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Letter

Seasonal and daily movement patterns of an alpine passerine suggest high flexibility in relation to environmental conditions

Arnaud G. Barras, Felix Liechti and Raphaël Arlettaz

A. G. Barras (https://orcid.org/0000-0003-0850-6965) ✉ (arnaud.barras@vogelwarte.ch) and R. Arlettaz, Division of Conservation Biology, Inst. of Ecology and Evolution, Univ. of Bern, Bern, Switzerland. – AGB and F. Liechti (https://orcid.org/0000-0001-9473-0837), Swiss Ornithological Inst., Sempach, Switzerland.

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Mountains naturally offer variable habitat conditions, but their biodiversity is currently facing the extra challenge of adapting to rapid environmental shifts that are much more pronounced than in the lowlands. Among adaptive responses, intra- and inter-seasonal movements represent potentially important coping strategies for wildlife that remain largely unexplored. We investigated the seasonal and daily 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 light-level geolocators and multi-sensor loggers. Of the birds traced to their non-breeding grounds, 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 flexible daily elevational movements, especially upon spring arrival on the breeding grounds in relation to date and snowfall occurrence, suggesting adaptive potential in response to environmental variation. This study shows how modern technology can deliver deeper and valuable insights into movements, behavioural patterns and life-history strategies for relatively little-studied animal species. By doing so, it paves the way for refined assessments of species' vulnerability to ongoing global change while providing basic conservation guidance.

Keywords: accelerometer, conservation, elevational movements, geolocator, migration, ring ouzel

Introduction

Rapid environmental change is imposing novel and multifaceted challenges on living organisms worldwide (Parmesan 2006). As summarized in the famous expression 'adapt, move or die', movement represents a central coping strategy. While it can take place over several generations, movement also enables mobile organisms to track favourable environments over their lifetime or their annual cycle, the latter being commonly described as migration (Newton 2008). To do so, they must rely on a suite of environmental cues that inform the direction and timing of movements (Newton 2008, Bauer et al.

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2020), but which may become increasingly unreliable in the context of global change (Winkler et al. 2014). For migratory birds breeding in highly seasonal environments such as arctic and alpine ecosystems, the timing of arrival needs to be finely tuned to a very brief time window with suitable conditions (Wingfield et al. 2004, Winkler et al. 2014), which defines a short reproduction season (Boyle et al. 2016). Arriving too early or too late typically entails negative fitness consequences, such as increased mortality or reduced reproductive output (Martin et al. 2017, Lerche-Jørgensen et al. 2018). An additional challenge in these extreme and unpredictable environments is the pronounced spatial and interannual variability in environmental conditions, exacerbated by the ongoing environmental change (Schär et al. 2004). Ultimately, the persistence of these populations therefore largely depends on the maintenance of flexible behavioural strategies, which are adjusted to changing environmental cues (Winkler et al. 2014, Beever et al. 2017).

Fine-grained information on individual movements is crucial to assess the frequency and flexibility of certain strategies, as well as the role of environmental cues. Generally, the movement ecology of birds in mountain ecosystems is still poorly known, even among well-investigated taxa from temperate biomes (Boyle and Martin 2015, Resano-Mayor et al. 2017). For instance, within-breeding season movements (Frey et al. 2016, Ceresa et al. 2020) or facultative latitudinal migration of species long considered as resident (Resano-Mayor et al. 2020) have been unveiled only recently, adding to our historical knowledge of seasonal elevational migration (Barçante et al. 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 and Martin 2015). The pronounced spatiotemporal heterogeneity that characterizes mountain ecosystems thus appears to foster regular movements throughout the annual cycle (Martin 2001), both latitudinally and elevationally. Yet, we still lack detailed data on movement strategies and their underlying mechanisms for a large range of mountain bird species.

The rapid development of sophisticated tracking devices offers novel opportunities to study individual bird movements at unprecedented spatial and temporal scales, with the potential to tackle key conservation challenges (Katzner and Arlettaz 2020). For small birds, light-level geolocators (GLS) enable the tracking of individuals throughout the annual cycle by means of simple measures of light intensity coupled with an internal clock. Still, this technology is not accurate enough to detect small-scale latitudinal movements (Fudickar et al. 2012), let alone elevational shifts. The tracking of such movements is possible with GPS devices, which are now successfully deployed on small passerines (McKinnon and 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 GLS with other sensors such as barometers and accelerometers have been developed (Liechti et al. 2018). As in GLS, 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 some of these new tracking technologies (mainly GLS and MSL). 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 and Bauer 1988, Keller et al. 2020). It is believed to overwinter mainly in the Atlas Mountains in Morocco and Algeria (Glutz von Blotzheim and 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 and Briggs 2006). Nonetheless, winter observations at the southern boundary of species' breeding range (French western Alps and Pyrenees; Glutz von Blotzheim and Bauer 1988) suggest that some 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). 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 wintering grounds 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). Here, we used various tracking technologies to unravel the migration timing, routes and behaviour of ring ouzels breeding in the central European Alps.

Methods

Fieldwork and material

Birds were captured and ringed at a single study site in Valais, Switzerland (46°19′50″, 7°25′50″, 1800–2100 m a.s.l.) 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 and Winkler 2020).

We used four types of loggers to record ring ouzel locations: simple geolocators (hereafter GLS; model GDL2, Swiss Ornithological Inst. (SOI), Switzerland); remote-download geolocators (hereafter also termed GLS; model GDL-uTag, SOI, Switzerland); multi-sensor loggers (hereafter MSL; model GDL3-PAM, SOI, Switzerland) and GPS loggers (model nanoFix-GEO, PathTrack Ltd, UK).

In addition to light intensity, the deployed MSL measured acceleration and atmospheric pressure at 5-min intervals (Liechti et al. 2018). GPS was 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 for GLS and MSL, and Teflon ribbon for GPS. The different types of loggers (Supporting information) 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). We equipped a total of 59 individuals with 62 GLS or MSL (three individuals were equipped on two different years) as well as 16 individuals with GPS between 2015 and 2019 (Supporting information).

Analyses

All analyses were performed with the software R ver. 4.0.4 (<www.r-project.org>). We first compared the apparent survival rate of birds equipped with loggers with those of a control group (only colour-ringed), based on Bayesian Cormack–Jolly–Seber models from visual re-sightings (following Kéry and Schaub 2012), fitted in JAGS via the package *jagsUI* (Kellner 2021). For the analysis of loggers' data, we used the packages *TwGeos* (Wotherspoon et al. 2016), *GeoLight* (Lisovski and Hahn 2012), *SGAT* (Sumner et al. 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 to 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. Given the long break between first migratory flights just after the breeding season and those in late summer and autumn, we first distinguished between a post-breeding period, when birds most likely leave the study area to reach moulting areas, and the actual autumn migration period, when ring ouzels travel to their overwintering grounds after moulting. The post-breeding period started on the day of the first migratory flight in June or July and lasted up to the autumn migration departure, which was defined as the first migratory flight after 1 August. The non-breeding (i.e. overwintering) period was defined when a bird had stayed at the same place for at least two weeks in a row after 1 October. Lastly, the spring migration period started with the first migratory flight in March and ended when birds were back in the study area.

In a second step, we converted readings of atmospheric pressure into metre above sea level (hereafter m a.s.l.) 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 elevation 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 elevation (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 first summarized the elevation 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. For the period between spring arrival on the breeding grounds and start of the breeding season (set as 10 May if the bird was not captured before), we also calculated the difference between mean elevation readings during the night and the day. We tested for the effect of day of year and snowfall occurrence on these daily elevational movements by fitting a linear model, in which the individual identity of the bird was also included as an explanatory factor to control for individual variation.

Finally, we derived geographic positions of the nine birds for which light-intensity data was available and of sufficient quality. We first defined defined sunrise and sunset times (hereafter 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 flights as residency periods, given the noise in the data and thus the need of longer periods to estimate accurate locations. For GLS, the distinction was done using the function *changeLight* in *GeoLight*, again setting a threshold of eight days for distinguishing a residency period. We used 'in-habitat' calibration of the sun elevation angles (zero and median) for parameterizing the error distribution around the twilight times (Lisovski and 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 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 track was fixed at the known breeding location, as was the endpoint, except for the individual whose logger stopped recording in the middle of winter. To fit the Estelle model, we first drew 1000 initial samples using a 'modifiedGamma' model (i.e. relaxed model, allowing negative errors on twilight times), tuning 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 2000 iterations to ensure convergence.

Results

Only seven out of the 62 GLS/MSL were retrieved by recapture of the tagged bird, while data from another four GLS could be downloaded remotely in the field. Two additional GLS-tagged individuals had lost their logger at the time of recapture. We thus retrieved data from, in total, five MSL and six GLS, from eleven different individuals. For MSL, data covered a full year except for one device that had stopped recording in February in the year following tagging. Regarding GLS, a too short light stalk on loggers fitted in the first year caused intense shading and prevented the use of data from 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 16 GPS by recapture but both had malfunctioned, with locations available for only one GPS for just a month after deployment.

In subsequent years following ringing, we resighted 33.9% (20/59) of the individuals equipped with GLS and MSL, and 18.8% (3/16) of the GPS-tagged birds, to be compared with 29.9% (64/214) of the ring ouzels from the control group. Apparent survival rates of GLS- and MSL-tagged birds did not differ from the control group ($\beta = 0.26$, 95% CI: −0.94 to 1.91), while we evidenced a detrimental effect of the slightly heavier GPS loggers ($\beta = -1.46$, 95% CI: −2.92 to −0.17).

Migratory schedule

We obtained a complete annual migratory schedule for four individuals, and partial for a fifth (Table 1). Migratory movements (i.e. flights ≥30 min) took place almost exclusively at night (mean = 96.7%, range: 92.7–98.8%). Post-breeding movements started between the second half of June and the first 10 days of July (Table 1). For one bird (AdM-3), we did not detect any migratory flight but only a short nocturnal flight (<30 min) during this time of the year, which was defined as the start of the post-breeding period. Actual departures into fall migration were observed 45–103 days after the onset of post-breeding movements, differing markedly between all five individuals (Table 1). Most of the autumn migratory flights occurred in October for all birds (Fig. 1; Supporting information). Inter-individual differences in the onset of fall migration produced large variation 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, Supporting information). 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 (Supporting information). 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).

Table 1. Summary statistics and schedule of migration from the five ring ouzel individuals equipped with multi-sensor loggers. The total distance indicates the great circle distance from the breeding site to the furthest winter 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' stands for the number of nights with ascertained migratory flight activity.

	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
Start of post-breeding period	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^{-1})	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^{-1})	128.7	117.5	93.4	253.8	–
Cumulative flight hours	21.3	36.2	40.8	41.7	–

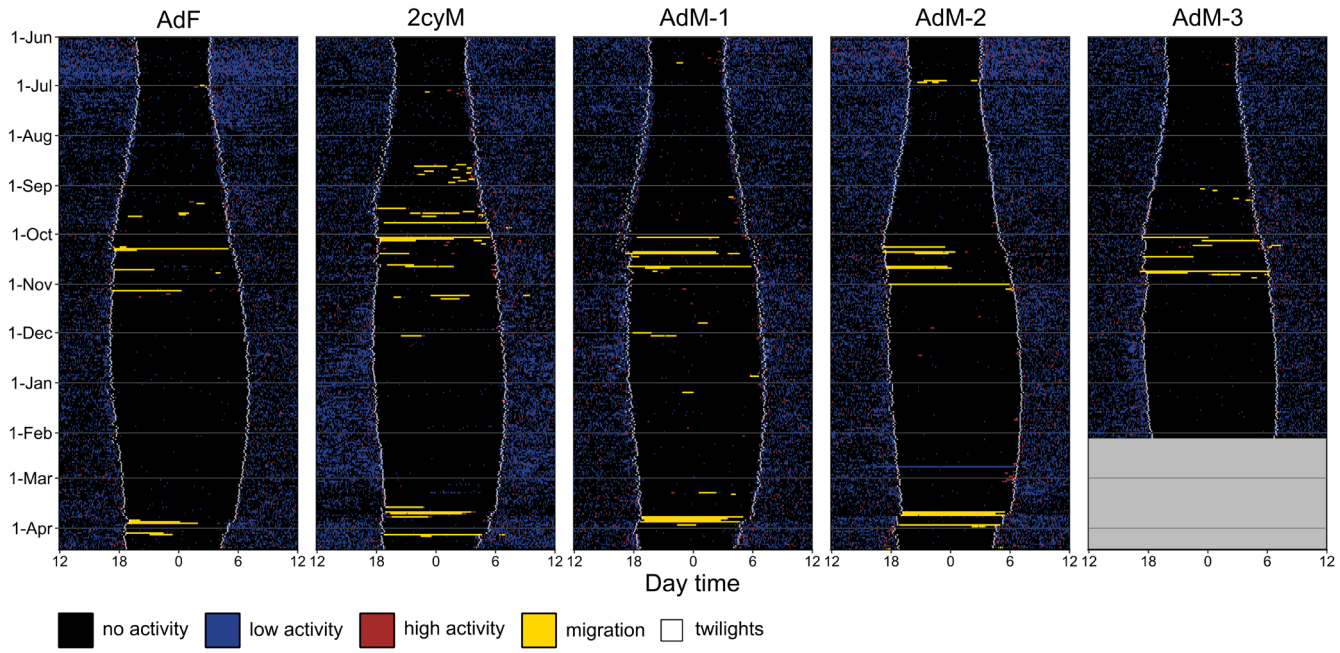

Figure 1. Actograms of five ring ouzels equipped with multi-sensor loggers, showing the annual activity pattern as classified into four categories of behaviour. Small white dots show the timing of the twilights as estimated from the individual light sensor of the tag. The cut between two successive 24-h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

Migration routes

The GPS information available from a single bird revealed a 140-km eastwards movement at the end of June and early July (over 20 days), in line with the findings on post-breeding movements obtained with MSL on other individuals. 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). During the autumn and spring migration periods, 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 short residency periods (i.e. stopovers) for most of our birds. For non-breeding grounds, however, GLS 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 (Supporting information), but could indicate that it stayed in different locations across the Atlas mountains and corroborate significant winter movements as evidenced by MSL. 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).

Elevational 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 a.s.l.; Fig. 3), indicating movements to sites mostly above the timberline after reproduction. The median elevation of stopovers during the autumn migration (in contrast to their location, the elevation of stopovers was easily retrieved from barometer data) was generally above 1860 m a.s.l. (Fig. 3), but three birds stopped below 1000 m a.s.l. for a single day. The maximal estimated flight elevation was reached during the fall nocturnal migration by bird AdF on 10 October, with 4270 m a.s.l. The median elevation of non-breeding grounds was always greater than 1500 m a.s.l. for every individual, irrespective of their location. Elevation readings during spring stopovers appeared generally lower than those on autumn stopovers, but not for all individuals (Fig. 3). Finally, year-round measurements revealed periods with marked elevation differences between day and night within a 24-h cycle (Supporting information). Birds were then clearly commuting every day to areas located either below (pre-breeding) or above (post-breeding) the elevation of their location overnight. This phenomenon, congruent with direct field observations, was particularly

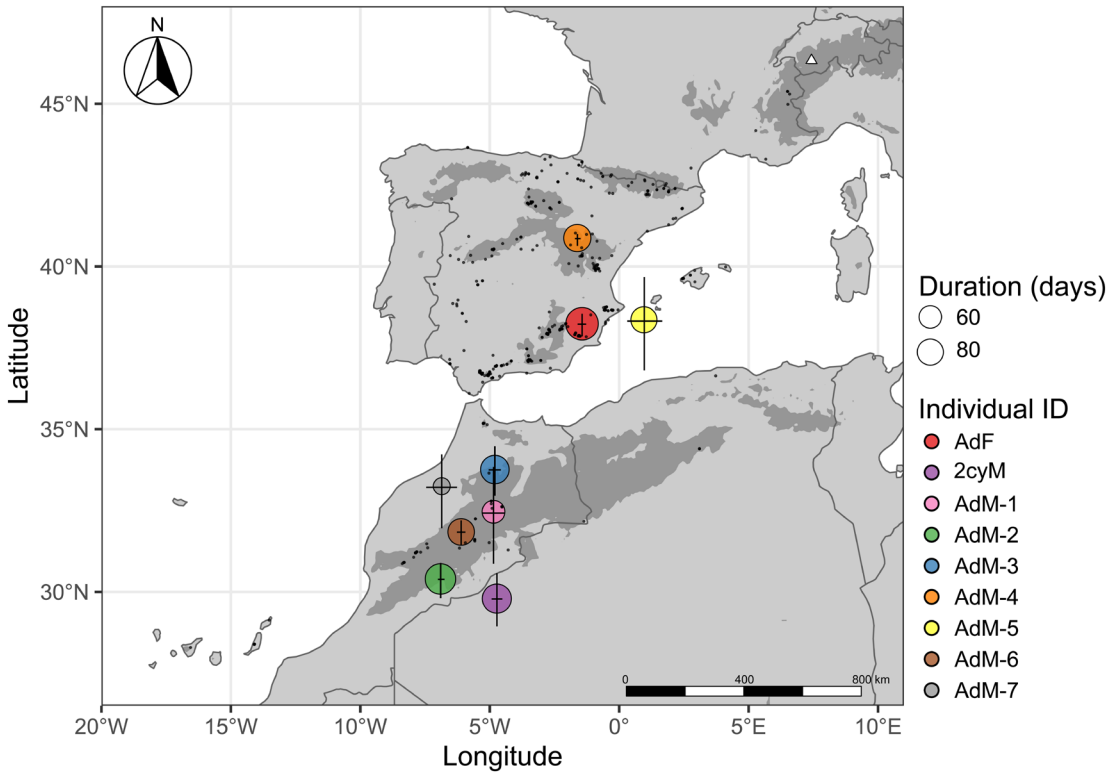

Figure 2. Longest stationary winter locations of nine ring ouzel individuals as retrieved from geolocator data. Error bars around locations represent 95% credible intervals while the size of each circle is proportional to stay duration. Winter sightings of ring ouzels (December–February) are shown as 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 a.s.l.

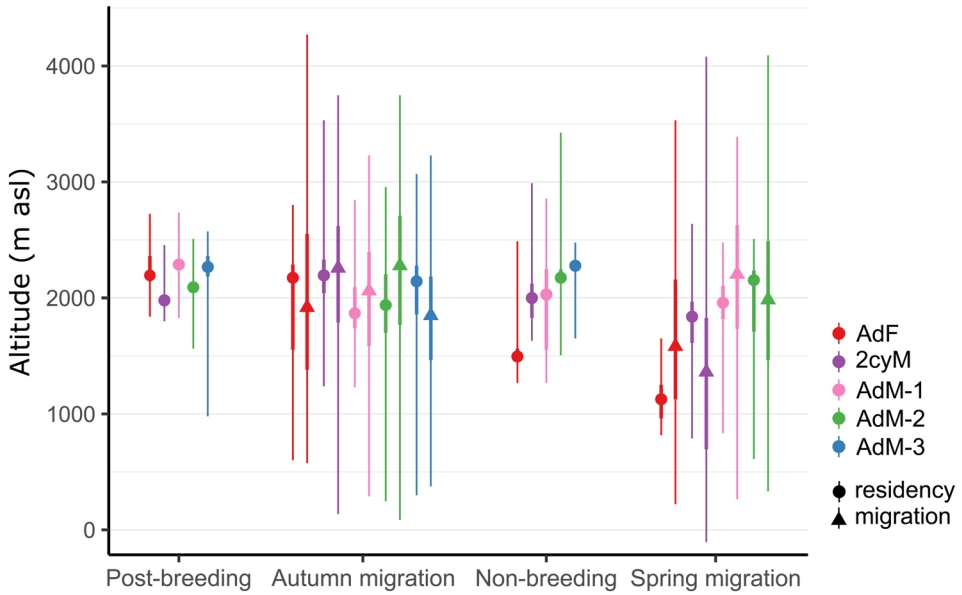

Figure 3. Median elevation estimates, at four stages of the annual cycle, for five ring ouzels equipped with multi-sensor loggers. For autumn and spring migration, readings during stopovers (circles) are separated from those during active, mostly nocturnal migration (triangles). Bold bars represent the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

marked in the weeks following spring arrivals, when birds flew to foraging grounds situated several hundred meters below the breeding area (Fig. 4). Day of year had a negative effect on the amplitude of these elevational movements ($\beta = -13.64$, $p < 0.001$), indicating that the daily commute distance progressively decreased as the season advanced. Snowfall occurrence, on the other hand, showed a positive effect ($\beta = 198.55$, $p < 0.001$), thus triggering movements also later in the season (late-April to early-May; Fig. 4), at a time when females start laying eggs and brooding..

Discussion

Using archival tracking technology, we documented the seasonal movements of Alpine ring ouzels breeding in the Swiss Alps. From a technical viewpoint, although 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

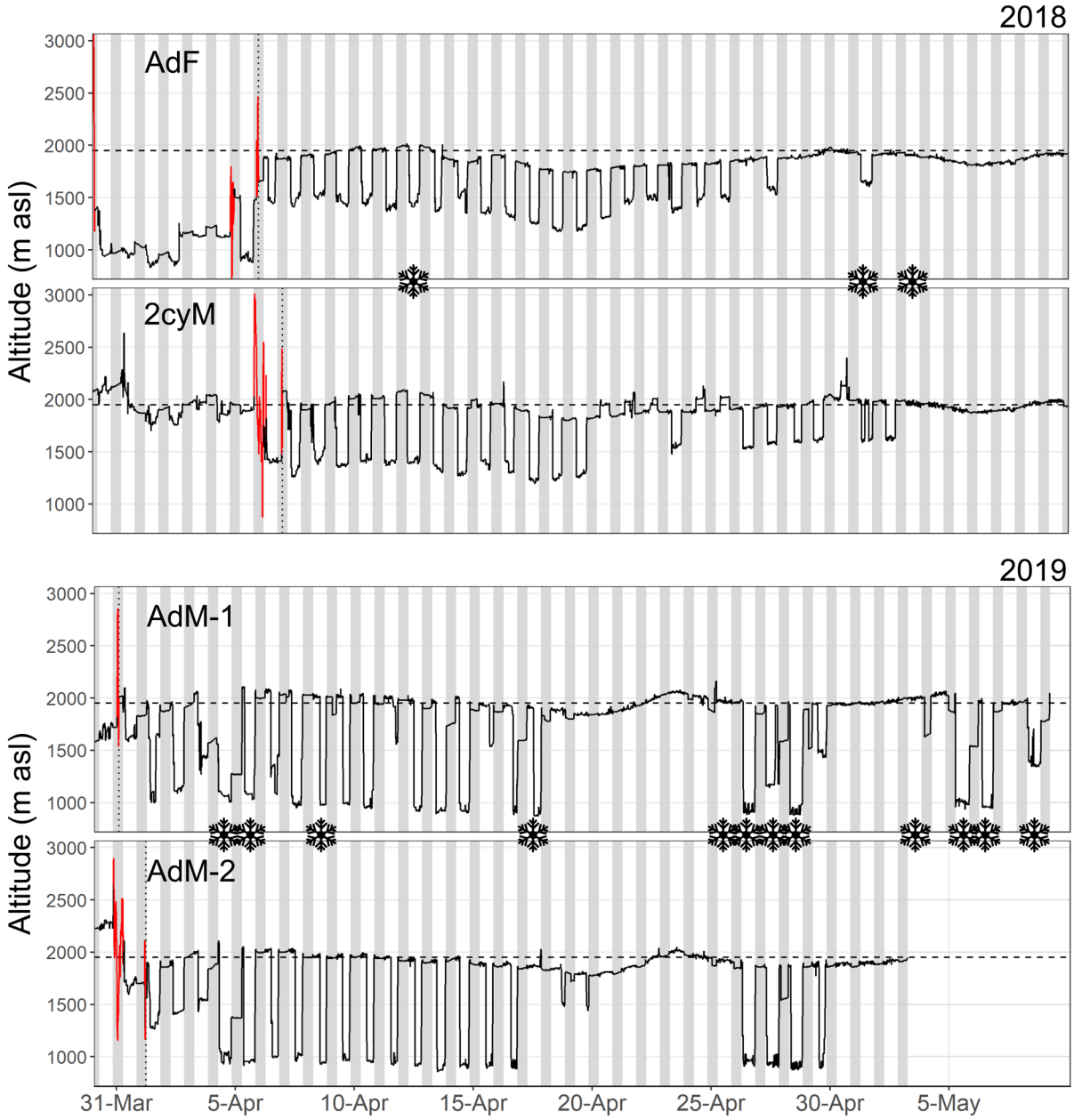

Figure 4. Continuous elevation estimates (5-min intervals) from four ring ouzels upon arrival (date: vertical dotted line) on the breeding grounds in spring. Grey zones symbolize nighttime and the horizontal dashed lines indicate the mean elevation of the study area. Elevation estimates displayed in 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 a.s.l.).

estimates. Multi-sensor loggers thus provide valuable additional information 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 locations and migratory behaviour of the ring ouzel. We found that the species is tightly associated with mountain ranges and high elevations at all stages of its life cycle, including during migratory stopovers. This highlights 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 been documented in the Nearctic (Martin 2001, Boyle and Martin 2015). For the ring ouzel, mountain massifs actually constitute a network of stepping stones in the western European landscape that is otherwise dominated by less suitable lowland habitat. The behavioural pattern illustrated here may be partly shared by at least another typical inhabitant of European alpine ecosystems, the white-winged snowfinch *Montifringilla nivalis* (Resano-Mayor et al. 2020). Given the faster climate shifts in mountain regions (Pepin et al. 2015) and an ultimately shrinking habitat towards mountain summits, these high-elevation species are regarded as especially vulnerable to rapid climate change (La Sorte and Jetz 2010). The strong reliance on mountains for various parts of the annual cycle might render them even more sensitive to changing climatic conditions, compared to other alpine species which regularly use lowland habitats (e.g. northern wheatear *Oenanthe oenanthe* or water pipit *Anthus spinoletta*).

Our results confirm the important role played by the Atlas Mountains for wintering ring ouzels (Glutz von Blotzheim and Bauer 1988, Ryall and Briggs 2006, Sim et al. 2015): two-thirds of the tracked 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 unrecognized key wintering hotspot, at least for this Alpine population. Overwintering in Spain certainly entails shorter, i.e. energetically less demanding flights for Alpine ring ouzels, but the availability of food resources could also play an important role in the choice of the non-breeding grounds. 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 dispersal (Herrera 1985, Zamora 1990, Ryall and Briggs 2006, Rumeu et al. 2009). Since thrushes are known to actively track food resources (Tellería et al. 2011, 2014), the high spatiotemporal variability in the availability of juniper berries could influence 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 somewhat resilient to the progressive loss of their foraging habitat in the Maghreb region, notably in Morocco where juniper forests are systematically overexploited for firewood (Ryall and Briggs 2006).

Finally, we also evidenced remarkable patterns of elevational movements. Ring ouzels performed daily elevational movements that have to our knowledge never been documented in such detail at the individual level apart from aerial insectivores (Dreelin et al. 2018). The most patent demonstration of this phenomenon was upon arrival of ring ouzels on their Alpine breeding grounds in April, when those are still covered by a dense snowpack. Birds typically overnight in their future breeding territories, males vocally signalling their occupancy at dawn and dusk (Glutz von Blotzheim and Bauer 1988). The rest of the day, they apparently visited snow-free meadows at lower elevations to forage, usually in the montane and subalpine belts, depending on seasonal, year-specific snow conditions. Later in the season, with the advancement of the snowmelt which frees the first patches of alpine grasslands within the breeding area, they stopped commuting, but daily movements resumed following new snowfall (Fig. 4). Retreating to lower elevations in response to adverse weather conditions at the breeding site is a behaviour that has been described for numerous bird species in several mountain ranges (O'Neill and Parker 1978, Hahn et al. 2004, Boyle et al. 2010). Nonetheless, it remains unclear if daily visits to the breeding site are common under these conditions (this study) or if birds rather continuously stay at low elevations for a few days (Hahn et al. 2004).

Daily elevational migration may enable birds to settle in high-elevation breeding grounds very early in the year, sometimes when those are still inhospitable, and thus some sort of insurance against missing the brief time window suitable for breeding (Barras et al. 2020, 2021b). In addition, this strategy of early territory occupancy might provide a competitive advantage over other individuals or species that breed in the same habitat. Ring ouzels migrate much faster in the spring than in the autumn, a pattern commonly observed across various migration flyways and species (Nilsson et al. 2013, Schmaljohann 2018). This contrasts, however, 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, potentially waiting there for the snowmelt at their nearby breeding sites and/or building fat reserves (Sander et al. 2021, Kölzsch et al. 2016, de Zwaan et al. 2019). With their daily elevational movements, 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 continuing to accentuate into the future.

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Author contributions

Arnaud G. Barras: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (supporting); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Felix Liechti**: Conceptualization (equal); Funding acquisition (equal); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Raphaël Arlettaz**: Conceptualization (equal); Funding acquisition (equal); Project administration (lead); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

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Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.nzs7h44sd> (Barras et al. 2021a).

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