may even be more acute for migratory species, given the increased probability of a temporal mismatch between reproduction and the peak in food supplies (Visser, Both & Lambrechts 2004). Altogether, this calls for fine-grained mechanistic appraisals of the factors influencing optimal foraging strategies and reproductive tactics of mountain bird species (Chamberlain *et al.* 2012).

The Ring Ouzel (*Turdus torquatus)* is a migratory thrush species living in the mountain massifs of central and eastern Europe, the UK and Fennoscandia (Glutz von Blotzheim & Bauer 1988). Although demographically stable in various areas of its range (Lehikoinen *et al.* 2019), the species has undergone a recent but steady decline in Switzerland, where ca. 15% of the European population breeds (Knaus *et al.* 2018), and in the UK (Wotton *et al.* 2016). Climate change is considered as the most likely driver of the observed decline in Swiss populations occurring at low elevations, which resulted in an apparent upward range shift (Maggini *et al.* 2011; Knaus *et al.* 2018). In the UK, one of the underlying mechanisms is believed to be warmer summers that reduce prey availability after the breeding season (Beale *et al.* 2006). In effect, Ring Ouzels rely on specific habitat characteristics for efficient foraging that are highly seasonal and temporally limited, showing a preference for relatively high soil moisture and a short grass sward interspersed with bare and litter-covered ground (Sim *et al.* 2013; Barras *et al.* 2020; *Chapter 1*). The earlier onset of vegetation growth and reduction in soil moisture induced by warmer ambient temperatures, as well as more frequent droughts, may indeed drastically reduce the availability of belowground invertebrates (Peach *et al.* 2004; Pearce-Higgins 2010). This might induce food shortage, affecting both fledging success and post-fledging survival (Sim *et al.* 2015) and in turn negatively impacting demographic trajectories (Sim *et al.* 2011). Yet, quantitative evidence about the mechanisms at play is still lacking for the Ring Ouzel, as for many other mountain bird species.

Based on nest video monitoring in the Alps, we assessed, first, the diet composition of Ring Ouzel nestlings to identify key food resources during reproduction. Second, we quantified parental food provisioning activity, delivered prey biomass and female nestling attendance throughout the nestling period. Third, we related these measures to local weather factors, namely ambient temperature, precipitation, sunshine duration, and wind. Fourth, we explored how brood characteristics such as age and number of nestlings influence food provisioning. Finally, we assessed the seasonal variation in the mean dry weight and proportion of prey in the nestling diet.

MATERIALS AND METHODS

Study area and study species

The study area is situated in the Swiss Bernese Alps, in the canton of Valais (46.33 N, 7.43 E), spanning an altitudinal gradient between 1800 and 2200 m above sea level. The area covers around 200 ha and consists of a wooded summer pasture, characterized by a semi-open landscape where grasslands are interspersed with coniferous tree stands (European larch *Larix decidua* and Norway spruce *Picea abies)*, a typical breeding habitat for the Alpine Ring Ouzel *T. t. alpestris* (Glutz von Blotzheim & Bauer 1988). From standardized monitoring surveys of the whole area over the period 2015–2020 (three spring visits at dawn following a predefined walk transect), we estimated on average 40.7 territories/100 ha (see *Chapter 3*), i.e. a very high density for the Alps (Knaus *et al.* 2018).

Ring Ouzels are single-brooded in the study area, as assessed reliably with radiotracking during two breeding seasons (2015 and 2017; see *Chapter 1*), and we assume that this is the most common reproductive strategy in the Alps. Nests are built in trees, mostly in larches close to the trunk, at a height from 1.5 to 18 m. Females take care of nest building and brooding, with very few exceptions of male assistance in these tasks. Most birds leave the study area immediately after reproduction, before the end of June, partly spending the post-breeding period at higher elevations (Glutz von Blotzheim & Bauer 1988). Migration to overwintering grounds in southern Spain and North Africa occurs mostly in September and October (Glutz von Blotzheim & Bauer 1988; *Chapter 4*).

Data collection

Between April and June 2019, nests were located either during monitoring surveys (described above) or during specific weekly nest-searching sessions over the whole study area. Most nests were found by observing individuals carrying nest material, alarm displays or when incubating females were incidentally flushed. We checked nests regularly (every second or third day) from the ground, using a video camera mounted on a perch, in order to identify date of hatching and to record nestling age. Video monitoring was conducted on a subset of the nests (n = 12); those that were not readily accessible were discarded to minimize potential disturbances. Suitable nests had to be reachable with an 8-m ladder and offering the possibility to fix the video system nearby. The video set was attached to a tree 1–3 m from the nest and covered with a camouflage net (see picture in the Supplementary Materials, Fig. S1). It consisted of a Panasonic HC-V180 camcorder coupled with a 20,000 mAh power bank to film continuously.

Because the nestlings are not able to thermoregulate in their early days after hatching, no video monitoring took place until they were at least three days old. Fledging occurs usually at the age of 12–14 days. We aimed to film each nest twice, once during the first week (days 3–8) and once during the second week (days 9–14), in order to capture potential changes in the provisioning activity throughout the nestling period. However, due to logistic constraints or late nest discovery, only 8 out of 12 nests were filmed twice. A day of filming lasted approximately from 6 am to 9 pm. The video system was always installed at least one day before monitoring to ensure that birds get accustomed to its presence and would adopt a normal behaviour. In addition, we always discarded the first hour of video footage to avoid any bias in the estimates of provisioning rates due to potential disturbances when initiating the system at dawn.

On days of video monitoring, we recorded several weather variables. Ambient temperature was measured on an hourly basis using two iButtons (DS1921G-F5; Thermochron, Baulkham Hills, Australia) placed in a constantly shaded place at 0.5 m above ground in the centre of the study area. Hourly precipitation (mm/h) information was retrieved from the nearest weather station (Anzère: 46.305 N, 7.408 E, 3.2 km distance; MeteoSwiss) while information on sunshine duration (min/h) and wind speed (m/s) came from another nearby meteorological station (Montana: 46.299 N, 7.461 E, 4.1 km distance; MeteoSwiss), because these data were not available from the closer station. Since the range of hourly rainfall during video monitoring sessions was rather small (0.0–3.9 mm/h) and we did not expect a linear relationship with provisioning activity over this small range, we transformed this variable into a binary factor of precipitation occurrence.

Analysis

Diet composition

To assess diet composition, prey items were identified to order or family level, with the number of items delivered in each prey load quantified as accurately as possible, which was possible for all video monitored nests except one due to low image quality (n = 11). Earthworms (Lumbricidae) were visually assigned to a body size category: small, medium or large, estimated relative to bill length (small: shorter than the bill length, medium: less than twice the bill length, large: more than twice the bill length). To estimate biomass, we relied on estimates of the mean dry weight for each prey category (Supplementary Materials, Table S1). The dry biomass of Arachnida, Coleoptera adults and larvae, Lepidoptera larvae and adults, Hymenoptera, Diptera and Tipulidae larvae was retrieved from samples collected in a parallel study on the White-winged Snowfinch (*Montifringilla nivalis*) carried out in high-elevation habitats in the same region (Resano-Mayor *et al.* 2019). The mean dry biomass of earthworms was estimated from individuals sampled directly in the study area (10–20 individuals per size category). To increase sample size for nestling diet, we also considered pictures of provisioning parents taken between May 30th and June 13th, 2017, in the same study area from four nests ($n_{2017+2019} = 15$). Those pictures had been taken from a hide on the ground with a digital camera equipped with a 600 mm telephoto lens.

Provisioning rates

All analyses were performed in the software R 3.6.2 (R Development Core Team 2019). We first considered hourly provisioning rates, i.e. the number of provisioning events per hour. We distinguished rates either while pooling the data of two parents together (hereafter called 'sex-independent') or from data on males and females separately (hereafter 'sex-specific'). Sex-specific provisioning rates were readily estimated as parents are easy to distinguish from plumage colouration. Data was available for 12 different broods, including one where only the female was provisioning. We analysed the impact of ambient temperature, rainfall, sunshine duration and wind on both sex-independent and sex-specific parental provisioning rates. Prior to the analysis, Pearson's correlation coefficients (r) within any pair of explanatory variables were checked for collinearity but no $|r|$ was ≥ 0.7 (Dormann *et al.* 2013). All continuous explanatory variables were standardized (mean = 0 and standard deviation (sd) = 1) to enable comparison of effect sizes from model estimates.

In order to identify the best model explaining variation in provisioning rates (either sex-independent or sex-specific), we followed a two-stage selection approach, where a full model was first fitted (Supplementary Materials, Table S2), followed by a ranking of all possible nested models. The full model was specified as a mixed-effects model with all four weather variables as fixed factors, as well as time of day (linear and quadratic terms) since bird provisioning activity typically follows a daily unimodal pattern (Low *et al.* 2008). In addition, sex (factor coding for male or female) and interaction terms between sex and temperature, and sex and precipitation, were included as fixed effects in the sex-specific model. The non-independence of repeated measurements at the same nest and on the same day was accounted for with nested random intercepts ('nest' within 'day'). In order to select the most appropriate error distribution and to check for model assumptions fulfilment, we performed a visual assessment of the QQ-plots and scatter plots of the residuals. Based on that, we opted for a normal linear mixed-effects model (LMM) for sex-independent provisioning rates, and for a generalized LMM with Poisson error distribution for sex-specific rates. The latter Poisson LMM was also checked for overdispersion. We verified that there was no pattern of temporal autocorrelation in the model residuals with autocorrelation function plots, using the *acf_resid* function from the R-package 'itsadug' (van Rij, Martijn & Baayen 2017). Models were fitted using the *lmer* and *glmer* functions in the 'lme4' package (Bates *et al.* 2015).

Once the appropriate structure for the full model was defined, we proceeded with the second step, ranking candidate models (i.e. models with all possible combinations of explanatory variables from the full model) based on the Akaike Information Criterion adjusted for small sample size (AICc). Candidate models were ranked by AICc in ascending order using the *dredge* function from the 'MuMIn' package (Bartoń 2019). We reported all models within ΔAICc < 2 from the first-ranked one (i.e. competitive models), after the exclusion of models with uninformative parameters, i.e. more complex versions of better-ranked models resulting in higher AICc values (Arnold 2010). We also calculated marginal and conditional R^2 values of competitive models following Nakagawa and Schielzeth (2013), to evaluate the proportion of explained variance.

Biomass

From the number of identified prey items and their reference dry weight, we could also estimate the taxon-specific and total provisioned dry biomass. However, all prey items could not be identified, due to unfavourable light conditions or a partially hidden prey load in some provisioning events. Therefore, we used the mean biomass per provisioning event over an hour (hereafter mean biomass) rather than the sum of provisioned biomass. We discarded hours with incomplete data, i.e. in which prey items were quantified in less than 75% of the provisioning events, which concerned 46/240 (19.2%) hours in the sex-independent analysis and 109/468 (23.3%) hours in the sex-specific. One of the 12 nests was discarded as light conditions were too poor to allow prey identification. We followed the exact same two-stage selection approach as for the provisioning rates to identify top models explaining variation in the mean prey biomass per provisioning event. In this case, both sex-independent and sex-specific models were fitted as LMMs with a normal error distribution. No pattern of temporal autocorrelation was evidenced. As several models on the biomass suffered from singularity, we removed the random effect ‘day of year’ in the candidate models.

After identifying the top models explaining biomass variation of all prey categories considered together, we also aimed to describe how important weather variables influenced the biomass proportion of the main food source in the diet, namely earthworms. We thus fitted univariate normal LMMs for rainfall and temperature with earthworm biomass proportion (logit-transformed) as a response variable, considering only sex-independent data.

Nestling attendance

We measured nestling attendance as the time each female individual of a nest spent brooding in min/h (males never brooded). Again, we followed a similar approach to model variation in female nestling attendance as for the provisioning rates and delivered biomass. Data was available from 12 different nests. Yet, no acceptable model fit was obtained, due to the high frequency of hours with no attendance at all, especially in the second week. In addition, visual inspections of temporal autocorrelation plots revealed potential issues for several days and nests. For this part of the analysis, we thus only present descriptive statistics (mean ± sd) in relation to weather variables and season rather than model estimates.

Brood age and size

As information about the age and number of nestlings was not included in previous models, we wanted to describe potential relationships of the brood characteristics with parental provisioning rates, delivered biomass and female nestling attendance. We fitted univariate models for each of the three response variables and two explanatory variables, resulting in six models, without using any model selection approach. For this purpose, each of the response variables was averaged at the day level to avoid pseudoreplication and we again used normal LMMs with ‘nest’ as a random factor.

Seasonal patterns

Finally, we explored the seasonal trends in two parameters, namely prey weight and biomass proportion of earthworms. Prey weight was defined as the mean dry weight per delivered prey item (mg/item) over an hour. The biomass proportion of earthworms was again logit-transformed prior to model fitting. For each of these two variables, we used a normal LMM with linear and quadratic terms of date as fixed factors and nest identity as a random effect.

RESULTS

In 2019, the Ring Ouzel breeding season was slightly delayed compared to previous study years due to late and heavy snowfalls. We have indications that some of the earliest nesting attempts failed due to these adverse weather conditions, but those were not concerned by our video monitoring. Altogether, we found 28 nests with a confirmed reproduction attempt. At least 18 broods (64.3%) fledged, while two nests were depredated, one at egg stage and another one at an early nestling stage. The fate of the remaining nests is unknown. In two out of the twelve nests that were video monitored, we observed the loss of the smallest nestling between the first and the second video session. There were, on average, 3.4 nestlings (range 1–5) that fledged per successful nest monitored in 2019, with hatching spanning from May 27th to June 13th.

Diet composition

We identified 3998 prey items (n_{2017} = 450, n_{2019} = 3548) from 15 different nests (n_{2017} = 4, n_{2019} = 11) (Supplementary Materials, Table S1). In both years, earthworms constituted the bulk of the nestling diet, with a median (± median absolute deviation) per nest of 80.5 ± 13.5% of the items provisioned by parents and 90.1 ± 9.3% in terms of biomass (Fig. 1). Insect larvae were the second most important group in the nestling diet, but most items could not be identified to order level due to insufficient picture resolution. Identified larvae were either Lepidoptera, Coleoptera or Diptera (Tipulidae) (Fig. 1; Supplementary Materials, Table S1). Prey items that could not be identified made up 4.7 ± 3.1% of the total. Other invertebrate groups contributed less than 1% to the median biomass and abundance delivered to the nestlings at each nest.

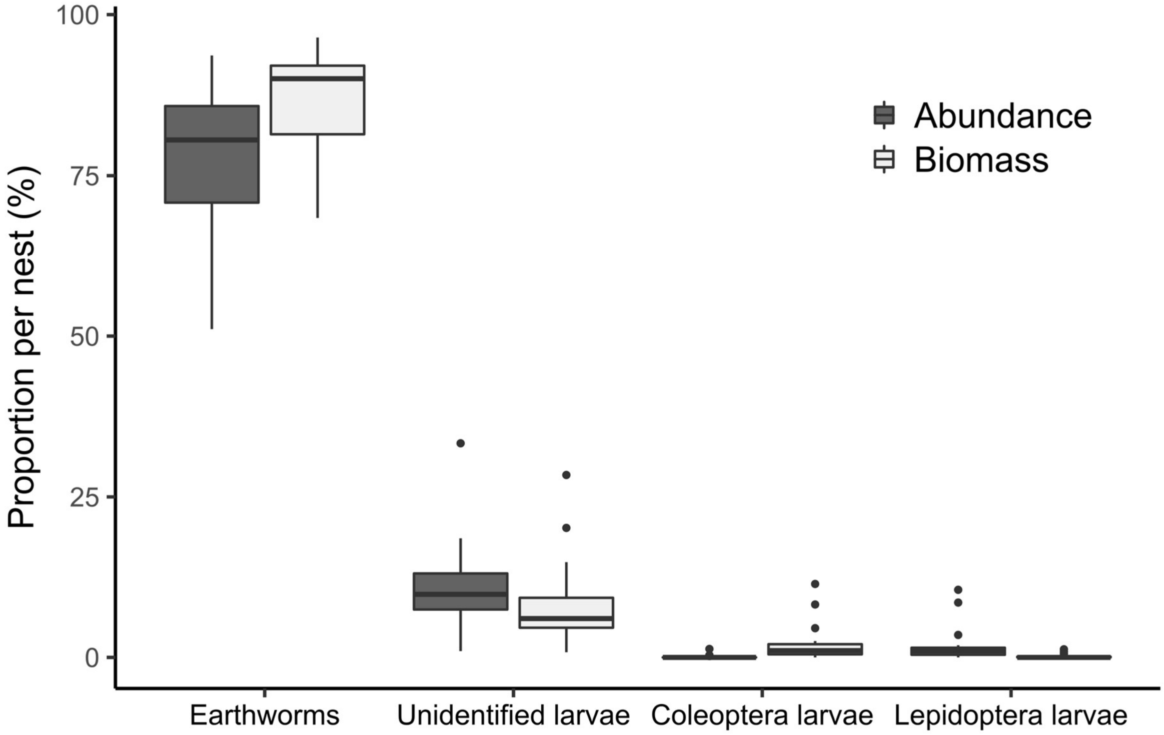

Figure 1 Proportion of the main invertebrate categories entering the diet of Ring Ouzel chicks in terms of abundance and biomass per nest. Prey categories with a median contribution < 1% for both prey abundance and biomass are not shown. Box plots represent the median (horizontal bar) as well as lower and upper quartiles (lower and upper hinges, respectively).

Provisioning rates

Our final dataset contained 1916 provisioning events from 12 different broods while nestlings were 3–13 days old. The mean hourly provisioning frequency (± sd) of the two adults together was 8.0 ± 3.4 (range 0–20). For the sex-independent analysis, we obtained a set of three best-supported models (Δ AICc < 2) from the selection procedure (Supplementary Materials, Table S2). Ambient temperature was retained in all models and had a strong negative effect on provisioning rates (Table 1a; Fig. 2a). Wind speed was as well retained in the top model with a negative effect (Table 1a). The marginal R^2 of the first-ranked model, i.e. variance explained only by fixed effects, was quite low (0.10) compared to conditional R^2 (0.27), indicating substantial variation within and between nests. Model selection for the sex-specific provisioning rates yielded two best-supported models, with again a top model showing negative effects of ambient temperature and wind speed (Table 1b), while sex of the provisioning parent was not retained in any models.

Biomass

The mean delivered biomass (± sd) per provisioning event and nest was 86.4 ± 23.6 mg (range 31.9–163.3 mg). Three best-supported models were obtained from the sex-independent analysis (Supplementary Materials, Table S2). Ambient temperature, as well as time of the day (linear and quadratic terms, unimodal relationship), were retained in all models. Temperature showed a strong negative effect on the provisioned biomass (Table 1c; Fig. 2b), whereas rainfall had a weak positive effect and was retained only in the first model. Again, marginal (0.11) and conditional R^2 (0.37) indicated that random effects explained a larger part of the variance. For the analysis of sex-specific provisioned biomass, three final competitive models were highlighted (Supplementary Materials, Table S2). In contrast to provisioning rates where no sex difference was evidenced, these models showed that males fed on average more biomass to the nestlings than females (Fig. 3). In the first-ranked model, the positive effect of rainfall on the provisioned biomass (Table 1d) was more pronounced than when considering both parents together (Table 1c), yet CI overlapped zero. This effect was replaced by a negative effect of sunshine duration in the second model, while the third model contained only the sex effect (Supplementary Materials, Table S2).

With respect to rainfall and temperature effects on the biomass proportion of earthworms, we showed a negative effect of high ambient temperature (β = -0.23, 95% CI: -0.52–0.07) and a positive effect of precipitation occurrence (β = 0.32, 95% CI: -0.57–1.21), although uncertainties around estimates were high.

Nestling attendance

Females spent on average (± sd) 7.1 ± 11.5 min/h to brood nestlings during the day (range 0–50 min/h). On average, nestling attendance was higher during precipitation (26.0 ± 12.1 min/h) compared to dry weather (6.1 ± 10.5 min/h), and in the first nestling week (12.8 ± 13.4 min/h) compared to the second week (1.5 ± 4.5 min/h). In the first week, nestling attendance was higher at low (15.2 ± 13.0 min/h) compared to high ambient temperatures (7.7 ± 13.0 min/h), considering the median temperature (13.5 °C) as a cutoff value.

Table 1 Coefficients estimates and 95% confidence intervals (CI) of the best-ranked model from the analyses of (a, b) provisioning rates and (c, d) delivered prey biomass in relation to weather variables and time of the day. (a, c) refer to sex-independent models while (b, d) are estimates based on individual, sex-specific models.

Variable	Coefficient estimate	Confidence interval	
		2.5%	97.5%
a. Provisioning rates, sex-independent			
Ambient temperature	-1.00	-1.63	-0.40
Wind	-0.46	-0.93	0.00
b. Provisioning rates, sex-specific			
Ambient temperature	-0.13	-0.21	-0.05
Wind	-0.06	-0.12	-0.00
c. Delivered mean prey biomass, sex-independent			
Ambient temperature	-8.16	-13.48	-2.84
Time of day	4.06	0.53	7.59
Time of day^2	-4.97	-9.19	-0.75
Rain occurrence (yes)	9.44	-2.80	21.69
d. Delivered mean prey biomass, sex-specific			
Rain occurrence (yes)	12.57	-0.43	25.58
Sex (male)	16.64	10.55	22.71

Variables names are displayed in bold if CI do not overlap zero

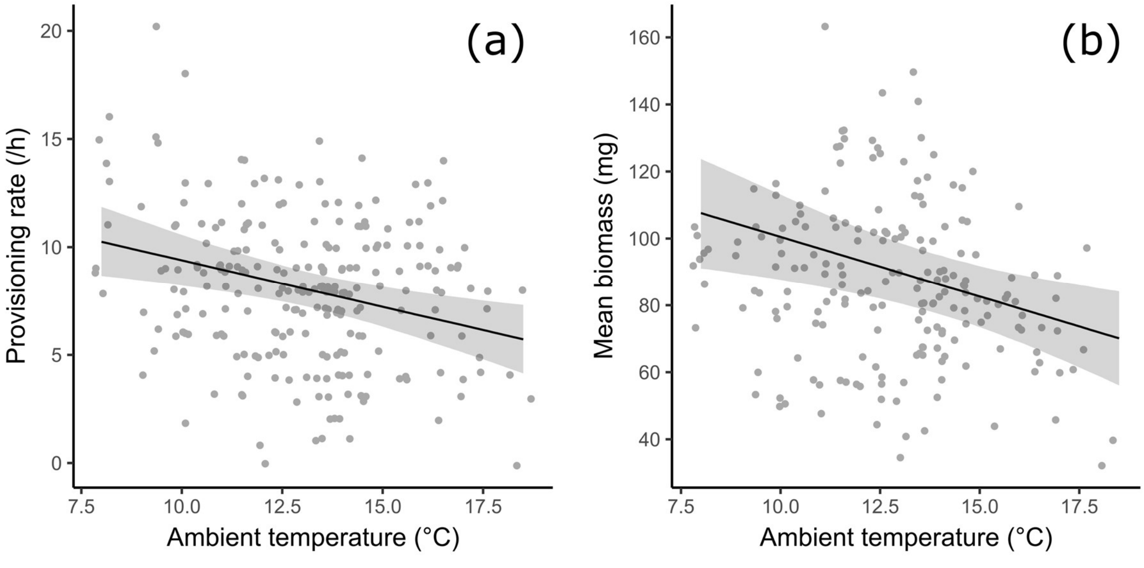

Figure 2 Relationships between (a) hourly provisioning rates and (b) hourly mean delivered prey biomass per feeding event vs. ambient temperature. Regression lines and 95% Bayesian credible intervals stem from the first-ranked model in the respective sex-independent analyses.

Brood age and size

The number of nestlings positively affected daily provisioning rates while their age had no clear effect (Table 2). On the contrary, the age of nestlings had a strong negative effect on attendance by the female, whereas we could not show any effect of brood size. Finally, neither the age nor the number of nestlings had detectable effects on the daily delivered biomass (Table 2).

Seasonal patterns

The mean dry weight of prey (± sd) was 41.5 ± 12.3 mg/item (range 14.2–83.3 mg, excluding an outlier at 112.6 mg). It showed a unimodal relationship with date (linear: $\beta = 0.49$,95% CI: -2.05–3.02; quadratic: $\beta = -2.19$, 95% CI: -3.96–-0.42), with a temporal decrease towards the end of the breeding season (Fig. 4a). The same seasonal decrease was evidenced for the biomass proportion of earthworms in the diet (Fig. 4b; linear: $\beta = 0.16$, 95% CI: -0.14–0.49; quadratic: $\beta = -0.30$, 95% CI: -0.51–-0.09).

Table 2 Coefficient estimates ± 95% CI for brood characteristics (age and brood size) in relation to the daily average in hourly provisioning rates, hourly mean of delivered prey biomass (per provisioning event) and hourly female nestling attendance, as drawn from univariate linear mixed-effects models.

Variable	Coefficient estimate	Confidence interval	
		2.5%	97.5%
Provisioning rates			
Age of nestlings	0.23	-0.47	0.89
Number of nestlings	0.78	0.09	1.48
Delivered mean prey biomass			
Age of nestlings	-5.75	-13.22	1.90
Number of nestlings	2.34	-5.48	10.13
Nestling attendance			
Age of nestlings	-6.90	-10.01	-3.80
Number of nestlings	0.86	-3.63	5.21

Variables names are displayed in bold if CI do not overlap zero.

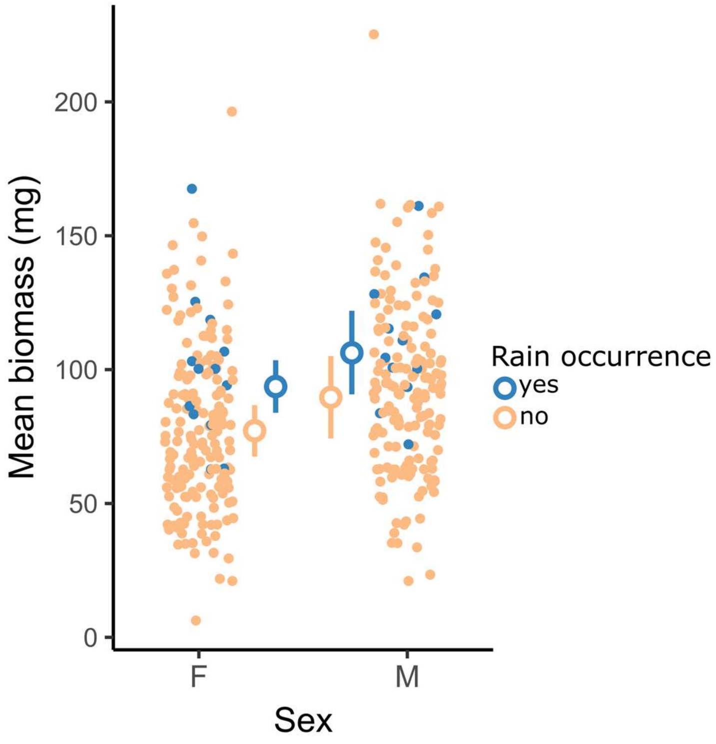

Figure 3 Effects of sex and precipitation occurrence on the hourly mean delivered prey biomass per feeding event. Empty circles depict model estimates and bars 95% Bayesian credible intervals from the first-ranked model.

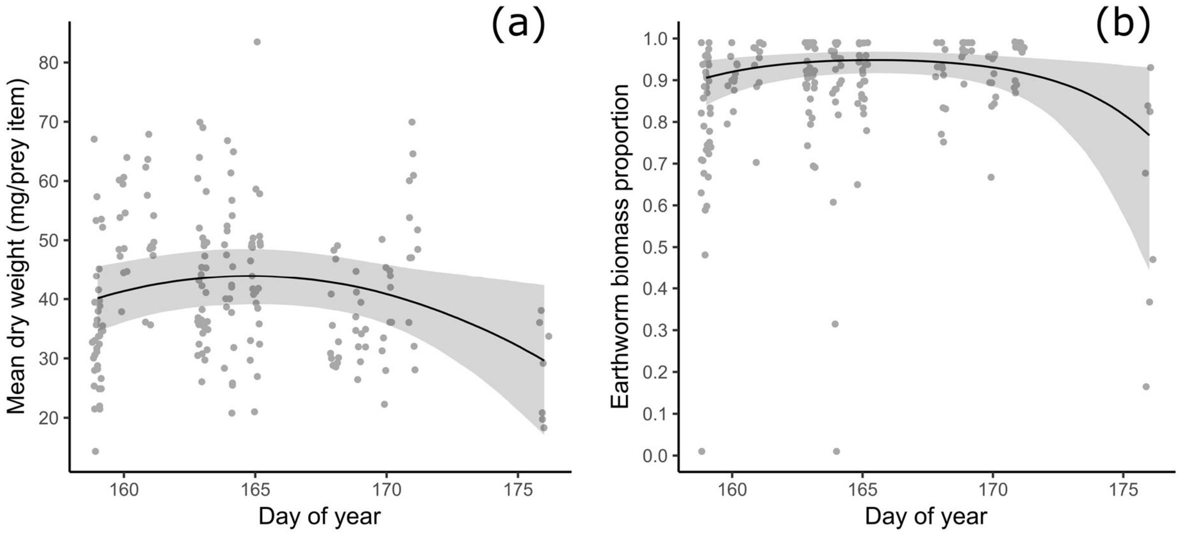

Figure 4 Seasonal variation in (a) the mean dry weight of delivered prey items per hour and (b) the biomass proportion of earthworms per provisioning event. Day 160 represents June 9th and shaded areas are 95% Bayesian credible intervals.

DISCUSSION

Mountain regions across the world are suffering from rapid and pronounced environmental change, impacting high-elevation biodiversity (La Sorte & Jetz 2010). The mechanisms at play in species' negative demographic trends remain poorly understood, however, as detailed knowledge of even basic species-specific ecological requirements is lacking. This study provides detailed insights into the nestling diet and patterns of parental food provisioning in a declining and emblematic alpine passerine, indicating how climate alterations and weather variations can mechanistically affect its trophic and breeding ecology. Indeed, the clear relationships between the provisioning efficiency of Ring Ouzel parents and weather circumstances highlight the challenges the species is facing. Parents forage most efficiently under cool ambient temperatures and during rainfall, which both boost the availability of the earthworms that constitute the bulk of nestlings' diet. Our findings further evidence a decrease in the mean dry biomass of prey items with the advancement of the reproductive season, suggesting a marked peak in staple food availability that temporally constrains breeding. Given the rapid increase in ambient temperatures and frequency of droughts forecasted for the Alps (Gobiet *et al.* 2014; CH2018 2018), Ring Ouzels thus appear particularly vulnerable to climate change.

The proportion of earthworms in the diet of Alpine Ring Ouzel nestlings was extremely high, both in terms of frequency (80%) and biomass (90%), in line with former faecal studies in the UK (70% of dry biomass from 60 nests; Burfield 2002) and previous qualitative appraisals from the Alps (Glutz von Blotzheim & Bauer 1988). Invertebrate larvae, in particular Coleoptera and Diptera (Tipulidae), also entered chick's diet but representing a minor fraction, as previously reported from British faecal analyses (Burfield 2002). Yet, discrepancies in diet composition might arise from different assessment methods: while faecal analyses often underestimate the presence of soft-bodied invertebrates in the diet (Moreby & Stoate 2000; Pearce-Higgins 2010), small prey items may be overlooked on pictures and videos (Douglas, Evans & Redpath 2008), in particular for multiple-prey loaders like the Ring Ouzel. The similarities in nestlings' diet composition in the two breeding populations is remarkable, especially considering the differences between the breeding habitat in the UK (heather moorland) and in the Alps (semi-open pastures), which host probably rather distinct invertebrate communities. Note, however, that a study using neck-collars in the Carpathians (in 39 nests) showed that Lepidoptera larvae were more important than earthworms in terms of biomass proportion (Korodi Gál 1970). This pattern was driven by a single species, *Hadena* *monoglypha*, and suggests that the Ring Ouzel can opportunistically adapt its diet to temporally or locally abundant and profitable invertebrate prey.

We suspect that the importance of earthworms is mostly driven by either high prey size and weight or their high digestibility for nestlings (Moreby & Stoate 2000), if not a combination of both. A predominance of large soft-bodied invertebrates in the composition of chicks' diet has been reported for numerous bird species, including at high elevations (e.g. Brodmann & Reyer 1999; Pearce-Higgins 2010; Resano-Mayor *et al.* 2019). Ring Ouzels are generally single-brooded in the Alps, where they reproduce particularly early compared to other sympatric mountain bird species and during the brief time window between the snowmelt onset and the growth of dense ground vegetation (Barras *et al.* 2020; *Chapter 1*). In contrast to soil invertebrates, grass-dwelling insects (e.g. Lepidoptera larvae and Orthoptera) are typically scarce so early in the season. Moreover, the Ring Ouzel, as many thrush species, is typically specialised in foraging on invertebrate prey present just below the soil surface. All our findings hence corroborate that earthworms represent a staple commodity for Ring Ouzels in Alpine treeline ecosystems.

The frequency and biomass of prey provisioning to chicks were negatively affected by ambient temperature, which was a better predictor than time of the day in all models. In altricial bird species, relationships between parental provisioning rates and ambient temperature are rather complex (e.g. Rauter, Brodmann & Reyer 2000; Geiser, Arlettaz & Schaub 2008). Prey provisioning is usually more frequent under high temperatures, due to increased invertebrate availability or activity (Geiser, Arlettaz & Schaub 2008; Low *et al.* 2008; Arlettaz *et al.* 2010; Winkler, Luo & Rakhimberdiev 2013) and because brooding requirements for thermoregulation of the chicks are reduced (Geiser, Arlettaz & Schaub 2008; Perez *et al.* 2016). Alternatively, however, provisioning is higher at low ambient temperatures as a parental response to fulfil the increased energy expenditure of actively thermoregulating nestlings (Rauter, Brodmann & Reyer 2000) or if prey availability is negatively affected by high ambient temperatures. As a matter of fact, earthworms respond to changes in ambient temperature and soil moisture by moving deeper into the soil under warm and dry weather conditions (Edwards & Bohlen 1996; Martay & Pearce-Higgins 2018; Onrust *et al.* 2019). This may underpin our observation of a slight but non-significant decrease in their biomass proportion in the diet with increasing ambient temperatures. Since earthworms are considered as climate-sensitive invertebrates (Pearce-Higgins 2010), mountain bird species that rely on them as a food source appear especially vulnerable in the face of climate change.

The weak positive effects of rainfall and overcast on the biomass delivered to the nestlings also suggest that earthworm availability was driving the patterns of parental provisioning activity. Nonetheless, we could not detect any increase in the proportion of earthworm biomass delivered under rainy conditions. Among insectivorous birds, rainfall usually exerts a negative effect on prey provisioning, and consequently breeding success, because it reduces the activity of flying insects and the accessibility of ground-dwelling invertebrates (Siikamäki 1996; Geiser, Arlettaz & Schaub 2008; Arlettaz *et al.* 2010; Perez *et al.* 2016; Schöll & Hille 2020). Ring Ouzels seem to stand out from other passerine bird species in this respect, obviously due to a trophic niche specialised on earthworms. Indeed, earthworms are more active in the upper ground layers and hence more accessible when the soil is humid and soft (Edwards & Bohlen 1996; Onrust *et al.* 2019), notably during or shortly after rainfall (Martay & Pearce-Higgins 2018) or during the snowmelt period. It is noteworthy that the larger prey biomass provisioned under such weather circumstances was mostly ascribable to exceptionally high amounts of food provided by the male, because then females were often found brooding nestlings to protect them from rainfall. The positive effect that wet and penetrable soils have on the availability of earthworms and other invertebrates (e.g. Tipulidae larvae) is thus key not only for birds in lowland agricultural landscapes (Peach *et al.* 2004; Smart *et al.* 2006; Onrust *et al.* 2019), but also in alpine ecosystems (Pearce-Higgins *et al.* 2010; Resano-Mayor *et al.* 2019; Barras *et al.* 2020; *Chapter 1*).

Our results further evidence a decrease in the mean dry weight of delivered prey items with the advancement of the breeding season. The parallel decrease in the earthworm fraction in prey biomass indicates that this reduction in prey weight was caused mostly by a diet shift towards smaller invertebrates. As we could not show any strong relationships between nestlings' age and daily provisioned biomass or provisioning frequency, this pattern likely results from a general drop in earthworm availability towards the end of the breeding season. This is in line with an established decrease in foraging habitat suitability with the advancement of the season due to progressive soil desiccation and ground vegetation densification (Barras *et al.* 2020; *Chapter 1*), with the aforementioned consequences on earthworm accessibility. This pattern will be further exacerbated in years with high summer ambient temperatures and prolonged droughts, negatively impacting the breeding success and first-year survival probability, such as reported for Ring Ouzels (Beale *et al.* 2006; Sim *et al.* 2011) and the European Golden Plovers (*Pluvialis apricaria*) in the UK (Pearce-Higgins *et al.* 2010), or Snowfinches in Italy (Strinella *et al.* 2020). In fact, the brood reduction that was observed on two occasions in our study (loss of the smallest nestling) suggests that food resources might actually be limiting (Magrath 1989; Siikamäki 1996). Single brooding and rapid movements to higher elevations just after fledging also point towards a short window of breeding opportunities (Barras *et al.* 2020; *Chapter 1*), as typically observed in alpine bird species (Boyle, Sandercock & Martin 2016). At this stage, however, this one-year study and the limited number of nests surveyed limit our ability to link demographic parameters such as productivity and juvenile survival rate to weather conditions. Finally, one ought to mention that a large fraction of the variation in provisioning rates and delivered biomass remained unexplained in our models, suggesting additional, unknown factors at play. Generally, we need more studies on the mechanical interlinks between climate, food supply and availability, and the demography of mountain birds (Chamberlain *et al.* 2012).

In conclusion, this study demonstrates that local weather considerably impacts the foraging ecology of an alpine bird during the reproductive period, with potential far-reaching consequences for population survival. Subject to a pace of warming double that recorded in the lowlands (Pepin *et al.* 2015), mountain birds face new challenges in meeting the food requirements of their offspring, notwithstanding the additional impacts of concomitant land-use change (Chamberlain *et al.* 2016). An earlier and accelerated spring snowmelt (Klein *et al.* 2016) can only accentuate the risk of a phenological mismatch for migratory species like Ring Ouzels, with potentially detrimental consequences for population dynamics (Visser, Both & Lambrechts 2004; McKinnon *et al.* 2012). While the breeding phenology of sedentary alpine specialists seems to be quite plastic (Martin *et al.* 2017), the question for non-resident species is whether they will gradually be able to anticipate their spring arrival on the breeding grounds. Last but not least, increasing frequency and magnitude of extreme weather events (Gobiet *et al.* 2014; CH2018 2018), such as prolonged drought periods (Beale *et al.* 2006) or late cold storms (Martin *et al.* 2017), may pose an additional challenge for mountain bird reproduction. Although we showed that provisioning activity peaked in wet and fresh weather conditions, cold storms characterized by abundant snowfall or frost in the core of the breeding season might lead to complete nesting failure (Martin *et al.* 2017), as observed in our study population at the beginning of the breeding season.

From a conservation perspective, measures aiming at directly boosting food availability in treeline ecotones would be beneficial for the Ring Ouzel, albeit challenging to implement. One could take advantage of current management practices of alpine grasslands in the Alps; extensively managed summer pastures, for instance, contribute to maintain a high density and biomass of earthworms (Steinwandter *et al.* 2017; Jernej *et al.* 2019) while keeping the grass sward short enough for efficient foraging. Moreover, some shading of the ground as well as a thicker litter layer generated by the tree canopy may buffer against excessive soil warming and desiccation compared to open areas above the treeline (Körner 2012; Müller *et al.* 2016). For this reason, supporting extensive, traditional summer pasturing in treeline ecosystems might contribute to maintain suitable foraging grounds under a changing climate. Further studies focusing on the response of other mountain birds and their invertebrate prey communities to environmental change and various management options (e.g. grazing intensity; see Douglas & Pearce-Higgins 2014) are yet needed to guide comprehensive conservation strategies for the mountain avifauna.

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SUPPLEMENTARY MATERIALS

Table S1 Reference values for mean dry weight per prey item, as well as overall abundance and proportion of the different taxonomic groups exploited by Ring Ouzel parents to provision nestlings (n = 15 nests).

Invertebrate category	Mean dry weight (mg/item)	Abundance	Proportion (%)
Lumbricidae (small)	21.1	1789	44.7
Lumbricidae (medium)	62.7	999	25.0
Lumbricidae (large)	112.6	427	10.7
Unidentified larvae	28.3	375	9.4
Unidentified	12.6	245	6.1
Coleoptera larvae	52.6	70	1.8
Tipulidae larvae	17.6	51	1.3
Lepidoptera larvae	14.6	15	0.4
Diptera adult	5.0	9	0.2
Hymenoptera adult	0.8	7	0.2
Coleoptera adult	3.2	6	0.2
Lepidoptera adult	2.1	4	0.1
Arachnida	4.4	1	0.0
Total	–	3998	–

Table S2 Set of best models, defined as within ΔAIC < 2 from the first-ranked model and obtained after the selection process for each of the different analyses.

Models	df	AICc	ΔAICc	weight	marg. R^2	cond. R^2
a. Provisioning rates, sex-independent						
Full model						
Temp + wind + time of day^2 + sunshine + rain						
Top models						
Temp + wind	6	1237.1	0.00	0.41	0.10	0.27
Temp + time of day	6	1237.1	0.03	0.41	0.09	0.26
Temp	5	1238.8	1.72	0.18	0.09	0.26
b. Provisioning rates, sex-specific						
Full model						
Temp + wind + time of day^2 + sunshine + rain + sex + sex x rain + sex x temp						
Top models						
Temperature + wind	5	1980.9	0.00	0.61	0.06	0.23
Temperature + time of day	5	1981.8	0.92	0.39	0.06	0.23
c. Delivered prey biomass, sex-independent						
Full model						
Temp + wind + time of day^2 + sunshine + rain						
Top models						
Temperature + time of day^2 + rain	7	1735.5	0.00	0.34	0.11	0.37
Temperature + time of day^2 + sunshine	7	1735.6	0.03	0.34	0.11	0.36
Temperature + time of day^2	6	1735.7	0.14	0.32	0.10	0.37
d. Delivered prey biomass, sex-specific						
Full model						
Temp + wind + time of day^2 + sunshine + rain + sex + sex x rain + sex x temp						
Top models						
Rain + sex	5	3462.3	0.00	0.50	0.07	0.25
Sunshine + sex	5	3463.4	1.18	0.27	0.07	0.24
Sex	4	3463.8	1.53	0.23	0.06	0.26

'df' stands for degrees of freedom and 'marg.' and 'cond. R^2' stand for marginal and conditional R^2 values (i.e. the proportion of explained variance by fixed effects only, and by both random and fixed effects, respectively). Models in (a) and (b) include nested random factors 'nest' and 'day of year'. Random factor 'day of year' was removed in models in (c) and (d) as leading to convergence issues. 'Temp' stands for temperature, 'x' for interactions and '2' as superscript indicates that both linear and quadratic terms were included.

Figure S1 Picture of the video monitoring system (in red circle) installed to record provisioning activity at a Ring Ouzel *Turdus torquatus alpestris* nest (in red square). Photo credits: A. G. Barras

Chapter 3

Variation in demography and life-history strategies across the range of a declining mountain bird species: is there potential to adapt to environmental change?

Variation in demography and life-history strategies across the range of a declining mountain bird species: is there potential to adapt to environmental change?

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Under review

ABSTRACT

There is increasing evidence that species- and population-specific responses to human-induced environmental change, and hence their adaptive potential, depend on the spatial variation in life-history traits and in demographic processes of local population dynamics. Yet, demographic parameters and their temporal variability remain mostly unknown for boreo-alpine species which are exposed to more pronounced climate change than species occurring at lower latitudes and elevations. We compared the demographic traits and dynamics of populations of Ring Ouzels (*Turdus torquatus*), an emblematic species of Western Palearctic mountain biomes, with the objective to identify the mechanisms underpinning their contrasting population trends. Using integrated population models fitted in a Bayesian framework, we estimated the survival probability, productivity, and immigration of two populations occurring in the Western European Alps, in France and Switzerland. The link between population growth rate and demographic parameters was assessed via perturbation analyses, while relationships between vital rates and weather variation during the breeding season were also examined. Juvenile apparent survival was lower and immigration rate higher in the Swiss compared to the French population, with the temporal variation in population growth rate driven by different demographic processes. If demographic rates only correlated weakly with weather circumstances during breeding, precipitation and the onset of snowmelt were two factors potentially playing a role in annual productivity and adult survival. Demography of these two Alpine populations indicate a slow life-history strategy, with a much lower productivity and higher adult survival compared to the sole population investigated so far in northern Europe. This study establishes that demographic characteristics can substantially vary across the range of a boreo-alpine passerine, essentially due to contrasted, potentially locally evolved life-history strategies. The question remains whether flexibility in life-history strategies is widespread among cold-adapted species and if this might provide adaptive potential for coping with current environmental change, i.e. by enhancing the chances of long-term population persistence.

Keywords: conservation, immigration, integrated population model, intraspecific variation, life-history, Ring Ouzel

INTRODUCTION

The evolution of diversity in life-history strategies is a central topic in evolutionary ecology (Partridge & Harvey 1988). It has become increasingly important from a conservation biology perspective, as understanding the type and flexibility of life-history strategies contributes to the estimation of adaptive potential (Forcada, Trathan & Murphy 2008), which will be decisive for accurately predicting the responses of biodiversity to environmental change (Reed, Schindler & Waples 2011; Swab *et al.* 2015). In this respect, life-history traits have already been recognized as good indicators of a species' sensitivity to global change and extinction risk (Jiguet *et al.* 2007; Pearson *et al.* 2014). Yet, the lack of knowledge of demographic characteristics across the distribution range of animal populations still limits our ability to assess their vulnerability to global change.

In the Western Palearctic, many taxa present a discontinuous distribution where they occupy mountain ranges at medium to high elevations at lower latitudes (i.e. Northern Africa and Europe), as well as taiga and tundra ecosystems at lower elevations and higher latitudes (i.e. Fennoscandia and Northwest Russia), thus covering a large latitudinal and elevational gradient. These species are referred to as boreo-alpine (or arctic-alpine) and are considered to be particularly vulnerable to climate change (Scridel *et al.* 2018) as the latter disproportionally impacts the aforementioned regions (Ernakovich *et al.* 2014). Yet, population trends of several boreo-alpine species differ markedly across their range (Lehikoinen *et al.* 2019) and it remains unclear if this results from contrasting rates of environmental change or from population-specific responses. Indeed, we might expect that intraspecific differences in life-history traits contribute to spatially heterogeneous sensitivity (Jiguet *et al.* 2007; Swab *et al.* 2015), which would have important implications for conservation management (Caswell 2000; Reed, Schindler & Waples 2011). This calls for more local studies to understand which ecological and demographic processes matter at the population level across latitudinal and elevational gradients (Chamberlain *et al.* 2012; Lehikoinen *et al.* 2019; Lundblad & Conway 2020). Finally, this knowledge would help to improve predictions of population resilience or resistance to new environmental circumstances (Pearson *et al.* 2014; Swab *et al.* 2015; Boyle, Sandercock & Martin 2016).

Birds have historically served as models to understand this variation (Lack 1947; Martin 2004). Indeed, despite a very consistent life cycle among species (Bennett & Owens 2002), avian life-history strategies span from one end of the well-known slow-fast continuum to the other, i.e. contrasting long-lived species reproducing slowly to those with short lives and fast reproduction (Sæther & Bakke 2000; Dobson 2007). In addition, broad geographical differences in life-history traits have been extensively documented in birds, first along a latitudinal gradient (Lack 1947), but also in relation to elevational gradients (Cody 1966). While faster life-histories are observed towards northern latitudes, there is evidence of the opposite pattern towards higher elevations (Hille & Cooper 2015; Boyle, Sandercock & Martin 2016), at least in temperate regions (Balasubramaniam & Rotenberry 2016). Such shifts have been evidenced both between and within species but are often limited to few life-history traits, such as clutch or egg size (Lack 1947; Cody 1966; Balasubramaniam & Rotenberry 2016). Several authors have stressed that a suite of demographic parameters should be included in intra- and interspecific comparisons across geographical gradients for better appraisals (Bennett & Owens 2002; Sandercock, Martin & Hannon 2005; Bears, Martin & White 2009; Lundblad & Conway 2020). Information on the demographic characteristics of bird species living at high elevations or latitudes should thus advance our knowledge of the ultimate and proximate drivers of life-history strategies (Bennett & Owens 2002; Martin 2004; Sandercock, Martin & Hannon 2005; Dobson 2007; Balasubramaniam & Rotenberry 2016), but research in this area is still disproportionally scarce (Chamberlain *et al.* 2012; Scridel *et al.* 2018).

The development of integrated population models (IPMs) has opened a range of opportunities to better assess the role of demographic processes in population dynamics (Besbeas *et al.* 2002; Schaub & Abadi 2011; Schaub & Kéry 2021). First, IPMs enable the simultaneous use of different types of demographic data in a combined model, leading to increased precision of demographic parameters, especially when sample sizes are small (Besbeas *et al.* 2002; Schaub *et al.* 2012). Second, estimates of parameters about which explicit information is lacking (e.g. immigration, productivity) can be obtained (Abadi *et al.* 2010; Schaub & Fletcher 2015). Third, a hierarchical formulation enables the separation of sampling from process variance, which translates into more reliable estimates of temporal variation in parameters (Kéry & Schaub 2012). All these advantages can be decisive when relationships between demographic parameters and variation in population growth rate or environmental variables need to be assessed (Besbeas *et al.* 2002; Schaub & Abadi 2011).

The present study focuses on the population dynamics of the Ring Ouzel (*Turdus torquatus*), a typical boreo-alpine thrush species breeding in mountain and upland ecosystems within the Western Palearctic (Keller *et al.* 2020). Although globally classified as ‘least concern’ (BirdLife International 2021), the species is nationally or regionally threatened following recent population declines. To the best of our knowledge, detailed demographic analyses have been performed only for a single declining population in Scotland, where juvenile and adult survival were identified as key parameters in population dynamics (Sim *et al.* 2011). Hence, the steady decline observed in the UK is probably caused by particularly low survival probabilities, but ecological drivers are still poorly understood (Sim *et al.* 2011). The succession of warm and dry summers associated with a decrease in territory occupancy over several sites in northern Great Britain could negatively impact survival through reduced food availability (Beale *et al.* 2006).

Here, we used IPMs to describe the local dynamics of two populations of Ring Ouzels in the French and Swiss Alps. Our aims were (1) to reliably estimate demographic rates, namely adult and juvenile apparent survival, immigration and productivity; (2) to identify key demographic rates contributing to temporal variation in local population growth rates using perturbation analyses; (3) to assess the relationships between annual demographic rates and a set of potentially important weather variables; (4) to compare estimates of demographic rates from these two Alpine populations with those from Scotland, i.e. at the north-western margin of the species' range, and discuss any discrepancies in the light of both their contrasting population trends and life-history theory; and (5) to provide a better base for predictions from a biological conservation perspective.

MATERIALS AND METHODS

Study species and study sites

Besides a subspecies occurring in the Middle East (*T. t. amicorum* in the Caucasus and Turkey), two other subspecies of Ring Ouzel are distinguished across the distribution range (Keller *et al.* 2020). *T. t. alpestris* breeds in central and southern Europe in semi-open forests, mostly within coniferous stands in the subalpine zone (Glutz von Blotzheim & Bauer 1988). In the Alps, most breeding pairs are single-brooded (65-75%; Glutz von Blotzheim & Bauer 1988) and annual survival probabilities are unknown. *T. t. torquatus* occupies more open areas in the British Isles, typically steep slopes of heather moorland, while it prefers semi-open habitats with bushes and shrubs in Fennoscandia (Burfield 2002). Double-brooding is common in the UK (e.g. 63% in Scotland; Sim, Rebecca & Wilkinson 2012), whereas it is apparently rare in Fennoscandia (Burfield 2002). Demographic parameters from a population in Scotland are presented in Table 1 (Sim *et al.* 2011). All three subspecies are short-distance migrants, with birds from western Europe sharing overwintering grounds in mountainous areas of southern Spain and North Africa (Glutz von Blotzheim & Bauer 1988; Sim *et al.* 2015).

We focused on two different breeding populations of *alpestris* Ring Ouzels in the Alps, one in the Vercors massif (Drôme, France; 44.78 N, 5.56 E) and one in Valais (Switzerland; 46.33 N, 7.43 E). The Vercors population is located at the western periphery of the Alpine range, approximately 225 km southwest of the Valais population, which has a more central position. Study sites cover 90 and 200 ha, respectively. In spite of weakly overlapping elevation ranges (Vercors: 1560–1760 m above sea level (m asl), Valais: 1720–2120 m asl), habitat configuration is similar in both sites and consists of summer cattle pastures interspersed with coniferous trees (*Pinus mugo uncinata* in Vercors, *Larix decidua* and *Picea abies* in Valais) close to the treeline. Both sites receive similar amounts of precipitation during the core of the breeding season (250–270 mm over April–June).

Data collection

Three types of data were collected at each study site: capture-mark-recapture (CMR), productivity and population size data. In Vercors, data collection occurred over the period 1999–2009. Birds were captured with mistnets and clap traps and ringed with unique colour-ring combinations on a yearly basis from March to July. Adults were defined as birds in their second calendar year or older and sexed based on plumage colouration (total number of ringed individuals: n_{male} = 94, n_{female} = 81). Juveniles were ringed directly at the nest or in its surroundings as fledglings (n_{juv} = 239). Specific sessions to re-sight ringed individuals were performed using binoculars or spotting scopes, with an even effort across the years. Productivity data was collected every year except in 1999, from an annual average of 10.5 nests (total = 105; range over years 3–24). Each nest was visited at least every sixth day and controlled from the ground with a mirror or camera fixed on a perch to monitor fledging success. Population surveys were performed on a subzone of the study area (32 ha) and consisted of 15 visits in May–June starting at dawn and along a predefined transect, performed each year except in 1999 and 2000. The territory mapping method (Bibby *et al.* 2000) was applied to estimate the annual number of breeding pairs.

In the Valais study site, the methods to capture and re-sight the birds were similar than in Vercors and were applied annually from March to June in years 2015–2020. Single and unique alphanumeric colour rings were used instead of colour ring combinations. While adult birds were captured on a yearly basis (total number of ringed individuals: n_{male} = 203, n_{female} =

107), juveniles were only ringed at the nest in 2017 and 2019 ($n_{\mathrm{juv}} = 80$). Direct information about productivity was thus only available for those two years, as well as in 2020 (total = 45; range over years 12–20). Population surveys were based on the same sampling design as in Vercors, except that it consisted of three visits per year in May–June and the total study area of 200 ha was covered.

Integrated population model

We used IPMs to estimate demographic parameters and population size (Besbeas *et al.* 2002; Schaub & Abadi 2011; Schaub & Kéry 2021). An IPM is based on a joint likelihood that is created by the likelihoods of each contributing dataset (Schaub & Abadi 2011; Kéry & Schaub 2012), in our case of the population survey, the productivity and the CMR data. We defined a multinomial likelihood to fit the Cormack-Jolly-Seber (CJS) model on the CMR dataset (Lebreton *et al.* 1992). This model separately estimates apparent survival, here with an age structure, and recapture probability. Juvenile apparent survival ($\phi_{juv,t}$) is defined as the probability that a juvenile ringed in year t survives and returns to the study area in year t+1. Apparent adult survival ($\phi_{ad,\mathrm{t}}$) is defined similarly, but applies to birds that are at least 1-year old. The recapture probability is defined as the probability of re-sighting a marked individual that is present in the study population. The productivity data was modelled with the Poisson likelihood, but differently for the two populations. For Vercors, we assumed that

$$J_t \sim Pois(R_t f_{VE,t})$$

where J_t is the total number of fledglings raised in year t in R_t monitored broods and $f_{VE,t}$ is the mean productivity in year t. Due to missing productivity data in the Valais population for half of the study years, we modelled productivity as

$$J \sim Pois(Rf_{VA})$$

where J is the total number of fledglings from R broods monitored over the years and f_{VA} is the mean productivity, which is assumed to be constant over time.

Lastly, the likelihood of the population survey data was formulated as a state-space model (Besbeas *et al.* 2002), which consists of state and observation processes to disentangle true variations in population size from observation errors (Kéry & Schaub 2012). The state process corresponds to a pre-breeding census, female-based matrix projection model. We distinguished three types of females, 1-year old birds (N_1), adults (at least 2-years old, N_{ad}) and immigrants (N_{imm}). The total number of females in year $t+1$ ($N_{tot,t+1}$) was defined as the sum of the number of females in these three stage classes:

$$N_{tot,t+1} = N_{1,t+1} + N_{ad,t+1} + N_{imm,t+1}$$

The temporal change in the numbers of females in each stage class was modelled with Poisson and binomial distributions to explicitly include demographic stochasticity:

$$N_{1,t+1} \sim Pois(\phi_{juv,t} f_t \frac{1}{2} N_{tot,t})$$

$$N_{ad,t+1} \sim Bin(\phi_{ad,t}, N_{to\ ,t})$$

$$N_{imm,t+1} \sim Pois(\omega_t N_{tot,t})$$

where ω_t is the immigration rate, i.e. the number of female immigrants in year $t+1$ as the proportion of females in year t, and f_t is the mean productivity at time t ($f_{VE,t}$ and f_{VA} for Vercors and Valais population, respectively), divided by two as we assumed an even sex ratio. The observation process, i.e. the relationship between observed (C_t) and true ($N_{tot,t}$) population size, was modelled using a Poisson distribution:

$$C_t \sim Pois(N_{to\ ,t})$$

Each demographic parameter was modelled with random time effects to estimate an overall mean and temporal variance (Kéry & Schaub 2012). Preliminary analyses revealed that the model fit was poor for both populations unless the immigration rate (ω_t) was assumed constant over the years. Hence, we were not able to estimate temporal variation of immigration.

The joint likelihood of the IPM was obtained by the product of all three different likelihoods under the assumption of independence of the datasets. Although this assumption may be violated in our datasets, several studies have shown that this has only a minor influence on parameter estimates (Schaub & Fletcher 2015; Schaub & Kéry 2021).

Model implementation

All models were fitted in a Bayesian framework, meaning that prior distributions of all unknown parameters had to be defined. We formulated vague priors for all parameters (see Supplementary Materials, Appendix S1) and used the program JAGS (Plummer 2003) to run our models using package 'jagsUI' (Kellner 2019) in program R 3.6.2 (R Development Core Team 2019). We ran three chains with 1,100,000 iterations including a 100,000 burn-in and a

1/100 thinning rate. R-hat diagnostics were used to assess convergence ($\hat{R} \leq 1.01$ for all parameters) and we report posterior means with 95% credible intervals (CRI) of the estimated parameters. R and JAGS codes for the fitted IPMs can be found in the Supplementary Materials, Appendix S1.

In order to identify an adequate model structure, we performed model selection based on the deviance information criterion (DIC), the Bayesian equivalent of the Akaike information criterion. Since the DIC is not reliable for hierarchical models (Millar 2009), we performed selection on the CJS models (i.e. using only the CMR data) with fixed instead of random time effects. We defined a set of candidate models that differed regarding time and sex effects (see Supplementary Materials, Table S1). Time effects on apparent adult and juvenile survival were retained in all models, as one goal of the study was the estimation of the temporal variability in demographic rates. Recapture probability was modelled as either constant or depending on sex and/or time effects. In the Vercors dataset, the sex was known for 10.9% of the juveniles, hence we also tested candidate models estimating sex-specific juvenile survival. We assigned a random sex to the other, unsexed individuals, assuming an even sex ratio (Nichols *et al.* 2004). For the Valais population, none of the marked nestlings was ever re-sighted in the study area, so that we considered only models with sex effects on adult survival or recapture probability (Supplementary Materials, Table S1). Candidate models were then ranked based on the DIC. To assess the goodness of fit of the CJS model, we performed frequentist tests using package 'R2ucare' (Gimenez *et al.* 2018). We further used the structure of the best CJS model in the IPM, but replaced fixed by random time effects.

Perturbation analyses

To assess the impact of demographic rates on population dynamics, we performed prospective and retrospective perturbation analyses. Prospective analyses address the question of how much would the population growth rate (λ) change if a given demographic rate changes by a small amount (Caswell 2000). We calculated elasticities as the proportional changes of λ when each demographic rate was changed by the same proportion in turn. Retrospective analyses address the question of how strongly the temporal variability of each demographic rate has contributed to the variability of the population growth rate (Caswell 2000). We applied transient life table response experiments (LTRE) for this purpose, as they fully account for the interplay between vital rates and population structure (Koons, Arnold & Schaub 2017). Again, we report posterior means along with 95% CRI of the computed perturbation quantities.

Effects of weather variables

In order to identify possible drivers of annual variation in demographic rates, we examined temporal relationships with environmental factors. We restricted our selection to weather variables collected in the direct surroundings of the study sites during the breeding season. Only few potentially important weather factors were included, based on known important relationships for mountain birds: ambient temperature and precipitation are key drivers of variation in demographic rates (Novoa *et al.* 2008; Chiffard *et al.* 2019; Strinella *et al.* 2020), and both influence parental provisioning of the Ring Ouzel in the Swiss Alps (Barras *et al.* 2021; *Chapter 2*). We assumed that spring precipitation has a positive effect on survival and productivity due to higher food availability, whereas ambient temperature has a negative effect. In addition, we considered the number of snow free days (defined as snow cover < 10 cm over a given period) as a proxy for the onset of snowmelt, since the latter is a main driver of foraging habitat suitability for the Ring Ouzel and other high-elevation bird species (Resano-Mayor *et al.* 2019; Barras *et al.* 2020; *Chapter 1*). Here, we hypothesized that an early snowmelt, i.e. a larger number of snow free days, is detrimental to survival and productivity.

In Vercors, data on precipitation (sum over April–June) and number of snow free days (sum over March–April) was provided by the closest meteorological station in Chichilianne (44.812 N, 5.571 E; 1010 m asl, 3.3 km distance) while temperature information (mean over April–June) was extracted from the 'Safran' surface model (Quintana-Seguí *et al.* 2008) over the corresponding grid cell (8 km resolution; centre 44.748 N, 5.518 E). In Valais, data on precipitation (sum over April–June), ambient temperature (mean over April–June) and number of snow-free days (sum over June–July) were obtained from the nearest meteorological stations for which this data was available (Anzère: 46.305 N, 7.408 E; 1614 m asl, 3.2 km distance — Montana: 46.299 N, 7.461 E; 1422 m asl, 4.1 km distance — Donin du Jour: 46.321 N, 7.367 E; 2390 m asl, 4.1 km distance, respectively). We recorded the number of snow free days over different months for Vercors and Valais, in order to capture the period of snowmelt, which occurred much later at the high-elevation weather station in Valais compared to Vercors. The snow height threshold at 10 cm was selected as this measure was the most reliable and available from both study sites. Despite the distance and elevation differences between weather stations and study sites, we assume that the annual variations in weather factors were equivalent.

All weather variables were standardized prior to the analyses and they were not correlated (Pearson's correlation coefficients $|r| < 0.7$). Fitting the explanatory weather variables directly as covariates in the IPM led to convergence problems ($\hat{R}$ > 1.1 for some parameters). For this reason, we ran bivariate correlation analyses (again using Pearson's *r*) between each weather variable and annual estimates of demographic rates from the IPM. We calculated these correlations for each MCMC draw such that the full uncertainty in the parameter estimates was accounted for. Moreover, this resulted in posterior distributions of the correlation coefficients allowing the computation of the probabilities that were positive or negative, depending on the sign of *r*.

RESULTS

Estimated demographic rates

The goodness-of-fit tests of the CJS models indicated no lack of fit for either CMR dataset (Vercors: X^2_{31} = 26.43, *P* = 0.70; Valais: X^2_{12} = 15.78, *P* = 0.20). Selection of models on the CMR data revealed that survival varied temporally, but was not different between sexes in both study populations. The recapture probability was also variable over time in Vercors, while it varied by sex in Valais (Supplementary Materials, Table S1).

Demography of the two populations differed markedly as revealed by the demographic parameter estimated from IPMs (Table 1). Productivity was higher on average (+44.8%) in the Valais compared to the Vercors population. On the contrary, juvenile apparent survival was around ten times higher in Vercors than in Valais and adult apparent survival was slightly higher in Vercors (+11.7%). The extremely low apparent survival of juveniles in the Valais population means that local recruitment was almost non-existent. Immigration was nearly four times as strong in the Valais compared to the Vercors population (+276%). The estimated mean population growth rate indicated a declining population in Vercors (λ = 0.93, 0.87–1.01; $p(\lambda < 1)$ = 0.96), while the Valais population appeared quite stable (λ = 1.04, 0.99–1.10; $p(\lambda < 1)$ = 0.07). Estimated population sizes were close to counts from the surveys (Fig. 1). Annual estimates of population growth rate, and adult and juvenile survival showed no clear temporal trend for either population, whereas productivity in Vercors appeared to be declining over the years (Fig. 1).

Effects of demographic rates on population growth rate

The growth rate of both populations was most sensitive to the variation of adult survival according to elasticities. The Valais population was more sensitive to immigration than to local recruitment (in terms of both productivity and juvenile survival), while the Vercors population growth rate was more sensitive to local recruitment than to immigration (Table 1). Stability of the Vercors population ($\lambda = 1$) would necessitate an increase in either mean adult survival of 10.6% (to 0.76), productivity of 55.8% (to 3.01), juvenile survival of 55.9% (to 0.21) or immigration rate of 67.0% (to 0.18). Transient LTRE, i.e. retrospective analyses, revealed that growth rate fluctuations in the Vercors population were primarily due to the variation in productivity, while survival parameters contributed less (Table 1). By contrast, the growth rate of the Valais population was essentially driven by the variation in adult survival (Table 1).

Table 1 Posterior means (with 95% credible intervals) of demographic rates and results from prospective (elasticities) and retrospective (transient LTRE) perturbation analyses as obtained from integrated population models for two Ring Ouzel (*alpestris*) populations in the Alps. Estimates of the present study are compared to reported demographic rates and characteristics of a *T. t. torquatus* population in Scotland (Sim *et al.* 2011).

Parameter	Valais (Switzerland)	Vercors (France)	Scotland (UK)
Demographic rates			
Adult survival (ϕ_{ad})	0.62 (0.39 – 0.85)	0.69 (0.59 – 0.82)	0.42
Juvenile survival (ϕ_{juv})	0.01 (0.00 – 0.15)	0.13 (0.07 – 0.22)	0.05
Productivity (f)	2.80 (2.33 – 3.31)	1.93 (0.85 – 3.55)	3.64
Immigration (ω)	0.41 (0.22 – 0.55)	0.11 (0.01 – 0.26)	–
Population growth rate (λ)	1.04 (0.99 – 1.10)	0.93 (0.87 – 1.01)	0.91
Growth rate elasticities			
Adult survival (ϕ_{ad})	0.59 (0.44 – 0.72)	0.75 (0.61 – 0.88)	–
Juvenile survival (ϕ_{juv})	0.02 (0.00 – 0.19)	0.14 (0.05 – 0.27)	–
Productivity (f)	0.02 (0.00 – 0.19)	0.14 (0.05 – 0.27)	–
Immigration (ω)	0.40 (0.21 – 0.54)	0.12 (0.01 – 0.26)	–
Summary	$\phi_{ad} > \omega > \phi_{juv} = f$	$\phi_{ad} > \phi_{juv} = f > \omega$	$\phi_{ad} > f_{early^*} > \phi_{juv} > f_{late}$
LTRE contribution (%)			
Adult survival (ϕ_{ad})	1.56 (0.00 – 4.38)	0.73 (-0.05 – 3.64)	–
Juvenile survival (ϕ_{juv})	0.20 (-0.23 – 2.35)	0.25 (-0.14 – 1.74)	–
Productivity (f)	–	0.75 (0.00 – 2.44)	–
Summary	$\phi_{ad} > \phi_{juv}$	$f > \phi_{ad} > \phi_{juv}$	$\phi_{juv} > f_{early} > \phi_{ad} > f_{late}$

[*] f_{early} and f_{late} refer to productivity of early and late broods, respectively, as those were tested separately in perturbation analyses in Sim *et al.* (2011)

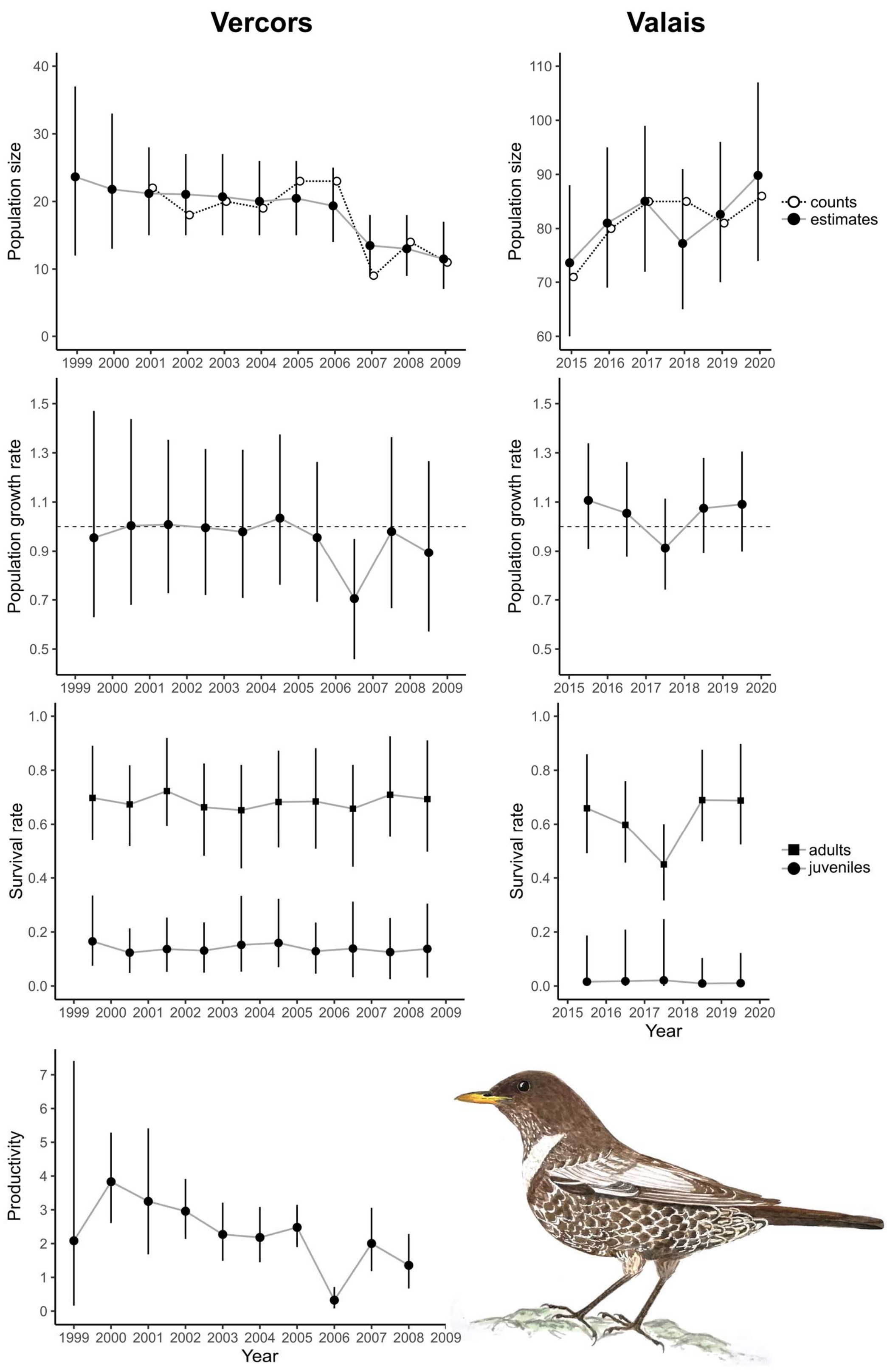

Figure 1 Mean estimates of annual population size (with actual counts also depicted), population growth rate, adult and juvenile apparent survival probabilities, and productivity for two Ring Ouzel populations in the Alps as obtained from an integrated population model. Error bars represent 95% credible intervals (CRI).

Effects of weather variables on demographic rates

Most of the temporal variation in demographic rates was not clearly explained by selected weather variables (Table 2). Nevertheless, best supported correlations were found with parameters that varied most. There was a high posterior probability ($p = 0.92$) for productivity in Vercors to be positively correlated with the amount of precipitation, but also with the number of snow free days ($p = 0.93$). It appears that the extremely low productivity in 2006, a dry year with a late snowmelt, was partly responsible for this pattern, while early snowmelt years resulted in higher productivity overall (Fig. 2). We could not assess if the relationship was similar in the Valais population, as annual estimates of productivity were not calculated due to missing data for some years. However, there was a high probability ($p = 0.89$) of years with an early snowmelt being associated with lower adult survival in this population (Table 2; Fig. 2).

Table 2 Mean Pearson's correlation coefficients r (with 95% credible intervals) between annual demographic rates and weather variables during the breeding season in two different populations of Ring Ouzels in the Alps, along with the probability of the correlation coefficient to be positive or negative, depending on the sign of r.

Parameter	Precipitation sum	Mean ambient temperature	Number of snow free days
Vercors population (n = 10 years)			
Adult survival (ϕ_{ad})	0.19 (-0.50 – 0.76) $p(r > 0) = 0.72$	-0.11 (-0.73 – 0.55) $p(r < 0) = 0.63$	0.02 (-0.59 – 0.63) $p(r > 0) = 0.52$
Juvenile survival (ϕ_{juv})	-0.08 (-0.69 – 0.56) $p(r < 0) = 0.60$	-0.06 (-0.65 – 0.61) $p(r < 0) = 0.58$	-0.02 (-0.63 – 0.58) $p(r < 0) = 0.52$
Productivity (f)	0.21 (-0.08 – 0.50) $p(r > 0) = 0.92$	-0.04 (-0.34 – 0.28) $p(r < 0) = 0.60$	0.39 (-0.19 – 0.66) $p(r > 0) = 0.93$
Valais population (n = 5 years)			
Adult survival (ϕ_{ad})	-0.03 (-0.63 – 0.56) $p(r < 0) = 0.54$	-0.05 (-0.66 – 0.59) $p(r < 0) = 0.56$	-0.39 (-0.89 – 0.33) $p(r < 0) = 0.89$
Juvenile survival (ϕ_{juv})	0.03 (-0.78 – 0.86) $p(r > 0) = 0.48$	-0.01 (-0.84 – 0.79) $p(r < 0) = 0.45$	0.02 (-0.79 – 0.86) $p(r > 0) = 0.48$

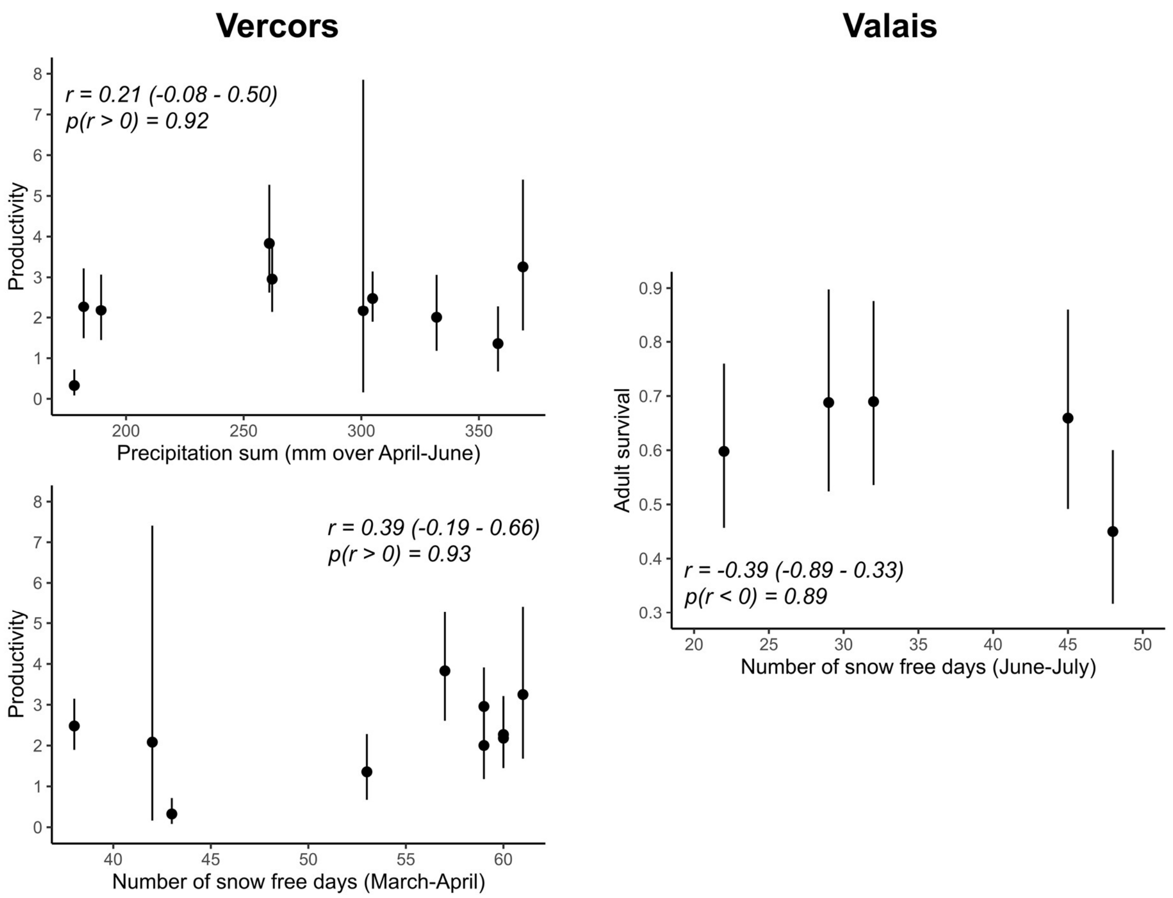

Figure 2 Relationships between demographic rates and weather variables for which the probability of a positive or negative correlation coefficient was high (p > 0,85), for each of the two study populations of Ring Ouzel. Error bars represent 95% CRI. Given are posterior means, 95% CRI of Pearson's correlation coefficients (r) and the probability of r being either positive or negative.

DISCUSSION

Using integrated population models, this study comprehensively characterized the contrasted dynamics of two geographically distinct populations of a mountain passerine in the French and Swiss Alps. Not only could we evidence marked differences between these two populations in a suite of demographic rates, but we also identified, thanks to retrospective perturbation analyses, the demographic mechanisms behind their divergent population trajectories. If we were unable to conclusively determine which environmental factors underpin the temporal variation observed in key demographic rates, there was some support for the potential roles played by precipitation and the temporal onset of the snowmelt.

Demographic differences between two alpine populations

Concerning the divergence in the demographic trajectories of our two study populations, the recent population growth rate in Valais (Switzerland) indicated a stable or even slightly increasing population size, while the Vercors (France) population declined in the first decade of this century. Although the periods of monitoring of the two populations did not overlap, independent data collected via a 'constant effort site' ringing scheme at the same Vercors study site in 2002–2020 (i.e. in the late phase and in prolongation of the period of the present CMR dataset) revealed a linear decrease in the number of annual captures of adult Ring Ouzels (β = -0.16, P = 0.04; Renous N. & Blache S., unpubl. data). This shows that the decline continued unabated beyond 2009, which was the last year of systematic CMR data collection at the French site. If the long-term national demographic trend for Ring Ouzel in Switzerland shows a linear decline of ca. 35% over the last three decades, the estimated density has decreased mostly at the lower margin of the elevation range (Knaus *et al.* 2018). Thus, the information at hand supports the general view that more marginal populations of Ring Ouzel, at lower elevations and at the periphery of the range, have been more affected than populations inhabiting the core of its Alpine distribution.

The demographic rates themselves also differed markedly between the two study sites. The Valais population was characterized by a higher immigration rate, and lower juvenile apparent survival and, to a lesser extent, adult survival than the Vercors population. Again, this matches the expectations regarding the demography of marginal vs. central populations, with more pronounced permanent emigration across age classes in core populations (Reichert, Fletcher & Kitchens 2021), as denoted by the lower apparent survival probabilities achieved locally in Valais. In contrast, the Vercors population appears geographically and demographically more isolated. The different sizes of our study areas of course directly influence estimates of immigration (Millon *et al.* 2019), but this renders our results even more conservative since the Vercors study area is smaller than the Valais one. Lower habitat suitability in Vercors, as typically observed at the distribution margin (Hampe & Petit 2005), may explain the lower average reproductive output achieved by breeding pairs compared to Valais, also rendering it less attractive for immigrants.

Results from the perturbation analyses also highlighted some discrepancies in the contribution of demographic rates to the dynamics of the two populations. Retrospective analyses revealed that productivity contributed most to growth rate annual variation in Vercors, while it was adult survival in Valais. Nonetheless, we call for caution when interpreting these results because productivity in Valais was modelled as a constant due to limited data. It is anyway very unlikely that productivity impacts population growth rate when one considers the extremely low local juvenile apparent survival in Valais. In the end, in both populations, the most prominent drivers of dynamics were clearly those showing marked temporal variability (Fig. 1), in line with numerous other demographic studies (Caswell 2000; Sæther & Bakke 2000). However, the demographic parameters that are revealed as important in retrospective analyses usually differ from those evidenced in prospective analyses. This is because natural selection reduces variation in demographic traits exhibiting a high elasticity, i.e. those contributing much to population growth rate, since variation of the latter has negative fitness consequences (Pfister 1998; Sæther & Bakke 2000). This was not obvious in our results, since adult survival was prominent in both prospective and retrospective appraisals. All in all, this suggests that the Valais population would be particularly vulnerable to variations in adult survival, while the Vercors population decline probably results from a series of years with low productivity.

Effects of weather conditions

We could detect only weak correlations of weather conditions during reproduction with demographic rates. In the case of Valais this is not that surprising given the brevity of the time series, which is reflected in the high level of uncertainty in the estimates. Furthermore, demographic parameters of altricial bird species inhabiting temperate biomes are often driven by weather circumstances during the non-breeding season (Sæther, Sutherland & Engen 2004), with time-lagged effects upon reproduction. We had to restrain our analysis to weather conditions during the breeding season because of limited knowledge about the whereabouts of wintering Alpine Ring Ouzels. Notwithstanding these issues, some interesting patterns emerged. First, productivity was positively associated with precipitation in Vercors, as expected, but contrary to what is generally observed among birds (Novoa *et al.* 2008; Arlettaz *et al.* 2010). This may easily be explained by the reliance of Ring Ouzel on earthworms for chicks provisioning (Barras *et al.* 2021; *Chapter 2*), their availability increasing with rainfall. Second, but contrary to our prediction, productivity was enhanced in years with an early onset of the snowmelt as observed in other mountain bird species (Novoa *et al.* 2008; Saracco *et al.* 2019). Yet, lower adult survival was observed in Valais in those very years with an early snowmelt, which points to negative carry-over effects in other stages of the life cycle. For instance, it could be that early snowmelt results in diminished soil moisture later in the season, limiting prey availability in the post-breeding and post-fledging periods.

Comparison across the range

To our knowledge, estimates of demographic rates exist for only one other Ring Ouzel population in Scotland (Sim, Rebecca *et al.* 2011). Scottish birds (subspecies *torquatus*) appear to have a totally different life-history strategy than Alpine birds. Compared to Vercors and Valais populations, they exhibit a much higher productivity (+88.6% and +30% fledglings per female and year, respectively), but lower adult annual survival (-39.1% and -32.3%, respectively) (Sim *et al.* 2011; Table 1). This sheer difference in productivity between the British uplands and the Alps has its source in the number of broods achieved per reproductive season. While double-brooding has never been observed in our two focal Alpine populations, it concerns more than half of the breeding females in the Scottish Highlands, with even triple-brooding observed in rare cases (Sim, Rebecca & Wilkinson 2012). This explains the higher breeding success of British birds. Yet, a greater reproductive effort probably entails higher intrinsic costs (Bennett & Owens 2002; Martin 2004; Dobson 2007) that are paid back in the form of reduced adult survival in Scottish Ring Ouzels. Single-brooding in the Alps most probably results from the shorter time window with suitable breeding conditions at higher elevations, mediated through prey availability (Boyle, Sandercock & Martin 2016; Lundblad & Conway 2020). In effect, the deep snowpack in the Alps impedes any access to the traditional foraging grounds when birds return from their winter quarters, whilst snow is most of the time absent at the same period in the British uplands. Later in the season, we have established a rapid decrease in the suitability of Alpine foraging habitat (Barras *et al.* 2020; *Chapter 1*), and thereby in prey availability. Of course, other factors could also play a role. Greater predation pressure on ground-nesting females in British uplands might select for higher productivity (Sandercock, Martin & Hannon 2005; Boyle, Sandercock & Martin 2016), although the larger communities of potential predators in the Alps somehow weaken this argument. Similarly, the slightly longer migration route of northern populations to overwintering grounds in North Africa and southern Spain might also entail some additional risks (Martin 2004; Sim *et al.* 2011), but this seems irrelevant in a short-distance migrant like the Ring Ouzel.

Regardless of the underlying mechanism, contrasted if not fairly divergent life-history strategies are manifest across the distribution range of the Ring Ouzel, with demographic characteristics of the Scottish Ring Ouzel population pointing towards a faster pace of life than in the Alps. Intraspecific differences in life-history traits have been evidenced for several bird species (Bears, Martin & White 2009; Bastianelli *et al.* 2017; Lundblad & Conway 2020) and typically emerge along eco-geographical gradients (Martin 2004; Boyle, Sandercock & Martin 2016). First, for any given species, the populations that inhabit the high latitudes show higher fecundity and lower adult survival than those closer to the tropics (Lack 1947; Martin 2004), which is precisely what we observe with the Ring Ouzel. Second, bird populations at higher elevations tend to adopt slower life-history strategies (Sandercock, Martin & Hannon 2005; Hille & Cooper 2015; Boyle, Sandercock & Martin 2016), which is also corroborated by the present results. In effect, our two Alpine populations occur at much higher elevations (1650–2100 m asl) than the Scottish population (350–850 m asl). Third, the geographic position of a population within its species range can also affect life-history traits: populations occurring at range margins should theoretically exhibit a slower pace of life than those in the core zones (Hampe & Petit 2005; Canonne *et al.* 2020). The pattern observed here between Scotland and the Alps is indeed exactly opposite, which challenges that generalization, although it could still explain the differences between Vercors and Valais, the former being peripheral and the latter central. Still, given the rather limited and non-overlapping periods of population monitoring, we cannot rule out that these differences within the Alpine range result from short-term weather effects rather than an evolutionary process.

Conservation implications and adaptive potential to environmental change

Declining in marginal zones (Vercors and Scotland), the Ring Ouzel still achieves a stable demography in the core of its range (Valais). This view is corroborated by recent observations and predictions of the species' demographic trajectories across the Swiss mountain massifs, where peripheral populations suffer more than central ones (Knaus *et al.* 2018; Barras *et al.* in press; *Chapter 5*). The findings that the more stable demography of the Valais population relies principally on immigration while it is characterized by a very low local juvenile recruitment indicates that we are in the presence of a complex metapopulation system, with numerous exchanges of individuals between subpopulations. Hence, a first lesson for management is that any conservation action should be envisioned at a much larger scale than the population under study, as evidenced for other species (Schaub *et al.* 2012; Schaub & Ullrich in press). A second series of lessons can be drawn from the local demographic population specificities. Low productivity is driving the negative demographic trajectory of the French population (this study), whereas reduced survival was identified as the reason for the decline in the UK (Sim *et al.* 2011). Local conservation interventions should thus focus on measures contributing to an amelioration of these respective demographic traits (e.g. habitat restoration to enhance reproductive output), in addition to keeping an eye on the underlying metapopulational issue.

As an emblematic mountain species with a typical, complex boreo-alpine distribution, the Ring Ouzel shows a pronounced geographic variation in the realization of its life-history tactics. This may indicate a high level of intrinsic potential for adjustments to environmental change in this species (Forcada, Trathan & Murphy 2008; Reed, Schindler & Waples 2011). For instance, an increase in the duration of the available temporal window for breeding, notably following modifications of snowfall regimes and an earlier snowmelt in spring at high elevations (Saracco *et al.* 2019), could provide room for adapting to even fairly rapid changes in environmental conditions. The question thus remains whether a similar variability is shared by other cold-adapted species (Forcada, Trathan & Murphy 2008) and whether it may suffice to achieve viable life history trade-offs in response to the novel challenges that future environments will impose on biodiversity (Reed, Schindler & Waples 2011). What is certain is that predictive models of species' future distribution ranges would certainly gain in accuracy by accounting for this variability in life-history traits.

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SUPPLEMENTARY MATERIALS

Table S1 Results of the CJS model selection process, with all tested candidate models ranked based on their DIC. The deviance, model complexity (pD), and the difference in DIC with the best-ranked model (ΔDIC) are displayed in addition. Symbols in the model list refer to the demographic parameters: adult apparent survival (ϕ_{ad}), juvenile apparent survival (ϕ_{juv}) and recapture/re-sighting probability (p). Notation in parenthesis indicates the presence (s: sex, t: time, $s+t$: sex and time) or absence (.: constant) of fixed effects for each parameter.

Model	DIC	deviance	pD	ΔDIC
Vercors population				
$\phi_{ad}(t)$, $\phi_{juv}(t)$, $p(t)$	278.34	253.92	24.43	0.00
$\phi_{ad}(s+t)$, $\phi_{juv}(t)$, $p(t)$	279.04	254.26	24.78	0.70
$\phi_{ad}(t)$, $\phi_{juv}(t)$, $p(s+t)$	281.08	253.99	27.09	2.74
$\phi_{ad}(s+t)$, $\phi_{juv}(s+t)$, $p(t)$	284.59	254.67	29.92	6.25
$\phi_{ad}(s+t)$, $\phi_{juv}(t)$, $p(s+t)$	284.65	256.62	28.03	6.31
$\phi_{ad}(s+t)$, $\phi_{juv}(s+t)$, $p(s+t)$	288.2	256.49	31.71	9.86
$\phi_{ad}(s)$, $\phi_{juv}(s)$, $p(.)$	288.38	283.63	4.75	10.04
$\phi_{ad}(s)$, $\phi_{juv}(s)$, $p(s)$	289.9	284.17	5.73	11.56
$\phi_{ad}(t)$, $\phi_{juv}(t)$, $p(s)$	291.38	271.71	19.68	13.04
$\phi_{ad}(t)$, $\phi_{juv}(t)$, $p(.)$	291.67	272.46	19.21	13.33
$\phi_{ad}(s+t)$, $\phi_{juv}(t)$, $p(.)$	294.82	271.26	23.56	16.48
$\phi_{ad}(s+t)$, $\phi_{juv}(t)$, $p(s)$	296.37	271.92	24.45	18.03
$\phi_{ad}(s+t)$, $\phi_{juv}(s+t)$, $p(.)$	299.52	270.45	29.07	21.18
$\phi_{ad}(s+t)$, $\phi_{juv}(s+t)$, $p(s)$	302.53	271.55	30.98	24.19
Valais population				
$\phi_{ad}(t)$, $\phi_{juv}(t)$, $p(s)$	112.32	101.74	10.58	0.00
$\phi_{ad}(t)$, $\phi_{juv}(t)$, $p(.)$	113.23	102.75	10.48	0.91
$\phi_{ad}(t)$, $\phi_{juv}(t)$, $p(t)$	114.89	102.02	12.87	2.57
$\phi_{ad}(t)$, $\phi_{juv}(t)$, $p(s+t)$	115.28	101.33	13.94	2.96
$\phi_{ad}(s+t)$, $\phi_{juv}(t)$, $p(t)$	116.52	103.19	13.33	4.20
$\phi_{ad}(s+t)$, $\phi_{juv}(t)$, $p(s+t)$	118.83	103.57	15.26	6.51
$\phi_{ad}(s+t)$, $\phi_{juv}(t)$, $p(.)$	121.87	107.62	14.25	9.55
$\phi_{ad}(s+t)$, $\phi_{juv}(t)$, $p(s)$	122.41	106.94	15.47	10.09

Appendix S1 JAGS code for the integrated population models as called from R, for (A) the Vercors (VE) population, and (B) the Valais (VA) population.

```
#---------------------------------------------------------------#
#### A. Integrated Population Model code for the VE population ####
#---------------------------------------------------------------#

nyears <- 11 # number of years covered by population data

sink("JAGSmodels/finalIPM_VE.jags")
cat("
model {
#-------------------------------------------------------------
#  Integrated population model
#  - Age structured model with 2 age classes: juveniles (1 cy) and adults (>=2cy)
#  - Age at first breeding: 1 year
#  - Prebreeding census, female-based
#  - Demographic rates (phia: adult survival, phij: juvenile survival, fec: 
productivity) are modelled as time-dependent (random effect)
#  - Recapture probability (p) is modelled as time-dependent
#  - Immigration (imm) is modelled as constant
#--------------------------------------------------------------

#-----------------------------------------
# 1. Defining priors for the parameters
#-----------------------------------------
# Initial population sizes
N1[1] ~ dcat(pn1)
NadSurv[1] ~ dcat(pnadSurv)
Nadimm[1] ~ dcat(pnadimm)

# Mean demographic parameters
l.mphij ~ dnorm(0, 0.01)
l.mphia ~ dnorm(0, 0.01)
l.mfec ~ dnorm(0, 0.01)
l.p ~ dnorm(0, 0.01)
mim ~ dunif(0,5)

# Precision of standard deviations of temporal variability
sig.phij ~ dunif(0, 10)
tau.phij <- pow(sig.phij, -2)
sig.phia ~ dunif(0, 10)
tau.phia <- pow(sig.phia, -2)
sig.p ~ dunif(0, 10)
tau.p <- pow(sig.p, -2)
sig.fec ~ dunif(0, 10)
tau.fec <- pow(sig.fec, -2)

# Distribution of error terms
for (t in 1:(nyears-1)){
   epsilon.phij[t] ~ dnorm(0, tau.phij)
   epsilon.phia[t] ~ dnorm(0, tau.phia)
   epsilon.fec[t] ~ dnorm(0, tau.fec)
   epsilon.p[t] ~ dnorm(0, tau.p)
   }

#-------------------------
# 2. Constrain parameters
#-------------------------
for (t in 1:(nyears-1)){
   logit(phij[t]) <- l.mphij + epsilon.phij[t]  # Juv. apparent survival
   logit(phia[t]) <- l.mphia + epsilon.phia[t]  # Adult apparent survival
```

```
   log(f[t]) <- l.mfec + epsilon.fec[t]         # Productivity
   omega[t] <- mim                              # Immigration
   logit(p[t]) <- l.p + epsilon.p[t]            # Recapture probability
   }

#-----------------------
# 3. Derived parameters
#-----------------------
mphij <- exp(l.mphij)/(1+exp(l.mphij))   # Mean juvenile survival probability
mphia <- exp(l.mphia)/(1+exp(l.mphia))   # Mean adult survival probability
mfec <- exp(l.mfec)                      # Mean productivity

# Population growth rate
for (t in 1:(nyears-1)){
   lambda[t] <- Ntot[t+1] / Ntot[t]
   logla[t] <- log(lambda[t])
   }
mlam <- exp((1/(nyears-1))*sum(logla[1:(nyears-1)]))   # Geometric mean

#---------------------------------------------
# 4. Likelihoods of the single data sets
#---------------------------------------------
# 4.1. Likelihood for population count data (state-space model)
   # 4.1.1 System process
   for (t in 2:nyears){
      N1[t] ~ dpois(0.5 * f[t-1] * phij[t-1] * Ntot[t-1])
      NadSurv[t] ~ dbin(phia[t-1], Ntot[t-1])
      Nadimm[t] ~ dpois(Ntot[t-1] * omega[t-1])
      }

   # 4.1.2 Observation process
   for (t in 1:nyears){
      Ntot[t] <- NadSurv[t] + Nadimm[t] + N1[t]
      y[t] ~ dpois(Ntot[t])
      }

# 4.2 Likelihood for capture-recapture data: CJS model (2 age classes, sex-
independent)
# Multinomial likelihood
for (t in 1:(nyears-1)){
   marray.j[t,1:nyears] ~ dmulti(pr.j[t,], r.j[t])
   marray.a[t,1:nyears] ~ dmulti(pr.a[t,], r.a[t])
   }

# m-array cell probabilities for juveniles
for (t in 1:(nyears-1)){
   q[t] <- 1-p[t]
   # Main diagonal
   pr.j[t,t] <- phij[t]*p[t]
   # Above main diagonal
   for (j in (t+1):(nyears-1)){
      pr.j[t,j] <- phij[t]*prod(phia[(t+1):j])*prod(q[t:(j-1)])*p[j]
      } #j
   # Below main diagonal
   for (j in 1:(t-1)){
      pr.j[t,j] <- 0
      } #j
   # Last column
   pr.j[t,nyears] <- 1-sum(pr.j[t,1:(nyears-1)])
   } #t

# m-array cell probabilities for adults
for (t in 1:(nyears-1)){
```

```
   # Main diagonal
   pr.a[t,t] <- phia[t]*p[t]
   # above main diagonal
   for (j in (t+1):(nyears-1)){
      pr.a[t,j] <- prod(phia[t:j])*prod(q[t:(j-1)])*p[j]
      } #j
   # Below main diagonal
   for (j in 1:(t-1)){
      pr.a[t,j] <- 0
      } #j
   # Last column
   pr.a[t,nyears] <- 1-sum(pr.a[t,1:(nyears-1)])
   } #t

# 4.3. Likelihood for productivity data: Poisson regression
  for (t in 1:length(time)){
    J[t] ~ dpois(rho[t])
    rho[t] <- R[t] * f[time[t]]
  }
}
",fill = TRUE)
sink()

# Discrete uniform distribution function
dUnif <- function(A, B){
   pprob <- c(rep(0, A-1), rep(1/(B-A+1), (B-A+1)))
   return(pprob)
}

# Bundle data
jags.data <- list(nyears = nyears, marray.j = marray.j, marray.a = marray.a, y =
popcount, J = J, R = R, time=time, r.j = r.j, r.a = r.a, pn1 = dUnif(1,10),
pnadSurv = dUnif(1,20), pnadimm = dUnif(1,20))

# Initial values
inits <- function(){list(l.mphij = rnorm(1, 0.2, 0.5), l.mphia = rnorm(1, 0.2,
0.5), l.mfec = rnorm(1, 0.2, 0.5), mim = runif(1,0,5), l.p = rnorm(1, 0.2, 1),
sig.phij = runif(1, 0.1, 10), sig.phia = runif(1, 0.1, 10), sig.fec = runif(1, 0.1,
10), sig.p = runif(1,0.1,10))}

# Parameters monitored
parameters <- c("phij", "phia", "f", "p","omega", "lambda", "mphij", "mphia",
"mfec", "mim", "mlam", "Ntot")

# MCMC settings
ni <- 1100000       # number of iterations
nt <- 100           # thinning rate
nb <- 100000        # burn-in
nc <- 3             # number of chains

# Call JAGS from R (RT 33.5 min)
IPM <- jags(jags.data, inits, parameters, "JAGSmodels/finalIPM_VE.jags", n.chains =
nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel = T)

#-----------------------------------------------------------------#
#### B. Integrated Population Model code for the VA population ####
#-----------------------------------------------------------------#

nyears <- 6 # number of years covered by population data

sink("JAGSmodels/finalIPM_VA.jags")
cat("
model {
```

```
#--------------------------------------------------------------
#  Integrated population model
#  - Age structured model with 2 age classes: juveniles (1 cy) and adults (>=2cy)
#  - Age at first breeding: 1 year
#  - Prebreeding census, female-based
#  - Demographic rates (phia: adult survival, phij: juvenile survival) are modelled
as time-dependent (random effect)
#  - Recapture probability (p) is modelled as sex-dependent
#  - Immigration (imm) and productivity (fec) are modelled as constant
#---------------------------------------------------------------

#-----------------------------------------
# 1. Defining priors for the parameters
#-----------------------------------------
# Initial population sizes

N1[1] ~ dcat(pn1)
NadSurv[1] ~ dcat(pnadSurv)
Nadimm[1] ~ dcat(pnadimm)

# Mean demographic parameters
l.mphij ~ dnorm(0, 0.01)
l.mphia ~ dnorm(0, 0.01)
mfec ~ dunif(0,5)
for (g in 1:2){
      mp[g] ~ dunif(0, 1)
     }

mim ~ dunif(0,5)

# Precision of standard deviations of temporal variability
sig.phij ~ dunif(0, 10)
tau.phij <- pow(sig.phij, -2)
sig.phia ~ dunif(0, 10)
tau.phia <- pow(sig.phia, -2)

# Distribution of error terms
for (t in 1:(nyears-1)){
   epsilon.phij[t] ~ dnorm(0, tau.phij)
   epsilon.phia[t] ~ dnorm(0, tau.phia)
   }

#-------------------------
# 2. Constrain parameters
#-------------------------
for (t in 1:(nyears-1)){
   logit(phij[t]) <- l.mphij + epsilon.phij[t]  # Juv. apparent survival
   logit(phia[t]) <- l.mphia + epsilon.phia[t]  # Adult apparent survival
   f[t] <- mfec                                 # Productivity
   omega[t] <- mim                              # Immigration
   }

for (g in 1:2){
        for (t in 1:(nyears-1)){
          p[g,t] <- mp[g]
          } # t
        } # g

#-----------------------
# 3. Derived parameters
#-----------------------
mphij <- exp(l.mphij)/(1+exp(l.mphij))    # Mean juvenile survival probability
mphia <- exp(l.mphia)/(1+exp(l.mphia))    # Mean adult survival probability
```

```
# Population growth rate
for (t in 1:(nyears-1)){
   lambda[t] <- Ntot[t+1] / Ntot[t]
   logla[t] <- log(lambda[t])
   }
mlam <- exp((1/(nyears-1))*sum(logla[1:(nyears-1)]))   # Geometric mean

#--------------------------------------------
# 4. Likelihoods of the single data sets
#--------------------------------------------
# 4.1. Likelihood for population count data (state-space model)
   # 4.1.1 System process
   for (t in 2:nyears){
      N1[t] ~ dpois(0.5 * f[t-1] * phij[t-1] * Ntot[t-1])
      NadSurv[t] ~ dbin(phia[t-1], Ntot[t-1])
      Nadimm[t] ~ dpois(Ntot[t-1] * omega[t-1])
      }

   # 4.1.2 Observation process
   for (t in 1:nyears){
      Ntot[t] <- NadSurv[t] + Nadimm[t] + N1[t]
      y[t] ~ dpois(Ntot[t])
      }

# 4.2 Likelihood for capture-recapture data: CJS model (2 age classes, sex-
dependent)
    # Define the multinomial likelihood
    for (g in 1:2){
      for (t in 1:(nyears-1)){
    marray.j[t,1:nyears,g] ~ dmulti(pr.j[g,t,], r.j[g,t])
    marray.a[t,1:nyears,g] ~ dmulti(pr.a[g,t,], r.a[g,t])
      }#t
    }#g

    # m-arrays cell probabilities for adults and juveniles
    for (g in 1:2){
      for (t in 1:(nyears-1)){
       q[g,t] <- 1-p[g,t]

       # Main diagonal
       pr.j[g,t,t] <- phij[t]*p[g,t]
       pr.a[g,t,t] <- phia[t]*p[g,t]

       # Above main diagonal
       for (j in (t+1):(nyears-1)){
          pr.j[g,t,j] <- phij[t]*prod(phia[(t+1):j])*prod(q[g,t:(j-1)])*p[g,j]
          pr.a[g,t,j] <- prod(phia[t:j])*prod(q[g,t:(j-1)])*p[g,j]
          } #j

       # Below main diagonal
       for (j in 1:(t-1)){
          pr.j[g,t,j] <- 0
          pr.a[g,t,j] <- 0
          } #j
        } #t

    # Last column: probability of non-recapture
    for (t in 1:(nyears-1)){
       pr.j[g,t,nyears] <- 1-sum(pr.j[g,t,1:(nyears-1)])
       pr.a[g,t,nyears] <- 1-sum(pr.a[g,t,1:(nyears-1)])
       } #t
    }#g
```

```
# 4.3. Likelihood for productivity data: Poisson regression
J ~ dpois(rho)
rho <- R * mfec
}
",fill = TRUE)
sink()

# Bundle data
jags.data <- list(nyears = nyears, marray.j = marray.j, marray.a = marray.a, y =
popcount, J = J, R = R, r.j = r.j, r.a = r.a, pn1 = dUnif(1,30), pnadSurv =
dUnif(1,60), pnadimm = dUnif(1,60))

# Initial values
inits <- function(){list(l.mphij = rnorm(1, 0.2, 0.5), l.mphia = rnorm(1, 0.2,
0.5), mfec = runif(1,0,5), mim = runif(1,0,5), mp = runif(2, 0, 1), sig.phij =
runif(1, 0.1, 10), sig.phia = runif(1, 0.1, 10))}

# Parameters monitored
parameters <- c("phij", "phia", "mp","omega", "lambda", "mphij", "mphia", "mfec",
"mim", "mlam", "Ntot")

# MCMC settings
ni <- 1100000       # number of iterations
nt <- 100           # thinning rate
nb <- 100000        # burn-in
nc <- 3             # number of chains

# Call JAGS from R (RT 11.3 min)
IPM <- jags(jags.data, inits, parameters, "JAGSmodels/finalIPM_VA.jags", n.chains =
nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel = T)
```

Chapter 4

Complex seasonal and day-to-day movements of an alpine passerine may act as an insurance against environmental variability

Complex seasonal and day-to-day movements of an alpine passerine may act as an insurance against environmental variability

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ABSTRACT

Mountains naturally offer very contrasting habitat conditions, but their biodiversity is nowadays facing the extra challenge of adapting to rapid environmental shifts that are much more pronounced than in the lowlands. Among the possible adaptive responses of wildlife, intra- and inter-seasonal movements represent an important coping strategy that remains largely unexplored. We investigated the seasonal and day-to-day movements of the Ring Ouzel *Turdus torquatus*, a European mountain bird species that is declining in many parts of its distribution. We tracked individuals breeding in the Swiss Alps using geolocators, multi-sensor loggers and GPS. Of the birds traced to their non-breeding quarters, two thirds reached the Atlas Mountains while one third stayed in Spain, a region potentially more significant for overwintering than previously thought. The birds remained mostly above 1000 m throughout the annual cycle, highlighting a strict association of Ring Ouzels with mountain habitats. We also evidenced daily elevational movements, especially upon spring arrival on the breeding grounds, which provides some noticeable behavioural flexibility, i.e. adaptive potential in response to environmental variation. This study shows how modern technology can deliver deeper insights into animal movements, paving the way for refined assessments of species vulnerability to ongoing global change while providing basic conservation guidance.

Keywords: accelerometer, altitudinal movements, barometer, conservation, high elevation, geolocator, migration, mountain bird

INTRODUCTION

Information on year-round movement patterns is key for animal species conservation (Webster *et al.* 2002). In effect, migratory decisions can directly determine individual survival and reproductive success (Marra, Hobson & Holmes 1998; Gill *et al.* 2001), impacting population dynamics (Norris & Marra 2007). The majority of animals inhabiting highly seasonal environments such as arctic and alpine ecosystems occupy their breeding habitat only during the short warm season. Consequently, the timing arrival at, and departure from these grounds needs to be finely tuned to the brief time window available for reproduction (Wingfield *et al.* 2004; Winkler *et al.* 2014). Given the particularly rapid pace of the environmental changes affecting these ecosystems (Flato & Boer 2001; Pepin *et al.* 2015), the capacity of birds to adjust and time their movement decisions in response to environmental shifts will be crucial for their long-term persistence (Dolman & Sutherland 1995; Winkler *et al.* 2014).

Movements of wildlife in mountain ecosystems have been little studied, even among well-investigated taxa such as mammals and birds of temperate biomes (Boyle & Martin 2015; Resano-Mayor *et al.* 2017). For instance, within-breeding season movements (Frey, Hadley & Betts 2016; Ceresa *et al.* 2020) or facultative latitudinal migration of bird species long considered as resident (Resano-Mayor *et al.* 2020) have been unveiled only recently, adding to our historical knowledge of seasonal altitudinal migration, i.e. vertical movements (Barçante, Vale & Alves 2017; Hsiung *et al.* 2018; Tsai *et al.* 2021). In the same line, the importance of high-elevation ecosystems as post-breeding or stopover grounds for migratory species may have been widely underestimated (Boyle & Martin 2015). The pronounced spatiotemporal heterogeneity that characterizes mountain ecosystems thus appears to foster regular movements throughout the annual cycle, both latitudinally and altitudinally. However, individual dispersal has remained poorly documented until the recent deployment of sophisticated tracking technology.

The rapid development of tracking devices offers novel opportunities to study individual bird movements at unprecedented spatial and temporal scales and thus to tackle key conservation challenges (Katzner & Arlettaz 2020). For small birds, geolocators (GL) enable tracking the whereabouts of individuals throughout the annual cycle by means of simple measures of light intensity coupled with an internal clock. Still, this technology alone is not accurate enough to detect small-scale latitudinal movements (Fudickar, Wikelski & Partecke 2012), without mentioning altitudinal ones. GPS tracking devices can fulfil this requirement and are now successfully deployed on small passerines (McKinnon & Love 2018), but the reduced lifespan of the embedded battery drastically limits the number of locations that can be collected. More recently, multi-sensor loggers (MSL) that combine GL with other sensors such as a barometer and/or an accelerometer have been developed (Liechti *et al.* 2018). Similarly to GL, MSL can collect data at high frequency and over long periods of time, additionally providing much deeper insights into individual spatial behaviour, including activity patterns, migratory schedules and flight altitude (Dhanjal-Adams *et al.* 2018; Liechti *et al.* 2018; Briedis *et al.* 2020). They thus represent a promising tool to better assess the three-dimensional movements of small animals such as passerines.

We investigated the annual movement patterns of a Western Palearctic passerine, the Alpine Ring Ouzel (*Turdus torquatus alpestris*), using these new tracking technologies. This subspecies of thrush breeds primarily in the mountain massifs of western and central Europe, from the Cantabrian to the Carpathian Mountains (Glutz von Blotzheim & Bauer 1988; Keller *et al.* 2020). It is believed to overwinter mainly in the Atlas Mountains in Morocco and Algeria (Glutz von Blotzheim & Bauer 1988) — in sympatry with individuals from the northern subspecies *T. t. torquatus* (Burfield 2002; Sim *et al.* 2015) — where the principal source of food is juniper (*Juniperus sp.*) berries (Ryall & Briggs 2006). Given the population declines observed in various parts of the species range, in particular at its periphery, it has been suggested that hunting and habitat deterioration in the principal migratory stopovers and/or on winter quarters may add to drivers negatively impacting the species on its breeding grounds (Burfield 2002; Sim *et al.* 2015). Yet, large-scale movements and thus migratory connectivity of the different Ring Ouzel populations are still poorly documented (Sim *et al.* 2015). This not only hampers understanding of the metapopulation system, but also impedes the development of an integral conservation management plan (Webster *et al.* 2002). Nonetheless, winter observations at the southern boundary of species breeding range (French western Alps and Pyrenees; Glutz von Blotzheim & Bauer 1988) suggest that central European populations are partially migratory or travel much shorter distances than their northern conspecifics, a classical pattern among European migrants (i.e. leapfrog migration; Newton 2008). This study used various tracking technologies to unravel the migration timing, routes and behaviour of Ring Ouzels breeding in the Central European Alps.

MATERIALS AND METHODS

Fieldwork and material

Birds were captured and ringed at a single study site in Valais, Switzerland (46.33 N, 7.43 E; 1800–2100 m above sea level) during the breeding season, i.e. in April–June 2015–2020. Captures were performed with 2.5-m high mistnets placed among potential foraging grounds or parallel to forest edges. Birds were sexed from plumage colouration and age — either second calendar year (2cy) or adult (> 2cy) — determined based on the presence of a moult limit in the greater coverts (Jenni & Winkler 2020).

We used four types of loggers to record Ring Ouzel locations: simple geolocators (hereafter GL; model GDL2, Swiss Ornithological Institute (SOI), Sempach, Switzerland); remote-download geolocators (hereafter also termed GL; model GDL-uTag, SOI, Sempach, Switzerland); multi-sensor loggers (hereafter MSL; model GDL3-PAM, SOI, Sempach Switzerland) and GPS loggers (GPS; model nanoFix-GEO, PathTrack Ltd, Otley, UK). In addition to light intensity, the deployed MSL measured acceleration and atmospheric pressure at 5-min intervals (see Liechti *et al.* 2018 for details). GPS were programmed to record position once a week. All types of loggers were fixed on the birds using a leg-loop harness, made of elastic rubber or inelastic threaded nylon as concerns GL and MSL, and Teflon ribbon for GPS. The different types of loggers (see details in the Supplementary Materials, Table S1) weighed at most 2.6% of the mean (± sd) body mass as measured from captured birds (males: 95.1 ± 5.1 g, n = 191; females: 100.8 ± 8.9, n = 91). The permit for bird capturing was delivered by the Swiss Federal Office for the Environment (F044-0799) and fitting of tracking devices was authorized by the Swiss Federal Food Safety and Veterinary Office, with all study protocols approved by the responsible ethics committee. Capturing and tagging were performed following all relevant guidelines and regulations of the abovementioned federal offices.

We equipped a total of 59 individuals with 62 GL or MSL (three individuals were equipped twice) as well as 15 individuals with GPS between 2015–2019 (see Supplementary Materials, Table S1). Only seven out of the 62 GL/MSL were retrieved by recapture of the tagged bird, while data from another four GL could be downloaded remotely in the field. Two additional GL-tagged individuals had lost their logger at the time of recapture. We thus retrieved data from, in total, 5 MSL and 6 GL. For MSL, data was complete (over one year) except for one device that had stopped recording as early as February in the year following tagging. Regarding GL, intense shading prevented data exploitation for two of them. Shading by feathers or the surrounding habitat may indeed strongly bias the measurements of sunrise or sunset times (hereafter twilights) and lead to spurious localizations. We additionally retrieved two out of the 15 GPS by recapture, but both had malfunctioned, with locations available for only one GPS for just a month after deployment.

On subsequent years following ringing, we re-sighted 33.9% (20/59) of the individuals equipped with GL and MSL, and 20% (3/15) of the GPS-tagged birds, to be compared with 29.9% (64/214) of the Ring Ouzels that had only been colour-ring marked at the study site and served as a control group. As assessed with Bayesian Cormack-Jolly-Seber models from visual re-sightings (following Kéry & Schaub 2012), apparent survival rates of GL- and MSL-tagged birds did not differ from the control group (β = 0.27, 95% CI: -0.92 to 1.66), while we evidenced a detrimental effect of the slightly heavier GPS loggers (β = -1.74, 95% CI: -3.32 to -0.42).

Analyses

All analyses were performed with the software R 3.6.2 (R Development Core Team 2019) using the packages ‘TwGeos’ (Wotherspoon, Sumner & Lisovski 2016), ‘GeoLight’ (Lisovski & Hahn 2012), ‘SGAT’ (Sumner, Wotherspoon & Hindell 2009) and ‘PAMLr’ (Dhanjal-Adams 2019), following the general framework described in Lisovski *et al.* (2020). Starting with data from the five MSL, we classified bird behaviour into four categories of activity (no activity, low activity, high activity and migration) based on acceleration measures, using the algorithm from the *classifyFLAP* function in ‘PAMLr’. We defined migratory flights as those equal or longer than 30 min, which corresponds to at least six consecutive readings with ascertained flight activity. Based on this data, we defined the migratory schedule and separated the annual cycle into four periods: post-breeding, autumn migration, non-breeding (i.e. overwintering) and spring migration (the locations during reproduction being irrelevant here). The post-breeding period started on the day of the first nocturnal flight in June or July and lasted up to the autumn migration departure, which was defined as the first true migratory flight after August 1st. We assumed that birds had reached their non-breeding residence area as soon as they had stayed for at least two weeks in a row at the same place after October 1st. Spring migration started with the first ascertained migratory flight in March.

In a second step, we converted readings of atmospheric pressure into m above sea level (hereafter m asl) using the function *altitudeCALC* in the ‘PAMLr’ package, which is based on the hypsometric equation that assumes standard atmospheric conditions (Stull 2016; Liechti *et* *al.* 2018). Hence, estimates of altitude are rather precise, but can be biased by natural variations in atmospheric pressure, i.e. influenced by the so-called ‘high- and low-pressure areas’. Such shifts in pressure are, however, fairly slow and minor (maximum of 2 hPa h^{-1}) so that they would not generate abrupt changes in estimated altitude (Liechti *et al.* 2018). Furthermore, daily fluctuations in atmospheric pressure, called atmospheric tides, reach at most 3 hPa in the tropics (Le Blancq 2011), potentially inducing a maximal daily altitudinal deviation of only ca. 30 m for a given location. We summarized the altitude information as the median and range (minimum to maximum) for each of the four periods of the annual cycle, treating readings during migratory bouts separately.

Finally, we derived geographic positions of the nine birds for which light-intensity data was available and of sufficient quality. We first defined twilights using ‘TwGeos’ and then categorized those into residency and movement periods. For MSL, this distinction was based on the migratory flights that were identified as described previously. We considered only periods of eight consecutive days without migratory flight as true stopovers, given the noise in the data and thus the need of longer periods to estimate accurate locations. For GL, the distinction was done using the function *changeLight* in ‘GeoLight’, again setting a threshold of eight days for distinguishing a stopover. We used ‘in-habitat’ calibration of the sun elevation angles (zero and median) for parameterizing the error distribution around the twilight times (Lisovski & Hahn 2012), i.e. using as a reference the period during which a bird was for sure present at its breeding site. We then modelled the migration trajectory as well as stopover and residency locations using ‘SGAT’. We chose a grouped Estelle model, where estimates within residency periods are grouped together to increase spatial precision (Lisovski *et al.* 2020). We forced residency periods to occur on land only, whereas movement was not constrained spatially but flight speed assumed to follow a gamma distribution ($\beta = 2.2$, sd = 0.08). The starting point of each trajectory track was fixed at the very breeding location, as was the end point, except for the individual whose logger stopped recording in the middle of winter. To fit the Estelle model, we first drew 1,000 initial samples using a ‘modifiedGamma’ model (i.e. relaxed model, allowing negative errors on twilight times), tuned it five times with 300 iterations using a ‘Gamma’ distribution. We shall here report median estimates ± 95% credible intervals (CI; based on 2.5 and 97.5% quantiles) from a final run with 2,000 iterations to ensure convergence.

RESULTS

Migratory schedule

We obtained a complete annual migratory schedule for four individuals, and partial for a fifth (Table 1). Most of the migratory movements took place at night (mean = 96.7%, range: 92.7–98.8%). Post-breeding dispersal started between the second half of June and the first decade of July (Table 1), although it consisted of only one single short nocturnal flight (< 30min) for bird AdM-3 (Fig. 1). Actual departures into fall migration were observed 45–103 days after the onset of post-breeding dispersal, differing markedly between all five individuals (Table 1). Most of the autumn migratory flights occurred in October for all birds (Fig. 1; Supplementary Materials, Fig. S1). Inter-individual differences in the onset of fall migration resulted in a large variation in the duration and speed of migration (Table 1), but the cumulative sum of flight hours varied little in all three adult males, with 44, 43 and 45 h, respectively (AdM-1, -2, -3; Table 1, Supplementary Materials, Fig. S1). The flight duration of the sole adult female (AdF) with a full tracking record was much briefer (31 h), owing to the shorter distance to her non-breeding site (Table 1). A fourth younger male (second calendar year; 2cyM) revealed high migratory activity in August and September already, resulting in a total of 75 h in migratory flights. The number of days necessary to reach the final non-breeding destination varied between 27 and 55 days (except for 2cyM that was hyperactive in the late summer, see above), although migratory flights occurred only during 7–13 nights (31 nights for 2cyM). Nocturnal migratory flights were also obvious for two individuals (2cyM and AdM-1) in December and January (Fig. 1), evidencing potentially significant movements in the middle of the winter (Supplementary Materials, Fig. S2). Spring migration from the four birds that yielded data took place in a fairly narrow temporal window of 9–20 days (Table 1, Fig. 1), being thus much shorter than fall migration, and also briefer in cumulative flight hours and number of migratory nights (Table 1).

Migration routes

An insufficient quality of data combined with migratory activity typically taking place around the equinoxes dramatically limited our ability to precisely reconstruct the migratory trajectories and locate the stopovers for most of our birds. Nevertheless, the GPS information available from a single bird revealed a 140 km eastwards movement at the end of June, hence initiating post-breeding dispersal, in line with the findings obtained with MSL. However, nocturnal flight durations of MSL-tagged birds at that time of the year (0.25–4.7 h in total) suggest that only one other bird could have covered a similarly long distance during the post-breeding period (AdM-2; Fig. 1). Concerning non-breeding grounds, GL and MSL data revealed that six birds spent the winter in North Africa, while three others most likely overwintered in the Iberian Peninsula (Fig. 2). Among the six birds wintering in Maghreb, two were localized in the Middle Atlas, two in the High Atlas and one in the Anti-Atlas, all five in Morocco. The location estimates of a sixth bird (2cyM) further south in Algeria are inconsistent with elevation readings (Fig. 3) and probably biased southwards (see also Supplementary Materials, Fig. S2); this individual may actually have overwintered in the Anti-Atlas or High Atlas massif. Among the three Ring Ouzels staying in Spain, one individual overwintered in the meridional Sistema Ibérico, (AdM-4), another in the Sistema Prebético (AdF), while the winter quarters of the third bird (AdM-5) are unclear (average locations in the Mediterranean) and could be situated in the eastern part of the Sistema Prebético (Fig. 2).

Altitudinal movements

The median elevation during the post-breeding period was, for all five birds tagged with MSL, above the average elevation of the core study area (i.e. > 1950 m asl; Fig. 3), indicating movements to sites mostly above the treeline after reproduction. The median elevation of stopovers during the autumn migration (contrary to their locations, the elevation of stopovers was easily retrieved thanks to the barometer sensor) was generally above 1860 m asl (Fig. 3), but three birds stopped below 1000 m asl for a single day. The maximal estimated flight altitude was reached during the fall nocturnal migration by bird AdF on October 10th, with 4270 m asl. The median elevation of non-breeding grounds was always at or above 1500 m asl for every individual, irrespective of their location. Spring stopover sites were on average at a lower elevation than autumn stopovers (Fig. 3). Finally, year-round measurements revealed periods with marked elevation differences between day and night within a 24-h cycle (Supplementary Materials, Fig. S3). Birds were then clearly commuting every day to areas located at either lower (pre-breeding) or higher (post-breeding) elevations than their overnighting sites. This phenomenon, confirmed via direct field observations, was particularly marked during the two to three weeks following spring arrivals, when birds flew to foraging grounds situated several hundred meters below the breeding area (Fig. 4). A similar behaviour was also detected later in the season, following late snowfalls (Fig. 4).

Table 1 Summary statistics and schedule of dispersal and migration from the five Ring Ouzel individuals equipped with multi-sensor loggers.

	AdF	2cyM	AdM-1	AdM-2	AdM-3
Age and sex	adult female	2nd-year male	adult male	adult male	adult male
Period	2017–2018	2017–2018	2018–2019	2018–2019	2019–2020
Total distance (km)	1158	2115	1868	2284	1739
Post-breeding dispersal start	2-Jul	5-Jul	17-Jun	28-Jun	19-Jun
Duration (days)	73	45	83	103	77
Autumn migration					
Departure	13-Sep	20-Aug	9-Sep	9-Oct	3-Sep
Duration (days)	54	83	46	27	55
Arrival	6-Nov	11-Nov	24-Oct	5-Nov	29-Oct
Nights on migration	11	31	8	7	13
Travel speed (km/day)	21.1	25.5	40.6	84.6	31.6
Cumulative flight hours	30.7	75.2	43.9	42.7	44.8
Spring migration					
Departure	27-Mar	19-Mar	11-Mar	22-Mar	–
Duration (days)	9	18	20	9	–
Arrival	5-Apr	6-Apr	31-Mar	1-Apr	–
Nights on migration	5	7	7	5	–
Travel speed (km/day)	128.7	117.5	93.4	253.8	–
Cumulative flight hours	21.3	36.2	40.8	41.7	–

The total distance indicates the great circle distance from the breeding site to the furthest non-breeding location, and not the whole trajectory distance. Travel speed has been calculated as total distance divided by the duration of migration (i.e. rounded number of days from the first to the last migratory flight). 'Nights on migration' stand for the number of nights with ascertained migratory flight activity.

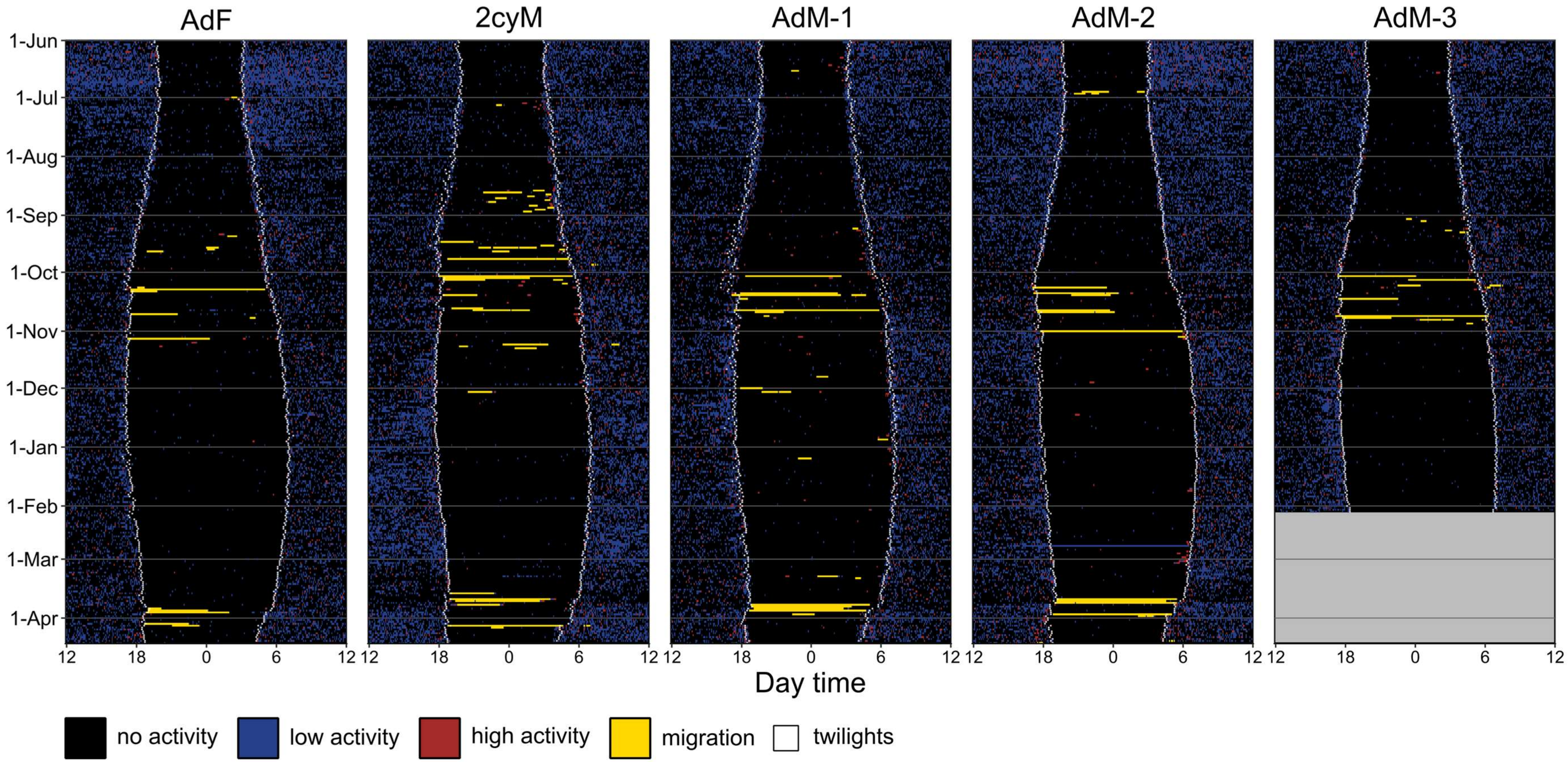

Figure 1 Actograms of five Ring Ouzels equipped with multi-sensor loggers, showing the annual activity pattern as classified into four categories of behaviour. Small white squares show the timing of the twilights as estimated from the individual light sensor of the tag. The cut between two successive 24-h periods is set at noon to enhance the visualization of a nocturnal migratory flight along a single line.

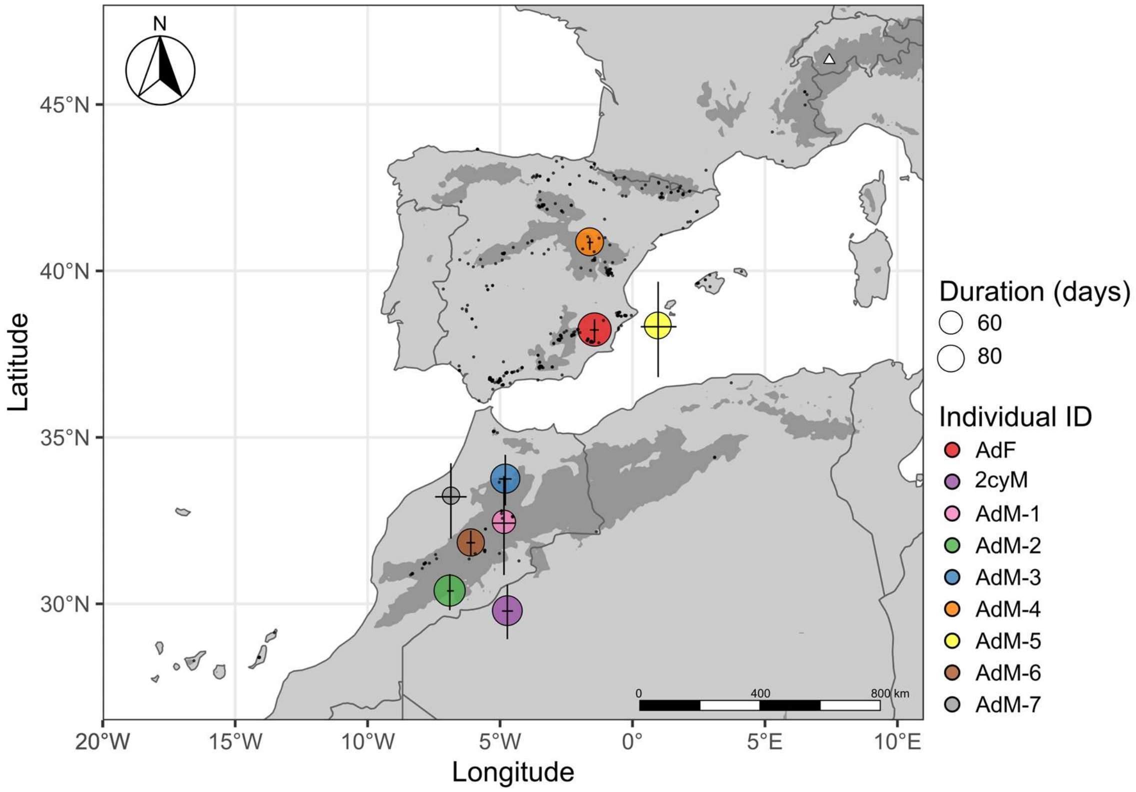

Figure 2 Longest stationary non-breeding location of nine Ring Ouzel individuals as retrieved from geolocator data. Error bars around locations represent 95% credible intervals while the size of circle is proportional to stay duration. Winter sightings of Ring Ouzels (December to February) are shown as small black dots and were accessed via GBIF (https://doi.org/10.15468/dl.p6ez7a). Areas shaded in dark grey are above the contour line of 1000 m asl.

DISCUSSION

Using electronic tracking technology, this study unravels the seasonal movements of Alpine Ring Ouzels breeding in the Swiss Alps. From a technical viewpoint, if modern tracking methods offer new opportunities for in-depth ecological research, we must not forget that geolocation is particularly challenging when deployed in mountainous environments. This is because the complex topography influences the measurement of day length, yielding less accurate location estimates. Multi-sensor loggers may constitute an interesting alternative as they enable measuring elevation and behaviour at an unprecedented fine temporal resolution. Here, it is the combination of different methods that provided us with a clear picture of the year-round whereabouts and migratory behaviour of the Ring Ouzel. The species is tightly associated with mountain ranges and high elevations at all stages of its life cycle, including during migratory stopovers. Our findings corroborate recent findings that temperate mountain ecosystems are important not only for the reproduction of Western Palearctic avifauna but also for its dispersal and migration, in line with what has recently been documented in the Nearctic (Boyle & Martin 2015). Mountain massifs actually constitute a network of stepping stones for this passerine species in the western European landscape that is otherwise dominated by unsuitable lowland habitat. This behavioural pattern observed in Ring Ouzels may be partly shared by at a least another typical inhabitant of European upland ecosystems, the White-winged Snowfinch *Montifringilla nivalis* (see Resano-Mayor *et al.* 2020). The strict reliance on mountains of these specialists of high elevations might render them more vulnerable to global environmental change than lowland wildlife. On the one hand, habitat conditions are going to worsen more rapidly for mountain-dwellers than for lowland species due to faster climate shifts at high elevations (Pepin *et al.* 2015). On the other hand, the area of suitable habitat will inexorably shrink due to the pyramid shape of mountains.

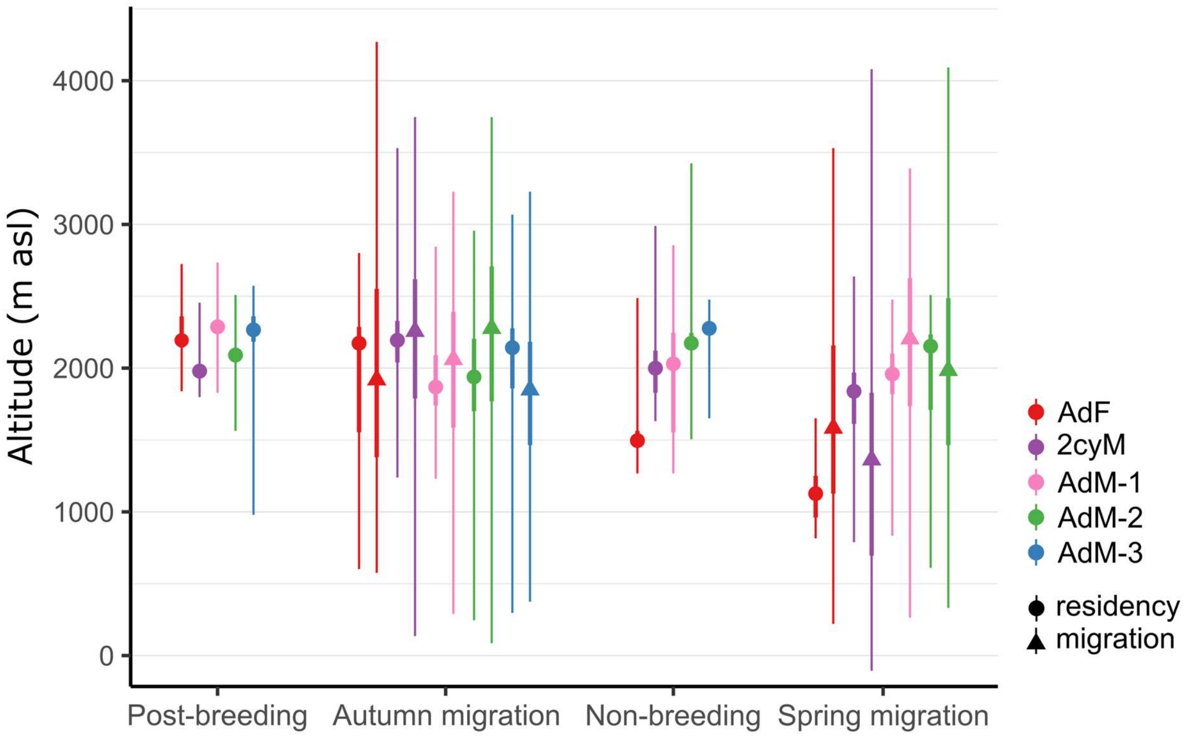

Figure 3 Median altitude estimates, at four stages of the annual cycle, for five Ring Ouzels equipped with multi-sensor loggers. For autumn and spring migration, readings during stopovers (circles) are separated from those during active, mostly nocturnal migration (triangles). Bold bars represent the lower to upper quartile range and thin bars the total range of readings (min to max).

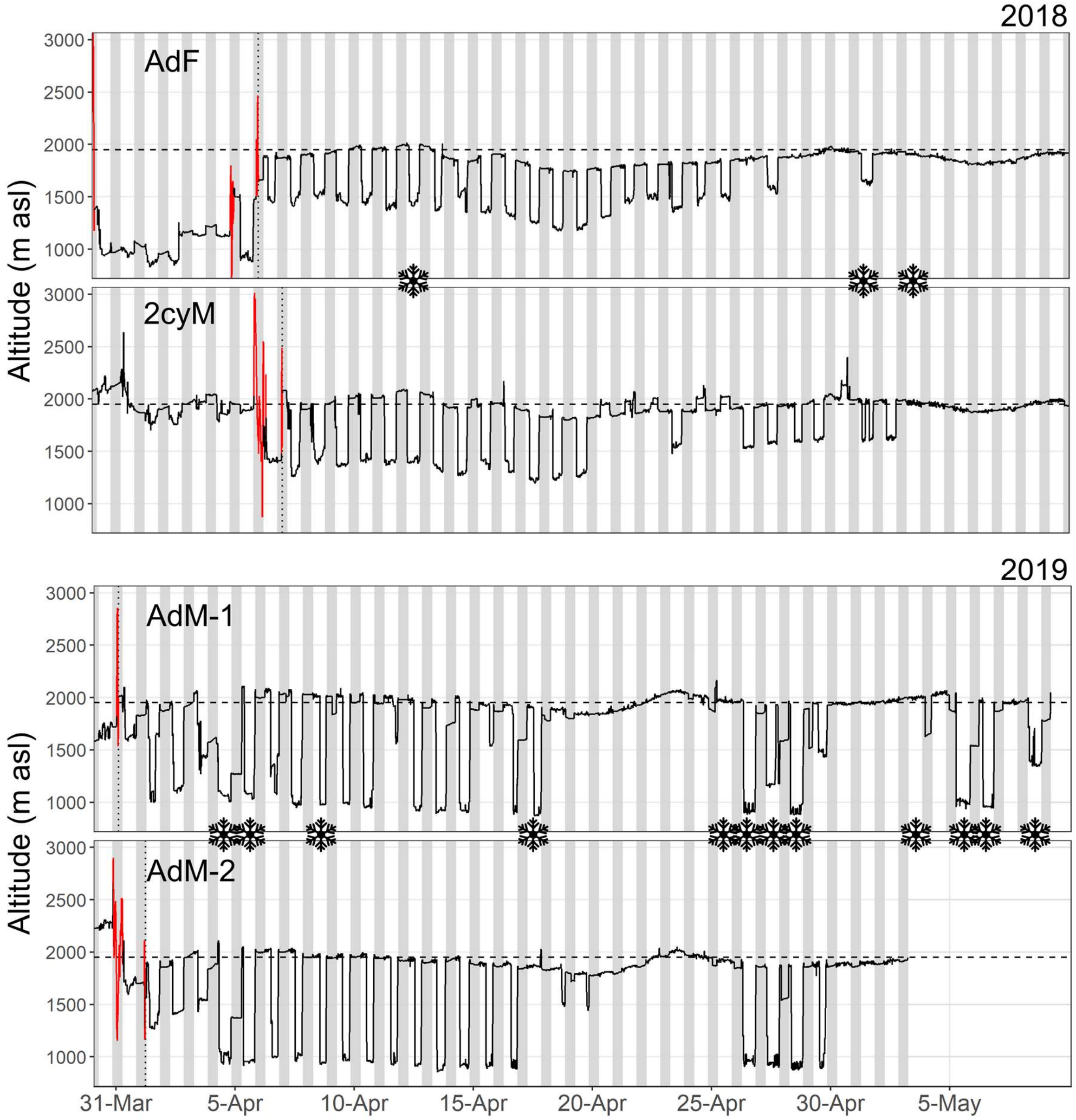

Figure 4 Continuous altitude estimates (5-min intervals) from four Ring Ouzels upon arrival (vertical dotted line) on the breeding grounds in spring. Grey zones symbolize nighttime and the horizontal dashed lines indicate the mean elevation of the study area. Altitude estimates displayed in red refer to migratory flights. Snowflake icons indicate a new snowfall (≥ 1 cm fresh snow) as measured at a nearby weather station (4.1 km distance, 2390 m asl).

Our results confirm the important role played by the Atlas Mountains for wintering Ring Ouzels (Glutz von Blotzheim & Bauer 1988; Ryall & Briggs 2006; Sim *et al.* 2015): two thirds of our birds spent the cold season in Maghreb. The remaining third overwintered in the Iberian Peninsula, suggesting that Spanish mountain ranges may represent another, so far unrated key wintering hotspot, at least for the Alpine population. Observations of Ring Ouzels in winter in the Atlas and Spanish massifs have shown that they feed mainly on juniper berries (of *Juniperus thurifera, communis, oxycedrus, phoenica* and *cedrus*), playing a key role in seed dispersion (Herrera 1985; Zamora 1990; Ryall & Briggs 2006; Rumeu, Padilla & Nogales 2009). Overwintering in Spain certainly entails shorter, i.e. energetically less demanding flights for Alpine Ring Ouzels. Nonetheless, the reason for choosing Spain may lie elsewhere. In effect, the fructification of junipers is highly cyclic in the Spanish highlands (Tellería *et al.* 2011; Tellería, Carrascal & Santos 2014), as it probably also is in North Africa (Ryall & Briggs 2006). Since thrushes are known to actively track food sources (Tellería *et al.* 2011; Tellería, Carrascal & Santos 2014), the local availability of juniper berries probably explains the whereabouts of Ring Ouzels in winter. Hence, the few sudden movements we could document in winter may correspond to relocations to regions providing good food supplies. An ability to move between feeding areas could make Ring Ouzels somehow resilient to the progressive loss of their foraging habitat in the Maghreb, notably in Morocco where juniper forests are systematically overexploited for firewood (Ryall & Briggs 2006).

Finally, this study also evidenced complex patterns of daily altitudinal movements, a behaviour that has to our knowledge never been documented in such detail at the individual level in a non-aerially foraging passerine. The most patent demonstration of this phenomenon is upon arrival from migration in April. At that time of the year, the breeding grounds of the Alpine Ring Ouzel are still under a dense snowpack. Birds typically overnight in their future breeding territories, males vocally signalling their occupancy at dawn and dusk (Glutz von Blotzheim & Bauer 1988). The rest of the day, they visit snow-free meadows at lower elevations to forage, usually in the montane and subalpine belts, depending on seasonal, year-specific snow conditions (Fig. 4). Later in the season, with the advancement of the snowmelt which frees the first patches of alpine grasslands within the breeding area, they stop commuting. Although we found no other reports of similar daily commuting of non-aerially foraging passerines in the literature, altitudinal movements to lower elevations triggered by adverse weather conditions at the breeding site were described several times (O'Neill & Parker 1978; Hahn *et al.* 2004; Boyle, Norris & Guglielmo 2010). We also observed such facultative movements after late snowfalls in the spring. Altitudinal migration may thus represent a sort of insurance against potential phenological mismatches, enabling birds to reach high-elevation breeding grounds very early, sometimes when those are still inhospitable. Indeed, Ring Ouzels migrate much faster in the spring than in the autumn, a pattern commonly observed in migratory species in Europe (Nilsson, Klaassen & Alerstam 2013). However, this contrasts with the migration strategy of other mountain or arctic bird species, that make prolonged pre-breeding stopovers at lower elevations or latitudes not far from their reproductive grounds, waiting there for the snowmelt at their nearby breeding sites and/or building fat reserves (Kölzsch *et al.* 2016; de Zwaan *et al.* 2019). With their daily commuting, Ring Ouzels have thus found an innovative solution to cope with the highly seasonal and unpredictable breeding environment that prevails at high elevation. The question remains whether this high spatial flexibility will also procure Ring Ouzel — and other cold-adapted bird species (Hahn *et al.* 2004; Wingfield *et al.* 2004; Resano-Mayor *et al.* 2020) — some buffer against the dramatic impacts of climate and land-use change that are going to accentuate into the future.

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SUPPLEMENTARY MATERIALS

Table S1 Details on the type and number of tracking devices fitted on Ring Ouzels in the Swiss Alps over the period 2015–2019.

	Simple geolocator	Remote-download geolocator	Multi-sensor logger	GPS logger
Abbreviation	GL	GL	MSL	GPS
Model	GDL2	GDL-uTag	GDL3-PAM	nanoFix-GEO
Producer	Swiss Ornithological Institute	Swiss Ornithological Institute	Swiss Ornithological Institute	PathTrack Ltd.
Weight with harness (g)	0.6	1.2	1.5	2.5
Material of harness	Threaded nylon	Elastic rubber	Elastic rubber or threaded nylon	Teflon ribbon
Number fitted				
2015	6	0	0	0
2016	0	0	0	15
2017	0	0	12	0
2018	0	0	19	0
2019	0	13	12	0
Total	**6**	**13**	**43**	**15**
Number retrieved	2	4	5	2
Exploitable data	0	4	5	1

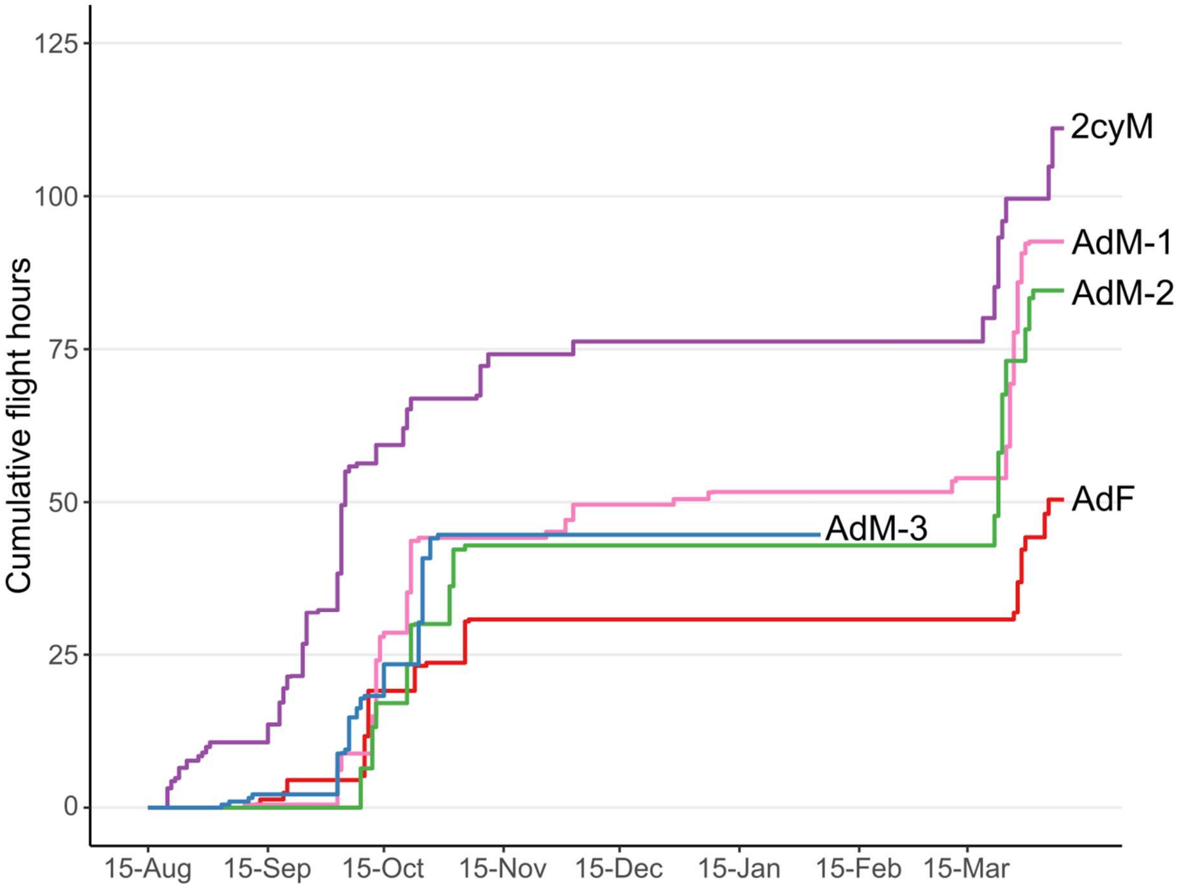

Figure S1 Cumulative flight hours of five Ring Ouzel individuals during the autumn migration, non-breeding and spring migration periods (August 15^{th} to April 10^{th}).

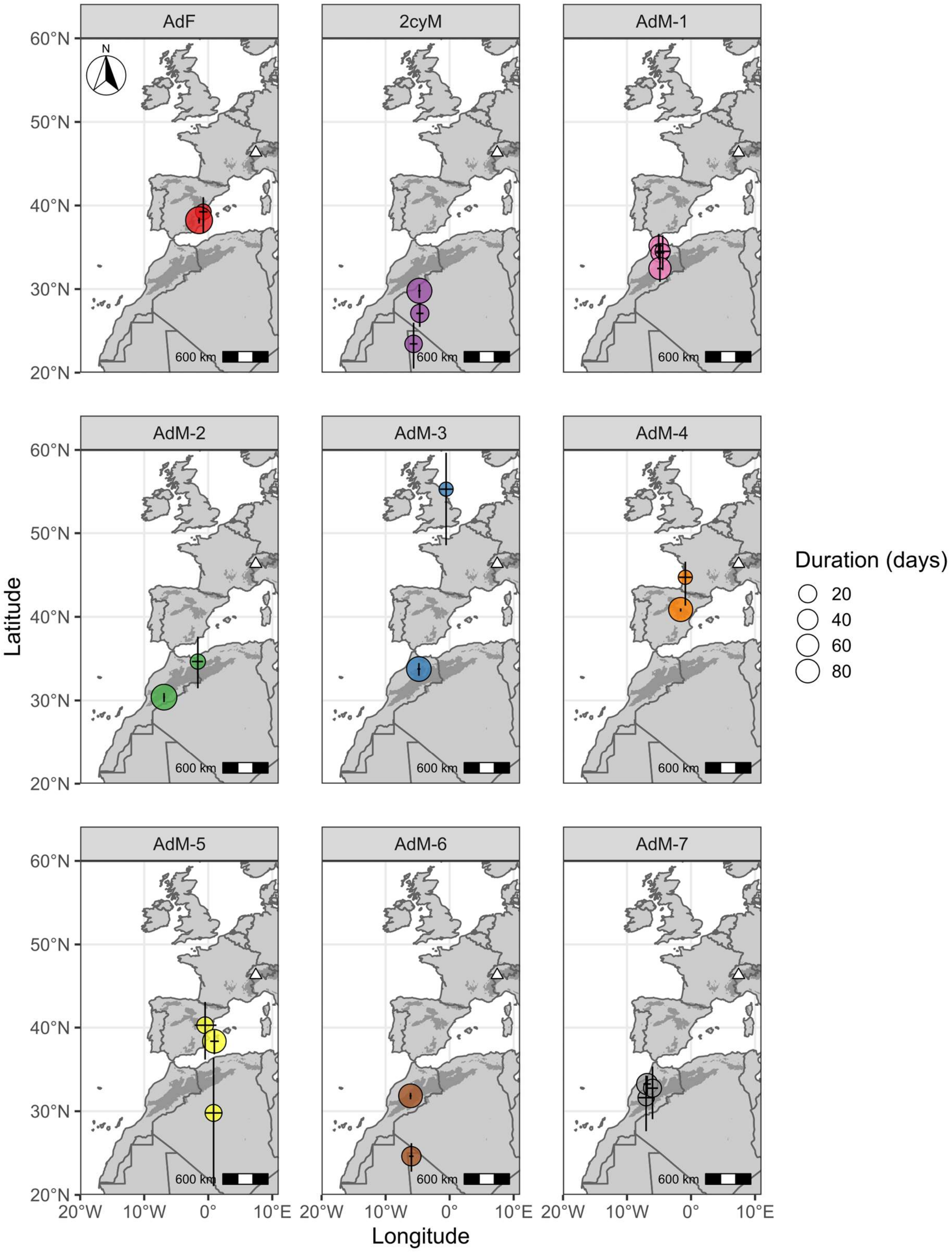

Figure S2 Estimated locations (± 95% CI bars) of the non-breeding residency periods (between October 15th and March 1st) for all nine Ring Ouzel individuals tracked with geolocators.

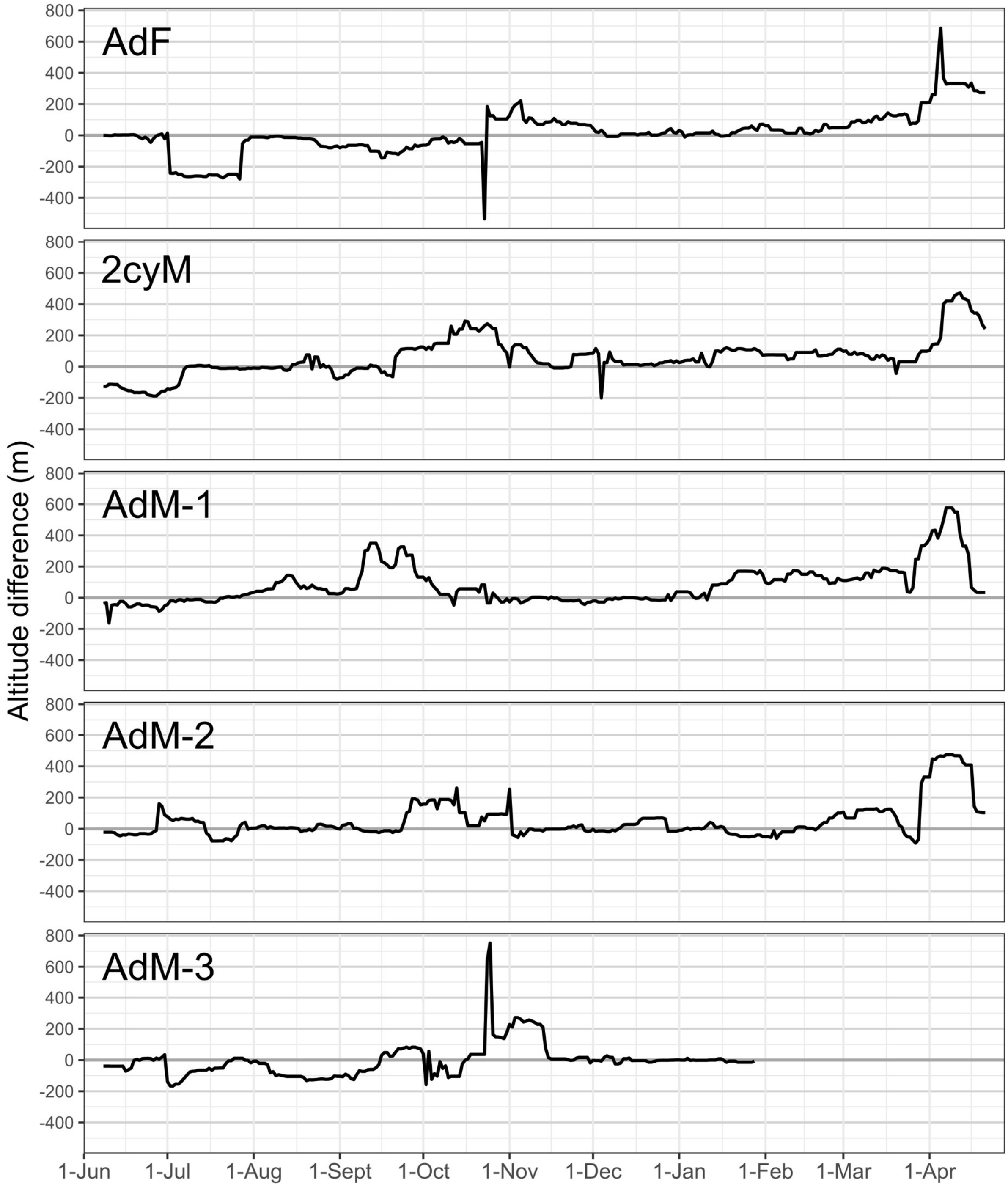

Figure S3 Difference in altitude (in meters) between night and day readings for five Ring Ouzel individuals equipped with multi-sensor loggers. A 15-days moving average has been applied to smooth peaks following migration flights at high or low elevations.

Chapter 5

Predictive models of distribution and abundance of a threatened mountain species show that impacts of climate change overrule those of land-use change

Predictive models of distribution and abundance of a threatened mountain species show that impacts of climate change overrule those of land-use change

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ABSTRACT

Climate is often the sole focus of global change research in mountain ecosystems although concomitant changes in land-use might represent an equally important threat. As mountain species typically depend on fine-scale environmental characteristics, integrating land-use change in predictive models is crucial to properly assess their vulnerability. Here, we present a modelling framework that aims at providing more comprehensive projections of both species' distribution and abundance under realistic scenarios of land-use and climate change, and at disentangling their relative effects. We used the Ring Ouzel (*Turdus torquatus*), a red-listed and declining mountain bird species, as a study model. Based on standardized monitoring data collected across the whole country, we fitted high-resolution ensemble species distribution models to predict current occurrence probability while spatially explicit density estimates were obtained from N-mixture models. We then tested for the effects of realistic scenarios of land-use (land abandonment vs. farming intensification) and climate change on future species distribution and abundance. Occurrence probability was mostly explained by climatic conditions, so that climate change was predicted to have larger impacts on distribution and abundance than any scenarios of land-use change. In the mid-term (2030–2050), predicted effects of environmental change show a high spatial heterogeneity due to regional differences in climate and dominant land-use, with farming intensification identified as an important threat locally. In the long-term (2080–2100), climate models forecast a marked upward range shift (up to +560m) and further population decline (up to -35%). Our innovative approach highlights the spatio-temporal heterogeneity in the relative effects of different environmental drivers on species distribution and abundance. The proposed framework thus provides a useful tool not only for better assessing species' vulnerability in the face of global change, but also for identifying key areas for conservation interventions at a meaningful scale.

Keywords: alpine grasslands, bird conservation, elevational shift, ensemble modelling, land-use intensification, N-mixture, treeline

INTRODUCTION

Mountain ecosystems are rapidly changing globally, under the influence of anthropogenic drivers (Huber, Bugmann & Reasoner 2006). Human-induced climate change represents a particular challenge for high-elevation biodiversity (Lehikoinen *et al.* 2019), through increasing ambient temperatures, altered hydrological cycles and more frequent extreme weather events (Beniston 2003); in effect, these phenomena are more acute in mountains than in the lowlands (Pepin *et al.* 2015; CH2018 2018). Moreover, species living at high elevations are particularly vulnerable due to their fine-tuned adaptations to naturally harsh environmental conditions and short periods of reproduction (Martin & Wiebe 2004), with a high risk of range contraction and fragmentation (Dirnböck, Essl & Rabitsch 2011) as well as phenological mismatches (Scridel *et al.* 2018). In parallel, changes in land-use are increasingly impacting mountain ecosystems and are considered an equally, if not more important threat than climate change in European cultural landscapes (Chamberlain *et al.* 2016; Mollet *et al.* 2018). Nevertheless, extant research predicting future species distributions has mainly focused on the effect of increasing ambient temperatures, while neglecting the role of land-use changes (Titeux *et al.* 2016; Sirami *et al.* 2017). Integrating land-use into future scenarios is, however, crucial to properly assess species vulnerability in the face of global change (Maggini *et al.* 2014; Howard *et al.* 2015) and thus make meaningful conservation recommendations (Braunisch *et al.* 2014), especially in ecosystems that are already heavily modified by humans.

Subalpine forests in Europe have been exploited for centuries (Mollet *et al.* 2018). In particular, the upper transition zone between wooded and open landscapes, the so-called treeline ecotone, has been largely shaped by anthropogenic activities (Körner 2012; Mollet *et al.* 2018). A long tradition of summer grazing by cattle and sheep has pushed the treeline to areas below the elevation threshold at which local environmental conditions naturally limit tree growth (Gehrig-Fasel, Guisan & Zimmermann 2007; Dirnböck, Essl & Rabitsch 2011; Körner 2012). In the Alps, as a result, the treeline belt consists of a complex mosaic of coniferous stands, patches of dwarf shrubs and grassland that can stretch over an elevational range of few hundred meters. This heterogenous habitat harbours a rich biodiversity (Körner 2012; Mollet *et al.* 2018), which is now threatened by a dichotomous trend of either agricultural abandonment or management intensification of traditional pastures and meadows (Tasser & Tappeiner 2002). On the one hand, less accessible or unproductive grasslands are not grazed or mown anymore, which leads to progressive shrub and ultimately forest encroachment (MacDonald *et al.* 2000; Laiolo *et al.* 2004). On the other hand, the management of biodiversity-rich grasslands is intensified through an increase in direct nitrogen input to enhance fodder productivity (Britschgi, Spaar & Arlettaz 2006; Andrey *et al.* 2014; Humbert *et al.* 2016). Both drivers, in some places accompanied by atmospheric nitrogen deposition, lead to the homogenization of mountain ecosystems, threatening these rich ecological communities that rely on semi-open and open habitats (Chamberlain *et al.* 2016; Bani *et al.* 2019; García-Navas *et al.* 2020).

In order to quantify the relative impacts of climate vs. land-use changes on species occurring in mountain environments, we chose as a model the Ring Ouzel (*Turdus torquatus*), a thrush species that inhabits exclusively mountain and upland ecosystems across its range (Glutz von Blotzheim & Bauer 1988). The subspecies *T. t. alpestris* is present in central Europe and typically breeds in semi-open subalpine forests. In Switzerland, its breeding population has been declining by more than one third in the 30 last years, mostly at lower elevations, resulting in a mean upward distribution shift of +84 m (Knaus *et al.* 2018). This strongly suggests that climate change, with a linear mean increase in ambient temperature of 0.9°C over the same period (Meteoswiss 2019), might be responsible for the decline (Beale *et al.* 2006; Barras *et al.* 2021; *Chapter 2*). Nevertheless, this climatic trend has been paralleled by accelerating land abandonment, which is the main driver of forest cover increase and upward shift in the country (Gehrig-Fasel, Guisan & Zimmermann 2007), with a 46,200 ha wooded area gain in the Swiss Alps from 1985 to 2009 (SFSO 2013). For a species relying strongly on semi-open habitats, a progressive forest closure may both lessen habitat suitability and negatively affect its demography. Moreover, the fertilization of mountain grasslands has also drastically increased, through direct and indirect (i.e. atmospheric) nitrogen inputs, favouring fast-growing nutrient-tolerant plant species (Tasser & Tappeiner 2002; Britschgi, Spaar & Arlettaz 2006; Andrey *et al.* 2014). Since Ring Ouzel relies on patches of short and sparse ground vegetation to forage (Burfield 2002; Barras *et al.* 2020; *Chapter 1*), high-productivity grasslands are usually avoided (Buchanan *et al.* 2003; von dem Bussche *et al.* 2008). Therefore, it is unknown to which extent these other, parallel changes in land-use could also contribute to species' fall, and by extension to the decline of other sympatric mountain species (Knaus *et al.* 2018; Lehikoinen *et al.* 2019).

Species distribution models (SDMs), which describe current relationships between species occurrence and environmental variables, offer the additional opportunity to predict the effect of different scenarios of environmental change on future habitat suitability, and consequently on species distribution and abundance (Guisan, Thuiller & Zimmermann 2017).

With the increasing availability of databases on species occurrence and environmental variables (e.g. from remote sensing), it is now possible to build models over wide geographic areas at a biologically meaningful resolution, i.e. matching the scale at which species perceive habitat and respond to environmental circumstances. These more accurate, finer-grained models are crucial to avoid the caveat of overestimating the effect of large-scale forces like climate and to better integrate local-driving forces such as functional species-habitat relationships into projections (Jiménez-Alfaro, Draper & Nogués-Bravo 2012; Chamberlain *et al.* 2013; Maggini *et al.* 2014). In addition, predictions of abundance are generally much more informative than mere estimates of occurrence probability, especially when it comes to assess the drivers of species declines and plan conservation action (Renwick *et al.* 2012; Virkkala & Lehikoinen 2014; Howard *et al.* 2015; Johnston *et al.* 2015). While the use of SDMs is on the increasing side in conservation research (Guisan, Thuiller & Zimmermann 2017), only few studies have simultaneously considered effects of land-use and climate change on bird species abundance (Renwick *et al.* 2012; Howard *et al.* 2015), and we are not aware of any that did so for predicting future species density.

In this study, we developed a framework to assess and predict the effects of climate and land-use changes on the Ring Ouzel in the Swiss Alps and Jura mountains. We used an ensemble modelling approach (Araújo & New 2007), based on precise species locations, to predict area-wide occurrence probability at a fine scale. We further fit N-mixture models (Royle 2004) to translate occurrence probability into abundance estimates and total population size. In particular, we aimed 1) to assess the relative importance of climate, land-use/cover and topography for characterizing species' habitat suitability; 2) to evaluate the impact of plausible scenarios of climate and land-use changes, and combination thereof, on species distribution and abundance in different areas, especially in relation to elevation; and 3) to delineate key areas that will remain or may become climatically suitable for Ring Ouzel in the future, so as to designate them as focal areas for targeted conservation management.

MATERIALS AND METHODS

Study area

Four biogeographical regions of Switzerland were considered, namely the Jura mountains, the northern, central (i.e. inner) and southern Alps (Gonseth *et al.* 2001; Fig. 1). The fifth region, the Plateau, was excluded since the Ring Ouzel does not breed and anyway very rarely occurs in the Swiss lowlands. These four regions vary in area (4,203; 11,486; 10,671; 3,671 km^2, respectively), mean elevation (816; 1,385; 2,144; 1,493 m above sea level (asl)) and also climate: the Jura and northern Alps are under the influence of an oceanic climate with regular precipitation all year round and low sunshine duration, the central Alps are under a continental (inner-Alpine) climate with very low precipitation, while the southern Alps are subject to the Insubrian climate (N Italy), characterized by intense precipitation events in spring and autumn, but also high sunshine duration (Price *et al.* 2015; CH2018 2018). The study area encompasses most of the climatic conditions experienced by Ring Ouzels across their whole breeding range (Supplementary Materials, Table S1) so that the risks of overestimating range shift or contraction in our predictions are deemed marginal. As a result of these contrasted circumstances, land-use varies considerably between our study regions: forests predominate in the southern Alps (49.1%) and Jura (47.4%), agricultural areas (mostly grasslands) have a wide coverage in the Jura (43.4%) and northern Alps (37.5%), whereas the central Alps are mostly dominated by unproductive land (e.g. bare or sparsely vegetated areas, glaciers, lakes; 49.5%) (SFSO 2013).

Species data

Ring Ouzel observations over the period 2013–2018 were gathered from various sources. We used observations from two standardized monitoring programmes, the Atlas of Swiss breeding birds (hereafter Atlas; Knaus *et al.* 2018) and the monitoring scheme of common breeding birds (hereafter MCBB; Schmid, Zbinden & Keller 2004), as well as casual observations reported to the official national birding exchange platform www.ornitho.ch. For the Atlas and MCBB, experienced volunteers systematically visited pre-selected 1-km^2 squares regularly spaced across Switzerland (Fig. 1). They recorded all bird observations on a map along a predefined walk transect (4–6 km) during three visits (only two for squares entirely above the treeline) between April–June in at least one year in the period 2013–2018. At the end of the season, the observations collected at each visit were aggregated into territories following a standardized protocol (for details see Schmid, Zbinden & Keller 2004; Kéry 2018). As Ring Ouzels are essentially single-brooded in the Alps (Glutz von Blotzheim & Bauer 1988), the estimated number of territories was unlikely to be inflated by potential relocations between a first and second brood. Concerning casual observations, we retained only precise enough (at least 50 m), confirmed records from May–June, discarding observations outside of the core reproductive period. We then grouped this information into three datasets: presence-only (PO), presence-absence (PA) and abundance (Fig. 1). In the PO dataset, data from territory locations and casual observations were combined (n = 8000). In the PA dataset, only territory centroids were retained as ascertained presence during breeding (n = 5169), whereas a number of ‘absence points’, equivalent to the number of territories, were generated and placed randomly in parts, or entire monitored 1-km^2 squares (throughout the study area) where no Ring Ouzel was observed. While we cannot totally exclude the selection of false absences which might impact predictions (Gu & Swihart 2004), the risk was greatly reduced by selecting only squares covered by the standardized monitoring programmes described above. The abundance data consists of the number of territories with at least one bird detected per visit (e.g. $n_1 = 7$; $n_2 = 8$; $n_3 = 6$) in each Atlas or MCBB 1-km^2 square (n = 1460). As a potential sampling bias could occur in the casual observations from the PO dataset (Fourcade *et al.* 2014), we applied spatial filtering by randomly removing nearby observations closer than 113 m. This distance represents the mean radius of an estimated home range, assuming strict territoriality in Ring Ouzel pairs (i.e. half the mean distance between territory centroids obtained from the Atlas and MCBB surveys).

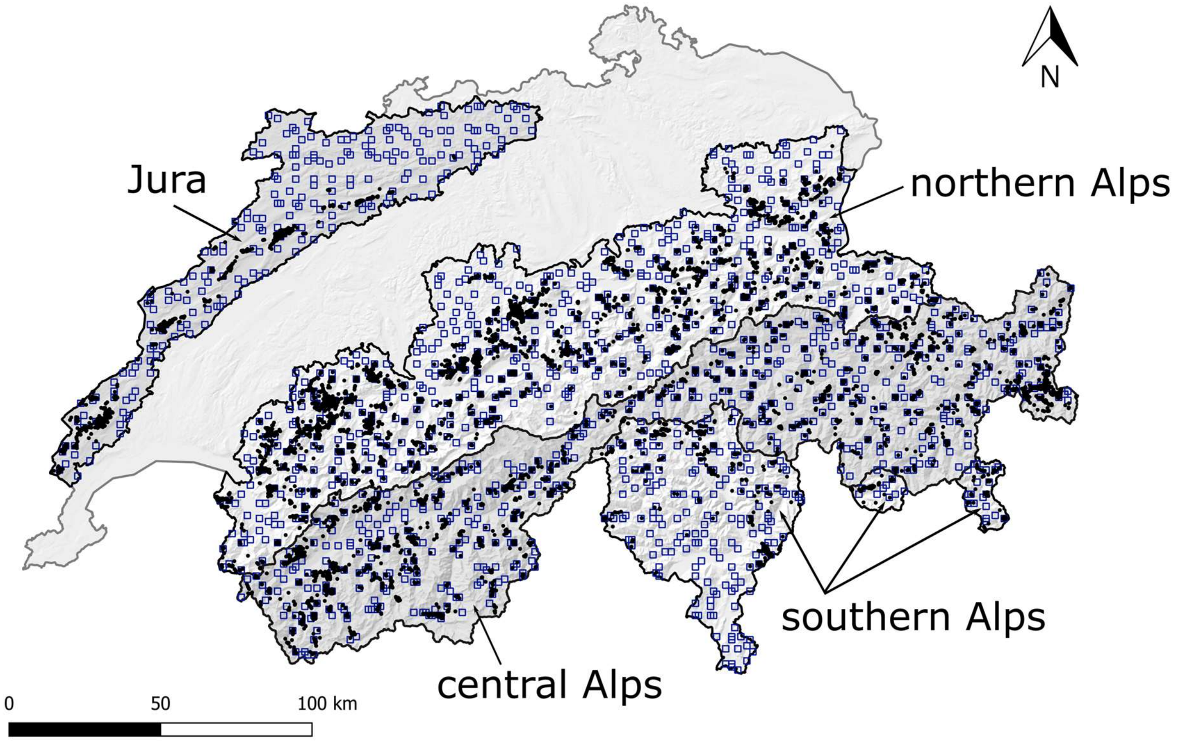

Figure 1 Map of Switzerland with depiction of the four study biogeographic regions. Black dots: locations of Ring Ouzel observations considered in the presence-only and presence-absence datasets. Empty blue squares: monitored 1-km2 squares in which abundance data were available.

Environmental data

We selected a set of environmental predictors referring to the literature on species-habitat relationships of the Ring Ouzel at various spatial scales (see Table 1), as well as on predictors that might be particularly important for mountain bird species in general. Predictors were classified into four categories, namely topography, climate, forest structure and land-use/cover. For topography, all variables were derived from a 25-m resolution digital elevation model (DEM) (Swisstopo 2005). Aspect (from which were derived eastness and northness), slope and the topographic position index (i.e. the position of a grid cell relative to the surrounding cells, indicating concavity or convexity of a landform) were all obtained using the raster analysis functions in the software QGIS 3.10 (QGIS Development Team 2020). Climate variables were compiled for the period 1996–2016 by the Swiss Federal Research Institute WSL (research unit ‘Land Change Science’), using the software Daymet (Thornton, Running & White 1997). The latter performs a gridded interpolation of weather variables based on a DEM and daily-resolution data from weather stations, here precipitation and temperature measured at, on average and respectively, 120 and 400 stations belonging to the network of the Federal Office of Meteorology and Climatology (MeteoSwiss). We extracted mean ambient temperature, total precipitation, precipitation seasonality, solar radiation and potential evapotranspiration over the Ring Ouzel breeding period (April–July), as well as the total winter precipitation (December–March) as a proxy for snow cover upon arrival of the birds in spring. All three forest structure variables (number of solitary trees, treeline length and distance to treeline) were derived from the topographic landscape model (TLM^{3D}) of Switzerland (Swisstopo 2018) as were the land cover variables ‘forest’ and ‘rock & screes’. For the grassland habitats, we combined information from the TLM^{3D} and the Swiss Land Use Statistics (SFSO 2013), to classify grassland areas into meadows and pastures, i.e. mown and grazed grasslands, respectively. Additionally, we used the normalized difference vegetation index (NDVI) as a proxy of grassland productivity (Pettorelli *et al.* 2005) and hence of management intensity (Weber, Schaepman-Strub & Ecker 2018). NDVI data were compiled in the Swiss Data Cube (www.swissdatacube.org; Giuliani *et al.* 2017) from Landsat 5 & 7 satellite pictures. To get rid of the effect of snow cover and capture essential information about maximum local vegetation productivity, we considered the maximum NDVI over the entire breeding season, averaged over the period 2005–2009. Then, for any given grassland type, we used the median NDVI value as a cut-off between low- and high-productivity categories. This resulted in four layers, namely pastures and meadows with two levels of productivity each.

All variables available as raster data were prepared as raster maps of 50-m resolution, either by resampling or aggregation (Table 1), subsequently assigning to each cell the mean value within circular moving window of 113-m radius (40,115 m^2) corresponding to the mean home-range size as described above. For vector data, namely treeline length and number of solitary trees, the total line length or point sum within a 113-m radius, respectively, was assigned to each 50 x 50 m cell.

Modelling

Prior to model fitting, we checked for pairwise correlations between all environmental predictors to reduce collinearity, considering a slightly more restrictive rejection threshold (Spearman's $|r_S| > 0.6$) than the rule-of-thumb (> 0.7; Dormann *et al.* 2013), given that several variable pairs showed correlations between 0.6–0.7 (Supplementary Materials, Fig. S1). At that step, five predictors were removed (see Supplementary Materials, Fig. S1 for details on the variable selection process). We further calculated variance inflation factors (VIF), which are based on R-squared values from the regression of each predictor on all others (Miles 2014), and confirmed that there were no multicollinearity issues (all VIF < 10). The whole model fitting and selection process was performed in the software R 3.6.1 (R Development Core Team 2019). A schematic summary of the model framework can be found in Fig. 2 and the ODMAP protocol of the modelling process following Zurell *et al.* (2020) is provided in the Supplementary Materials, Table S2.

Occurrence models

In order to model species' occurrence probability, we used an ensemble modelling approach, combining models fitted with different algorithms to account for the high variability among predictions (Thuiller 2004; Araújo & New 2007). Ensemble modelling is now routinely used in the field of species distribution modelling as it produces more robust predictions and allows to quantify uncertainties (Araújo & New 2007; Guisan, Thuiller & Zimmermann 2017). Here we fitted SDMs based on five commonly used algorithms: generalized linear models (GLM), random forest (RF), boosted regression trees (BRT), artificial neural network (ANN) and maximum entropy (MaxEnt). The MaxEnt model was fitted on PO data and 20,000 randomly generated background points, whereas all other four algorithms used PA data. Prior to model fitting, we partitioned each dataset into four spatially structured folds of equal size based on longitude and latitude, using the 'ENMeval' package (Muscarella *et al.* 2014).

Table 1 List of environmental variables included in the occurrence models, along with their possible ecological relevance for Ring Ouzel, as retrieved from the literature. For the data that were not directly available at 50-m resolution, the method of data aggregation/resampling is indicated.

Variables	Original resolution	Resampling method	Possible relationship	Source
Topography				
Elevation	25	average	Clear elevational optimum across the breeding range[1,2,3,4]	DEM[a]
Slope	25		Influence of topography on important soil characteristics for foraging[4,5,6] and on the preferred vegetation structure at the territory scale[1,2], e.g. through natural dynamic. Preference for nesting in steep slopes in the UK[3,4].	DEM[a]
Northness	25			DEM[a]
Eastness	25			DEM[a]
Topographic Position Index	25			DEM[a]
Climate				
Temperature Breeding Season (BS)	100	nearest neighbour	Importance of climatic factors detected at various spatial scales[2,3,7]. Functional links to the breeding ecology[4,5,6,7,8], mostly through the impacts on food availability.	MeteoSwiss/WSL[b]
Solar radiation BS	100			MeteoSwiss/WSL[b]
Potential evapotranspiration BS	100			MeteoSwiss/WSL[b]
Precipitation BS	100			MeteoSwiss/WSL[b]
Precipitation seasonality BS	100			MeteoSwiss/WSL[b]
Precipitation winter	100			MeteoSwiss/WSL[b]
Forest structure				
Treeline length	–	–	Selection for low distance to forest edges[1], or for open stands among mountain grasslands[2]. Avoidance of conifer plantations in the UK[3].	TLM3D[c]
Treeline distance	50			TLM3D[c]
Number of solitary trees	–			TLM3D[c]
Land-use/cover				
Low-productivity meadow cover	10	sum	Important role of mountain grassland cover and management, with preference for nutrient-poor over nutrient-rich grasslands at the territory scale[2,3]. Avoidance of dense and high grass swards for foraging[4,5].	TLM3D[c]/AS[d]/GRID[e]
High-productivity meadow cover	10			TLM3D[c]/AS[d]/GRID[e]
Low-productivity pasture cover	10			TLM3D[c]/AS[d]/GRID[e]
High-productivity pasture cover	10			TLM3D[c]/AS[d]/GRID[e]
Unused grassland cover	10			TLM3D[c]/AS[d]
Rock and screes cover	10		Absence of soil and therefore belowground invertebrate prey[9]. Preference for intermediate rock cover for nesting sites in the UK[3].	TLM3D[c]
Forest cover	10		Importance of intermediate forest cover[1,2]	TLM3D[c]

[1]Ciach and Mrowiec (2013); [2]von dem Bussche *et al.* (2008); [3]Buchanan *et al.* (2003); [4]Burfield (2002); [5]Barras *et al.* (2020); [6]Sim *et al.* (2013); [7]Beale *et al.* (2006); [8]Barras *et al.* (2021); [9]Hagedorn, Gavazov and Alexander (2019)

[a]Digital Elevation Model (Swisstopo 2005); [b]Prepared by the research unit 'Land Change Science' of the Federal research institute WSL from weather stations data from MeteoSwiss; [c]Topographic Landscape Model of Switzerland (Swisstopo 2018); [d]Aerial Statistics (SFSO 2013); [e]NDVI data compiled from the Swiss Data Cube (Giuliani *et al.* 2017)

We used this partitioned data to run a four-fold cross validation for each model, i.e. to evaluate spatial transferability, and evaluated model's performance with the area under the receiver operating characteristics curve (AUC; Bradley 1997) of the test folds. For fitting and selecting the different models, we used the package 'SDMtune' (Vignali *et al.* 2020). For each algorithm except the GLM, we first identified the combination of hyperparameters resulting in the best performing model in terms of mean test AUC using the *optimizeModel* function. Then, in all models, we sequentially removed variables having a permutation importance of less than 1% until an optimum in test AUC was reached, using the function *reduceVar*. The performance of the obtained model was evaluated through mean AUC and true skills statistics (TSS; Allouche, Tsoar & Kadmon 2006) on the test folds. Finally, we merged all four folds together to fit a final model from which variable importance and probability of occurrence over the whole study area were computed. Variable importance was estimated using ten permutations for each variable in each model. Concerning the occurrence probability, we further calculated the mean and standard deviation (sd) of the five model predictions. For MaxEnt models, we retained the 'cloglog' output, which is equivalent to the occurrence probability predictions of the other SDM algorithms used here (Phillips *et al.* 2017).

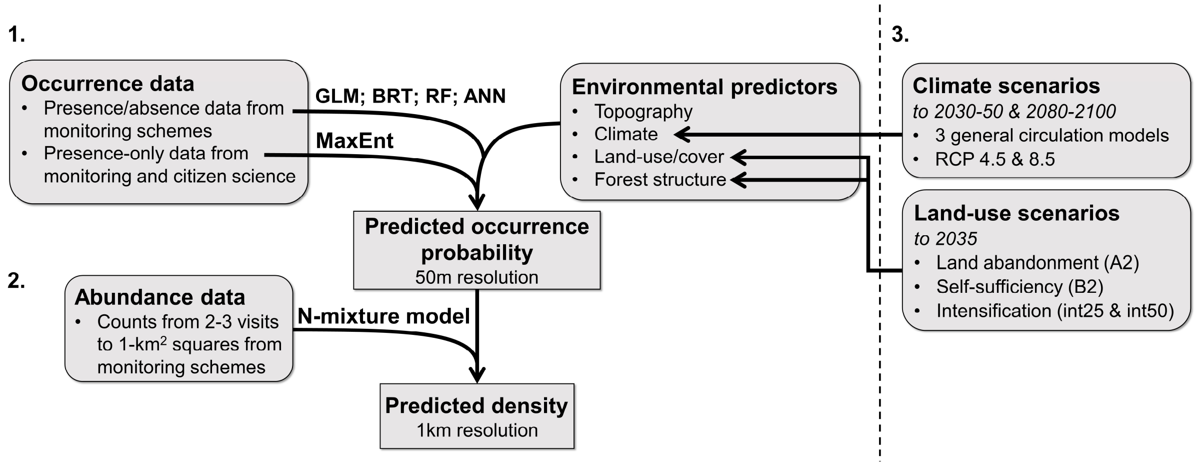

Figure 2 Modelling framework used in the present study. In a first step (1), occurrence probability was modelled at a 50-m resolution with a set of environmental predictors and two different datasets as inputs (presence-only & presence/absence), using five different algorithms (MaxEnt: maximum entropy, GLM: generalized linear model, BRT: boosted regression trees, RF: random forest & ANN: artificial neural network). In a second step (2), abundance per surveyed 1-km^2 square was modelled as a function of mean occurrence probability using an N-mixture model accounting for imperfect detection. In the final step (3), we used the fitted models to predict future occurrence probability and population density under different realistic scenarios of climate and land-use change.

Abundance model

To model species abundance in our 1-km^2 squares, we applied a binomial N-mixture model to the territory counts, which accounts for imperfect detection and therefore produces more reliable estimates of abundance (Royle 2004; Kéry & Royle 2016). Following the recommendations by Kéry (2018), we based our selection of the abundance mixture distribution on Akaike's Information Criterion but checked for potential identifiability problems, establishing that the zero-inflated Poisson distribution was the best option for our data. We fitted the model using the package 'unmarked' (Fiske & Chandler 2011) with covariates in the detection part being the survey date and session (1–3). For the abundance part of the model, we used as a covariate the mean occurrence probability in each 1-km^2 square, obtained from aggregating the results of the occurrence ensemble model to this resolution. Goodness of fit of the model was assessed by calculating the 'c-hat' value based on parametric bootstrapping with 1000 simulations (Kéry & Royle 2016), as well as by the root-mean-square error (RMSE) and the mean absolute error (MAE). We then produced an estimate of regional and total population sizes in Switzerland by rounding the number of breeding pairs per km^2 to integer values and summing up the abundance predictions for the area of interest. Finally, we also retrieved the density-weighted mean elevation (total and regional) of the species distribution, i.e. the average elevation of occupied squares with abundance estimates as weights.

Climate change scenarios

Future climate was modelled for two 20-years periods, in the mid- (2030–2050) and long-term (2080–2100), using data from the European branch of the coordinated regional climate downscaling experiment, EURO-CORDEX (www.euro-cordex.net; 0.11-degree resolution). Two representative concentration pathways (RCPs), RCP 4.5 and 8.5, were considered. RCPs represent possible scenarios of greenhouse gas emissions as described in the IPCC (2014), with RCP 4.5 being a moderate scenario assuming a decrease in emissions from 2050 onward, while RCP 8.5 represents an extreme scenario with a continuous increase up to 2100. Data were downscaled using the same regional climate model CLMcom-CCLM4-8-1, for three general circulation models (GCMs): CNRM-CERFACS-CNRM-CM5, ICHEC-EC-EARTH and MPI-M-MPI-ESM-LR, resulting in six climate scenarios for each period. Those GCMs were selected as their projections covered a broad range of possible future climatic conditions, although the first two GCMs are considered rather similar (Knutti, Masson & Gettelman 2013).

The resulting data was further downscaled using the delta change method (Anandhi *et al.* 2011). Using this method, the coarse-scale maps of future climate from EURO-CORDEX are expressed as anomalies relative to the baseline period 1996–2016. These anomalies are then interpolated bilinearly to 100 m and combined with the equivalent baseline fine-scale maps (from section 'Environmental data') to obtain absolute values, thus assuming that relative fine-scale differences in current climate will remain the same. All data was provided by the Federal Research Institute WSL.

Land-use change scenarios

As future land-use, we used the model predictions of Price *et al.* (2015) covering the whole of Switzerland. Using socio-economical and biogeographic variables, these authors predicted land-use by 2035 (i.e. matching the mid-term climate scenarios described above), along various storylines of climate change as described in the Special Report on Emission Scenarios IPCC (2000). Here, we retained the two different scenarios B2 and A2, which correspond to the RCPs 4.5 & 8.5, respectively, as defined in the newest IPCC assessments (Rogelj, Meinshausen & Knutti 2012). Under the A2 scenario (hereafter land abandonment), high economic and population growth with low support for conservation and agricultural subsidies is assumed; Price *et al.* (2015) predict that over 46,000 ha of pastures will be abandoned and encroached in the Alps and Jura, while another 28,000 ha of overgrown areas will become forest. Nevertheless, 19,000 ha of overgrown areas will be reconverted into pastures. Under the B2 scenario (hereafter self-sufficiency), population growth will be moderate and there will be high support for biodiversity conservation, as well as for maintaining extensive agriculture in remote areas; no pastures would be abandoned and transformed into forest, while 46,000 ha of overgrown areas will be converted back into grasslands. In both scenarios, no loss of forest was allowed.

Since the categories of land-use from Price *et al.* (2015) (hereafter LU categories) were not identical to the variables used as predictors in our models, we translated the scenario predictions into our land-use/cover and forest structure variables. For this, we identified raster cells where the LU category was predicted to shift according to Price *et al.* (2015) and changed the values of each of the retained predictors accordingly (see details in the Supplementary Materials, Fig. S2). For areas whose cover shifted toward grasslands under future scenarios, type (pasture or meadow) and productivity (low or high) were assigned according to the characteristics of the nearest grassland patch in the current landscape. Finally, we also simulated a farming intensification process of the managed grasslands up to two elevation thresholds (1635 and 2010 m asl), by changing the productivity of all meadows and pastures below the respective elevation-limit to ‘high productivity’. Elevation thresholds were defined as the 0.25 and 0.5 elevation quantiles of low-productivity pastures, so that scenarios would reflect an intensification of respectively 25 and 50% of the lower-elevation pastures (hereafter int25 & int50 scenarios). The same thresholds were then also applied to meadows. Land-use scenarios were calculated assuming constant climate, and in combination with climate change scenarios for the mid-term period only.

RESULTS

All SDMs of the ensemble individually show excellent (> 0.9) to good (> 0.8) predictive accuracy for the cross-validated mean test AUC (MaxEnt = 0.88, GLM = 0.91, BRT = 0.91, RF = 0.91, ANN = 0.91) and good (> 0.4) accuracy for TSS (MaxEnt = 0.62, GLM = 0.68, BRT = 0.67, RF = 0.66, ANN = 0.67) according to classification thresholds summarized in Guisan, Thuiller and Zimmermann (2017). The most important variable for explaining species occurrence was mean ambient temperature during the breeding season, with a clear optimum detected in all models at 5–10°C (see response curves in the Supplementary Materials, Fig. S3). Solar radiation was ranked second, followed by habitat variables like cover of forest and low-productivity pastures as well as the number of solitary trees present in the home range (Table 2), all showing curvilinear relationships but that differed between algorithms (Supplementary Materials, Fig. S3), so that it was difficult to define clear optimal ranges. Eleven other variables were retained in at least one of the five models, but all had relatively low permutation importance (Table 2).

The fit of the abundance (N-mixture) model was good as well as assessed by RMSE = 1.91 and MAE = 0.96 (see Supplementary Materials, Table S3 for parameter estimates). Calculation of the over-dispersion parameter ($\hat{c} = 1.5$) suggested slight over-dispersion in the zero-inflated Poisson model, which was taken into account by multiplying the variance-covariance prediction matrix by the ‘c-hat’ value (following Kéry & Royle 2016).

We estimated a current population size of 60,218 breeding pairs (95% CI: 53,070–67,349) in Switzerland, at a mean elevation of 1803 m asl. Abundance maps, in contrast to mere occurrence probability maps, identified clear population density hotspots in the landscape (Fig. 3), with 68 1-km^2 squares harbouring more than 20 breeding pairs each, 88% in the northern Alps and the rest in the central Alps (Fig. 3b). Concerning mid-term predictions, land-use scenarios had limited effects on the species range and population size (from +1.6% for A2 to -4.8% for int50), resulting in only small changes in mean elevation (from -1 m for B2 to +16 m for int25; Fig. 4). For the same time horizon, both climate scenarios delivered similar predictions with little changes in population size (on average -1.2% and -3.7% for RCP 4.5 & 8.5, respectively) but a clear upward elevational shift (on average +85.7 m and +144.7 m for RCP 4.5 & 8.5, respectively) which was consistent across the three different general circulation models used (Fig. 4). Effects of climate-change scenarios were much more pronounced for the end of the century (2080–2100) than in the mid-term, especially for the RCP 8.5 with a mean 30.5% (range 25.2–35.2%) decrease in population size and a +512 m (484–560 m) elevational shift (Fig. 3). When combining land-use change with the mid-term climate change scenarios, population size estimates were indicating additive rather than interactive effects of both drivers (Fig. 4).

Table 2 Permutation importance of retained environmental variables in each of the five models fitted for species occurrence (MaxEnt: maximum entropy, GLM: generalized linear model, BRT: boosted regression trees, RF: random forest, ANN: artificial neural network), as well as averaged across models. The importance of variables was set to zero in models in which there were not retained.

	Permutation importance (%)					
Variables	MaxEnt	GLM	BRT	RF	ANN	average
Temperature BS	81.4	72.6	68.3	79.5	56.9	71.74
Solar radiation BS	7.1	9.2	12	7	9	8.86
Forest cover	2.3	4.5	4.3	1.9	8.9	4.38
Low-productivity pasture cover	1.1	2.9	1	0.8	9.3	3.02
Number of solitary trees	1.8	2	4.5	2.3	3.4	2.8
Slope	4.2	2.1	2.2	1.6	1	2.22
Precipitation BS	0	1.6	3.7	3.9	1.7	2.18
High-productivity pasture cover	0	2.3	0	0.2	5.6	1.62
Northness	0	1.4	1.6	0.6	1.7	1.06
Precipitation seasonality BS	0	0.7	1.6	1.9	0.4	0.92
Rock and screes cover	2.2	0.1	0	0.1	0	0.48
Unused grassland cover	0	0.6	0	0	1.3	0.38
Low-productivity meadow cover	0	0	0.7	0	0.5	0.24
Eastness	0	0.1	0	0.2	0	0.06
High-productivity meadow cover	0	0	0	0	0.3	0.06
Topographic Position Index	0	0	0	0.1	0	0.02

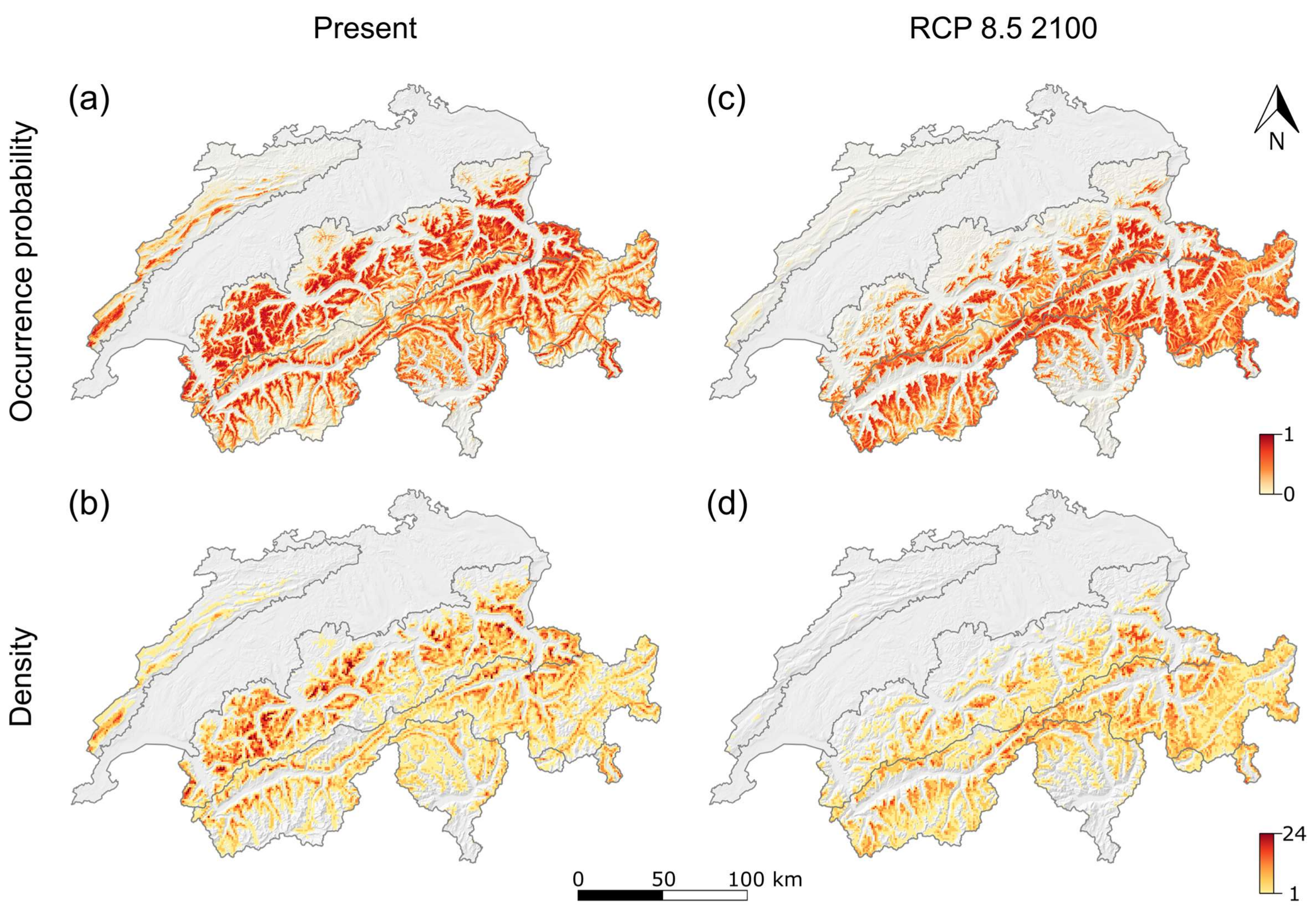

Figure 3 Spatial predictions of occurrence probability and population density of Ring Ouzels (number of breeding pairs per km^2) in Switzerland at present (a, b) and under the most extreme climate change scenario (RCP 8.5) for the period 2080–2100, considering the CNRM-CM5 general circulation model (c, d).

Looking at the biogeographic regions independently, our models predicted divergent responses of the different breeding populations. At this scale, the magnitude of change caused by climate change appeared much more pronounced than the different scenarios of land-use in the mid-term. The size of the populations occurring at lower elevations would clearly decrease (up to -100.0% and -69.2% in the Jura and northern Alps, respectively) whereas it would increase in the high-elevation regions (up to +33.9% and +29.6% in the central and southern Alps, respectively; Fig. 5). Especially under the most extreme climate-change scenario (RCP 8.5) toward the end of the century, we expect that the Ring Ouzel would become extinct in the Jura mountains and its Alpine population strongholds would shift from the northern to the central Alps (Fig. 5). Nevertheless, land-use change scenarios had also noticeable effects in some regions, such as a predicted decrease (-10.4%) in the northern Alps under a regime of farming intensification (here int50) and a slight increase (+5.5%) in the central Alps under land abandonment. The self-sufficiency scenario had no clear effects in any of the four regions (from -0.8% to +0.1%). Predictions of all scenarios per time periods and regions are summarized in the Supplementary Materials, Table S4.

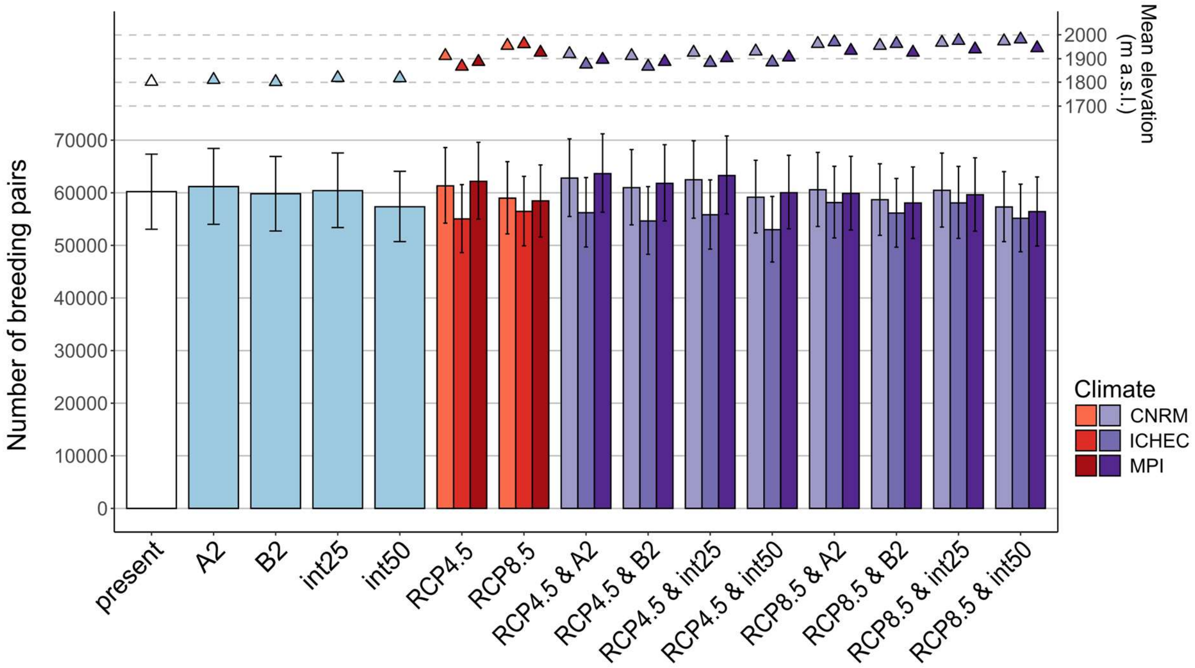

Figure 4 Present (very left) and mid-term (2030–2050) projected total population size (histogram) and density-weighted mean elevation (triangles) of the Ring Ouzel in Switzerland under various scenarios of land-use (A2, B2, int25, int50; blue bars) and climate change (RCP 4.5 & 8.5, red bars), either tested individually or in combination (purple bars). CNRM, ICHEC and MPI stands for different general circulation models (see Materials and Methods for more details). Error bars show 95% confidence intervals.

DISCUSSION

Taking as an example the Ring Ouzel, a threatened mountain bird species, this study presents an innovative approach for both modelling current species distribution and abundance and projecting them into the future under realistic scenarios of changes in climate and land-use. By not only focusing on distribution ranges but also integrating actual population size estimates, our analytical framework provides more realistic assessments of species' vulnerability to environmental change, while at the same time yielding key spatial information for targeted conservation planning.

Current occurrence and abundance predictions

Habitat suitability was modelled here over a wide geographic range but choosing a scale (home-range) at which fine-grained, ecologically functional species-habitat relationships were integrated (Jiménez-Alfaro, Draper & Nogués-Bravo 2012; Chamberlain *et al.* 2013). All species distribution models within our ensemble had good predictive accuracy and emphasized that Ring Ouzel occurrence is mostly driven by climate, namely the mean ambient temperature, here integrated over the breeding season. Although it is generally recognized that climate is a weaker predictor of bird occurrence than habitat circumstances at finer scales (Thuiller 2004; Howard *et al.* 2015; Brambilla *et al.* 2019), there are several examples of alpine species for which ambient temperature remains a crucial predictor at territory scale (Chamberlain *et al.* 2013; Brambilla *et al.* 2019; Jähnig *et al.* 2020). The second most important variable was solar radiation during the breeding season, with an optimum toward higher values. Yet, as solar radiation increases with elevation ($r_S = 0.44$; see Supplementary Materials, Fig. S1), its effect probably underpins the species association with high elevations rather than with sun-exposed areas. Despite their lower relative importance, habitat variables were also high-ranked, corroborating former findings regarding species' preferences for a forest-grassland mosaic (von dem Bussche *et al.* 2008; Ciach & Mrowiec 2013; Barras *et al.* 2020; *Chapter 1*). The most important grassland type was the fraction of low-productivity pastures in the home range, a proxy for extensively-managed pastures characterized by low nutrient inputs (Weber, Schaepman-Strub & Ecker 2018). This is in accord with the known preferences of Ring Ouzels for nutrient-poor grasslands (Buchanan *et al.* 2003; von dem Bussche *et al.* 2008) and foraging sites with short and sparse grass swards (Burfield 2002; Barras *et al.* 2020; *Chapter 1*).

Our modelling framework also delivered spatially explicit predictions about Ring Ouzel population abundance. Those mirrors the spatial distribution of habitat quality more accurately than maps of occurrence probability (Renwick *et al.* 2012; Howard *et al.* 2015; Johnston *et al.* 2015) and enabled the delineation of high-density hotspots. Furthermore, our abundance estimates allowed delimiting species' distribution range, this without relying on the arbitrary thresholds that are conventionally used for converting occurrence probability into presence-absence data (Guisan, Thuiller & Zimmermann 2017) and can strongly affect the extent of forecast range shifts (Thuiller 2004; von dem Bussche *et al.* 2008). Finally, the density-weighted mean elevation of breeding birds, in other words the 'center of gravity' of the entire Swiss population, could be calculated. The latter is crucial to highlight elevational or latitudinal shifts that might be invisible when looking only at mere distribution maps (Virkkala & Lehikoinen 2014). Yet, using mean occurrence probability to predict abundance relies on the assumption that abundance and occurrence depend on the same factors (Brown 1984), which might not hold true in some cases (e.g. Johnston *et al.* 2015) although it was used successfully in others (e.g. Hill *et al.* 2017). Our approach resulted in a good fit, apparently delivering a reliable estimate of total population size (95% CI: 53,070–67,349 breeding pairs) when compared to quantitative appraisals by the last national Atlas (50,000–75,000; see Knaus *et al.* 2018).

Effects of climate and land-use scenarios

According to our models, the magnitude of predicted changes in population size and mean elevation was overall much larger for climate change scenarios than for any land-use scenario, especially at the regional level (Fig. 5). A noticeable exception to that general pattern was the scenario of increased grassland productivity in the northern Alps, whose detrimental effect on population size was equivalent to the moderate scenario of climate change. This highlights that further intensification of grassland management (or steady increase in nitrogen atmospheric deposition) could have additional negative effects regionally. In contrast, grassland abandonment resulted only in minor changes in population size, contradicting our hypothesis that forest encroachment would be detrimental to Ring Ouzels (see Bani *et al.* 2019). As a matter of fact, the foreseen increased habitat suitability in newly forested areas above the current treeline simply compensated for any habitat loss through vegetation encroachment at lower elevations. This is in line with findings from Chamberlain *et al.* (2013), who predicted positive effects of forest upward expansion for other treeline passerines in the European Alps, but not with observations of a net range loss reported for those species in Bani *et al.* (2019), suggesting complex responses of the bird community in treeline ecotones.

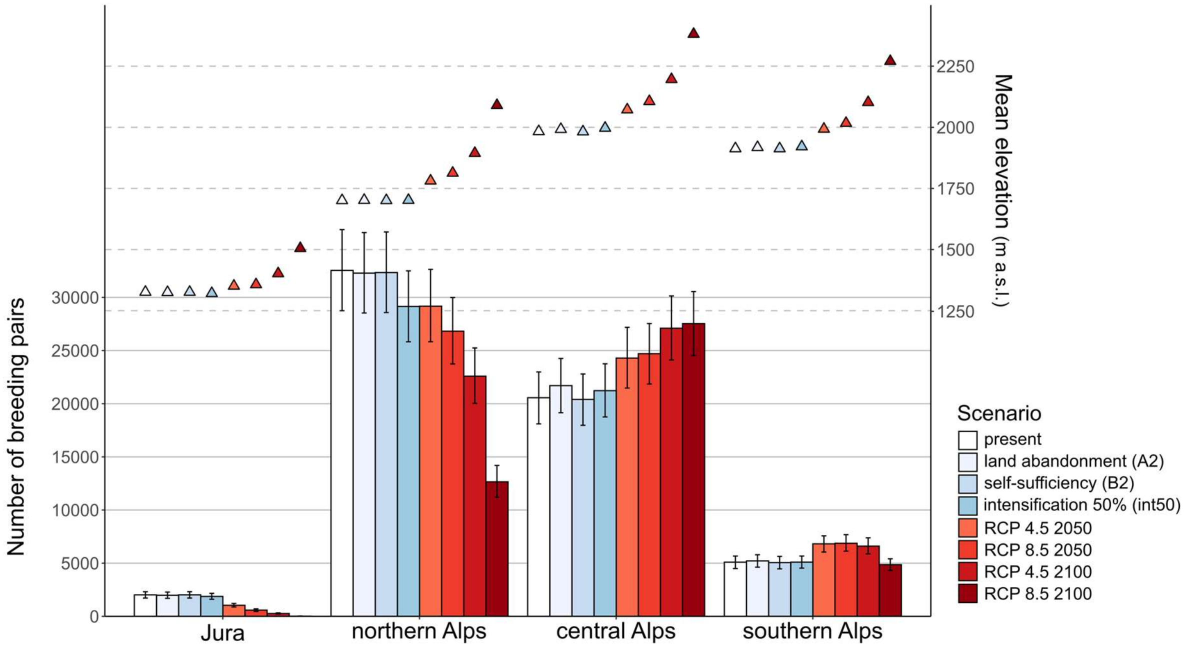

Figure 5 Present and projected population size (histogram) and density-weighted mean elevation (triangles) of the Ring Ouzel in each of the four Swiss biogeographic regions considered, under various scenarios of land-use (blue bars) and climate change (red bars). Land-use scenarios refer to 2035 whereas climate change scenarios are for two periods (2030–2050 & 2080–2100), considering the CNRM-CM5 general circulation model. Error bars show 95% confidence intervals.

Concerning climate change scenarios, Ring Ouzel populations are likely to react differently with respect to the study region. Populations occurring at low elevations (Jura & northern Alps) are projected to decline further into the future, whilst populations located closer to the main axis of the Alpine chain (here central — or inner — and southern Alps) are predicted to increase, a pattern confirmed by recent estimates of regional population trends (Knaus *et al.* 2018). At the national level and in the mid-term, this would result in an elevational upward range shift by ca. 100 m but with an apparent demographic stability under both climate change scenarios. By the end of this century, however, the most extreme climate change scenario predicts a further loss of one third of the total Swiss population and a particularly marked upward range shift of almost 500 m. This would cause the extinction of the species from the Swiss Jura (Fig. 3d; Fig. 5) and a halving of the number of breeding pairs in the current species stronghold (northern Alps). Note that all these scenarios assume a high dispersal ability of the species, i.e. an immediate colonization of suitable habitat, which is a reasonable assumption for a short-distance migrant bird.

Model implications and limitations

Our results suggest that the recent decline observed in Ring Ouzel populations inhabiting lower mountain ranges in Switzerland and neighbouring countries like France and Germany (Knaus *et al.* 2018; Anger *et al.* 2020) is mainly due to climate change. The intensification of grassland management in Ring Ouzel breeding habitat might have played an additional role, especially at lower elevations, analogous to the severe impact it exerted upon other grassland passerines (e.g. Britschgi, Spaar & Arlettaz 2006). In contrast, it is unlikely that land abandonment has and will contribute much to the decline of the species in Switzerland. Indeed, the high intervention scenario in which forest encroachment is extensively combated (e.g. via targeted forestry measures or grazing) had no discernible effects on the Swiss population size although local changes in habitat suitability were obvious. In this context, implementing the above habitat management measures to buffer the negative effects of climate change at lower elevations (see Braunisch *et al.* 2014) would make little sense. Instead, given that new suitable breeding habitat will appear through natural afforestation above the actual treeline, habitat management measures implemented at the advancing range-margin may represent a more promising adaptive strategy (Pearce-Higgins *et al.* 2011).

We decided not to account for changes in vegetation in our climatic scenarios, in contrast to land-use scenarios. First, it is unclear whether factors that increasingly impact low-elevation forests, e.g. wildfires or insect outbreaks, will represent important drivers in subalpine forests in the future (Schumacher & Bugmann 2006). Second, uncertainties about the pace of upward shifts in vegetation and soil development are high (Dirnböck, Essl & Rabitsch 2011; Hagedorn, Gavazov & Alexander 2019). In effect, treelines are predicted to lag behind climate change for 50–100 years due to the slow growth of trees at high elevation (Körner 2012). In addition, grazing and browsing by livestock, and more and more, by growing and expanding populations of wild ungulates, especially red deer *Cervus elaphus*, will hamper spontaneous afforestation (Schumacher & Bugmann 2006; Didion *et al.* 2011). Still, the question remains to which extent wild ungulates can compensate for the decrease in domestic livestock, i.e. whether their effectiveness in keeping open and semi-open habitats in the long run is comparable (San Miguel-Ayanz, Perea García-Calvo & García-Olalla 2010). Under these circumstances, one can expect an amplifying spatial mismatch between the optimal climatic niche and suitable habitat configuration for all treeline species whose occurrence largely depends on climatic factors (Chamberlain *et al.* 2013; Bani *et al.* 2019). This is obvious in our projections predicting above all an absolute decrease in population density rather than upward shifts in Ring Ouzel hotspots (Fig. 3b & 3d). Nevertheless, pasture abandonment can lead to more rapid upward shifts of the treeline (Gehrig-Fasel, Guisan & Zimmermann 2007; Körner 2012), such that the accuracy of our predictions toward the end of the century may be contingent upon long-term modifications in land-use. Those are, however, excessively challenging to predict (Verburg, Tabeau & Hatna 2013), which motivated our choice of relatively short-term projections (to 2035; Price *et al.* 2015). Even within that timeframe, the evolution of the national socio-political and economical contexts remains difficult to predict, which might limit the general applicability of our framework.

Recommendations for species conservation

The innovative approach used here allowed us to identify current hotspot areas for the Ring Ouzel as well as sites that will remain or become suitable in the future. With that information, we could designate areas in the landscape where conservation efforts should be deployed in priority for maintaining habitat quality in the long run. As main management measures, we recommend to avoid further grassland intensification in the northern Alps and Jura mountains, especially in recognized hotspots with high Ring Ouzel density, and to carefully monitor and manage shifting treelines in the central and southern Alps (Mollet *et al.* 2018). Regarding the latter, it remains contentious whether habitat should be managed in a way that assists tree migration to higher elevations or whether it should be slowed down (Chamberlain *et al.* 2013; Bani *et al.* 2019; García-Navas *et al.* 2020). In the Alps, upward shifts in treelines have already been documented, being mainly ascribed to woody vegetation encroachment following pastoral abandonment (Gehrig-Fasel, Guisan & Zimmermann 2007; Dirnböck, Essl & Rabitsch 2011). At a first glance, this temporary habitat gain may provide a short-term window of opportunity for several treeline species (Laiolo *et al.* 2004). However, treeline upward shifts are also considered as a major threat (Bani *et al.* 2019; García-Navas *et al.* 2020), since open Alpine grasslands, which harbour a very rich biodiversity, would decrease in area as a result (Dirnböck, Essl & Rabitsch 2011; Chamberlain *et al.* 2013). This is, first, because of the pyramid shape of mountains, and second, because grasslands risk to get squeezed between a moving treeline and rocky substrates where soil development is especially slow (Hagedorn, Gavazov & Alexander 2019). An elegant solution to solve this apparent conservation dilemma would be to maintain extensive pasturing in mountain ecosystems, via financial incentives to farmers, as it probably represents the best management trade-off in the long-term (Laiolo *et al.* 2004; Bani *et al.* 2019). This would allow keeping both biodiversity-rich open Alpine grasslands and semi-open wooded pastures whose habitat heterogeneity is key for Ring Ouzel and a number of associated treeline species of birds and mammals (Braunisch, Patthey & Arlettaz 2016; Mollet *et al.* 2018; Rehnus *et al.* 2018).

Conclusions

By modelling and projecting species occurrence and abundance at a fine scale under realistic scenarios of changes in climate and land-use, the original framework deployed in this study represents a valuable tool not only for assessing species' vulnerability to environmental change and disentangling between different drivers, but also for delivering spatially explicit information for planning conservation interventions. Indeed, forward-looking approaches such as the present one would be the crux to properly identify and rank threats to biodiversity while delineating areas where adaptive and targeted conservation action should be prioritized. A wider use of this framework would allow to better predict abundance and distribution changes of species in the face of global change, accounting for regional specificities (Lehikoinen *et al.* 2019). The growing availability of both species and environmental data at unprecedented spatial resolutions offers new avenues for such an exemplary modelling of other threatened mountain species, providing that basic knowledge on their ecological requirements exists.

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SUPPLEMENTARY MATERIALS

Table S1 Range (min–max) of climate variables across the European range of the Ring Ouzel (ca. 95% of the whole species range) and within the area considered in this study. Species range was available at a 10x10 km resolution and accessed via the 'Eionet' portal (http://cdr.eionet.europa.eu/) while climate variables were extracted from 'WorldClim' (www.worldclim.org; Fick & Hijmans 2017) at a spatial resolution of 2.5 minutes (ca. 4.5 x 4.5 km). The third column shows the range of climate data used in this study (50 x 50 m). See Table 1 of the main manuscript for a description of the climate variables.

Climate variable	Ring Ouzel range	Study area (Swiss Alps & Jura)	
	WorldClim	WorldClim	Climate data WSL
Temperature mean BS (°C)	-7.58 – 17.94	-7.58 – 16.52	-8.83 – 18.47
Precipitation sum BS (mm)	55 – 871	55 – 771	195 – 1367
Precipitation seasonality BS	0.01 – 0.73	0.01 – 0.31	0.03 – 0.39
Solar radiation BS (kJ m^{-2} day^{-1})	14380 – 23195	17986 – 23195	7013 – 27673

Table S2 ODMAP (Overview, Data, Model, Assessment and Prediction) protocol of the whole modelling process, following recommendations of Zurell *et al.* (2020)

OVERVIEW	
Authorship	
Contact	Arnaud G. Barras, arnaud.barras@iee.unibe.ch
Study link	https://doi.org/10.1111/ddi.13247
Model objective	
Model objective	Forecast and transfer
Target ouptut	Occurrence probability and abundance
Location	
Location	Switzerland
Scale of analysis	
Spatial extent	6.087789, 10.544688, 45.8185, 47.49406 (xmin, xmax, ymin, ymax)
Spatial resolution	50 m
Temporal extent	2013–2018
Temporal resolution	*NA*
Boundary	political
Biodiversity data	
Observation type	citizen science, standardized monitoring data
Response data type	point occurrence, counts
Predictors	
Predictor types	climatic, habitat, topographic
Hypotheses	
Hypotheses	We wanted to test the effect of land-use and climate on the current distribution, as well as the effects of realistic scenarios of change on the future occurrence probability and abundance of the species. Potentially relevant and important species-environment relationships were retrieved from the literature on the species; see Table 1 in the associated manuscript for details.
Assumptions	
Model assumptions	We assume that the large climatic and topographic gradient covered by the study area accommodate the full niche of the species. We also assume that the species is at equilibrium with its environment and retains its niche in space and time.
Algorithms	
Modelling techniques	MaxEnt, ANN (artificial neural networks), RF (random forest), GLM (generalized linear models), BRT (boosted regression trees)
Model complexity	We used an ensemble modelling approach to produce more robust predictions and quantify uncertainties in those predictions.
Model averaging	Average of predictions of all 5 algorithms
Workflow	
Model workflow	Model workflow can be seen in Fig. 2 of the corresponding manuscript.
Software	
Software	R (version 3.6.1) with package *SDMtune, ENMeval, unmarked*
Code availability	Available upon reasonable request; see vignette for *SDMtune* here (https://consbiol-unibern.github.io/SDMtune/index.html)

Table S2 (continued)

Data availability	Data not available due to restrictions (used under license)
DATA	
Biodiversity data	
Taxon names	Ring Ouzel (*Turdus torquatus alpestris*)
Taxonomic reference system	*NA*
Ecological level	species
Data sources	Swiss Ornithological Institute (www.vogelwarte.ch)
Sampling design	Standardized monitoring protocol and casual observations records
Sample size	Presence-only dataset: n = 8000 occurrence records Presence/absence dataset: n = 5169/5169 Count dataset: n = 1460 sampling units
Clipping	4 biogeographic regions of Switzerland (Jura, northern Alps, central Alps and southern Alps)
Scaling	See Table 1
Cleaning	Spatial sampling bias in casual observation records was corrected by spatial filtering (>113m)
Absence data	Sampled randomly within visited monitoring squares where no observation was performed
Background data	Sampled randomly across the study area
Errors and biases	Detection probability for count data was accounted for by N-mixture models
Data partitioning	
Training data	Four-fold cross validation based on spatially structured folds (based on long/lat)
Validation data	Four-fold cross validation based on spatially structured folds (based on long/lat)
Predictor variables	
Predictor variables	See Table 1
Data sources	See Table 1
Spatial extent	6.087789, 10.544688, 45.8185, 47.49406 (xmin, xmax, ymin, ymax)
Spatial resolution	See Table 1
Coordinate reference system	EPSG:4326
Temporal extent	Topography: 2005 Climate: 1996–2016 Forest: 2018 Land-use/cover (based on NDVI): 2005–2009 Land-use/cover (all others): 2018
Data processing	See Table 1
Dimension reduction	Variable set selected based on important species-environment relationships described in the literature.
Transfer data	
Data sources	Price *et al.* (2015) Climate: ‘Land Change Science’ group of the Federal research institute WSL
Spatial extent	6.087789, 10.544688, 45.8185, 47.49406 (xmin, xmax, ymin, ymax)
Spatial resolution	Land-use: 100 m Climate: 100 m
Temporal extent	Land-use: 2035 Climate: 2030–2050 & 2080–2100
Models and scenarios	Land-use: B2 & A2 from Price *et al.* (2015) Climate: RCP 4.5 & 8.5 (based on regional climate model CLMcom-CCLM4-8-1 and 3 general circulation models CNRM-CERFACS-CNRM-CM5, ICHEC-EC-EARTH and MPI-M-MPI-ESM-LR)

Table S2 (continued)

Data processing	Land-use: see Supplementary Materials, Fig. S2; Climate: same as for climate predictor variables
Quantification of novelty	no quantification
MODEL	
Variable pre-selection	
Variable pre-selection	*NA*
Multicollinearity	
Multicollinearity	Check of pairwise correlations between all environmental predictors, considering a Spearman's $\lvert r_S \rvert>0.6$ as rejection threshold for one variable of the pair. In addition, checking that all VIF<5.
Model settings	
MaxEnt	final variables (forest, lp_past, rockscrees, slope, soltrees, srad_47, tave_47), feature combination (selection c(l,lq,h); final lq), iterations (selection seq(100,1000,100); final 600), regularization (selection seq(0.1,2,0.1); final 0.4), notes (for tuned hyperparameters, 'selection' indicates range of tested values and 'final' the value in the final model), remark (code for variables are the same as used in the Supplementary Materials, Fig. S1)
ANN	final variables (forest, hp_mead, hp_past, lp_mead, lp_past, northness, prec_47, precseas_47, slope, soltrees, srad_47, tave_47, unusedgrass), size (selection seq(1,10,1); final 9), decay (selection seq(1e-3,1e-2,1e-3); final 0.001), rang (selection seq(0.1,1,0.1); final 0.4), notes (for tuned hyperparameters, 'selection' indicates range of tested values and 'final' the value in the final model)
RF	final variables (eastness, forest, hp_past, lp_past, northness, prec_47, precseas_47, rockscrees, slope, soltreesnbr, srad_47, tave_47, TPI), mtry (selection seq(2,8,1); final 5), nodesize (selection seq(1,5,1); final 5), ntree (selection seq(100,700,100); final 300), notes (for tuned hyperparameters, 'selection' indicates range of tested values and 'final' the value in the final model)
GLM	final variables (eastness, forest, forest_quad, hp_past, lp_past, lp_past_quad, northness, prec_47, prec_47_quad, precseas_47, precseas_47_quad, rockscrees, soltrees, soltrees_quad, srad_47, srad_47_quad, tave_47, tave_47_quad, slope, slope_quad, unusedgrass), family (binomial), notes (suffix '_quad' indicate quadratic terms)
BRT	final variables (forest, lp_mead, lp_past, northness, prec_47, precseas_47, slope, soltrees, srad_47, tave_47), distribution (bernoulli), nTrees (selection seq(500,7500,500);final 3000), interactionDepth (1), shrinkage (selection seq(0.005,0.1,0.005); final 0.01), bagFraction (0.5), notes (for tuned hyperparameters, 'selection' indicates range of tested values and 'final' the value in the final model)
Model settings (extrapolation)	clamping for Maxent
Model estimates	
Coefficients	Mean of predictions per cell over all 5 algorithms.
Variable importance	Assessed using 10 permutations for each variable in each final model; see Table 2

Table S2 (continued)

Model selection – model averaging – ensembles	
Model selection	Tuning of hyperparameters for each algorithm (except GLM) using the *optimizeModel* function in package *SDMtune* and maximizing cross-validated mean test AUC (for hyperparameters combination, see Model settings above). Further stepwise removal of variables for which permutation importance <1% until optimum in mean test AUC was reached.
Model ensembles	Mean of occurrence probability predicted by all 5 algorithms ('cloglog' output considered for Maxent)
Analysis and Correction of non-independence	
Spatial autocorrelation	Potential spatial autocorrelation was not accounted for as several algorithms were fitted, and no single method could be used to account for it in all.
Threshold selection	
Threshold selection	No threshold selected since abundance estimates were predicted directly from the N-mixture model.
ASSESSMENT	
Performance statistics	
Performance on training data	*NA*
Performance on validation data	AUC, TSS
Performance on test data	*NA*
Plausibility check	
Response shapes	Fit of the abundance model was assessed visually from a plot of fitted values against observed data, and from RMSE and MAE metrics
Expert judgement	Prediction map of the current occurrence probability and abundance were checked by experts and compared to independent predictions from the last national Atlas in Knaus *et al.* (2018)
PREDICTION	
Prediction output	
Prediction unit	Occurrence probability map at 50-m resolution and abundance map at 1000-m resolution for present and future (under various scenarios of land-use and climate change)
Uncertainty quantification	
Scenario uncertainty	By using various scenarios of land-use and climate change (different RCP, different model chains), as well as scenarios of no change, we cover a range of possible outcomes for land-use and climate.
Novel environments	Not visualized

Table S3 Parameter estimates, standard error (se) and 95% confidence intervals (CI) of the N-mixture model used to predict abundance while correcting for imperfect detection. Abundance parameters are on the log-scale and detection probability parameters are on the logit-scale. Intercept for the detection probability model part is defined as for visit n°1.

Model parameters	Estimate	se	95% CI
Abundance (λ)			
Mean occurrence probability	4.780	0.10	4.587 – 4.977
Detection probability (p)			
Day of year	-0.328	0.04	-0.406 – -0.251
Visit n°2	0.205	0.05	0.101 – 0.309
Visit n°3	0.044	0.07	-0.097 – 0.184

Table S4 Predictions of population size (number of breeding pairs; with 95% confidence interval limits) and density-weighted mean elevation (m asl) of the Ring Ouzel population, for Switzerland as a whole (total) and per biogeographic region (N_Alps: northern Alps; C_Alps: central Alps; S_Alps: southern Alps) for all the considered scenarios of land-use and climate change. For land-use, present: present land-use; A2: land abandonment; B2: self-sufficiency; int25: intensification 25%; int50: intensification 50%. For climate, present: present climate; CNRM/ICHEC/MPI stands for the general circulation models; see legend of Fig. 4; RCP4.5 & 8.5 stands for the IPCC greenhouse gas emission scenario (IPCC 2014); 2050 or 2100 stands for the two considered prediction periods (2030–2050 and 2080–2100, respectively).

Scenario		Region	Population size	Lower 95% CI	Upper 95% CI	Elevation
Climate	Land-use					
present	present	total	60218	53070	67349	1803
		Jura	2021	1722	2314	1326
		N_Alps	32539	28748	36376	1701
		C_Alps	20563	18103	22989	1983
		S_Alps	5095	4497	5670	1913
present	A2	total	61185	54007	68431	1811
		Jura	1983	1694	2285	1325
		N_Alps	32284	28534	36096	1702
		C_Alps	21702	19153	24256	1992
		S_Alps	5216	4626	5794	1918
present	B2	total	59823	52736	66911	1802
		Jura	2023	1723	2318	1326
		N_Alps	32339	28575	36155	1701
		C_Alps	20403	17970	22798	1982
		S_Alps	5058	4468	5640	1913
present	int25	total	60415	53397	67570	1819
		Jura	1877	1606	2166	1322
		N_Alps	31212	27627	34883	1708
		C_Alps	22040	19460	24625	1993
		S_Alps	5286	4704	5896	1919
present	int50	total	57348	50722	64087	1818
		Jura	1875	1606	2164	1321
		N_Alps	29147	25824	32497	1702
		C_Alps	21228	18756	23753	1997
		S_Alps	5098	4536	5673	1921
CNRM RCP4.5 2050	present	total	61323	54233	68608	1912
		Jura	1038	885	1212	1351
		N_Alps	29174	25826	32637	1781
		C_Alps	24291	21473	27186	2072
		S_Alps	6820	6049	7573	1993

Table S4 (continued)

CNRM RCP8.5 2050	present	total	58985	52187	65917	1955
		Jura	583	459	705	1357
		N_Alps	26824	23743	29990	1813
		C_Alps	24705	21854	27541	2106
		S_Alps	6873	6131	7681	2017
ICHEC RCP4.5 2050	present	total	55037	48627	61557	1867
		Jura	1244	1042	1440	1349
		N_Alps	28238	24986	31516	1750
		C_Alps	20731	18317	23200	2036
		S_Alps	4824	4282	5401	1965
ICHEC RCP8.5 2050	present	total	56467	49927	63130	1962
		Jura	633	519	760	1374
		N_Alps	25535	22596	28551	1817
		C_Alps	24094	21318	26910	2114
		S_Alps	6205	5494	6909	2033
MPI RCP4.5 2050	present	total	62178	55005	69596	1887
		Jura	1573	1362	1828	1341
		N_Alps	29662	26213	33126	1761
		C_Alps	24175	21414	27100	2052
		S_Alps	6768	6016	7542	1977
MPI RCP8.5 2050	present	total	58464	51600	65296	1926
		Jura	877	708	1048	1341
		N_Alps	28933	25589	32285	1794
		C_Alps	23463	20713	26177	2091
		S_Alps	5191	4590	5786	2008
CNRM RCP4.5 2100	present	total	56562	50240	63098	2061
		Jura	266	213	327	1402
		N_Alps	22590	20035	25245	1894
		C_Alps	27103	24116	30139	2196
		S_Alps	6603	5876	7387	2102
CNRM RCP8.5 2100	present	total	45067	40061	50187	2287
		Jura	17	10	29	1505
		N_Alps	12654	11201	14195	2090
		C_Alps	27536	24528	30549	2381
		S_Alps	4860	4322	5414	2270
ICHEC RCP4.5 2100	present	total	54204	47993	60550	1984
		Jura	505	407	640	1372
		N_Alps	24696	21871	27593	1834
		C_Alps	24298	21547	27077	2135
		S_Alps	4705	4168	5240	2060
ICHEC RCP8.5 2100	present	total	39028	34794	43473	2363
		Jura	1	0	3	1551
		N_Alps	10020	8894	11240	2168
		C_Alps	25314	22623	28115	2444
		S_Alps	3693	3277	4115	2341

Table S4 (continued)

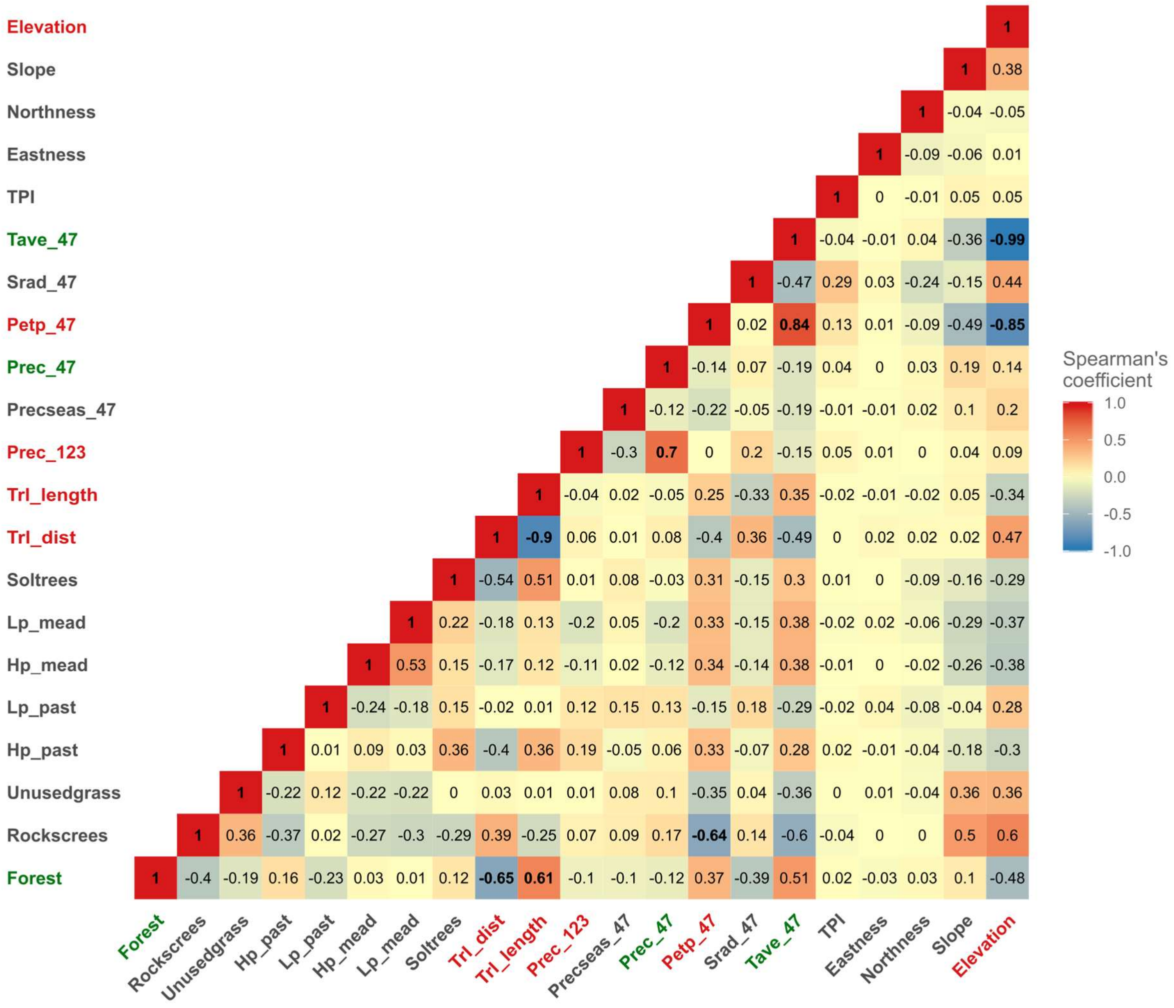
MPI RCP4.5 2100	present	total	58936	52238	65788	2000
		Jura	635	525	766	1376
		N_Alps	25726	22780	28687	1844
		C_Alps	26019	23099	29019	2152
		S_Alps	6556	5834	7316	2072
MPI RCP8.5 2100	present	total	41473	36826	46135	2294
		Jura	23	10	32	1496
		N_Alps	12419	10995	13905	2084
		C_Alps	24870	22117	27561	2398
		S_Alps	4161	3704	4637	2304
CNRM RCP4.5 2050	A2	total	62798	55494	70253	1920
		Jura	1010	866	1189	1350
		N_Alps	29006	25656	32431	1782
		C_Alps	25816	22795	28875	2078
		S_Alps	6966	6177	7758	1996
ICHEC RCP4.5 2050	A2	total	56219	49691	62899	1876
		Jura	1213	1019	1412	1348
		N_Alps	28015	24779	31270	1750
		C_Alps	22045	19502	24685	2043
		S_Alps	4946	4391	5532	1970
MPI RCP4.5 2050	A2	total	63651	56301	71216	1896
		Jura	1549	1337	1793	1340
		N_Alps	29416	26006	32866	1762
		C_Alps	25761	22822	28857	2060
		S_Alps	6925	6136	7700	1981
CNRM RCP4.5 2050	B2	total	60981	53906	68220	1912
		Jura	1040	888	1212	1351
		N_Alps	29017	25676	32461	1781
		C_Alps	24127	21309	26997	2072
		S_Alps	6797	6033	7550	1993
ICHEC RCP4.5 2050	B2	total	54644	48301	61178	1867
		Jura	1244	1043	1442	1349
		N_Alps	28033	24830	31323	1750
		C_Alps	20570	18180	23037	2036
		S_Alps	4797	4248	5376	1966
MPI RCP4.5 2050	B2	total	61799	54642	69146	1887
		Jura	1574	1364	1830	1341
		N_Alps	29463	26025	32910	1761
		C_Alps	24025	21265	26903	2052
		S_Alps	6737	5988	7503	1977
CNRM RCP4.5 2050	int25	total	62482	55169	69894	1926
		Jura	971	825	1139	1345
		N_Alps	28256	24958	31557	1788
		C_Alps	26192	23116	29322	2079
		S_Alps	7063	6270	7876	1996

Table S4 (continued)

ICHEC RCP4.5 2050	int25	total	55829	49289	62454	1883
		Jura	1148	974	1344	1344
		N_Alps	27242	24075	30408	1757
		C_Alps	22405	19783	25074	2045
		S_Alps	5034	4457	5628	1969
MPI RCP4.5 2050	int25	total	63282	55992	70807	1903
		Jura	1469	1269	1700	1336
		N_Alps	28629	25326	31980	1768
		C_Alps	26164	23169	29320	2060
		S_Alps	7020	6228	7807	1981
CNRM RCP4.5 2050	int50	total	59161	52367	66182	1931
		Jura	969	824	1139	1344
		N_Alps	26001	23080	29076	1786
		C_Alps	25416	22440	28418	2084
		S_Alps	6775	6023	7549	2000
ICHEC RCP4.5 2050	int50	total	52994	46841	59304	1885
		Jura	1146	971	1343	1344
		N_Alps	25315	22397	28248	1753
		C_Alps	21657	19164	24266	2049
		S_Alps	4876	4309	5447	1972
MPI RCP4.5 2050	int50	total	60023	53164	67135	1906
		Jura	1467	1267	1699	1336
		N_Alps	26527	23519	29622	1765
		C_Alps	25297	22416	28338	2066
		S_Alps	6732	5962	7476	1985
CNRM RCP8.5 2050	A2	total	60584	53586	67674	1963
		Jura	569	448	688	1355
		N_Alps	26641	23575	29755	1814
		C_Alps	26331	23292	29383	2111
		S_Alps	7043	6271	7848	2020
ICHEC RCP8.5 2050	A2	total	58142	51415	65039	1970
		Jura	615	507	746	1373
		N_Alps	25365	22433	28341	1817
		C_Alps	25790	22837	28864	2119
		S_Alps	6372	5638	7088	2035
MPI RCP8.5 2050	A2	total	59884	52934	66936	1934
		Jura	861	693	1029	1339
		N_Alps	28709	25434	32073	1795
		C_Alps	25013	22117	27938	2097
		S_Alps	5301	4690	5896	2012

Table S4 (continued)

CNRM RCP8.5 2050	B2	total	58690	51917	65516	1955
		Jura	584	460	705	1357
		N_Alps	26672	23607	29792	1814
		C_Alps	24580	21732	27368	2106
		S_Alps	6854	6118	7651	2017
ICHEC RCP8.5 2050	B2	total	56149	49658	62728	1963
		Jura	635	520	760	1374
		N_Alps	25378	22461	28371	1817
		C_Alps	23952	21200	26721	2114
		S_Alps	6184	5477	6876	2033
MPI RCP8.5 2050	B2	total	58067	51313	64916	1926
		Jura	875	709	1049	1341
		N_Alps	28738	25455	32120	1794
		C_Alps	23300	20581	25992	2092
		S_Alps	5154	4568	5755	2009
CNRM RCP8.5 2050	int25	total	60472	53485	67549	1968
		Jura	549	428	664	1352
		N_Alps	26016	23027	29077	1820
		C_Alps	26762	23663	29843	2111
		S_Alps	7145	6367	7965	2019
ICHEC RCP8.5 2050	int25	total	58077	51330	65022	1976
		Jura	589	477	702	1369
		N_Alps	24799	21923	27749	1824
		C_Alps	26215	23211	29364	2119
		S_Alps	6474	5719	7207	2034
MPI RCP8.5 2050	int25	total	59641	52706	66651	1940
		Jura	827	665	986	1334
		N_Alps	28026	24801	31299	1801
		C_Alps	25404	22473	28366	2098
		S_Alps	5384	4767	6000	2012
CNRM RCP8.5 2050	int50	total	57308	50711	64024	1974
		Jura	548	428	664	1352
		N_Alps	23943	21199	26724	1820
		C_Alps	25956	22963	28988	2117
		S_Alps	6861	6121	7648	2024
ICHEC RCP8.5 2050	int50	total	55160	48783	61643	1982
		Jura	586	475	701	1369
		N_Alps	22882	20253	25512	1824
		C_Alps	25448	22544	28487	2125
		S_Alps	6244	5511	6943	2039
MPI RCP8.5 2050	int50	total	56423	49888	63019	1945
		Jura	826	665	985	1334
		N_Alps	25781	22838	28743	1800
		C_Alps	24618	21779	27492	2103
		S_Alps	5198	4606	5799	2016



	Forest	Rockscrees	Unusedgrass	Hp_past	Lp_past	Hp_mead	Lp_mead	Soltrees	Trl_dist	Trl_length	Prec_123	Precseas_47	Prec_47	Petp_47	Srad_47	Tave_47	TPI	Eastness	Northness	Slope	Elevation
Elevation																					1
Slope																				1	0.38
Northness																			1	-0.04	-0.05
Eastness																		1	-0.09	-0.06	0.01
TPI																	1	0	-0.01	0.05	0.05
Tave_47																1	-0.04	-0.01	0.04	-0.36	**-0.99**
Srad_47															1	-0.47	0.29	0.03	-0.24	-0.15	0.44
Petp_47														1	0.02	**0.84**	0.13	0.01	-0.09	-0.49	**-0.85**
Prec_47													1	-0.14	0.07	-0.19	0.04	0	0.03	0.19	0.14
Precseas_47												1	-0.12	-0.22	-0.05	-0.19	-0.01	-0.01	0.02	0.1	0.2
Prec_123											1	-0.3	**0.7**	0	0.2	-0.15	0.05	0.01	0	0.04	0.09
Trl_length										1	-0.04	0.02	-0.05	0.25	-0.33	0.35	-0.02	-0.01	-0.02	0.05	-0.34
Trl_dist									1	**-0.9**	0.06	0.01	0.08	-0.4	0.36	-0.49	0	0.02	0.02	0.02	0.47
Soltrees								1	-0.54	0.51	0.01	0.08	-0.03	0.31	-0.15	0.3	0.01	0	-0.09	-0.16	-0.29
Lp_mead							1	0.22	-0.18	0.13	-0.2	0.05	-0.2	0.33	-0.15	0.38	-0.02	0.02	-0.06	-0.29	-0.37
Hp_mead						1	0.53	0.15	-0.17	0.12	-0.11	0.02	-0.12	0.34	-0.14	0.38	-0.01	0	-0.02	-0.26	-0.38
Lp_past					1	-0.24	-0.18	0.15	-0.02	0.01	0.12	0.15	0.13	-0.15	0.18	-0.29	-0.02	0.04	-0.08	-0.04	0.28
Hp_past				1	0.01	0.09	0.03	0.36	-0.4	0.36	0.19	-0.05	0.06	0.33	-0.07	0.28	0.02	-0.01	-0.04	-0.18	-0.3
Unusedgrass			1	-0.22	0.12	-0.22	-0.22	0	0.03	0.01	0.01	0.08	0.1	-0.35	0.04	-0.36	0	0.01	-0.04	0.36	0.36
Rockscrees		1	0.36	-0.37	0.02	-0.27	-0.3	-0.29	0.39	-0.25	0.07	0.09	0.17	**-0.64**	0.14	-0.6	-0.04	0	0	0.5	0.6
Forest	1	-0.4	-0.19	0.16	-0.23	0.03	0.01	0.12	**-0.65**	**0.61**	-0.1	-0.1	-0.12	0.37	-0.39	0.51	0.02	-0.03	0.03	0.1	-0.48

Figure S1 Spearman’s correlation coefficients between all pairs of variables, with in bold those above the selected threshold $|r_S|>0.6$. Names of variables that were removed at this step are displayed in red, and those that were retained are in green. We preferentially retained climate variables, with higher general importance for bird distributions (e.g. Tave_47 over Elevation), that were also projected in future scenarios (e.g. Tave_47 over Petp_47), and for which we assumed a more direct influence on the breeding ecology (e.g. Prec_47 over Prec_123). For land-use/cover variables, we retained those that were most closely corresponding to the land-use categories in given land-use scenarios (see Supplementary Materials, Fig. S2; e.g. Forest over Trl_length and Trl_dist). Variables in black were not correlated to any of the remaining variables and hence all retained. Variables full name and description can be seen in Table 1 of the main manuscript, where the order of variables on the left column is the same as here.

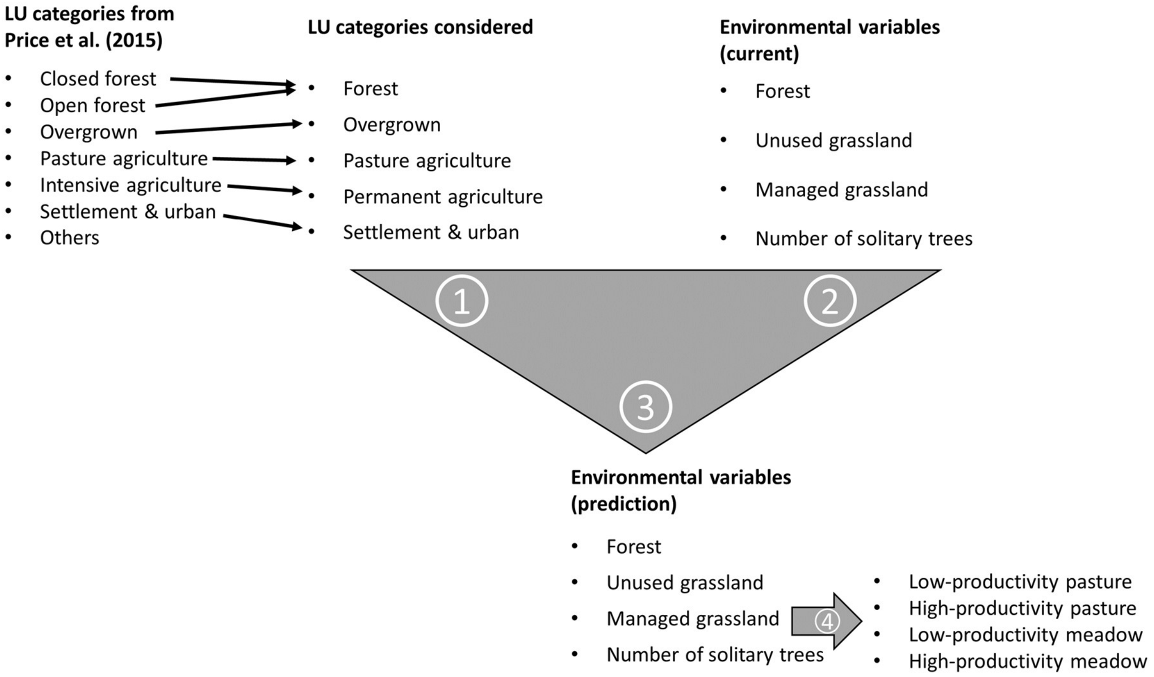
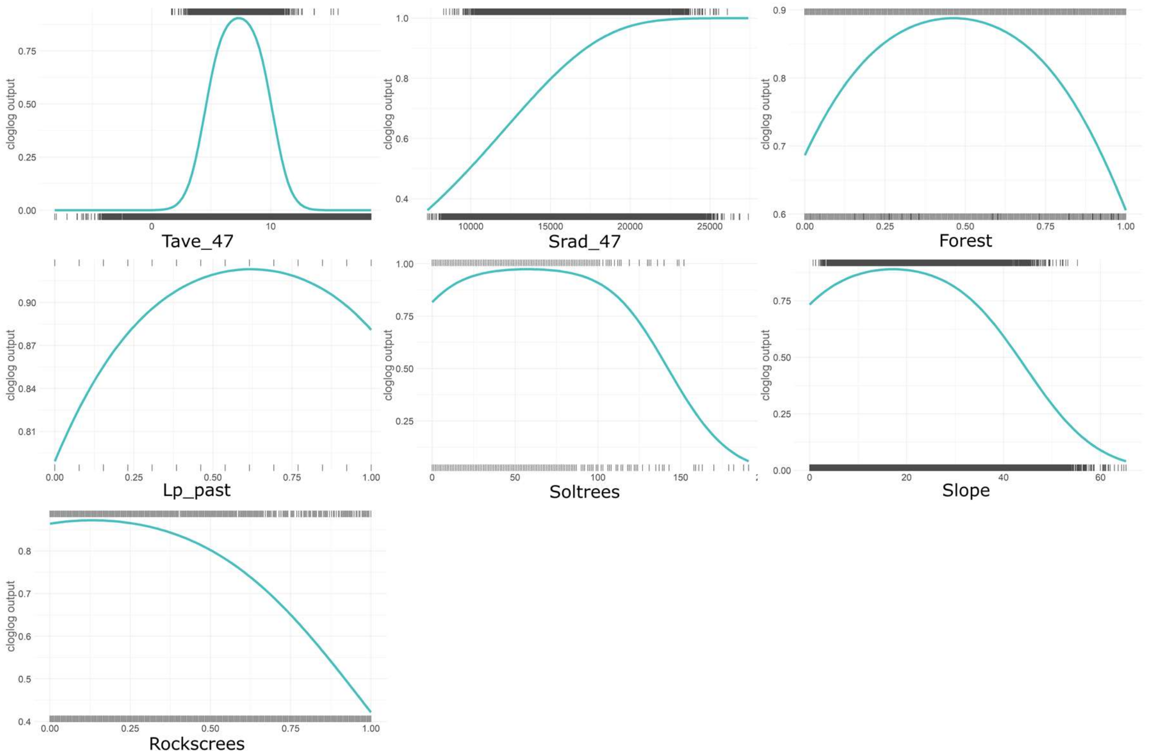


Figure S2 Schematic representation of the translation of the land-use scenarios A2 & B2 from *Price et al.* (2015) to the set of environmental variables retained in our models. The seven main categories in the model of Price *et al.* (2015) were reduced to five LU categories (summing up ‘open-’ and ‘closed forest’, renaming ‘intensive agriculture’ as ‘permanent agriculture’ and removing ‘others’). We then translated the changes in LU categories (according to the respective LU scenario) into changes in the environmental variables that were retained in our final models and represented land-use or cover. The category ‘rock & screes’ was maintained constant, as the pace of soil development at higher elevations is difficult to predict (Hagedorn, Gavazov & Alexander 2019). For each LU category, we ① identified cells where a gain in the given LU category would occur under the respective scenario (A2 or B2); ② retrieved values of each environmental variable in the cells where the given LU category occurs in the current state, so as to obtain possible values of environmental variables in areas covered by the respective LU category; ③ sampled randomly and without replacement values from ② to edit the values in the cells identified in ①, doing that for each variable and each of the 5 LU categories. In a final step ④ we allocated predicted ‘new’ managed grasslands to one of the 4 possible management types based on the nearest current management type in the surrounding landscape, using Euclidean allocation in QGIS 3.10 (QGIS Development Team 2020).



MaxEnt

Figure S3 Marginal response curves (i.e. with all other predictors set to their mean value) of retained predictors in the final species distribution models of the ensemble. MaxEnt: maximum entropy, GLM: generalized linear model, BRT: boosted regression trees, RF: random forest & ANN: artificial neural network**.** See Supplementary Materials, Fig. S1, and Table 1 for the meaning of the variable abbreviations

GLM

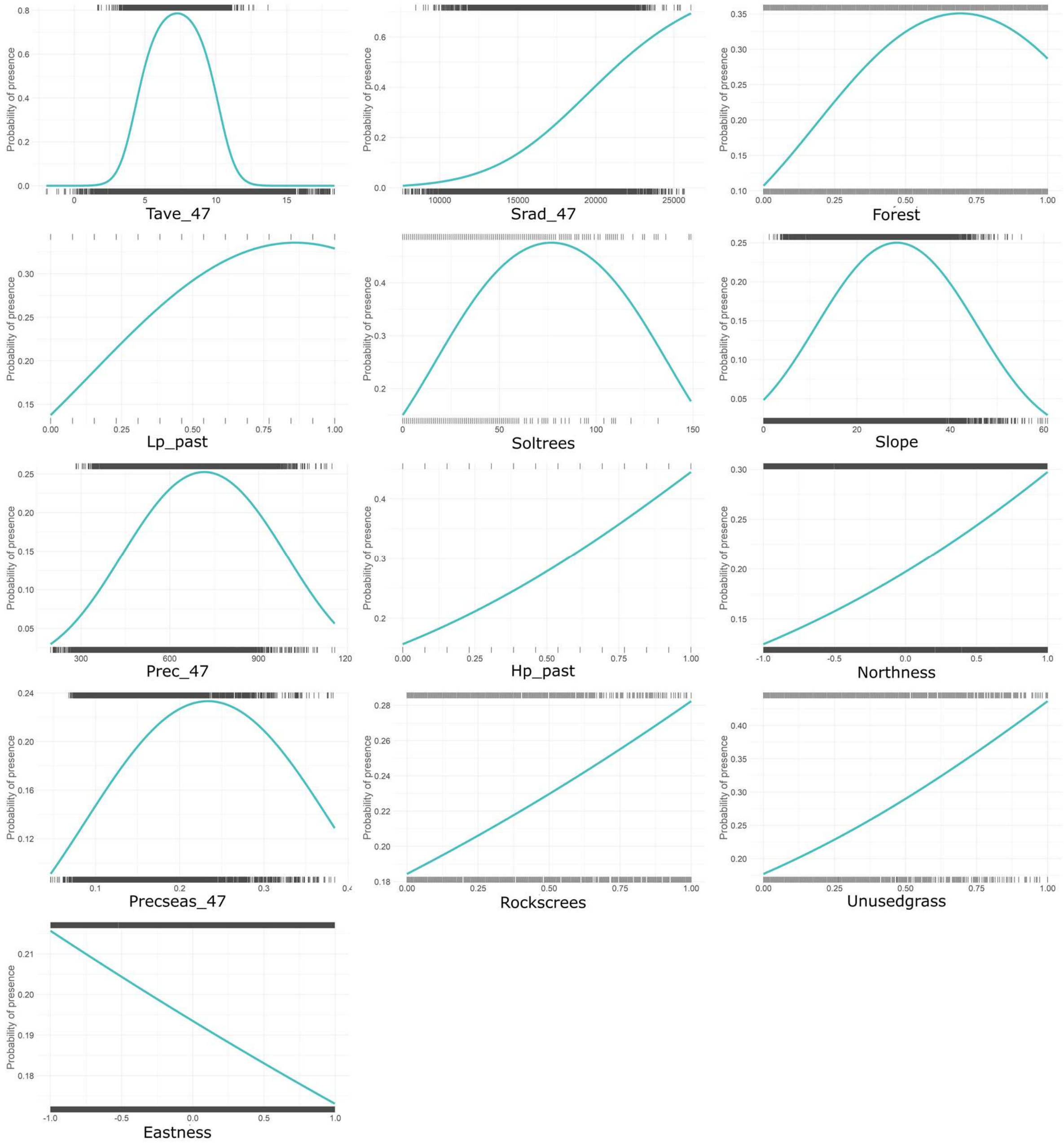


Figure S3 (continued)

BRT

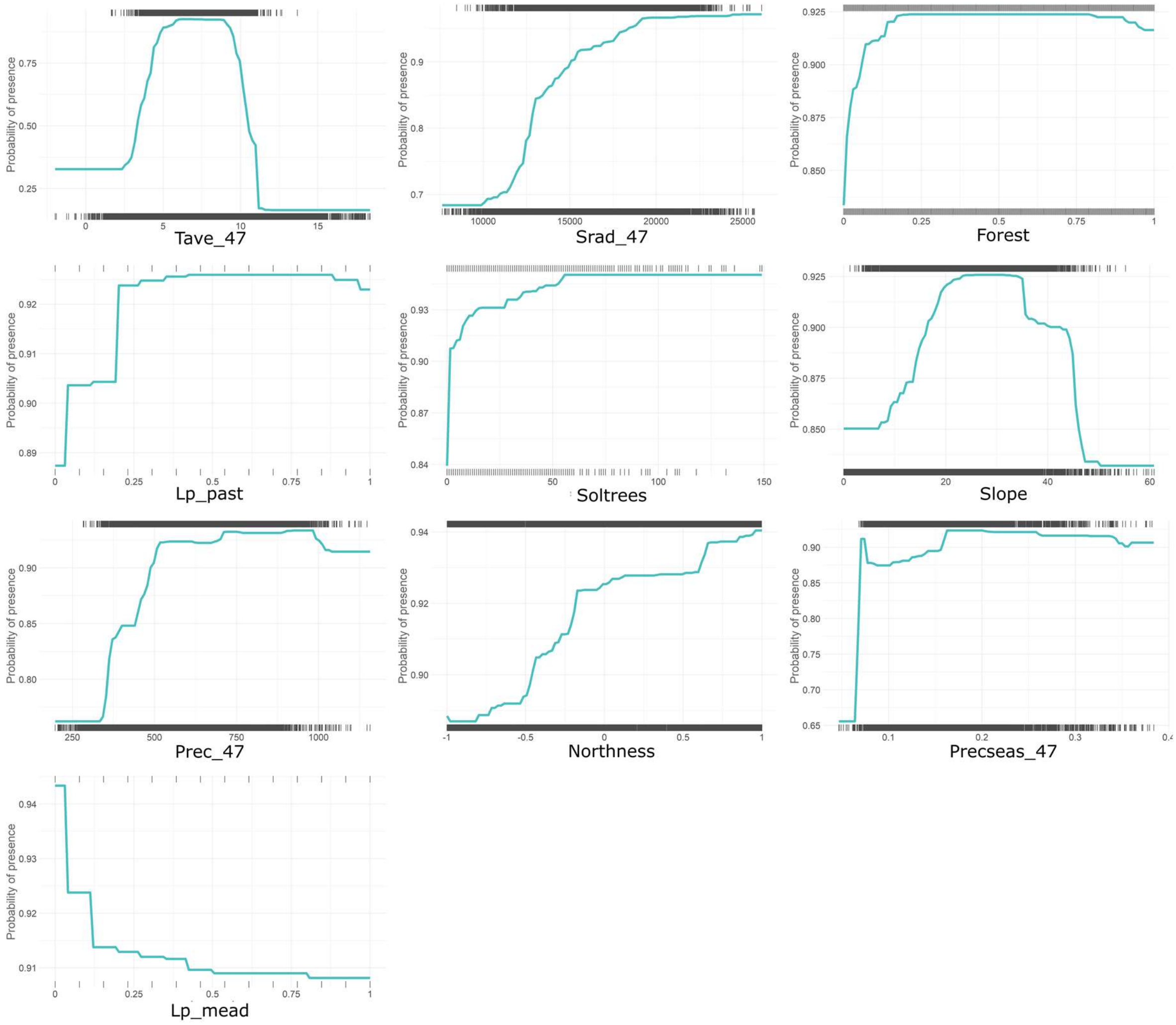


Figure S3 (continued)

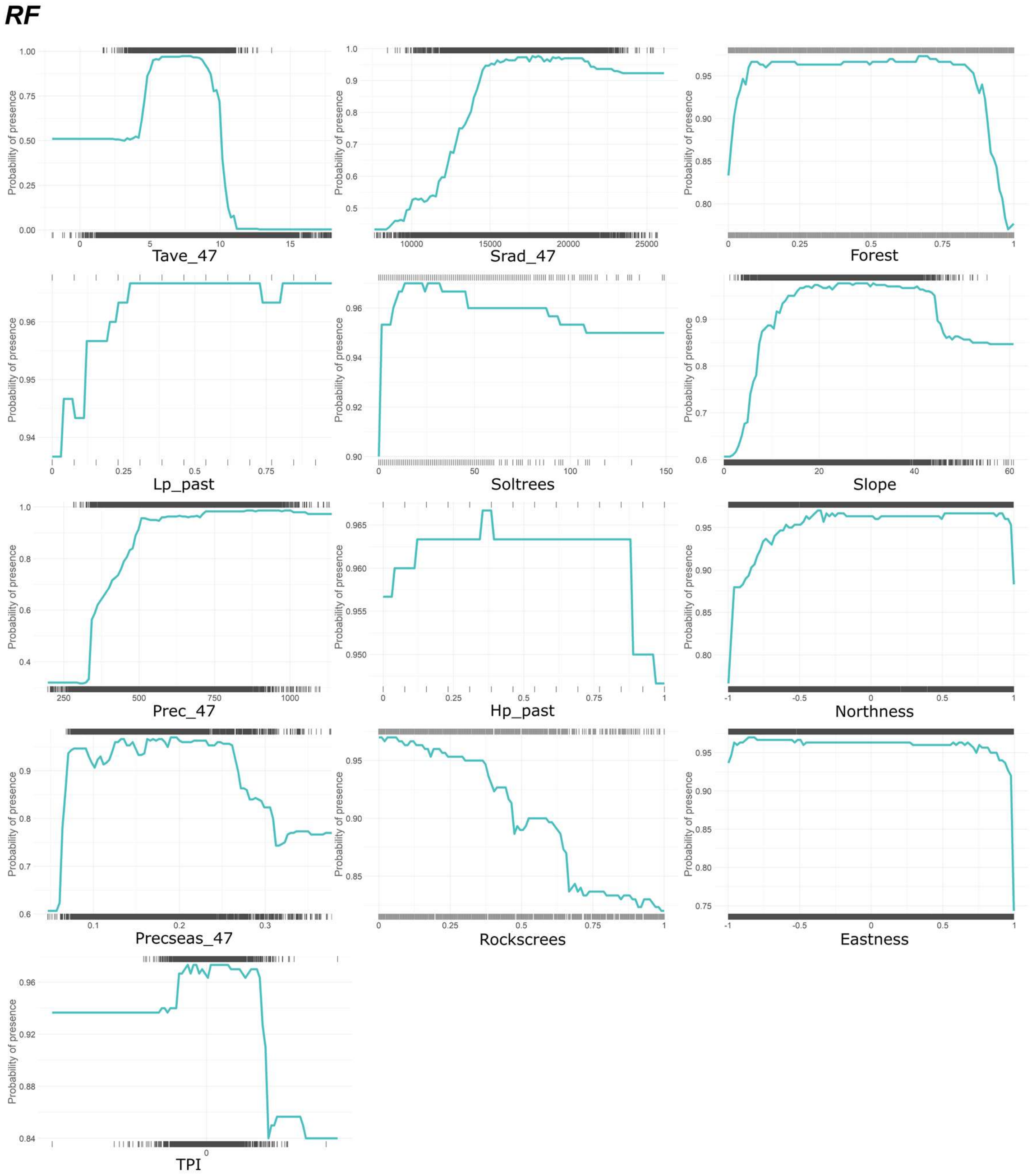


Figure S3 (continued)

ANN

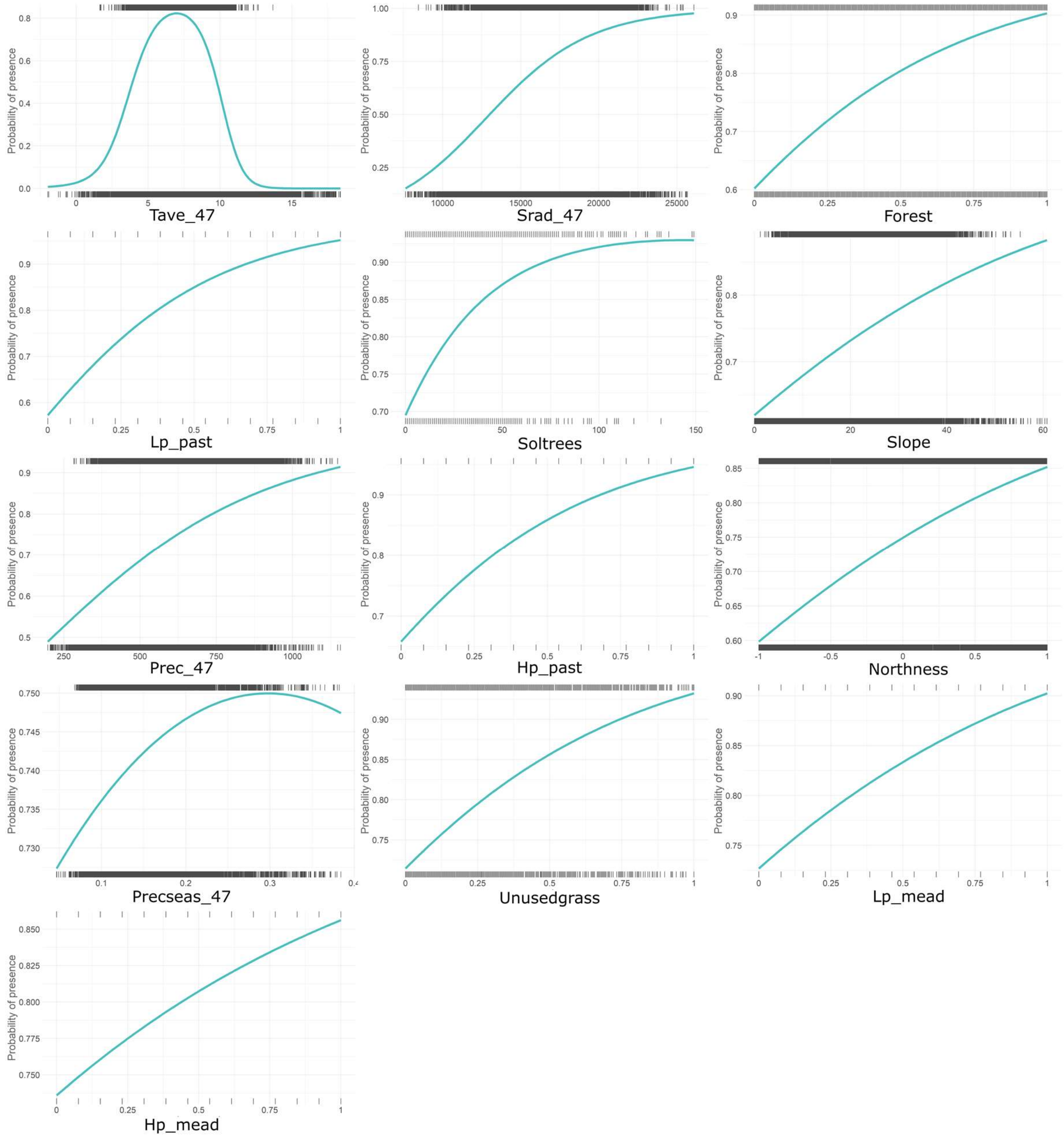


Figure S3 (continued)

GENERAL DISCUSSION

Despite a consensus on mountain wildlife's vulnerability to rapid environmental change, a mechanistic understanding of its impact on species and populations is still largely lacking. This insufficient knowledge currently represents a major impediment to the development and implementation of management interventions that could alleviate the detrimental effects of anthropogenic drivers. In many instances, it remains unclear if land-use constitutes an additional threat that may exacerbate the impact of climatic alterations or an opportunity for climate change adaptation strategies (Pearce-Higgins *et al.* 2011; Braunisch *et al.* 2014). In a rapidly changing world, research to determine main ecological and demographic constraints on the distribution and abundance of high-elevation organisms is thus of fundamental importance (Chamberlain *et al.* 2012; Chamberlain & Pearce-Higgins 2013). In this dissertation, we seek to fill these gaps in knowledge for the Ring Ouzel, an emblematic and locally threatened bird species typical of European mountain ranges, with the ultimate objective of building the evidence base for future species conservation.

Main findings

In *Chapter 1,* we identify crucial drivers of habitat selection during the energetically critical period of nestling provisioning by describing the optimal foraging habitat profile, namely sites characterized by soft and moist soils, where a short and sparse grass sward enables easy access to the ground layer. We interpret this selection pattern as the result of a trade-off between prey accessibility and abundance, in line with other studies on ground-foraging bird species (Atkinson, Buckingham & Morris 2004; Schaub *et al.* 2010; Resano-Mayor *et al.* 2019). We also demonstrate how the availability of suitable foraging grounds is rapidly decreasing after the complete melt of the snowpack, as soils desiccate and dense ground vegetation grows, defining a narrow time window of foraging opportunities.

Because prey availability is most likely playing a fundamental role in the pattern evidenced above, we focus on the nestling diet and provisioning behaviour in *Chapter 2*. We show that earthworms constitute the bulk of delivered prey items, in terms of both abundance (80%) and biomass (90%), corroborating former appraisals (Glutz von Blotzheim & Bauer 1988; Burfield 2002). We also evidence how provisioning activity and efficiency vary in relation to prevailing weather conditions, both being reduced in warm and dry weather contexts that coincide with low earthworm availability (Martay & Pearce-Higgins 2018; Onrust *et al.* 2019). This relationship probably underpins the decreasing size of prey items and lower proportion of earthworms delivered to nestlings as the season advances, highlighting strong temporal constraints on breeding, as in *Chapter 1*.

In *Chapter 3*, we delve into the demographic characteristics of two populations of Alpine Ring Ouzel with contrasting trends, revealing marked differences in a suite of traits: the growing focal population from the Swiss Alps shows a higher immigration rate and productivity but a much lower apparent juvenile survival than the declining population from the French Vercors, which appears rather isolated. In addition to this spatial variation, we evidence temporal variability in annual demographic rates that we cannot clearly link to weather variables, although they were to some extent correlated to the amount of spring precipitation and the onset of snowmelt. A comparison of the demographic traits of our two focal populations with those of Scottish birds (i.e. Northern Ring Ouzels; Sim *et al.* 2011) suggests a slower life-history strategy in the Alps, in accordance with theoretical predictions along geographical gradients (Boyle, Sandercock & Martin 2016).

While several factors might explain the variations in survival and reproduction that we report in *Chapter 3*, a few could act during the non-breeding period, warranting deeper insights into the annual cycle. This was our goal in *Chapter 4*, where we unveil the complex annual movement and behavioural patterns of individual Ring Ouzels breeding in the Swiss Alps. We show that overwintering takes place at high elevation (≥ 1500m above sea level), either in Spain or in North Africa, which are considered as the main non-breeding quarters of the species (Glutz von Blotzheim & Bauer 1988; Sim *et al.* 2015). We also reveal that this association with mountain features is sustained year-round, even during migratory stopovers. Our data further demonstrate how Ring Ouzels settle on breeding territories very early in the spring, at a time with extended snow cover, through daily commuting to lower elevations where snow-free foraging areas are available. This behaviour is presumably an adaptation to the unpredictable environmental fluctuations of seasonal ecosystems such as mountains (Hahn *et al.* 2004; Wingfield *et al.* 2004) and enables birds to start defending their territories while the breeding grounds are still largely inhospitable.

Lastly, in *Chapter 5*, we integrate knowledge on species-specific ecological requirements — gained especially from *Chapters 1 & 2* — to build a fine-scale model of occurrence probability and abundance over the whole Swiss breeding range and to project future effects of environmental change. We show that even at the home-range scale, ambient temperature remains the single most important predictor of Ring Ouzel occurrence, something evidenced for several alpine bird species (Brambilla *et al.* 2019; Jähnig *et al.* 2020). Other retained predictors corroborate the known species' preferences for a mosaic of semi-open forest and low-intensity pastures (von dem Bussche *et al.* 2008). At present, we estimate ca. 60,000 breeding pairs in Switzerland, with strongholds located in the northern Alps. In the future, we forecast a significant upward range shift, leading to extinction in the Jura mountains and shifting strongholds toward the inner Alps. Generally, our models predict that climate change will have larger impacts on population size than possible land-use alterations.

Temporal constraints on breeding

The duration of the reproduction season in birds is generally shorter at higher elevation, on average by ca. 42–57% as estimated from intraspecific comparisons (Boyle, Sandercock & Martin 2016; Martin *et al.* 2017). This is mostly a consequence of a later clutch initiation imposed by harsh weather conditions in early spring (Boyle, Sandercock & Martin 2016), but also due to a brief seasonal peak in food availability that limits the possibility for replacement or second broods (Martin & Wiebe 2004; Martin *et al.* 2017). Our results suggest that prey availability plays an important role in defining the breeding season duration of Alpine Ring Ouzels. In effect, the availability of suitable foraging habitat quickly decreases as the season advances (*Chapter 1*), having apparent repercussions for provisioning activity and efficiency of parental birds (*Chapter 2*). The existence of strong temporal constraints on breeding are corroborated by observations of rapid post-fledging movements toward higher elevations (*Chapter 1*), as well as post-breeding dispersal in the second half of June already (*Chapter 4*). Furthermore, there are strong indications that the brevity of the breeding season constitutes an important driving force in the slow life-history strategy observed in the Alps (*Chapter* 3; Boyle, Sandercock & Martin 2016). Indeed, Alpine Ring Ouzels usually manage to raise a single brood only (Glutz von Blotzheim & Bauer 1988), resulting in lower annual productivity compared to their double-brooded British conspecifics (Burfield 2002; Sim *et al.* 2011).

Given the rapid pace of climate change, the challenge to match the reproductive effort with the flush in food resources is likely to increase in complexity in the future (Visser, Both & Lambrechts 2004; Møller, Rubolini & Lehikoinen 2008), especially for organisms breeding in highly seasonal environments (Martin & Wiebe 2004; McKinnon *et al.* 2012). Increasing ambient temperatures and an earlier snowmelt are inducing an advancement of spring phenological events in arctic and alpine regions (Wipf & Rixen 2010; Klein *et al.* 2016), so that a lack of response in breeding phenology should be associated with fitness costs (Møller, Rubolini & Lehikoinen 2008). The very early arrival of Alpine Ring Ouzels on breeding grounds (*Chapter 4*) could therefore represent an insurance against potential phenological mismatches. The peak in prey availability may not only advance, however, but may also be reduced in dimension and duration following more frequent extreme weather events such as summer droughts (Beale *et al.* 2006; Pearce-Higgins 2010) or late cold snaps (Martin *et al.* 2017). In addition to indirect effects, extreme weather can also directly affect breeding success or even adult survival (Moreno & Møller 2011), so that an early reproduction onset also entails risk, especially for income breeders (Pearce-Higgins & Green 2014). Flexibility in life-history traits (*Chapter* 3: Martin & Wiebe 2004; de Zwaan *et al.* 2019) or opportunistic altitudinal movements (*Chapter* 4; Hahn *et al.* 2004) could thus act as important coping strategies to increasingly stochastic environmental conditions.

Prominent threat of climate change

The first pastoral activities in the European Alps are dated back to 5000–3000 BC and led, through burning and logging, to the progressive opening of subalpine forests and a subsequent increase in grassland cover (Schwörer *et al.* 2015; Mollet *et al.* 2018). These traditional silvi-agricultural land-use systems have persisted up to today and artificially lowered and stretched the treeline ecotone over a large altitudinal amplitude (Gehrig-Fasel, Guisan & Zimmermann 2007; Mollet *et al.* 2018). The resulting extended mosaic of semi-open coniferous forest and grassland now constitutes the core breeding zone of Alpine Ring Ouzels (von dem Bussche *et al.* 2008; Ciach & Mrowiec 2013). In this work, we detail how traditional summer pasturing may have positive effects on both prey accessibility and abundance for the Ring Ouzel (*Chapters 1 & 2*). We also evidence how a mosaic landscape is favoured by the species (*Chapter 5*) and could buffer detrimental impacts of heatwaves and droughts on prey availability (*Chapter 2*). Moreover, we show that the type and intensity of agricultural management have an influence on Ring Ouzel occurrence (*Chapter 5*), as highlighted in former studies (Buchanan *et al.* 2003; von dem Bussche *et al.* 2008). This raised the question of whether current land-use trends such as land abandonment or farming intensification may be driving the observed decline to some extent, as for other mountain bird species (Laiolo *et al.* 2004; Korner, Graf & Jenni 2018). Our predictive model actually reveals that the intensification of mountain grassland management would lead to a noticeable decrease in population size in the northern Alps (*Chapter 5*). This is an exception, however, as climate effects should largely overrule possible impacts of land-use change in all other regions in the coming decades.

While we forecast overwhelming climate change effects on the future distribution and abundance of the Ring Ouzel, assessing their magnitude is associated with large uncertainties. Indeed, there is a broad range of possible mechanisms by which climate disruption can impact mountain taxa (Chamberlain & Pearce-Higgins 2013; Scridel *et al.* 2018), many of them being indirect and implying altered species interactions (Gilman *et al.* 2010; Cahill *et al.* 2013). Here, we show how weather conditions may impact the demography of Ring Ouzel populations (*Chapter 3*) through effects on food availability (*Chapters 1 & 2*), which probably represents a widespread phenomenon for mountain wildlife (Pearce-Higgins 2010; Pearce-Higgins *et al.* 2010). By incorporating proxies for these crucial relationships in our predictive distribution model (*Chapter 5*), we aimed to capture and upscale these indirect ecological mechanisms. We notably highlight a possible future mismatch between optimal climatic conditions and suitable breeding or foraging habitat for the Ring Ouzel (*Chapter 5*), as upward shifts in vegetation or invertebrate prey will lag behind climate change (Körner 2012; Hagedorn, Gavazov & Alexander 2019). Nonetheless, it is difficult to assess whether, and to what extent, indirect effects are encompassed in our predictions. For instance, presumably important drivers such as predation (Ims *et al.* 2019) or interspecific competition (Scridel *et al.* 2018; Brambilla *et al.* 2020) were not specifically accounted for in our models, but their intensity may depend on environmental variables that were integrated. Last but not least, climatic factors outside the breeding season can exert an important influence on population trends (e.g. Chiffard *et al.* 2019), making an assessment of climate change effects even more challenging for migratory species (*Chapter* 3; Sæther, Sutherland & Engen 2004). This is particularly relevant for the Ring Ouzel, given its year-round reliance on climate-sensitive ecosystems (*Chapter 4*).

Management recommendations

Throughout this thesis, we underline some of the mechanisms by which summer grazing by cattle may benefit the Ring Ouzel. Hence, it potentially represents the best instrument for appropriate habitat management below the actual treeline. First, summer grazing probably increases the suitability of foraging grounds, by maintaining an extensive but short grass field layer (< ca. 10cm), interspersed with bare ground areas through trampling (Pittarello *et al.* 2016). There are also indications that managed pastures host a higher abundance of soil-dwelling invertebrates compared to abandoned grasslands (Steinwandter *et al.* 2017; Jernej *et al.* 2019), at least as long as overgrazing is avoided. At a coarser scale, the semi-open vegetation structure of wooded pastures should guarantee the retention of optimal soil conditions via the buffering effect on soil desiccation of canopy shading and a thicker litter layer (James *et al.*

2003; Müller *et al.* 2016). A high number of scattered, isolated trees (> 5 m) should therefore be promoted at the landscape scale while strictly controlling for the formation of dense forest stands. This may require selective tree felling and forest opening interventions where the forest has already reached later successional stages. In such cases, we recommend taking advantage of possible synergies with other habitat management plans, e.g. for other priority bird species at the treeline like the Black Grouse *Lyrurus tetrix* (Patthey *et al.* 2012; Braunisch, Patthey & Arlettaz 2016; Pradervand, Jacot & Spaar 2018). In recently encroached grasslands, however, browsing by livestock should apparently suffice to suppress rejuvenation and restore the appropriate, biodiversity-rich habitat structure, provided that clear guidelines are followed (see Koch *et al.* 2013). The maintenance of summer pastures in the Alps is nevertheless contingent upon substantial governmental subsidies, which certainly questions their long-term persistence in numerous regions (Mack & Flury 2008).

In addition, our projections highlight that realistic land-use change scenarios for Switzerland, including country-wide interventions to reduce grassland encroachment, would not have major effects on the distribution and population size of the Ring Ouzel in the medium-term (to 2035). This underlines that the management interventions listed above, even if deployed on a large scale, would have only limited effectiveness for species conservation in a context of rapid climate change. The question arises then as to whether maintaining habitat quality at low elevations at all costs represents an appropriate climate change adaptation strategy, or if facilitating shifts at the advancing range margin, i.e. at higher elevations above the current treeline, would not be a more promising option (Pearce-Higgins *et al.* 2011). These two strategies are certainly not mutually exclusive, and spatially explicit models might constitute the key to prioritize their implementation in space and time (Braunisch, Patthey & Arlettaz 2016; Brambilla *et al.* 2019). A possible solution would be (1) to maintain or restore habitat quality in current Ring Ouzel density hotspots that are predicted to remain climatically suitable, and (2) to assist the natural dynamic of treeline upward shifts in areas with high climatic suitability projected in the future, while ensuring that it does not jeopardize important ecological communities of open alpine grasslands (Chamberlain *et al.* 2013).

Further perspectives

Although we believe that the findings of this PhD thesis make a significant contribution to the understanding of possible effects of global change on mountain birds in general, and on the Alpine Ring Ouzel in particular, many questions were raised throughout the research process. Some particular aspects that were not covered here would in our opinion deserve further investigation:

1. Despite its crucial importance in driving many aspects of Ring Ouzel autecology, prey availability was never directly measured within the framework of this thesis. As food availability has a strong influence on population demography of short-lived bird species, it appears crucial to understand how the phenology and seasonality of key food resources are altered by environmental change (Pearce-Higgins 2010; Pearce-Higgins & Green 2014). This is currently hindered by excessively rare monitoring of invertebrate populations at high elevation. We therefore call for multi-year studies on above- and belowground prey availability in mountain ecosystems, similar to research carried out in the Arctic (e.g. McKinnon *et al.* 2012; Saalfeld *et al.* 2019), to better understand how intra- and interannual fluctuations may impact alpine birds.

2. Climatic effects on demography are notoriously difficult to detect (Sæther, Sutherland & Engen 2004) and often require long time series of high-quality data. Owing to logistic constraints, detailed demographic studies on mountain bird populations remain challenging to implement but have been increasing in recent years (e.g. Bastianelli *et al.* 2017; Chiffard *et al.* 2019; Strinella *et al.* 2020). Some revealed a clear impact of climatic conditions on demographic parameters, but often in unexpected ways or with significant spatial heterogeneity. An intensive monitoring of populations in various temperate mountain regions across the globe — for example through the development of constant-effort ringing stations in subalpine or alpine zones — will in our opinion prove fundamental to better understand and predict their response to new environmental circumstances.

3. Finally, purposely narrowing the focus on the European Alps in this last section, there is a need to properly quantify how rapid changes in the management regime of mountain grasslands affect the avifauna, especially within the subalpine and alpine zones. This requires, first, a proper baseline to establish distribution and abundance of

mountain bird species in the whole Alpine arc, and second, a spatially replicated long-term monitoring of bird communities in regions subjected to the most drastic land-use changes. In addition to hosting emblematic mountain specialists, the Alps may act as a refuge for farmland bird species that widely vanished from the lowlands following farming intensification (Archaux 2007; Knaus *et al.* 2018; Keller *et al.* 2020). Alpine countries thus bear an international responsibility for their conservation and are bound to preserve this unique heritage.

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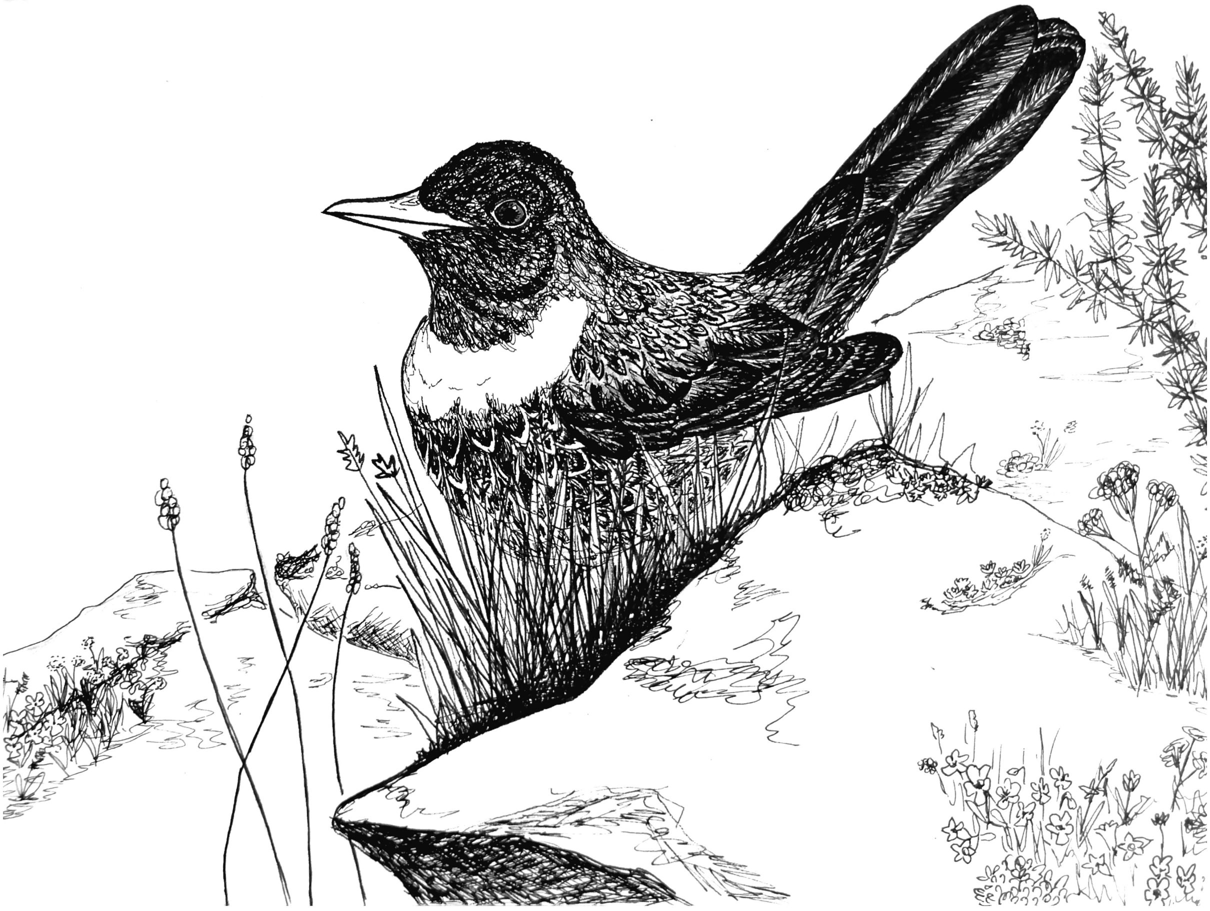

Declaration of consent

on the basis of Article 18 of the PromR Phil.-nat. 19

Name/First Name	Barras Arnaud Gian
Registration Number	11-509-684
Study program	Phil.-nat. Ökologie und Evolution

Bachelor ☐ Master ☐ Dissertation ☑

Title of the thesis	Assessing the response of mountain birds to rapid environmental change: conservation ecology of the Alpine Ring Ouzel (*Turdus torquatus alpestris*)
Supervisors	Prof. Dr. Raphaël Arlettaz Dr. Veronika Braunisch

I declare herewith that this thesis is my own work and that I have not used any sources other than those stated. I have indicated the adoption of quotations as well as thoughts taken from other authors as such in the thesis. I am aware that the Senate pursuant to Article 36 paragraph 1 litera r of the University Act of September 5th, 1996 and Article 69 of the University Statute of June 7th, 2011 is authorized to revoke the doctoral degree awarded on the basis of this thesis.

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