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Research Article

Autumn bat migration across the mountain barrier in Central Europe

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Abstract

Knowledge of bat migration routes and phenology is still incomplete, especially for small-bodied species. Here we report on autumn migration over a mountain barrier (1200 – 1400 m a.s.l.) and analyse differences between short- and long-distance migrants based on acoustic monitoring of the number and direction of bat flights. The number of flights over the mountain passes peaked in September and then slowly declined. This pattern occurred for both long-distance and short-distance migrants, but long-distance migrants had a longer migration season. All bats migrated preferentially during milder weather (relatively dry, high temperature and low wind). As the migration season progressed, the proportion of southerly flights increased, and this tendency was stronger for long-distance migrants than for short-distance migrants. It appears that a proportion of the movements of short-distance migrants were associated with individuals commuting across the ridge to swarming and wintering sites on either side of the ridge. We conclude that long-distance migrants differ from other species only quantitatively: they have a longer migratory season and their migratory direction to the south is more defined. We hypothesise that the migration strategy of long-distance migrants depends on maximising the use of good weather windows rather than on persistent migration regardless of conditions.

Introduction

Four key characteristics of migratory movements have been highlighted: i) migration is persistent and tends to be linear in space, ii) it involves the movement of individuals over a larger spatial scale than their usual activities, iii) migratory movements tend to be periodic and involve movement between habitats of different quality, and iv) migration results in the redistribution of individuals within a spatially extended population (Dingle and Drake, 2007). For bats, most species meet these criteria (Webber and McGuire, 2022), although there is often some variability in the tendency to migrate within a population. Migration is often partial (Smith et al., 2022), sex-specific (Lehnert et al., 2018; O'Mara et al., 2016; Cryan, 2003), and migrating individuals make situational decisions about their routes (Voigt et al., 2023; O'Mara et al., 2019). Also neighbouring populations can differ significantly in their migratory habits (Lehnert et al., 2018; Popa-Lisseanu and Voigt, 2009). At an evolutionary level, the tendency to migrate is not a conservative trait and migration is poorly explained by phylogenetic relationships between taxa. Instead, it appears that ecological factors affecting a particular species or population are critical (Webber and McGuire, 2022).

The largest European migratory bat, the greater noctule (*Nyctalus lasiopterus*), covers about 155–210 km per night (maximum 445 km; Vasenkov et al. 2023). In general, however, the performance of migratory bats in terms of distance travelled or speed is not impressive compared to similarly sized birds (Hedenström, 2009). The migratory speed of bats averages between 10 and 60 km/h (Lagerveld et al., 2024; Micalizzi et al., 2023; Roby et al., 2019; Bruderer and Popa-Lisseanu, 2005), and individuals typically travel less than 100 km per night (Hurme et al., 2025; Lagerveld et al., 2024; Rydell et al., 2014; Hedenström, 2009). This is a result of bats' specific migratory strategy of wandering combined with continuous replenishment of energy stores (Roby et al., 2019; Dechmann et al., 2017; Jonasson and Guglielmo, 2016; Krüger et al., 2014; Krauel and McCracken, 2013; Šuba et al., 2012; Voigt et al., 2012). Migrating bats also enter prolonged periods of torpor when environmental conditions deteriorate. This so-called torpor-assisted migration allows them to reduce their resting energy requirements and accumulate energy for flight while taking advantage of periods of favourable weather (Webber and McGuire, 2022; Baloun and Guglielmo, 2019; Brabant et al., 2019; Pettit and O'Keefe, 2017; McGuire et al., 2014). Indeed, many studies have shown that bat flights are more intense at higher temperatures (Lagerveld et al., 2021; Martin et al., 2017), lower winds (Voigt et al., 2015), preferably in the direction of migration (Hurme et al., 2025; Haest et al., 2021; Lagerveld et al., 2021; Dechmann et al., 2017) and in the absence of precipitation (Voigt et al., 2011).

Given the fly-and-forage strategy and sensitivity to weather conditions, one would expect geographical barriers such as seas or mountain ranges to be a major challenge for migratory bats. The data supporting this hypothesis are mixed. For example, *M. myotis* populations on either side of the Strait of Gibraltar are genetically isolated from each other (Castella et al., 2000), although the distance they have to travel across the open sea is only 14 km. Migrating bats have also been observed to take detours from the general direction of migration, apparently to reduce the distance travelled over water (Lagerveld et al., 2024; McGuire et al., 2012). On the other hand, numerous bat species have been repeatedly recorded at offshore wind farms, 60–80 km from the coast (Boshamer and Bekker, 2008; Ahlén et al., 2007; Ahlén, 1997) and there is evidence that *Pipistrellus nathusii* can fly around 200 km across the open sea (Lagerveld et al., 2024). In the mountains, a negative correlation between altitude and bat activity has been described (Diggins and Ford 2022; Widerin and Reiter 2018; Wolbert et al. 2014; but see Muthersbaugh et al. 2019). The recent discovery of *Miniopterus schreibersi* expanding its range north of the Carpathian Mountains was most likely made possible by crossing the ridge alongside the river gorge (Piksa and Gubała, 2021). However, the altitude range

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of migrating *P. nathusii* reaches 2500 m above sea level (Lagerveld et al., 2024), and several bat species have been detected in the Alps at about 2200 m (Caprio et al., 2020) and even 3100 m (Widerin and Reiter, 2018), demonstrating that they can cross high mountains.

Despite technological developments in animal tracking methods, even the smallest GPS loggers currently available (Wild et al., 2022) exceed the '5 % body weight' rule (Aldridge and Brigham, 1988) for many species. Therefore, acoustic monitoring of echolocating bats remains a useful tool for sampling bat movements and contributing to the knowledge of their migration routes, which are important for conservation purposes (Voigt et al., 2024) and for understanding potential pathogen spread pathways (Melaun et al., 2014).

Here, we use acoustic monitoring to investigate the timing and ecological determinants of autumn bat migration across the Karkonosze Mountains on the Czech-Polish border (Fig. 1). Previous research (Furmankiewicz and Kucharska, 2009) has shown the existence of a migration route along the lowland river valley towards this massif, which may represent a significant challenge for migratory bats – it extends from north-west to south-east, perpendicular to the expected migration axis in Central Europe, has a significant relative altitude (800–1200 m from the foothills) and a harsh climate on the ridge, which is very different from the climate in the surrounding lowlands. The average temperature on the ridge is around 6 °C lower than in the foothills, and there are also considerable differences in wind strength (Sobik et al., 2013). The study was carried out using the acoustic survey method proposed by Jarzembowski (2003) and implemented in recent projects (Cortes and Gillam, 2020; Bartonička et al., 2019; Furmankiewicz and Kucharska, 2009), which allows bat flights to be divided into fractions with different directions. We tested whether the variation in the number of bat passes across the ridge could be explained by the advance of the migratory season, atmospheric conditions and the migratory habits of the species (long-distance vs. short-distance migrants; the 1000 km limit was adopted as a criterion for distinguishing long-distance migrants, following Strelkov 1969). Our hypothesis was that the migration of the first group would be more persistent, i.e. more directional and also less dependent on atmospheric conditions. This is because potential detours and weather-related disruptions would accumulate into delays proportional to the length of the migration route. Long-distance migrants should therefore be selected for a more straightened out and weather-independent flight than other species. We also looked for a qualitative difference between the two groups: we expected the seasonal dynamics of migration to be decreasing for short-distance migrants and non-monotonic (inverted U-shaped with a mid-season peak) for long-distance migrants. The rationale behind this hypothesis was that most short-distance migrants are recruited locally and their numbers should gradually decline as the season progresses. In contrast, long-distance migrants may originate from local and diverse northern populations, so the number of individuals at the barrier should first accumulate and then decrease (Caprio et al., 2020; Widerin and Reiter, 2018).

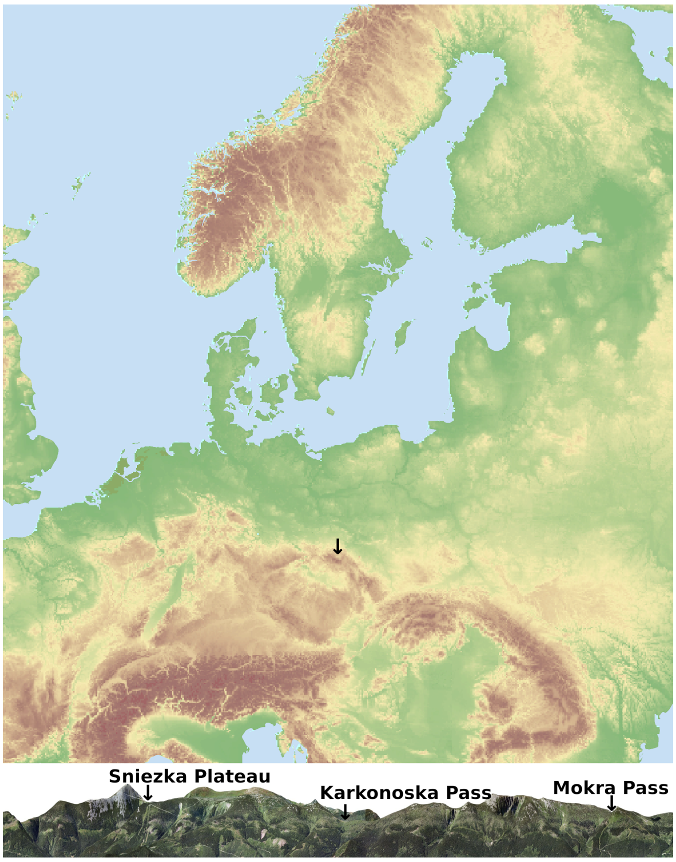

Figure 1 – The upper panel shows Central Europe, marking the Karkonosze Mountains with an arrow. The lower panel is a panoramic view of the Karkonosze Massif (north facing) with three data collection sites. Graphics courtesy of Karkonosze National Park.

Materials and methods

Study area

We conducted our study in the Giant Mountains, also known as the Krkonoše (in Czech) or Karkonosze (in Polish; we will use the latter name in the following), which are part of the Sudetes. The Sudetes (about 300 km long, stretching longitudinally) and the Carpathians form an almost unbroken line of about 850 km from west (51° N, 15° E) to east (48° N, 25° E; Fig. 1).

The Karkonosze massif has a ridge that averages between 1200 and 1400 m. The most prominent peak is Sněžka (Czech pronunciation: sηε ∫ka) or Śnieżka (Polish pronunciation: σηεşka; German: Schneekoppe), which lies on the border between the Czech Republic and Poland. At 1603.3 metres (5260 ft), its summit is the highest point in the Czech Republic. The tree line is at 1200–1250 m. In the sub-alpine and alpine zone on the ridge, with dwarf mountain pines (*Pinus mugo*), peat bogs and meadows, vegetation stops between the end of September and mid-May (Głowicki, 1993), and snow remains on average for 160–180 days per year (Sobik et al., 2013).

Data collection

We recorded bat activity on 34 nights between 20 July and 25 October in 2013 and 2014 at three sites on the Karkonosze ridge, distributed along a straight line of 16.6 km (18.2 km measured along the ridge). The first and westernmost site, surrounded by dwarf mountain pines, is the Mokra Pass (1290 m a.s.l.) in the sub-alpine zone. The middle one, 7 km to the east, is the Karkonoska Pass (1198 m), which borders the tree line. Finally, the easternmost and highest site (1389 m) was established in a patch of dwarf mountain pine on the Sniezka Plateau, which lies on the border between the subalpine and alpine zones (Fig. 1).

At each site we recorded bat activity continuously (without setting frequency or sound pressure triggers) from 30 minutes before sunset to sunrise. This ranged from about 8 hours per night at the start of the migration season in July to 14 hours per night at the end of October. We used Song Meter SM2Bat (Wildlife Acoustics; Maynard, USA) broadband ultrasonic recorders equipped with two ultrasonic omnidirectional microphones (SMX-US, Wildlife Acoustics), one facing north and the other south, mounted on 2 m poles 10 m apart on the north-south axis. This arrangement allowed stereo recording in two separate channels and subsequent analysis of flight direction (see below). Sound files were stored on SD cards using WAC 5 lossless compression and a sampling rate of 192 kHz (16 bit). In total, over 34 nights at three sites, we collected 1153.38 hours of recordings. No bat activity was recorded at one site-night. However, since both the recorder and the microphones appeared to be working properly, the recording was included in the dataset.

Meteorological data were provided by the Institute of Meteorology and Water Management (Instytut Meteorologii i Gospodarki Wodnej) observatory on Sniezka, the highest peak within the massif. During the period of bat migration monitoring, medians and interquartile ranges for overnight temperatures (°C) were 7.8 (4.9–9.9), precipitation (mm) 0.01 (0.0–0.2) and wind strength (m/s) 9.9 (7.7–12.0). The median wind direction was 240° (194–294), which roughly corresponds to the WSW on the compass (from the perspective of bats flying over the ridge, this is the crosswind). As the migration season progressed, the temperature linearly decreased at an average rate of 0.09 °C per night. Correlations between date and other weather variables were negligible.

We used Adobe Audition software (Adobe Systems Incorporated; California, USA) to find, visualise and identify bat calls. We manually scrolled through the recordings and searched for vocalisations. The unit of bat vocal activity was defined as a sequence: a series of ultrasonic pulses in which the distance between individual pulses was less than the distance between individual adjacent sequences. The same person (MJ) assigned all sequences to taxa and function, using her expert knowledge based on literature on the identification of Central European bat species (Russ, 2021; Barataud, 2015; Sachanowicz and Ciechanowski, 2005; Altringham, 2003; Řehák, 2000; Ahlén and Baagøe, 1999; Barataud, 1996; Ahlén, 1990, 1981). The most important criteria for identifying species are listed in Tab. S1. We distinguished three functions of vocalisations: 'navigational' sequences used by bats to determine their position in space and to detect possible obstacles, foraging calls (feeding buzzes; Neuweiler 2000), and social calls (Fenton, 2003).

Where possible, we determined the bat flight direction from the difference in call arrival times between the two microphones recording the stereo file (Cortes and Gillam, 2020; Bartonička et al., 2019; Furmankiewicz and Kucharska, 2009; Jarzembowski, 2003). If the sequence of pulses appeared first in the northern channel and then in the southern channel (with a delay of 1–3 ms, depending on the species), we classified the flight as southerly (N → S). The reversal, i.e. the sequence in the southern channel continued in the northern channel, was classified as a northward flight (S → N). In about 60 % of the sequences, the flight direction could not be determined: either the bat was recorded in two channels simultaneously, or in only one channel.

The analysis revealed the presence of 11 taxa (Tab. S2). In the statistical analysis, we focused on 6 species – *E. nilssonii*, *E. serotinus*, *N. noctula*, *P. pipistrellus*, *P. nathusii* and *Myotis* spp. – which together contributed more than 90 % of the recorded navigation sequences. The taxa were divided into two groups: long-distance migrants (*N. noctula* and *P. nathusii*) and short-distance migrants (the remaining species and *Myotis* spp.). Long-distance migrants are species that regularly fly over 1000 km in seasonal migrations from northern Europe (Hutterer et al., 2005; Steffens et al., 2004; Strelkov, 1969). The second group is less homogeneous, as it includes species that hibernate and breed in within the range of up to 50–100 km away (e.g. *B. barbastellus*), as well as species that can undertake migrations of several hundred kilometres (e.g. *P. pipistrellus* or *Myotis* spp.). *P. pipistrellus* is also known to migrate over long distances, but most of its movements indicate short distances (Steffens et al., 2004).

Statistical analysis

Statistical analyses were performed in the R environment (version 3.6.3; R Core Team 2022), sometimes using additional libraries listed below. Whenever possible, effect sizes and their 95 % confidence intervals are presented instead of P values. Effect sizes for some non-parametric analyses (Spearman rank correlation, difference between medians) were calculated using the 'DescTools' library (Signorell, 2025). General linear mixed models (GLMMs) were fitted using the 'lme4' library, version 1.1-33 (Bates et al., 2015) and checked using diagnostic tests included in the 'DHARMa' package, version 0.4.3 (Hartig, 2020).

The variables describing the weather – temperature, wind strength and direction, and precipitation – are averages calculated from a series of hourly measurements taken throughout the night. After exploratory data analysis, we decided to remove wind direction due to its low variability (the vast majority of the night was dominated by crosswinds blowing from the WSW). To avoid multicollinearity and to save degrees of freedom in GLMMs, we applied principal component analysis to the remaining standardised (with a mean of 0 and a standard deviation of 1) weather variables. The PCA revealed two principal components with eigenvalues greater than 1, cumulatively explaining 81.6 % of the total variance. The first PC, accounting for 45.8 % of the variance, loaded positively with temperature ($r = 0.52$) and negatively with wind strength ($r = -0.74$) and precipitation ($r = -0.43$). The second component, accounting for 38.9 % of the variance, was also positively correlated with temperature ($r = 0.66$) and negatively with precipitation ($r = -0.75$), but did not explain the variance in wind strength ($r = 0.03$). In subsequent analyses, the weather was represented only by the values of PC1, as it was well correlated with all the component weather variables and easy to interpret: higher values of PC1 corresponded to 'good' weather (windless and dry nights with relatively high temperatures), while low values indicated 'poor' weather (relatively wet, windy and cool).

In all analyses where seasonality was a predictor, the date was presented as consecutive days from 20 June (taken as 1). Analyses of the seasonal dynamics of activity changes (i.e. the number of echolocation sequences) of different taxa were performed using Poisson regression. For each species, a linear model and a second degree polynomial model were fitted (see Tab. S3). Their AIC values were then compared and the model with the lower value was accepted as the final (Burnham and Anderson, 2002).

GLMMs – Poisson with log links and binomial with logit links – were used to investigate the potential influence of migratory habits and environmental factors, including weather conditions, on the variation in bat activity and the directionality of their flights. The model specifications, together with a list of the random and fixed effects used, are described in the results. We diagnosed the GLMMs using the DHARMa test battery. In particular, both models passed the combined adjusted quantile test, the KS test for correct distribution of residuals within and between groups, and the outlier test. The Poisson GLMM was also tested for overdispersion.

Results

Altogether, during 34 nights in three locations on the main ridge of the Karkonosze, we recorded 4407 bat passes, including 4069 (92.3 %) passes with navigation sequences, 251 (5.7 %) with foraging sequences and 87 (2.0 %) with social calls. The proportion of passes with navigation sequences increased during the season ($r_s = 0.727$; 95 % CI: 0.512–0.857) at the expense of the proportion of foraging sequences, which decreased ($r_s = -0.724$; 95 % CI: -0.855–-0.507). After 10 September, foraging calls were only sporadically recorded (median = 1 per night compared to 11 per night during the previous period; difference = 10, 95 % CI: 5–14). The proportion of social calls did not vary significantly over the season ($r_s = -0.136$; 95 % CI: -0.458–0.218), but their number was generally low (median of 2 per night, interquartile range: 0 to 4). In all subsequent analyses we only consider bat passes with navigation sequences (hereafter: bat passes).

Of the 4069 bat passes, 2372 (58.3 %) had no detectable direction and 1697 (41.7 %) were recorded by two detectors placed on the North – South axis (see Methods). N → S passes accounted for 72.8 % (95 % CI: 70.6–74.9) of all directional passes and significantly outnumbered S → N passes (27.2 %; 95 % CI: 25.1–29.4).

The number of bat passes varied between the three recording sites (Friedman two-way ANOVA: chi-squared = 38.95, $df = 2$, $P < 0.001$): within the same night the Karkonosze Pass, which was the lowest location, was usually the most frequented site (2062 passes, 50.7 % of the total number), with a median nightly difference of 21 (95 % CI: 9–32) more bat passes than the Mokra Pass (1022 passes, 25.1 %) which, in turn, did not differ from the Sniezka Plateau (985 passes, 24.2 %; median difference = 1.95 % CI: -2–6). Summarized across the three sites, the number of bat passes per night increased with ambient temperature ($r_s = 0.41$, 95 % CI: 0.08–0.66), decreased with precipitation ($r_s = -0.35$, 95 % CI: -0.61–-0.01) and tended to decrease with wind strength ($r_s = -0.27$, 95 % CI: -0.56–0.08). Using the first component of the PCA describing atmospheric conditions (see Methods), it was possible to encapsulate the relationships between bat activity and weather (Fig. 2). Thus bat passes were more frequent in nights when the weather was generally 'milder', as indicated by the higher PC1 values ($r_s = 0.36$, 95 % CI: 0.02–0.62). The number of bat passes also tended to decrease with the date of observation ($r_s = -0.67$, 95 % CI: –0.82––0.45). Because weather, as expressed by the value of PC1, deteriorated with date ($r_s = -0.34$, 95 % CI: –0.61–0.00) along with bat activity, simple correlation analysis could not disentangle relationships between these variables, and we further addressed this issue in multivariable analysis (see below).

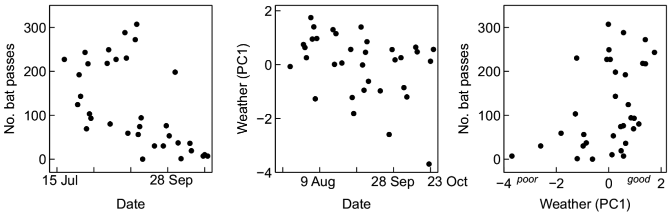

Figure 2 – Correlations between date, weather and number of bat passes through the ridge of the Karkonosze. Each point represents one night.

In total, we recorded the presence of at least 11 bat species (Tab. S2). This is a conservative estimate because the sequences identified as belonging to the genus *Myotis*, which accounted for more than 9 % of the total, were not classified into species. In the subsequent analyses, only the 6 most frequent taxa that accounted for at least 10 % of the total guild were included: *Eptesicus nilssonii*, *E. serotinus*, *Nyctalus noctula*, *Pipistrellus pipistrellus*, *P. nathusii* and *Myotis* spp. To quantify changes in their presence on the ridge during the migration season, we fitted a linear and second polynomial Poisson regression models. In all cases polynomial models produced a much better fit, as indicated by the ΔAIC (Tab. S3). Thus all taxa showed a non-monotonic seasonal dynamics: the number of navigation sequences tended to increase at the beginning of the migration season, reached a peak between August and September and then decreased to values around zero in November (Fig. 3). In addition, a simple comparison, not taking into account potential covariates, suggested that the long-range migratory species (*N. noctula* and *P. nathusii*) appeared on the ridge on average later than the short-distance migrants (*E. nilssonii*, *E. serotinus*, *P. pipistrellus* and *Myotis* spp.): the difference in the mean date of appearance between the two groups was 10.3 days (95 % CI: 6.2–14.4).

To test the general hypothesis that the variation in the occurrence of bats on the ridge is explained by the advance of the migratory season, the sensitivity of bats to atmospheric conditions, and their propensity for long-distance migration, we constructed a Poisson GLMM in which the number of bat passes was predicted by date (entered in the model as a quadratic term), weather (PC1 value), and migratory habits (short- v. long-range migrants). The model also included an interaction between migratory habits and date (to test for differences in the timing of the appearance of long-distance and short-distance migrants) and an interaction between migratory habits and weather (to test the hypothesis that long-distance migrants are relatively less sensitive to atmospheric conditions). Year, location, species, and an observation ID were entered into the model as random intercepts. The results (Fig. 4 and Tab. S4) supported and clarified the findings of univariate analyses described above. Thus, the number of bat passes covaried not linearly with date. A milder weather increased the number of bat passes regardless of the date of observation. Long-distance migrants showed a significant tendency to appear later in the migration season than short-distance migrants. Finally, contrary to our expectations, short- and long-distance migrants responded similarly to weather conditions: their activity decreased when the weather deteriorated.

In the following model, a binomial GLMM (Fig. 4, Fig. 5 and Tab. S4), we included only bat passes on the North-South axis, and the explained variable was the proportion of N → S passes. We used the same set of predictor variables as before, except that date was entered as a linear term only, and the same set of random terms. The model showed that the proportion of N → S bat passes gradually increased as the migration season progressed, and this effect was significantly stronger for long distance migrants compared to short distance migrants (Fig. 5). There was also a marginally significant trend suggesting that in favourable weather conditions, long-distance migrants made a higher proportion of N → S passes than short-distance migrants.

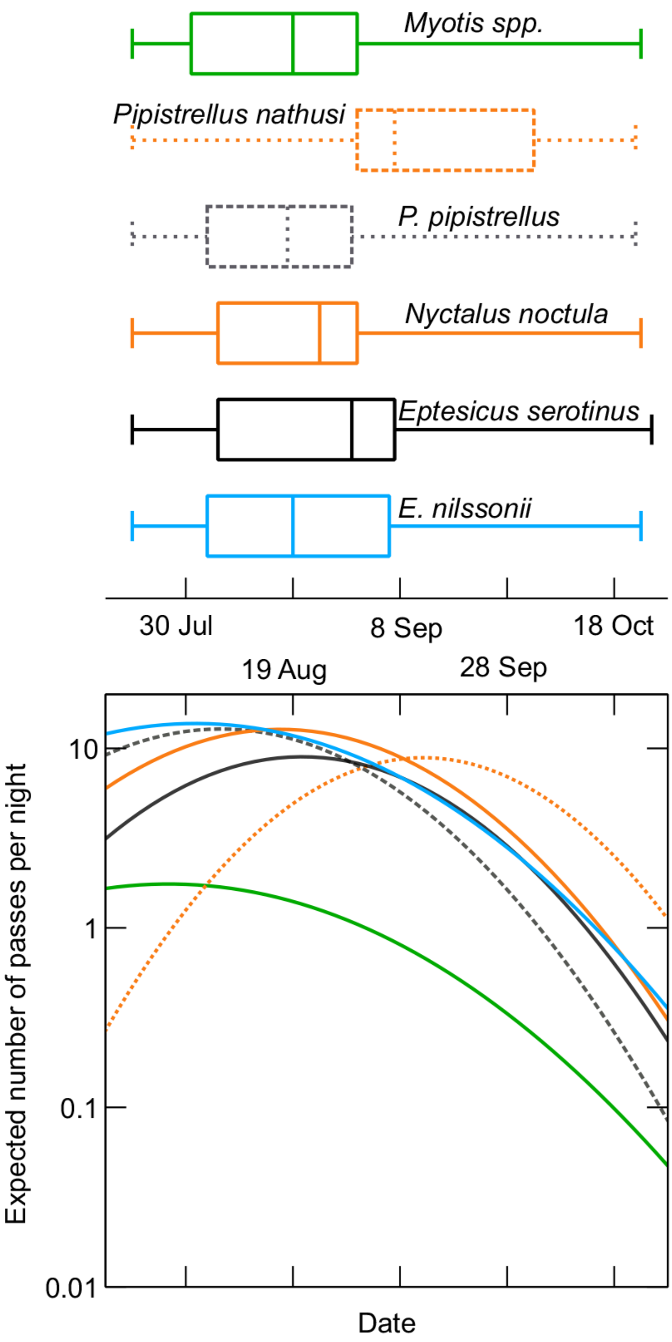

Figure 3 – Seasonal changes in the number of bat passes through the ridge of the Karkonosze. Upper panel: the distribution of observation dates for different species (ranges, quartiles and medians). Lower panel: the expected number of passes per one site/night calculated from the Poisson polynomial regression models (see Tab. S3). Note the logarithmic scale on the vertical axis. On both panels, each species is represented with the same unique colour and line.

Discussion

Of the three sites on the ridge where bat detectors were placed, bats preferred the lowest, 92 and 191 m lower than the other two, supporting the hypothesis that the Karkonosze massif may be a barrier for bats. Similarly, lower elevations were preferentially selected by bats in the Alps (Widerin and Reiter, 2018). On the north-south axis, the dominant vector of bat passage was N → S, so a large proportion of individuals appearing on the ridge must be autumn migrants. This finding is consistent with the known direction of seasonal migration of long-distance bat migrants in Europe (Hutterer et al., 2005; Steffens et al., 2004) and studies of bat migration across mountain passes in the Alps (Caprio et al., 2020; Widerin and Reiter, 2018).

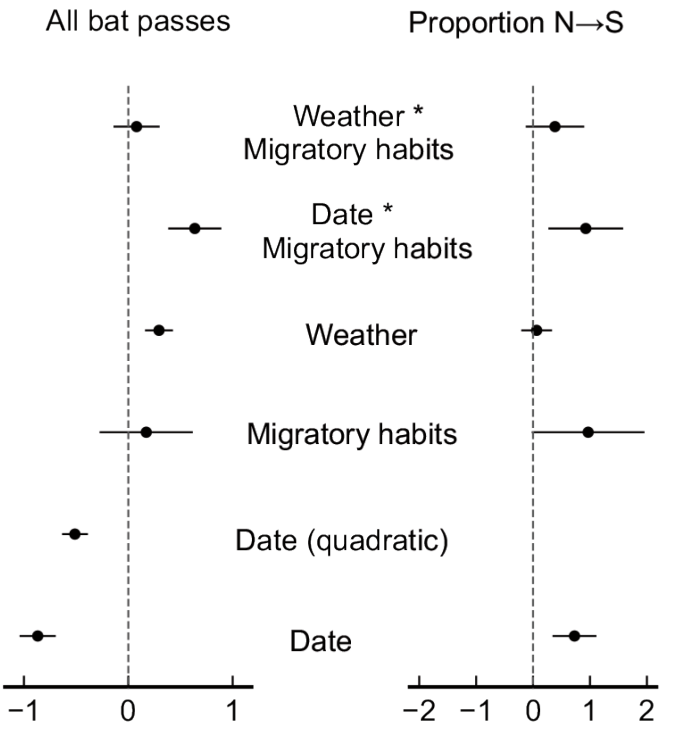

Figure 4 – Effect sizes (beta coefficients ±95 % confidence intervals) of GLMMs explaining variation in the number and direction of bat passes on the ridge of the Karkonosze during the migration season.

Foraging sequences from the second decade of September were only sporadically recorded, suggesting that bats came to the ridge mainly because it was on their migration route and that movements were not related to foraging activity on the ridge. However, we cannot exclude the possibility that some local individuals commute across the ridge between foraging sites (Widerin and Reiter, 2018), swarming sites (Dekeukeleire et al., 2016; Piksa et al., 2011; Furmankiewicz, 2008; Rivers et al., 2006; Parsons and Jones, 2003) and daily roosts on the northern and southern slopes. Particularly at the beginning of the migration season (July and August), such movements may be quite frequent, as indicated by the almost equal proportion of N → S and S → N passes during this period (Fig. 5).

Of the 11 taxa that appeared on the ridge, two – *Nycatlus noctula* and *Pipistrellus nathusii* – were identified from the literature as long-distance migrants, regularly travelling 1000 km or more. We did not find any traits that distinguished this group from the other species. In particular, species for which we had a large sample of passes across the ridge showed an inverted U-shaped seasonal activity, with mid-autumn peaks, suggesting that the individuals recorded were not only from the local population, but that the flow of migrants was fed by external populations further north.

The only significant differences between long-distance and short-distance migrants were in terms of the magnitude of the same traits. First, the average date of migration was later for long-distance migrants (Fig. 4). We conclude that this is because this group had a relatively higher proportion of individuals from distant northern European populations that arrived later. Another possible explanation is that local long-distance migrants delay the start of their migration, meaning they cross the ridge relatively late in the season. Second, long-distance migrants were more persistent in terms of flight direction (higher proportion of N → S passes) and this difference widened with season (Fig. 5). Intuitively, one would expect migration directionality to increase with date: as the season progresses, migrating bats have less time to reach hibernacula, so they should fly more persistently southwards. This effect must be particularly strong for long-distance migrants, whose hibernacula may be quite distant. For short-distance migrants, the time pressure is much less, because they are closer to their wintering grounds. In addition, their choice of hibernation sites is not strictly determined by large-scale geographical climate variability. Data from ringing centres (Hutterer et al., 2005; Steffens et al., 2004), show that species that fly short distances tend to have a fairly freely defined migration direction. In the Karkonosze, hibernation sites of many species are located on both the northern and southern slopes and there is evidence from ringing, that individuals breeding south of the Karkonosze may overwinter on the northern side of the massif (Furmankiewicz et al., 2022). In summary, these migrations from the south to hibernacula on the northern slopes of the Karkonosze, plus the chaotic movements of local ‘across-the-ridge commuters’ (see above), may add up and reduce the observed proportion of N → S passes in short-distance migrants.

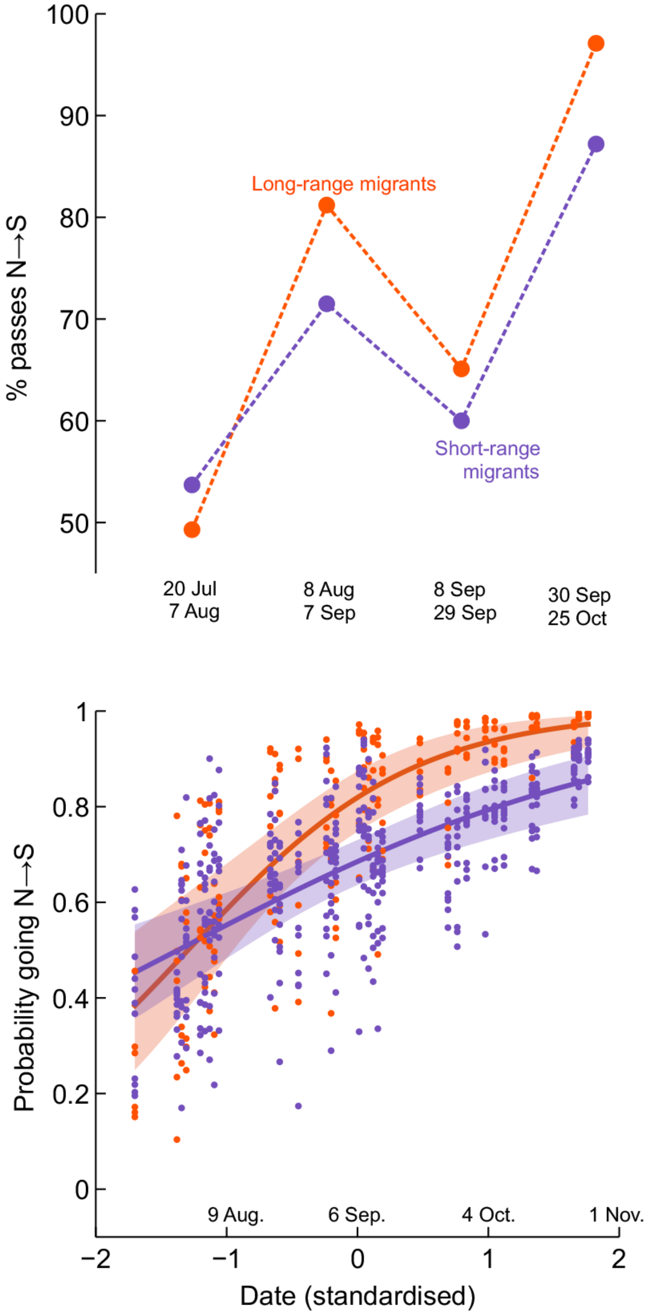

Figure 5 – Direction of bat passes by short-distance (violet) and long-distance (orange) migrants on the ridge of the Karkonosze. The upper panel shows seasonal changes in the percentage of N → S passes. The lower panel shows predictions of the GLMM explaining seasonal variation in the proportion of N → S passes. Each point represents the predicted value for one species at one date and observation site. Regression lines are shown with 95 % confidence intervals.

As predicted, we found some support for the hypothesis that bat movements depend on weather conditions: the total number of bat passes was higher when the weather was favourable (relatively high temperature, low wind and precipitation), and this effect was independent of date. A similar pattern has been found in several other studies (Hurme et al., 2025; Widerin and Reiter, 2018; Dechmann et al., 2017; Voigt et al., 2015; Reynolds, 2006). We expected that long-distance migrants would be less sensitive to weather conditions than short-distance migrants. On the contrary, both groups responded quite similarly to changing weather conditions. A marginally significant trend in our study suggests that in 'good' weather, long-distance migrants make a higher proportion of N → S passes than short-distance migrants (Fig. 4, right panel). This may indicate that species in the former group are not selected to cope well with inclement weather, but rather to maximise the use of favourable weather windows. It appears that our study was the first to test the relationships between species' migratory range and weather sensitivity, so at this stage there is a lack of published work to place our results in a wider context.

In conclusion, the results obtained suggest that bats migrate through the Karkonosze Mountains, a massif with the character of a geographical barrier (altitude of 800–1200 m from the foothills), perpendicular to the known direction of bat migration in Europe. We found no signature trait that distinguishes long-distance migrants from other bat species that cross the ridge, and the differences between them are only quantitative. For long-distance migrants, the migration season is longer and the migration itself is more persistent in terms of directionality than for the short-distance migrants. Throughout the season, higher numbers of bats appeared on the ridge when weather conditions were good, and we hypothesise that selection pressure to use good weather windows is particularly strong in long-distance migrants.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Parameters of bat echolocation calls used for species identification.

Table S2 Number of bat passes with navigation sequences on the ridge of the Karkonosze in autumn.

Table S3 Univariate regression models describing seasonal changes in the number of bat passes on the ridge of the Karkonosze in autumn.

Table S4 Effect sizes of GLMMs explaining variation in the number (Poisson model with log links) and direction (binomial model with logit links) of bat passes on the ridge of the Karkonosze.