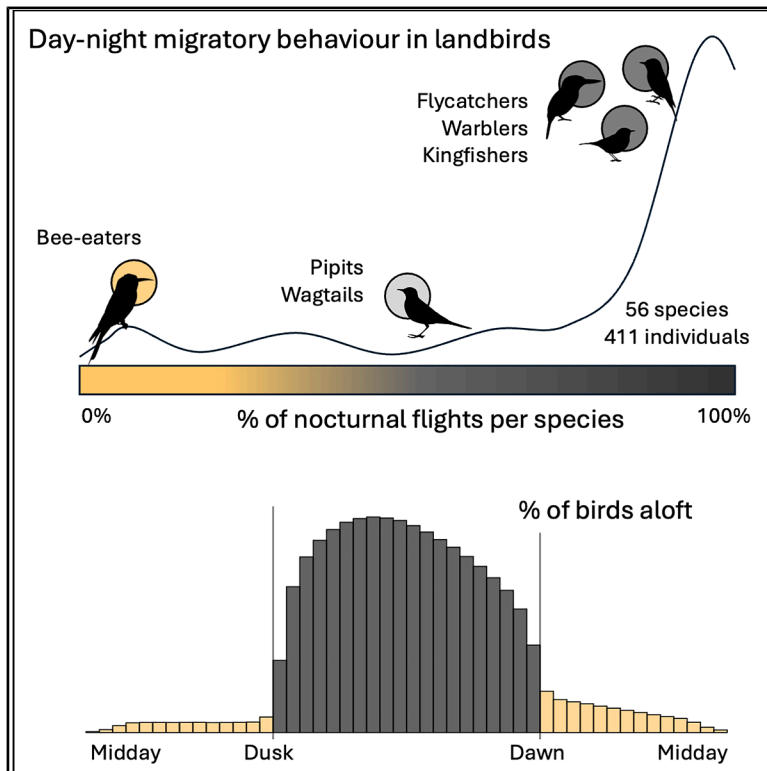


Current Biology

Multi-sensor tracking reveals the extent of nocturnal migration in landbirds

Graphical abstract



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In brief

Dufour et al. combine multi-sensor geolocator data from 411 individuals across 56 landbird species to quantify nocturnal and diurnal migratory flight. They show that nocturnal migration is the dominant strategy among small landbirds, is phylogenetically conserved, and that several species previously considered diurnal migrants in fact fly exclusively at night.

Highlights

- Multi-sensor geolocators are uniquely suited to quantify flight timing in landbirds
- Nocturnal flights dominate (82%) across 56 small- to medium-sized landbird species
- Departures and landing times cluster around civil dusk and dawn
- Nocturnal flight timing shows moderate to strong phylogenetic signal

Report

Multi-sensor tracking reveals the extent of nocturnal migration in landbirds

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SUMMARY

Most bird species are diurnal but drastically change their diel cycle of activity to migrate at night. Nocturnal migration has been documented using different methods (e.g., experiments, radar and radio tracking, and acoustic monitoring), but accurately quantifying the proportion of nocturnal versus diurnal flight at the individual and species levels, and understanding how this behavior evolved across the avian tree, has remained methodologically challenging.^{1–3} Such uncertainty is not only of theoretical importance but also limits our ability to mitigate conservation threats, particularly from light pollution and building collisions.^{4–6} With multi-sensor geolocators recording light, barometric pressure, and activity,^{7,8} we reconstructed high-resolution migratory trajectories^{9,10} for 411 individuals from 56 small- or medium-sized landbird species across four continents and measured the proportion of each flight that occurred during night or day. Our species-level quantification confirmed nocturnal migration as the dominant strategy among small landbirds, while also providing precise flight proportion estimates across a broad taxonomic sample and refining the classification of several species previously described as partial or facultative diurnal migrants. We found that birds initiated and ended migratory flights near civil dusk and dawn, thereby maximizing nocturnal travel. The phylogenetic signal we detected indicates that nocturnal migration is largely conserved within lineages. While nocturnal migration confers multiple advantages, the relative importance of the proposed drivers remains to be determined.^{11,12} Our study provides species-specific quantification of nocturnal migration, highlights tracking gaps across taxa and regions, and opens new avenues for studying the evolutionary, ecological, and sensory drivers of nocturnal migratory flights.

RESULTS AND DISCUSSION

Multi-sensor geolocators allow quantification of nocturnal flight timing

The nocturnal migration of otherwise diurnal birds has long fascinated scientists and remains an important, unresolved

question.¹³ It represents a unique exception to the general pattern of diel activity rhythm in diurnal animals, which are typically active during the day and inactive at night.^{14,15} The first studies of nocturnal migration relied on moon-watching, experimental observations, including the quantification of migratory restlessness (*Zugunruhe*), and ringing activities and were later

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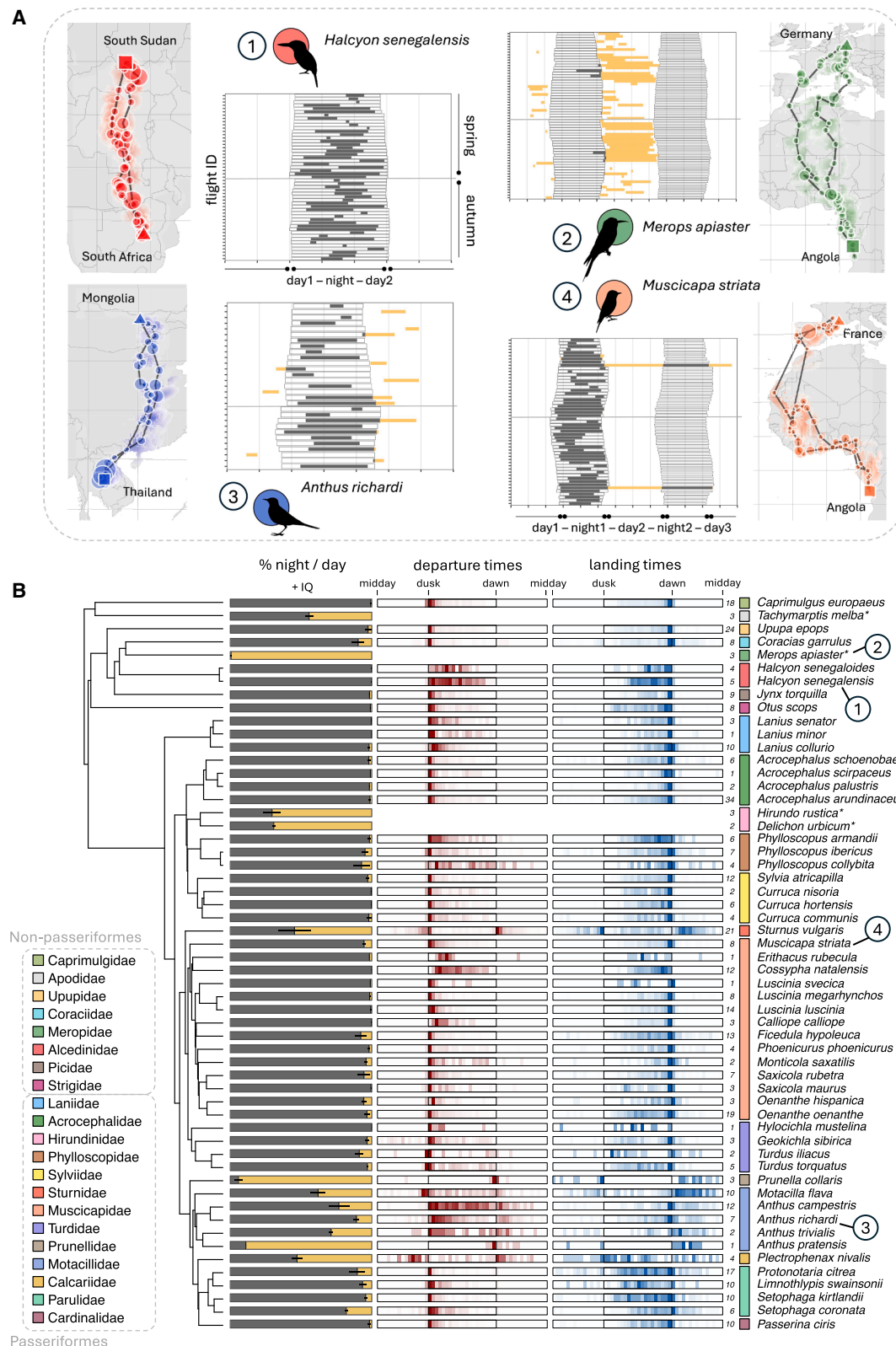
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complemented by radar observations, acoustic monitoring, and thermal imaging.^{16–19} Radar studies have long confirmed that nocturnal migration is the dominant strategy across the majority of Palearctic songbird species,^{20,21} and large-scale weather radar programs in North America have similarly focused on nocturnal movements as the established norm.^{1,22} More recently, individual-tracking studies have begun to reveal that birds may initiate flights at multiple times throughout the night, highlighting some individual variation in flight onset and duration.^{23,24} Yet, despite this wide range of methods, each comes with limitations, and none can accurately quantify diurnal and nocturnal flight activity at both the individual and species levels with detailed temporal-spatial resolution. For example, while automated radio-telemetry has been extensively used to document departure date and time, it cannot determine flight durations or landing times; similarly, acoustic monitoring fails to detect silent species, and radar monitoring is unable to distinguish between individual species.³ Visual observations of

some migratory species while they are flying during daytime may suggest diurnal migration, but these observations are often based on opportunistic encounters, and without detailed information on individual behavior, this interpretation remains speculative. As a result, while nocturnal migration is well established as the dominant strategy in many songbird groups, precisely quantifying the proportion of nocturnal versus diurnal flight at the individual and species level across a broad taxonomic and geographic range was unrealistic with earlier methods. Indeed, the literature often remains vague when classifying species as diurnal or nocturnal migrants, with many simply described as migrating during both periods (see Horton et al.⁶ and Adamík et al.²⁵). This uncertainty hampers both our theoretical understanding of diel activity rhythms and our ability to assess conservation risks, with nocturnal species being much more susceptible to light pollution, building, and wind turbine collisions.^{4–6}

Here, we used multi-sensor geolocators to obtain detailed individual behavioral tracking throughout the annual cycle. By



combining a unique set of published and unpublished tracking data, we analyzed data from 411 small- to medium-sized migratory individual landbirds to accurately quantify the proportion of migratory flights at night (Figures 1 and S1). Individuals belonged to 56 species from four continents and were from 21 families within 7 orders, and all but two species (one owl and one nightjar) were diurnal. These geolocators are ultra-light tags (averaging <1 g; see STAR Methods) that record light, barometric pressure, and, in most cases, accelerometer data but do not transmit information automatically and therefore must be retrieved to access the data.^{7,8} With data sampling intervals ranging from 5 to 30 min depending on the model, we were able to determine the precise timing of each migratory flight, defined by a clear drop in pressure data corresponding to altitude gain in flight and associated with high accelerometer measurements (of the same duration as the variation in pressure, see Nussbaumer et al.⁹ and Dhanjal-Adams et al.²⁶). We applied state-of-the-art geopositioning methods to track individual locations and then calculated civil dawn and civil dusk (i.e., first time in the morning and last time in the evening when the solar depression angle was above -6°) at different stages of each individual's annual cycle. This allowed us to determine the proportion of migratory flight that occurred during daytime versus nighttime.^{9,10}

Nocturnal migration is the dominant strategy in small- to medium-sized landbirds

Across all species, we found that, on average, 82% of all migratory flights occurred solely at nighttime (interquartile range of 79%–98%). When excluding flights involving the crossing of major ecological barriers, during which nocturnal migratory flights sometimes extended into the daytime,²⁷ this increased to 85% of migratory flights occurring at nighttime (interquartile range across species of 90%–99%). Forty-one species (out of 56; 73%) had more than 90% of their migratory flights occurring at night, confirming that nocturnal migration is the dominant strategy across a broad diversity of small landbirds (see Figure 2).

For species whose migratory timing had previously been estimated by visual observations, it was revealed that several species traditionally considered to migrate both during day and night instead conducted most of their migratory flights at night. For example, the Eurasian hoopoe *Upupa epops* and the tree pipit *Anthus trivialis* perform 91% and 71% of their migratory flights at night, respectively, whereas previous observations suggested these were instead mostly diurnal migrants (see also Briedis et al., which contradicts previous expectations for tawny pipit *Anthus campestris*,²⁸ and Vgants et al. for common starling *Sturnus vulgaris*²⁹). These findings highlight that apparent diurnal activity does not necessarily reflect the timing of migratory flight.

Yet, important exceptions to this predominance occur, with certain species showing a clear tendency to migrate during the day. In the case of the European bee-eater *Merops apiaster*, which relies on thermal updrafts to facilitate soaring flight, observing diurnal migratory activity (0.1% nocturnal flights) was expected.³⁰ However, this new approach also revealed that certain migratory flights of bee-eaters, particularly those corresponding to the crossing of the Sahara Desert, may start several hours prior to sunrise (see Figure 1A). Also, among the exceptions, hirundines have long been regarded as predominantly diurnal migrants, sometimes also making use of thermal currents. Yet, our approach reveals that the two studied hirundine species performed a substantial share of their migratory flights at night, with an average nocturnal proportion of 38%.^{31,32} Then, three alpine accentors *Prunella collaris* tracked from southern France to their breeding grounds in the Alps performed most of their migratory flights during daytime. However, this may reflect the atypical ecology of this short-distance and altitudinal migrant rather than a family-level pattern, as other Prunellidae, such as the duncock *Prunella modularis*, are regularly recorded migrating at night.^{33–35}

Finally, certain groups, such as pipits and wagtails (Motacillidae) or species like the snow bunting *Plectrophenax nivalis*, also appeared to perform more daytime flights than other species (often short flights, e.g., Richard's pipit *Anthus richardi* in Figure 1A). In the case of the snow bunting, tracked individuals bred at very high latitudes ($>78^\circ$ north) and hence conducted a substantial portion of their migratory flights during polar day. This example illustrates facultative diurnal migration under continuous daylight and reflects the same trade-off observed in high-latitude radar studies, in which preserving migratory progress takes precedence over adhering to nocturnality.³⁶

Several species in our study were represented by small sample sizes. Nevertheless, we found very little intraspecific variation, with an average interquartile range of proportion of nocturnal flights across species of 0.036 when excluding flights across ecological barriers (also 0.036 when all flights were included; Figure 3). We suspect that variation in the proportion of nocturnal flights is primarily driven by migratory route choice and the need to cross ecological barriers (see spotted flycatcher *Muscicapa striata* in Figure 1A), although species differ in their propensity to prolong flights into daytime when facing such crossings.^{27,37,38} In another example, the common starling performed its longest flights, usually during long marine crossings, mostly at night, whereas shorter flights tended to occur during the day (Figure S3).²⁹ Excluding these barrier-crossing flights tends to lower the estimated proportion of nocturnal migration and increases the estimated intraspecific variation, because

positional uncertainty. Each horizontal bar in the activity plots represents one migratory flight (flight ID, flights ordered sequentially across the annual cycle), shown relative to night periods (white bars), with a gray horizontal line separating autumn and spring migration. For individuals flying into the day (spotted flycatcher *Muscicapa striata*) or primarily during the day (European bee-eater *Merops apiaster*), two consecutive nights are included to visualize the full flight duration.

(B) Shows a phylogenetic tree alongside three bars per species: (1) the proportion of migratory flight occurring during the night (dark gray) versus day (yellow), with intra-species variation shown as interquartile ranges (black lines); (2) departure; and (3) landing times across a standardized diel cycle, with normalized nighttime centered between dusk and dawn. Alongside, we present the number of tracked individuals indicated next to each species name with a color-coded family. Dusk and dawn times are based on a solar depression angle of -6° (see STAR Methods). For species marked with an asterisk (*), flight timing was more difficult to estimate accurately due to non-stop flying or aerial feeding behavior (see STAR Methods). The proportion of migratory flights occurring at night versus during the day is estimated here, excluding barrier-crossing flights (see Figure 3A). See Figures S1 and S2, Table S1, and Data S1.

not all tracked starlings undertook such long marine crossings (Figures 3 and S3).

Most species synchronized the departure and landing of migratory flights close to civil dusk and civil dawn. Specifically, 92% and 96% of species synchronized departures and landings more closely with civil twilight than with actual sunset or sunrise, respectively, suggesting that nocturnal migrants tend to maximize travel time during the night (Figure S2).^{11,24,39} However, some species-specific exceptions exist. For instance, the three intra-tropical migrants tracked in Africa, the woodland kingfisher *Halcyon senegalensis*, the mangrove kingfisher *H. senegaloides*, and the red-capped robin-chat *Cossypha natalensis*, are exclusively nocturnal migrants, yet their departures and landings appeared less tightly synchronized with the end and start of civil twilight (Figure 1 and Rime et al.⁴⁰). A similar pattern was observed in some other species (starling, wagtails, and pipits), which also performed some of their flights during the day (Figure S3).

Phylogenetic structuring of flight timing of migratory landbirds

To describe the phylogenetic structuring of nocturnal migration and to assess whether this behavior tends to be conserved within lineages, we investigated phylogenetic signal in nocturnal flight patterns across species. Across both metrics of nocturnal flight proportions, including or excluding barrier-crossing flights, we detected a consistent phylogenetic signal, though its strength varied (Table S1). Pagel's λ was nearly identical and significant in both cases ($\lambda = 1.015$ and 1.008 , $p < 0.001$), pointing to strong phylogenetic structuring and suggesting that nocturnal migration is largely conserved within lineages. Blomberg's K^* indicated a significant and consistent signal in both cases (0.723 , $p = 0.001$ and 0.746 , $p = 0.002$), suggesting that the phylogenetic structuring of nocturnal migration is robust regardless of whether barrier-crossing flights are included. Collectively, these results show that nocturnal migration is moderately to strongly shaped by phylogeny and evolutionary history, as is the case for the tendency to evolve seasonal migration itself.^{41,42} The overall consistency across all indices and the strengthened signal in the expanded dataset reinforce the interpretation that nocturnal migration is largely conserved within lineages, though convergent evolution or behavioral plasticity under similar ecological pressures cannot be excluded.

To assess whether the detected phylogenetic signal could reflect shared ecological conditions among related species, we ran phylogenetic generalized least squares (PGLS) models incorporating breeding latitude and total migration distance as covariates (two variables *a priori* expected to influence nocturnal flight proportions, see Sivakumar et al.³⁶). Neither factor predicted nocturnal flight proportion after accounting for phylogenetic relatedness (breeding latitude: $p = 0.101$; migration distance: $p = 0.567$; Figure S4), suggesting that the phylogenetic structuring of nocturnal migration reflects true evolutionary conservatism rather than shared ecology alone.

Several hypotheses have been proposed to explain nocturnal migration, but, for the most part, they remain untested (see Alerstam¹²). A first hypothesis proposes that nighttime flights offer more favorable aerodynamic conditions, as birds avoid turbulence and strong winds.⁴³ This has also been proposed as a

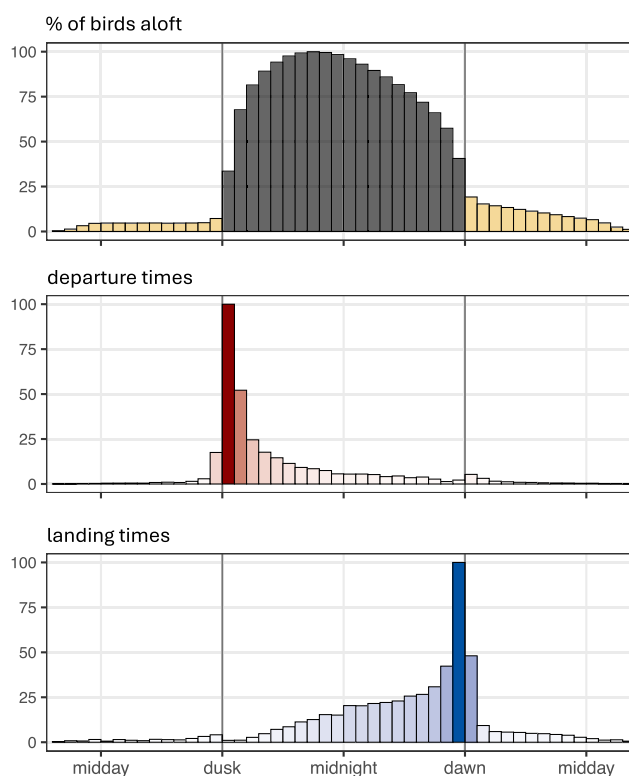


Figure 2. Distribution of migratory flight timing between day and night across all pooled flights (12,542 flights) from 411 individuals, totaling 84,477 h of flight

The top panel shows the proportion of birds aloft over a normalized 24-h cycle, with 77% of the migratory flights occurring during nighttime. The middle panel illustrates normalized departure times, with shading from light pink to dark red indicating the relative percentage of departures (darker shades indicate higher concentrations). The bottom panel shows normalized landing times, with shading from light to dark blue reflecting the relative percentage of landings. Dusk and dawn times are based on a solar depression angle of -6° (see STAR Methods). All proportions within panels are rescaled between 0 and 1.

See also Figure S2 and Data S1.

key driver of nocturnal migration in insects, in which radar studies have shown that nocturnal migrants achieve greater travel speeds and tighter directional control than their diurnal counterparts.^{44,45} A related hypothesis on physiological conditions proposes that nocturnal flight allows birds to avoid overheating from solar radiation exposure and from evaporative water loss because of cooler, more humid air. This is consistent with the extreme diel flight altitude changes recently documented in different species.^{27,37,46} A third hypothesis points to predator avoidance,^{47,48} and a fourth highlights the use of celestial cues after sunset and into the night for orientation,²⁴ alongside solar and magnetic cues that also provide mechanisms for orientation.^{49,50} Finally, a fifth hypothesis suggests that nocturnal migration in otherwise diurnal species evolved to maximize foraging opportunities during the day.^{51,52} This may explain why species such as hirundines, swifts, and bee-eaters, which are able to feed on the wing, distribute their migratory flights between day and night and are capable of performing rapid, uninterrupted migratory journeys in just a few days (e.g., in alpine

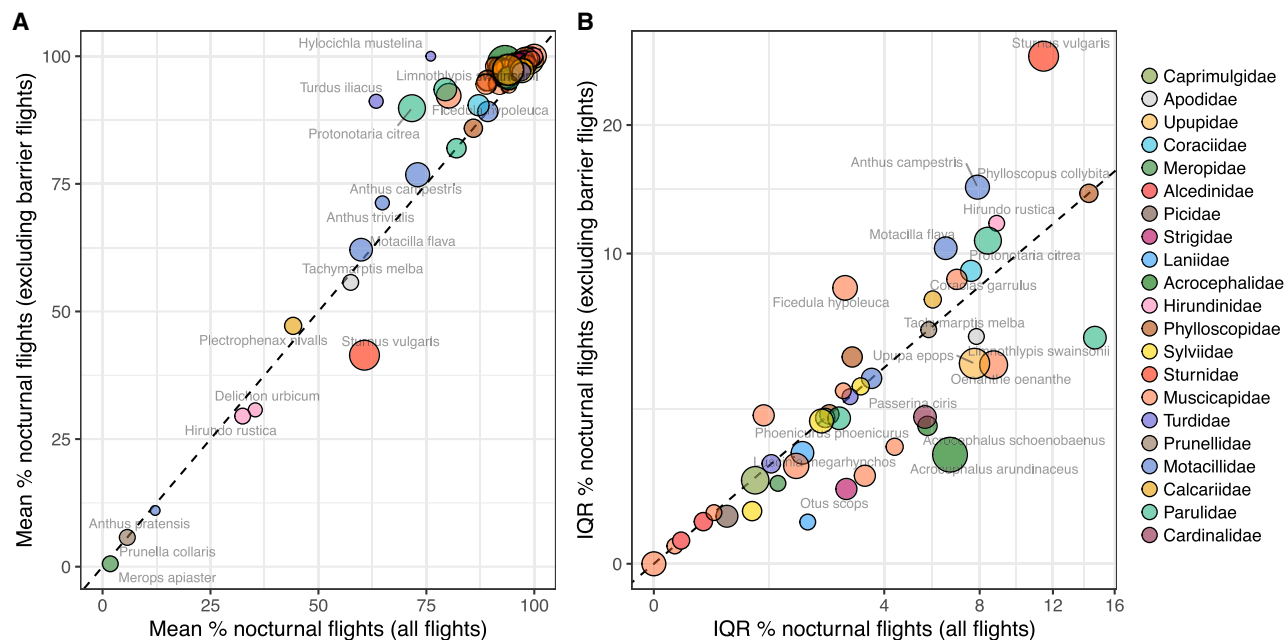


Figure 3. Effects of ecological barrier crossing on the mean and variation of the proportion of nocturnal migratory flight

(A) Average proportion of nocturnal migratory flights per species, with and without barrier-crossing flights. Species above the dashed line show a higher proportion of diurnal flights when crossing barriers (see STAR Methods).

(B) Intraspecific variation in nocturnal migratory activity per species, expressed as interquartile range (IQR), with and without barrier-crossing flights; species above the dashed line exhibit increased variation attributable to barrier crossing. Axes in (B) are square-root transformed for readability.

In (A) and (B), dot size is proportional to the number of tracked individuals. Only species with ≥ 3 individuals are included.

See also Figure S3 and Data S1.

swift³²). There is also some indication that Palearctic migrants adopt a more flexible timing (i.e., less tightly synchronized with civil twilight, as compared with those in North America or elsewhere) when they reach their wintering quarters south of the Sahara (see Adamík et al.⁵³). By adopting nocturnal flight strategies similar to those of intra-African migratory species, they may perform shorter, more opportunistic flights that allow them to efficiently track patchy or ephemeral food resources.^{40,54} While our data cannot directly test these hypotheses, some patterns are at least consistent with certain predictions. The near-universal synchronization of departures and landings with civil dusk and dawn is consistent with both the celestial orientation and predator avoidance hypotheses, whereas the exceptions (e.g., aerial feeders) align more naturally with the foraging hypothesis. Future studies combining multi-sensor tracking with environmental data such as wind, temperature, and predator activity would allow more direct tests of these competing explanations.

Conclusion

Our study highlights the unique value and spatiotemporal resolution of multi-sensor geolocators as the most suitable method currently available to quantify the proportion of nocturnal versus diurnal migration in small- to medium-sized landbirds and also to investigate their behavior en route. This approach, however, comes with inherent limitations because it relies on species that have sufficient site fidelity to enable archival tag recovery in subsequent years. As a result, our dataset is subject to taxonomic and geographic biases, with certain groups (e.g.,

Passerellidae and Tyrannidae) remaining underrepresented (Figure 4). Among the groups most notably absent from our dataset are the Fringillidae, of which several members (e.g., crossbills and siskins) are presumed, from visual observations and ringing studies, to undertake substantial daytime migration. Including such species in future analyses would likely reveal a broader continuum of diurnal and nocturnal strategies than captured here and would refine estimates of the overall prevalence of nocturnal migration across landbirds. Expanding taxonomic coverage to currently underrepresented groups would also allow testing whether the phylogenetic conservatism detected here holds across a broader avian tree or whether certain lineages have independently evolved flexible diel strategies. Furthermore, combining multi-sensor tracking with concurrent environmental measurements (e.g., wind, temperature, and predator activity) would enable direct evaluation of the competing mechanistic hypotheses for nocturnal migration that our descriptive framework cannot resolve. By providing a synthesis of both published and unpublished datasets, we hope this work will encourage new collaborations, promote wider use of multi-sensor tracking technology, and draw attention to the current taxonomic and geographic gaps.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Paul Dufour (paul.dufour80@gmail.com).

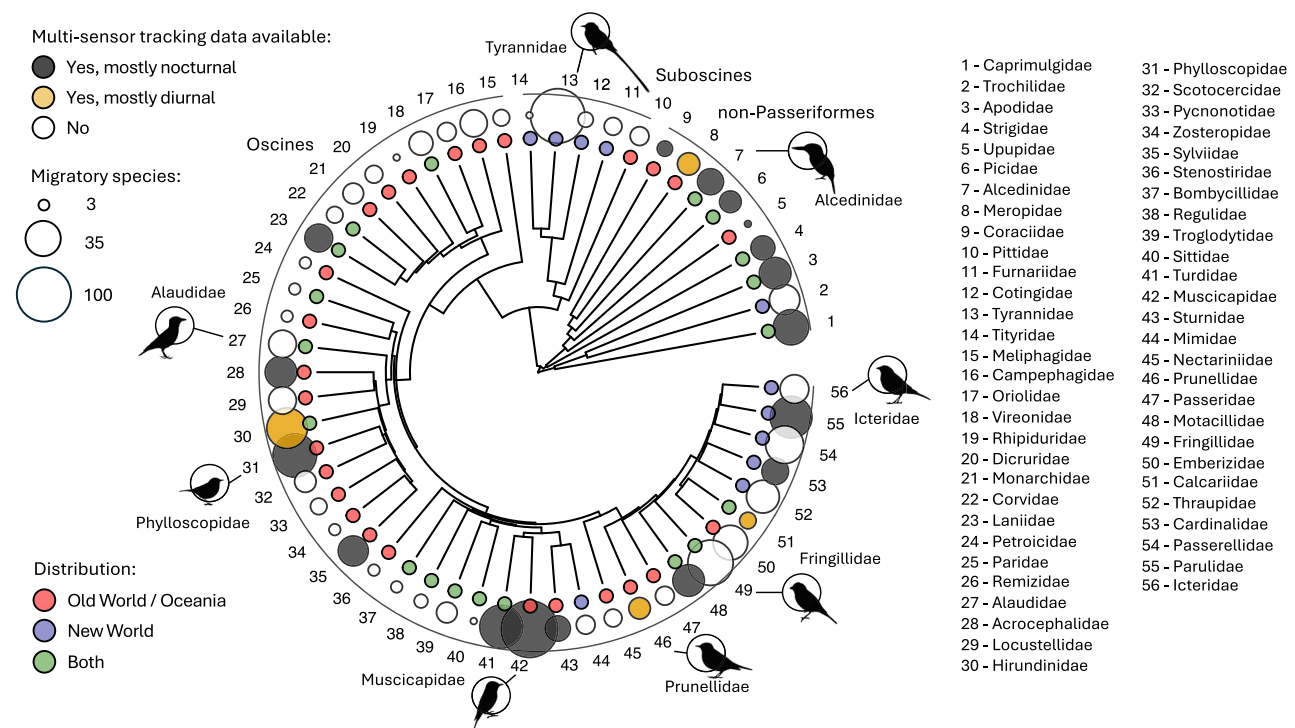


Figure 4. Phylogenetic distribution of multi-sensor tracking data, nocturnality, and diurnality across migratory landbird families

The phylogenetic tree includes all migratory landbird families. For each family, the outer circle indicates whether multi-sensor tracking data are available and, if so, the average proportion of nocturnal migratory flights across tracked species within that family, represented by a color ranging from yellow (>50% diurnal) to dark gray (>50% nocturnal). White circles indicate families for which no multi-sensor tracking data are currently available. Circle size is proportional to the total number of known migratory species within each family. Migration strategies were taken from Dufour et al.⁵⁵ Inner colored dots indicate the geographic distribution of each family (pink, Old World and Oceania; blue, New World; green: both). Family names and their corresponding numbers are listed to the right of the figure.

See also [Data S1](#).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All data necessary to reproduce this publication are available in [Data S1](#). It provides information about the estimated proportion of nocturnal flights for each individual.
- The study does not report any original code.
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

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AUTHOR CONTRIBUTIONS

P.D. designed the paper with R.N., B.H., and M. Briedis. P.D. performed analyses, visualizations, and wrote the first version of the paper. P.D., R.N., J.B.W., Y.R., P.M.-T., M. Briedis, E.J., V.C.-L., P.C.-L., G.R., T.Z., P.D.-V., S. Szarmach, D.K., and K.J.G. analyzed tracking data. All authors were involved in the data collection in the field. All authors contributed to the revisions.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Estimated proportions of nocturnal migratory flights per individuals, with or without barrier crossing flights	This paper, Data S1	DOI of the paper
Software and algorithms		
Rstudio	RStudio Team https://www.rstudio.com/	Rstudio 4.4.1
R package GeoPressureR	Nussbaumer et al. ^{9,10}	https://github.com/Rafnuss/GeoPressureR
R package clootl	Miller et al. ⁵⁶	https://cran.r-project.org/web/packages/clootl/index.html
R package nlme	Pinheiro and Bates ⁵⁷	https://cran.r-project.org/web/packages/nlme/index.html
R package phylosignal	Keck et al. ⁵⁸	https://cran.r-project.org/web/packages/phylosignal/index.html
R package geosphere	Hijmans et al. ⁵⁹	https://cran.r-project.org/web/packages/geosphere/index.html
Other		
Multi-sensor geolocators	Swiss Ornithological Institute	GDL3-PAM 1.2-2g
Multi-sensor geolocators	Migrate Technology	BARP30Z11-7-DIP, DARK30Z11-DIP, CARP30Z11-7-DIP, CARP30B1-7-DIP 0.3-0.6g
Multi-sensor geolocators	Lund University	CAnMove 1g

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

All birds were captured and tagged for the purposes of this study under permits issued by museums or the relevant local authorities in each participating country or region involved.

METHOD DETAILS

Geolocators and species data

We collected both published and unpublished multi-sensor tracking data from 411 individuals of 56 different species, originating from 83 populations across 25 countries spanning four continents (see [Figure S1](#); [Table S2](#)). We collected varying numbers of loggers per species, with a minimum of one for five species ([Table S2](#)) and a maximum of 35 for the great reed warbler *Acrocephalus arundinaceus* (7.4 loggers per species on average). Note that in some cases of partial migratory species, such as the meadow pipit *Anthus pratensis*, seven loggers were retrieved from the same population, but only one bird migrated.

Multi-sensor loggers refer to small devices that can include sensors such as light, accelerometer, and pressure. After deployment, the same individuals must be recaptured in subsequent years to recover the tags and access the data. Except for alpine accentor in France, Richard's pipit in Spain and red-capped robin-chat and mangrove kingfisher in Kenya, which were tagged on their wintering grounds, all individuals were tagged on their breeding grounds. Therefore, all tagged birds were experienced individuals that had completed at least one-way migration before tagging.

The data were collected using different types of multi-sensor loggers, which always included at least a pressure sensor, with varying recording intervals ranging from 5 to 30 minutes. These loggers were manufactured by the Swiss Ornithological Institute⁷ (model GDL3-PAM, 1.2–2.0 g with harness), the Lund University^{8,60} (<1.2 g with harness), or Migrate Technology (models BARP30Z11-7-DIP, DARK30Z11-DIP, CARP30Z11-7-DIP, CARP30B1-7-DIP, with respective weights of 0.35 and <0.55 g including harness). Most models featured at least light, accelerometer, and pressure sensors, though some (e.g., DARK30Z11-DIP) only included pressure sensors. When present, light data were always recorded at 5-minute intervals. Pressure and activity data were recorded at intervals ranging from 5 to 30 minutes.

The species tagged ranged in weight from 7 g (the smallest, common chiffchaff *Phylloscopus collybita*) to 150 g (the heaviest, European roller *Coracias garrulus*). The devices never exceeded 5% of the body mass of the tagged birds. All devices were mounted

using leg-loop harnesses made of either stretchy elastic thread or tressed UV-proof thread, with diameters between 0.7 and 1.0 mm depending on the species' size. Birds were captured and tagged following strict ethical guidelines and under various licenses issued by national or regional authorities. A list of reference programs or project codes for unpublished data is provided in the [acknowledgments](#).

Estimations of nocturnal and diurnal flight times

To determine what fraction of each migratory flight occurred during the night versus the day, we first modeled the trajectory of each track following the approach presented in Nussbaumer et al.^{9,10} using the *GeoPressureR* R package (version 3.2). This package is based on geolocation estimation of stopover sites (as well as wintering or breeding areas) throughout the annual cycle, using either pressure data alone or a combination of pressure and light data. In general, we followed all the steps presented in the online tutorial: <https://raphaelnussbaumer.com/GeoPressureManual/>.

First, we separated stationary periods and migratory flights by manually labelling the geolocators' pressure and/or activity (i.e., accelerometer) measurements. Stationary periods were characterized by a limited variation in consecutive pressure measurements indicating an absence of change in altitude as well as by consistently low activity measurements. Migratory flights typically displayed a clear drop in atmospheric pressure, corresponding to in-flight altitude gain, and consistently high activity measurements (which forms a high activity plateau of the same duration as the variation in pressure). If both pressure and activity data are available, labeling is done using activity data; otherwise, it is done using pressure data. To enable comparison between all individuals, especially those with different data recording intervals, we only labeled flights that lasted at least 40 minutes. See <https://raphaelnussbaumer.com/GeoPressureManual/labelling-tracks.html> and⁶¹ for examples.

Second, we built separate probability maps based on atmospheric pressure and light intensity data (sunrise and sunset times) to estimate the position of each bird during each stationary period. For the pressure-based maps, the time series of the geolocator pressure measurements during stationary periods were matched with the one-hour atmospheric pressure at surface level from ERA5 re-analysis dataset (spatial resolution: $0.1 \times 0.1^\circ$) to produce a likelihood map of the geolocator's position.⁹ The resulting likelihood map included the information of both the temporal variation of pressure and the absolute values of pressure corresponding to the altitudinal range within each grid cell. Stationary periods identified through pressure and/or activity measurement labeling were directly used to estimate the probability maps calculated with light intensity data. For those, we calculated likelihood estimates using an "in-habitat" calibration from the equipment and retrieval periods (as described in Lisovski and Hahn⁶² and Lisovski et al.⁶³) fitting the distribution of zenith angle with a kernel density estimation. Note that we did not use light intensity data (but only atmospheric pressure) for nocturnal species (like Eurasian scops-owl *Otus scops*) or species spending most of daytime under cover (like siberian ruby-throat *Calliope calliope*; see later for details about all individuals).

Finally, we constructed the trajectories of each bird using a Hidden Markov Model as presented in Nussbaumer et al.¹⁰ The observation model consisted of the likelihood maps generated from pressure and light data (or only pressure data). The movement model used the information of flight duration derived from the labelling and a parametric equation defined as the cubic root of the mechanical power required for the average airspeed computed for a transition, accounting for the different species size and shape. Using this model, we generated the most likely migration trajectory of the birds.

From the most likely trajectory, we then used the *path2twilight* function in the *GeoPressureR* R package to calculate the theoretical twilight times at each location for specified dates. Since civil twilight is a commonly used celestial cue (see Cooper et al.²⁴), we estimated twilight times using a solar depression angle of -6° . We also calculated twilight times using a solar depression angle of 0° , corresponding to sunrise and sunset times, to assess whether departure and landing events align more closely with civil twilight than with sunrise or sunset. Once we had the start and end of civil twilight estimated at each stopover location, we used the *stap2-flight* function to convert the stationary period data frame into a flight data frame where flights are computed as the difference between the end of a stationary period to the start of the next one. For each flight, using the civil twilight information, we then estimated the duration of the flight that occurred during the night versus the day.

Note that we favored this method of using estimation of geo-positioning over direct calculation from raw light data to estimate civil twilight times because it provides consistency across all individuals, especially since some species or types of loggers either do not record light data or produce data of insufficient quality. Although there is inherent uncertainty in geolocation, we expect the biases to be relatively small, given that variations in civil twilight times are minimal across relatively large geographic distances.

Cases of aerial feeders and non-stop flying species

Unlike species that undertake long flight phases only during migration, aerial insectivores, such as swallows, swifts, and bee-eaters, spend most of the day flying while foraging. This makes it harder to identify migratory flights from foraging flights using the pattern described in other species: a drop in pressure data combined with a sustained plateau of high activity.

Using pressure and accelerometer data, we found that most species (except swifts) typically perch at ground level for most nights. We therefore defined migratory flights as pronounced daytime activity periods (high accelerometer data) occurring between two nights that differed in mean atmospheric pressure by at least 3 hPa. Following this labeling approach and combining it with light-level data, we used *GeoPressureR* to estimate the most likely migration trajectory. We iteratively refined the labeling process until the resulting trajectory appeared coherent and did not suggest numerous back-and-forth movements, which would imply that the total duration of labeled flight was overestimated relative to the time required for the migration (see Nussbaumer et al.¹⁰).

For the only non-stop flyer in our dataset, the Alpine Swift, we first estimated the migration route, including main wintering and major stopover sites, from light data using GeoLight following Lisovski et al.⁶⁴ We then identified migration periods from shifts in sunrise and sunset, isolated these intervals in the pressure and accelerometer data, and manually labeled segments consistent with migratory behavior. These segments were marked by prolonged high-activity plateaus in the accelerometer data, probably induced by increased flapping flights, which were not observed outside migration periods. The trajectory was then interpolated to match flight events, and local sunrise/sunset times were estimated to determine day vs. night flight proportions like in other species.

For both aerial feeders and non-stop flyers, we acknowledge that this manual labeling can introduce more observer bias than in other species, so we did not calculate precise departure or landing times. Still, our estimates clearly show multiple partially or fully nocturnal migratory flights, a behavior previously unknown or poorly documented in these species.^{31,65} Moreover, even with a latitudinal error margin of ~ 1000 km, sunset variation is minimal (0–2 min in September; 5–9 min in October) across West Africa (5–15° N), making our nocturnal/diurnal flight proportions reasonably robust at the species level.

Ecological barrier crossing flights

Ecological barriers are natural geographic features or environmental conditions that significantly hinder the migration of species. For migratory animals, these barriers can restrict access to suitable habitats, increase travel risks, and influence migration routes and timing.^{66,67} When crossing large marine expanses, migratory landbirds have no opportunity to land. If the crossing takes longer than a single night, part of the flight must necessarily occur during the day. To enable consistent comparisons across species and populations, some of which may not face such ecological barriers, we also estimated nocturnal and diurnal flight times excluding flights that involved barrier crossings. We focused on two key ecological barriers: marine expanses over 500 km and the Sahara Desert.

The 500 km marine threshold was informed by tracking data from five northern wheatears *Oenanthe oenanthe* undertaking their first autumnal flight from Ouessant island to northwest Iberia. These birds took an average of 11.1 hours to complete the ~ 500 km journey, departing at civil dusk and arriving a few hours after civil dawn.²⁷ This suggests that 500 km is close to the upper limit of what small passerines can fly overnight without needing to continue into the day. Therefore, we used 500 km as a conservative threshold beyond which flights starting in the evening are likely to involve daytime movement. We chose northern wheatear tracking data specifically because they provided empirically grounded estimates of overnight flight distance for a small passerine undertaking a well-defined sea crossing, rather than relying on theoretical flight range estimates. This threshold is conservative as species capable of longer overnight flights would require a greater crossing distance before daytime prolongation becomes necessary.

To classify a flight as crossing an ecological barrier, we considered whether at least half of its duration occurred within the defined polygon representing that barrier. This criterion ensures that the majority of the flight is meaningfully associated with the barrier environment, while also accounting for uncertainties in trajectory estimation and barrier boundaries. We used a global polygon of all marine expanses and a polygon representing the boundaries of the Sahara Desert as defined in.⁶⁸

QUANTIFICATION AND STATISTICAL ANALYSIS

Phylogenetic modelling

We generated a maximum clade credibility phylogenetic tree including all 56 bird species examined in this study using the *clootl* R package,⁵⁶ which accesses the Cornell Lab of Ornithology Open Tree of Life Avian Phylogeny (version Aves v1.4).⁶⁹ It represents one of the most up-to-date and comprehensive avian phylogenetic frameworks currently available, synthesizing phylogenetic information from all recently published studies (see⁶⁹).

We used four indices to evaluate the phylogenetic signal in the proportion of nocturnal flight time, whether including or excluding ecological barrier crossing flights: Pagel's λ , Blomberg's K, Abouheif's Cmean and Moran's I index.⁷⁰ Overall, values of λ , K, I and Cmean larger than zero denote deep relationships between species' traits and phylogeny.⁷⁰ Under a Brownian Motion (BM) model of trait evolution, Pagel's λ and Blomberg's K are expected to be equal to 1. When values of λ and K are close to 0, there is no phylogenetic signal in the studied trait, that is, there is phylogenetic independence, and the trait has evolved independently of phylogeny and close relatives are not more similar than distant relatives. Here, we used Blomberg's K*, a modification of the original Blomberg's K (see Blomberg and Garland⁷¹) that is more robust across different tree shapes and trait distributions. The I and Cmean are autocorrelation indices and measure how similar trait values are between neighboring species on the phylogeny; they are not based on any evolutionary model and large deviations from 0 are representative of strong phylogenetic signal.⁷⁰ We evaluated all four metrics because they are complementary and capture different aspects of phylogenetic signals. We used the *phylosignal* R package to run these analyses.⁵⁸

To assess whether the phylogenetic structuring of nocturnal migration could be attributed to shared ecological conditions among related species rather than true evolutionary conservatism, we ran phylogenetic generalized least squares models (PGLS) using the *nlme* R package.⁵⁷ We used the species-level mean proportion of nocturnal flights (including barrier-crossing flights) as the response variable, and breeding latitude and total migration distance as ecological covariates (see Figure S4). Breeding latitude was computed as the mean absolute latitude of capture locations per species from our tracking dataset. Total migration distance was estimated as the cumulative great-circle distance between consecutive stopover locations along the most likely trajectory of each individual, averaged per species, using the *geosphere* R package.⁵⁹