

# Complex Seasonal and Day-to-day Movements of an Alpine Passerine May Act as an Insurance Against Environmental Variability

Arnaud Gian Barras (✉ [arnaud.barras@iee.unibe.ch](mailto:arnaud.barras@iee.unibe.ch))

University of Bern

Felix Liechti

Swiss Ornithological Institute

Raphaël Arlettaz

University of Bern

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## Research Article

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# Abstract

Mountains naturally offer very contrasted 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 declines 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 transhumance, especially upon spring arrival on the breeding grounds, which provides some noticeable behavioural flexibility, i.e. adaptative 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.

## Introduction

Information on year-round movement patterns is key for animal species conservation<sup>1</sup>. In effect, migratory decisions can directly determine individual survival and reproductive success<sup>2,3</sup>, impacting population dynamics<sup>4</sup>. 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 of arrival at, and departure from these grounds needs to be finely tuned to the brief time window available for reproduction<sup>5,6</sup>. Given the particularly rapid pace of the environmental changes affecting these ecosystems<sup>7,8</sup>, the capacity of birds to adjust and time their movement decisions in response to environmental shifts will thus be crucial for their long-term persistence<sup>6,9</sup>.

Movements of wildlife in mountain ecosystems have been little studied, even among well-investigated taxa such as mammals and birds of temperate biomes<sup>10,11</sup>. For instance, within-breeding season movements<sup>12,13</sup> or facultative latitudinal migration of bird species long considered as resident<sup>14</sup> have been unveiled only recently, adding to our historical knowledge of seasonal altitudinal migration, i.e. vertical transhumance<sup>15-17</sup>. In the same line, the importance of high-elevation ecosystems as post-breeding or stopover grounds for migratory species may have been widely underestimated<sup>10</sup>. 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 bird individual movements at unprecedented spatial and temporal scales and thus to tackle key conservation challenges<sup>18</sup>. 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<sup>19</sup>, without mentioning altitudinal ones. GPS tracking devices can fulfil this requirement and are now successfully deployed on small passerines<sup>20</sup>, 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 barometer and accelerometer have been developed<sup>21</sup>. 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<sup>21-23</sup>. They thus represent a promising tool to better appraise 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<sup>24,25</sup>. It is believed to overwinter mainly in the Atlas Mountains in Morocco and Algeria<sup>24</sup> – in sympatry with individuals from the northern subspecies *T. t. torquatus*<sup>26,27</sup> – where the principal source of food are juniper (*Juniperus sp.*) berries<sup>28</sup>. 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<sup>26,27</sup>. Yet, large-scale movements and thus migratory connectivity of the different ring ouzel populations are still poorly documented<sup>27</sup>. This not only hampers understanding of the metapopulation system, but also impedes the development of an integral conservation management plan<sup>1</sup>. Nonetheless, winter observations at the southern boundary of species breeding range French western Alps and Pyrenees;<sup>24</sup> 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;<sup>29</sup>. This study used various tracking technologies to unravel the migration timing, routes and behaviour of ring ouzels breeding in the Central European Alps.

## 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 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 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 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).

Table 1

Summary statistics and schedule of dispersal and 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' stand for the number of nights with ascertained migratory flight activity.

	<b>AdF</b>	<b>2cyM</b>	<b>AdM-1</b>	<b>AdM-2</b>	<b>AdM-3</b>
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	-

## Migration routes

An insufficient quality of data combined with a 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 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 timberline 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 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).

## 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 daylength, 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<sup>10</sup>. 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 least another typical inhabitant of European upland ecosystems, the white-winged snowfinch *Montifringilla nivalis* see<sup>14</sup>. 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<sup>7</sup>. On the other hand, the area of suitable habitat will inexorably shrink due to the pyramid shape of mountains.

Our results confirm the important role played by the Atlas Mountains for wintering ring ouzels<sup>24,27,28</sup>: 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<sup>28,30-32</sup>. 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<sup>33,34</sup>, as it probably also is in North Africa<sup>28</sup>. Since thrushes are known to actively track food sources<sup>33,34</sup>, 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<sup>28</sup>.

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 signaling their occupancy at dawn and dusk<sup>24</sup>. 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 transhumance 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<sup>35-</sup>

<sup>37</sup>. 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 <sup>38</sup>. 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 <sup>39,40</sup>. With their daily transhumance, 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 <sup>5,14,35</sup> – some buffer against the dramatic impacts of climate and land-use change that are going to accentuate into the future.

## 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 coloration and age – either second calendar year (2cy) or adult (>2cy) – determined based on the presence of a moult limit in the greater coverts <sup>41</sup>.

We used four types of loggers to record ring ouzel locations: simple geolocators (hereafter GL; model GDL2, Swiss Ornithological Institute (SOI), Switzerland); remote-download geolocators (hereafter also termed GL; model GDL-uTag, SOI, Switzerland); multi-sensor loggers (hereafter MSL; model GDL3-PAM, SOI, Switzerland) and GPS loggers (GPS; model nanoFix-GEO, PathTrack Ltd, UK). In addition to light intensity, the deployed MSL measured acceleration and atmospheric pressure at 5-min intervals see <sup>21</sup> 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 Table S1) weighted at most 2.6% of the mean ( $\pm$  SD) body mass as measured from captured birds (males:  $95.1 \pm 5.1$  g,  $n = 191$ ; females:  $100.8 \pm 8.9$ ,  $n = 91$ ). 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 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 resighted 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 resightings following <sup>42</sup>, apparent survival rates of GL- and MSL-tagged birds did not differ from the control group ( $\beta = 0.27$ , 95% CI: -0.92 to 1.66), while we evidenced a detrimental effect of the slightly heavier GPS loggers ( $\beta = -1.74$ , 95% CI: -3.32 to -0.42).

## Analyses

All analyses were performed with the software R version 3.6.2 <sup>43</sup> using the packages *TwGeos* <sup>44</sup>, *GeoLight* <sup>45</sup>, *SGAT* <sup>46</sup> and *PAMLR* <sup>47</sup>, following the general framework described in Lisovski, et al. <sup>48</sup>. 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 1<sup>st</sup>. 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 1<sup>st</sup>. 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 <sup>21,49</sup>. 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<sup>-1</sup>) so that they would not generate abrupt changes in estimated altitude <sup>21</sup>. Furthermore, daily fluctuations in atmospheric pressure, called atmospheric tides, reach at most 3 hPa in the tropics <sup>50</sup>, 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<sup>45</sup>, i.e. using as a reference the period during which a bird was for sure present at its breeding site. We then modeled 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<sup>48</sup>. 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 5 times with 300 iterations using a 'Gamma' distribution. We shall here report median estimates  $\pm$  95% credible intervals (CI; based on 2.5 and 97.5% quantiles) from a final run with 2'000 iterations to ensure convergence.

## Declarations

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## Author contributions:

All authors contributed to the study conception and design. Data collection and analysis was performed by AB. AB lead writing of the manuscript and all authors read, thoroughly edited and approved the final manuscript.

## Conflicts of interest:

The authors declare that they have no conflict of interest

## Permit:

Permission for bird capturing was delivered by the Swiss Federal Office for the Environment (F044-0799) and authorization for fitting birds with tracking devices by the Swiss Federal Food Safety and Veterinary Office.

## Data accessibility statement:

Data that support the findings of this study will be made available from the figshare repository upon publication.

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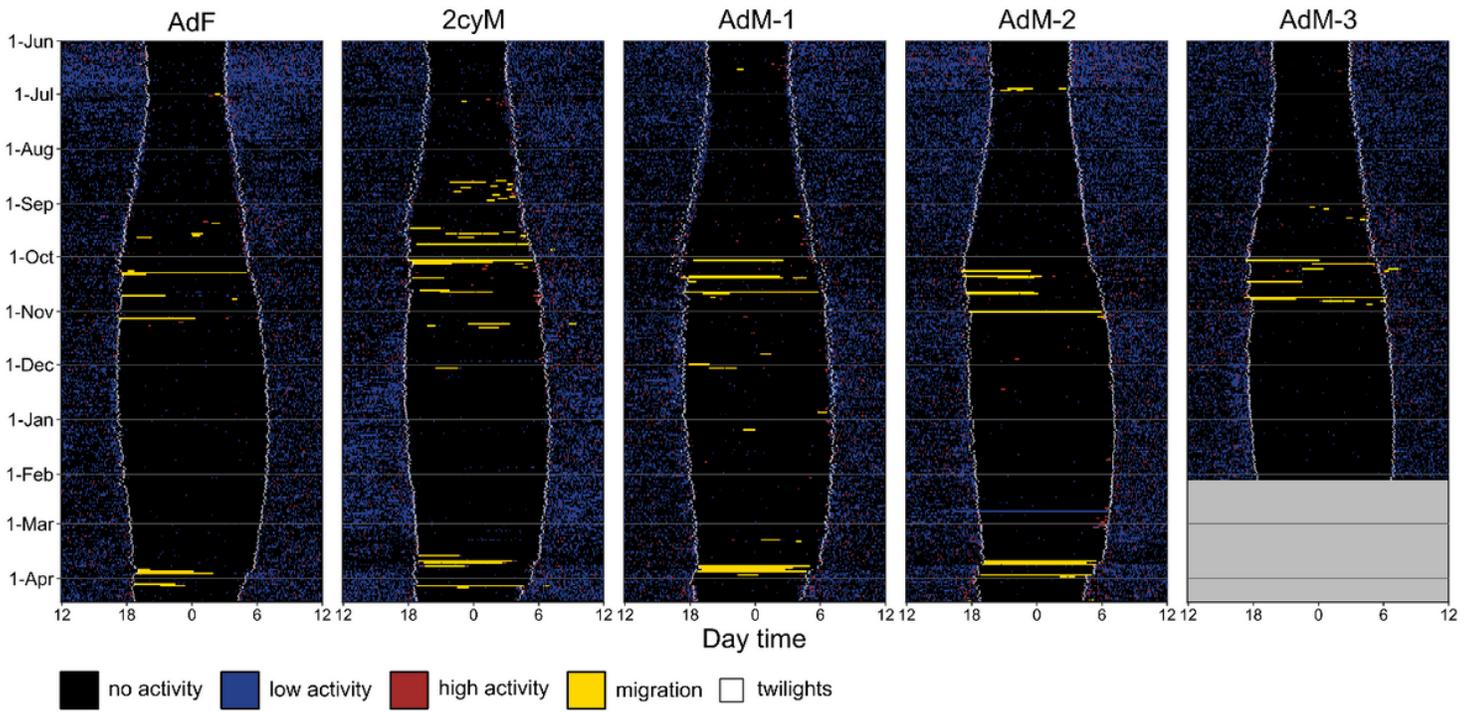
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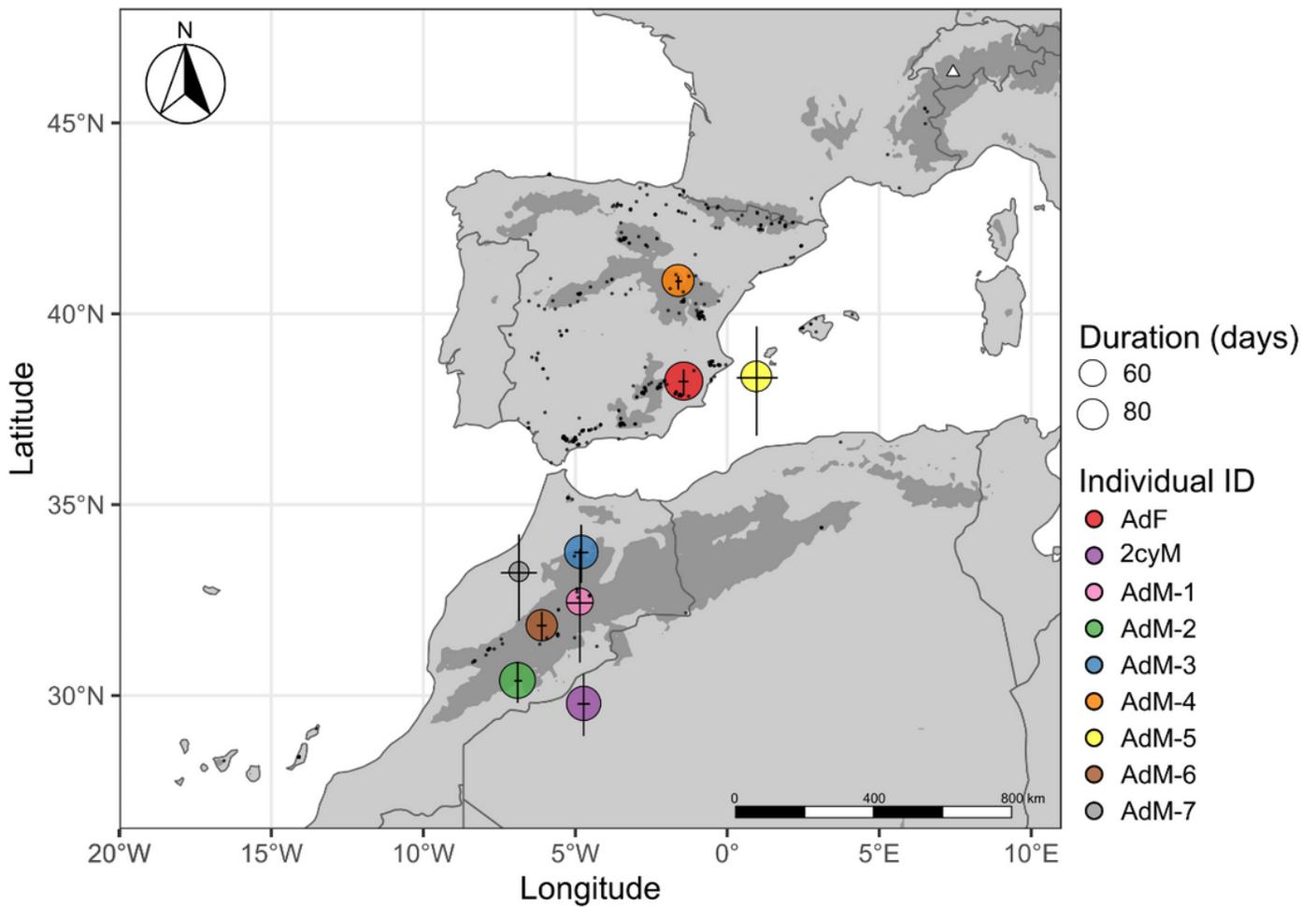
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## Figures



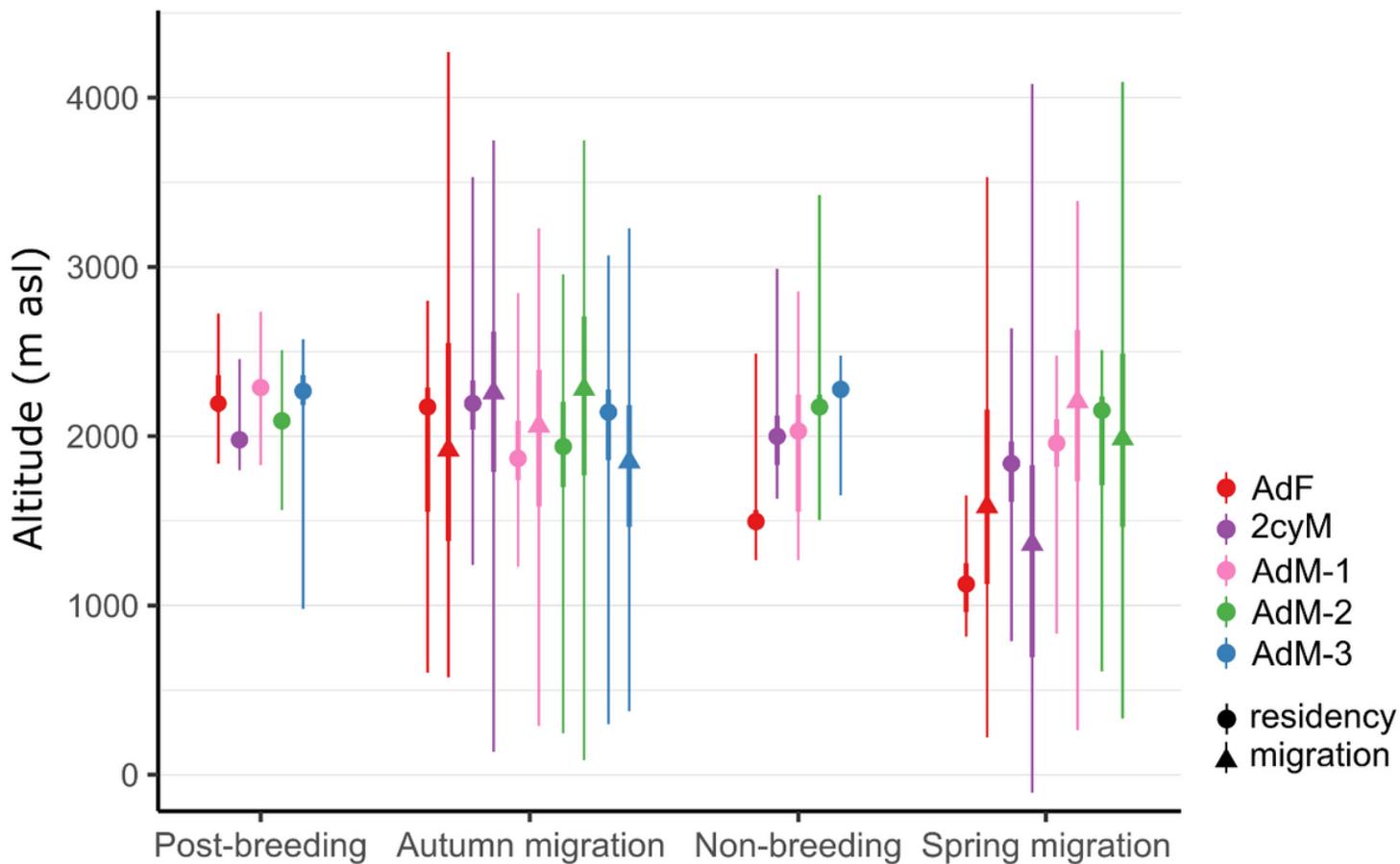
**Figure 1**

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.



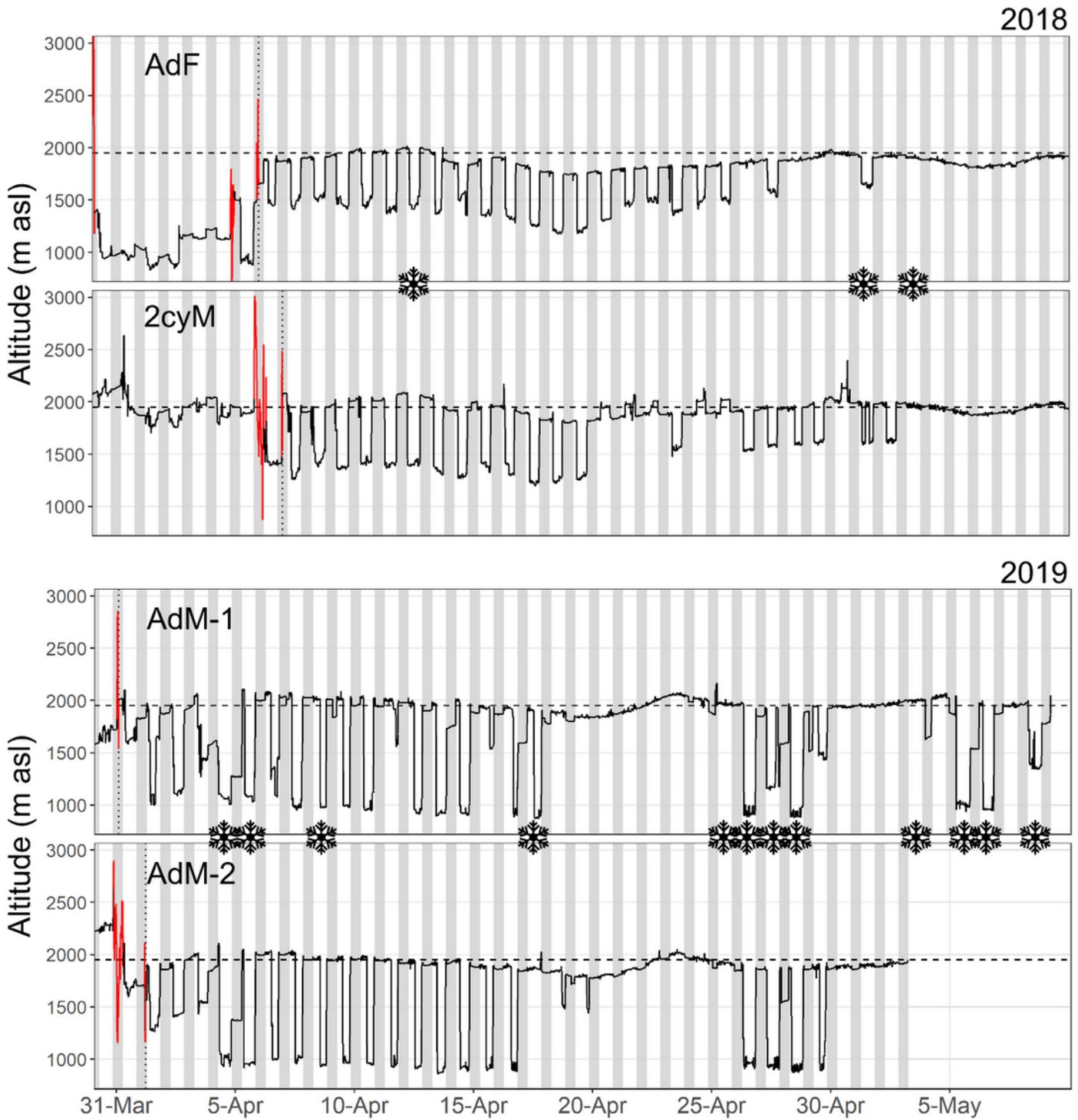
**Figure 2**

Longest stationary winter locations 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.



**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 (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. Altitude estimates displayed in red refer to migratory flights. Snowflake icons indicate a new snowfall ( $\geq 1$  cm fresh snow) as measured at a nearby weather station (4.1 km distance, 2390 m asl).

## Supplementary Files

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