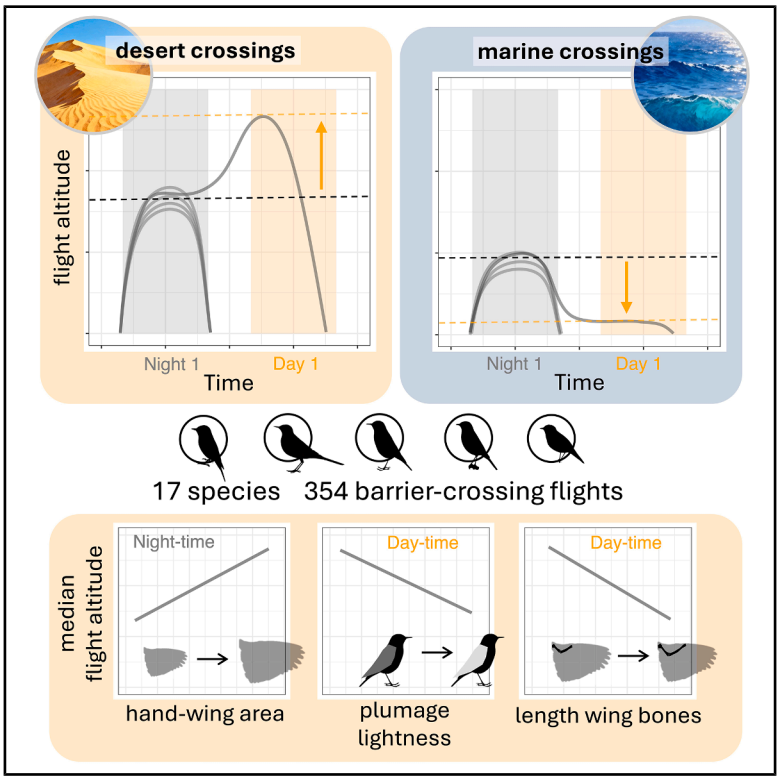
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Article

Ecological barrier crossing strategies in small migratory birds depend on wing morphology and plumage color

Graphical abstract



Highlights

- Small migratory birds shift altitude markedly when crossing deserts and marine barriers
- Small birds fly higher over the Sahara than over marine areas, especially during daytime
- Wing traits and plumage color influence how birds cross ecological barriers
- Darker plumage and shorter wing bones relate to higher Sahara flight in daytime

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In brief

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Article

Ecological barrier crossing strategies in small migratory birds depend on wing morphology and plumage color

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SUMMARY

Recent tracking technologies have revealed remarkable diel flight altitude changes over the Sahara Desert in small migratory birds. However, the drivers and traits behind these strategies remain poorly understood, partly because few species and barriers have been studied. Using a dataset from 67 recovered multi-sensor loggers across 17 species, we examined how small landbirds cross two major marine barriers (the Bay of Biscay, the Mediterranean Sea) and the Sahara. We then used a comparative approach to test the influence of wing morphology, wing structure, and plumage color on flight altitude. Birds showed important differences across barriers: over the desert, they averaged 1,600 m at night and 2,800 m during prolonged daytime flights, while marine crossings occurred lower (750 m), sometimes just above water. Flight altitude increased with wing area, and species with shorter wing bones and darker plumage flew higher over the Sahara, likely to enhance heat dissipation and reduce solar heating. These findings refine hypotheses on barrier-crossing strategies and suggest broader ecological and evolutionary implications.

INTRODUCTION

Birds undertake some of the most spectacular annual migrations in the animal kingdom, with several billion birds traveling twice a year between their breeding and wintering grounds.[1] In the Palearctic-African migratory corridor, it has been estimated that 2.1 billion songbirds and near-passerines migrate each season between Europe and sub-Saharan Africa,[2] where they face several major ecological barriers. Ecological barriers are geographical features, such as deserts, mountains, or seas, that can impact birds' migration because they provide little food resources, nowhere to land, or harsh climatic conditions[3] (see also[4]). Between Western Europe and sub-Saharan Africa, migratory birds can face marine barriers and the Sahara Desert, which locally extends over 2000 km. In some cases, birds can avoid and bypass these barriers, but under certain circumstances, they either choose or are forced to cross them.[5]

How small migratory birds cross such large ecological barriers has long remained a mystery.[6] However, technological advances in recent decades, especially the miniaturization of tracking devices, have significantly expanded our understanding of their behaviors. Radar studies first provided evidence that small migratory birds mostly migrate at night, with some birds regularly extending their flight into the day when crossing large barriers such as the Sahara Desert.[7–10] Light patterns recorded by light-level geolocators were then confirmed that this strategy is probably common among small migratory species.[11] Finally, the use of multi-sensor loggers, including temperature, accelerometer, and pressure sensors, has recently enabled accurate measurements of both the duration and altitude of these flights.[12–14] They notably revealed extremely high-altitude flights and diel cycles of flight dynamics during the Sahara crossing for different species (in *Acrocephalus arundinaceus* and *Upupa epops*[15,16]) and low daylight sea-crossing flights in *Caprimulgus europaeus*.[17]

Several hypotheses have been proposed to explain these crossing strategies, mostly, desert crossings. These hypotheses are related to factors such as predation, vision range, solar

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radiation, diel variation in ambient temperature, and wind support.[16,18–20] Regarding solar radiation, Sjöberg et al.[21] tested the hypothesis that birds fly at higher altitudes during daytime to mitigate the effect of extra heating from solar radiation. Using temperature data recorded by the loggers, the authors found that birds flying at the same altitude were warmer during the day than at night, which suggests that climbing during the day to colder altitudes might counterbalance the heating from solar radiation.[19,21] Few hypotheses have so far been proposed regarding marine crossings, partly due to the difficulty of identifying such events from data issued from geolocators carried by small species ([17], see also[22,23]).

Other factors, including wing morphology and plumage color, may influence barrier-crossing behavior, but they have been so far rarely tested. A recent study showed significant associations between hand-wing index (used as a proxy for flight efficiency) and road-crossing probability in the Amazonian forest,[24] suggesting that wing morphology could be used to study barrier crossing abilities. Previous studies indeed suggested that species with more elongated wings (i.e., higher aspect ratio) are more likely to undertake prolonged flights over the Sahara.[12] Wing morphology can influence both energy efficiency and lift generation[25–28]: for example, higher aspect ratio wings generally improve flight efficiency, whereas larger winged birds (i.e., higher hand-wing area) can likely generate more lift with less effort, enabling them to sustain flight at higher altitudes where the air is thinner. Conversely, some wing shapes may not generate sufficient lift to reach higher elevations, where the air is thinner, during barrier crossings.[29–31] However, whether species with higher aspect ratio wings or larger wings tend to cross barriers at higher altitudes, or complete longer uninterrupted desert or marine crossings, remains unclear. In addition, a recent study showed that the structure of the bird wings can also be linked to heat dissipation, with higher temperatures associated with relatively longer wing bones (i.e., combined humerus and ulna lengths) in Passeriformes (as predicted by Allen's Rule).[32] We hypothesized that species with relatively shorter wing bones (and thus potentially less vascularized wings) may struggle to dissipate heat during prolonged flight and might compensate by flying at higher altitudes to cool down. This would be even more important during the daytime, as solar radiation also contributes to overheating. Regarding plumage color, Delhey et al.[33] found that migratory birds generally have lighter plumage. Because darker birds absorb more solar radiation and heat up faster than lighter ones, the authors suggested that migrants could have evolved reflective plumage to prevent overheating.[34] It remains to be tested whether darker species fly at higher altitudes, particularly during daytime, to mitigate excess heat from solar radiation. Testing these hypotheses has been challenging due to difficulties in tracking small species and pinpointing their exact locations during migration (see[35,36] for uncertainties of geo-positioning with light-level geolocators). While multi-sensor loggers have improved the geo-positioning,[37] they still require recapturing individuals after their migration to retrieve data, and few species have so far been equipped.

In this study, we equipped more than 300 individuals with multi-sensor loggers and analyzed sea and desert crossings of 67 retrieved individuals of 17 small migratory bird species that migrate between western Europe and their sub-Saharan wintering grounds. Our aim was to study how small migratory birds cross two major types of ecological barrier: marine and desert areas. First, we investigated whether barrier-crossing strategies differed among species, hypothesizing that morphological and plumage characteristics influence how individuals navigate ecological barriers. Specifically, we expected species with longer and larger wings to fly at higher altitudes and undertake longer flights,[29,30] particularly over the Sahara, where the risk of overheating from solar radiation is higher. We also predicted that species with relatively shorter wing bones and darker plumage would ascend to cooler altitudes, especially during daytime crossings, to either dissipate heat or reduce heat absorption.[21,33] To test these predictions, we used a recently developed geo-positioning method that integrates activity, light, and pressure data,[37,38] allowing us to accurately estimate where, when, and how each individual crossed the different ecological barriers. We then examined whether interspecific differences in flight altitude across the two barrier types were associated with morphometric traits and plumage color.

RESULTS

A total of 67 multi-sensor loggers (6 GDL3-PAM and 59 CARP30Z11-7-DIP) were retrieved on 17 different species (Table 1). Analysis of the trajectories revealed 312 flights over the Sahara Desert and 42 flights over the Mediterranean Sea or the Bay of Biscay (see Table 1; Figure S2).

We found significant differences in flight altitudes between species when crossing the Sahara (average of 1614 with a standard-deviation of 1048 m above sea level; Figure 1A; Table S1). For example, *Lanius senator* (1033 ± 796 m asl, $n = 17$ flights) and *Phoenicurus phoenicurus* (1323 ± 1111 m asl, $n = 17$ flights) flew at lower altitudes than *Acrocephalus arundinaceus* (2466 ± 1420 m asl, $n = 6$ flights; Table S1). When flights extended into daytime, we found that 12 out of 14 species (85%) climbed to higher elevations compared to their night-time flight altitudes (paired t test for all flights: t = 5.11, df = 76, p-value <0.001; average of 2630 ± 1521 m asl; Figures 1A and 2). Among the 25 flights in which a clear change in altitude between night and day was visually detected, 68% of climbs began before the onset of civil twilight, and 36% occurred within the 20 min preceding civil twilight. Interestingly, three species, *Caprimulgus europaeus, Curruca hortensis,* and *Monticola saxatilis* did not exhibit any prolonged flights during daytime (see Figure 1C). Half of the flights over the Sahara lasted the duration of the night, i.e., between 10 and 14 h (50%; Figure 1A). Flights lasting less than 10 h were less common (30%), and about 20% of flights extended beyond the first night, lasting up to 45 h. When flights continued beyond one night, and the following day, birds typically remained in flight until at least the morning of the second night.

For sea crossings, flights generally lasted between 10 and 20 h, depending on the sea extent to cross (Figure 1B). Several individuals performed flights at very low altitudes, probably close to the sea surface (average of 774 ± 747 m asl; see STAR Methods regarding possible uncertainty in the estimation of flight altitude). We found that 19 of the 42 marine crossing flights (45%)

Table 1. List of small migratory species tracked by multi-sensor loggers in this study

Species (english)	Species (latin)	Loggers	Desert flights	Desert prolonged flights (>14h)	Marine flights
European Nightjar	*Caprimulgus europaeus*	2	23	0	1
Eurasian Scops-owl	*Otus scops*	4	28	1	2
Eurasian Hoopoe	*Upupa epops*	4	23	2	5
Woodchat Shrike	*Lanius senator*	3	17	1	0
Great-reed Warbler	*Acrocephalus arundinaceus*	2	23	6	0
Sedge Warbler	*Acrocephalus schoenobaenus*	5	9	3	5
Western Orphean Warbler	*Curruca hortensis*	6	25	0	0
Greater Whitethroat	*Curruca communis*	1	2	1	1
Spotted Flycatcher	*Muscicapa striata*	5	15	7	0
Common Redstart	*Phoenicurus phoenicurus*	4	17	6	0
Common Rock Thrush	*Monticola saxatilis*	1	7	0	1
Whinchat	*Saxicola rubetra*	6	29	6	0
Northern Wheatear	*Oenanthe Oenanthe*	7	36	3	9
Common Nightingale	*Luscinia megarhynchos*	3	12	2	1
Western Yellow Wagtail	*Motacilla flava*	7	16	13	9
Tawny Pipit	*Anthus campestris*	5	26	9	8
Tree Pipit	*Anthus trivialis*	2	4	4	0
	Total	67	312	64	42

The number of loggers retrieved is indicated per species, as well as the number of flights above the desert (Sahara Desert) and the marine (Mediterranean Sea and Bay of Biscay) barriers.

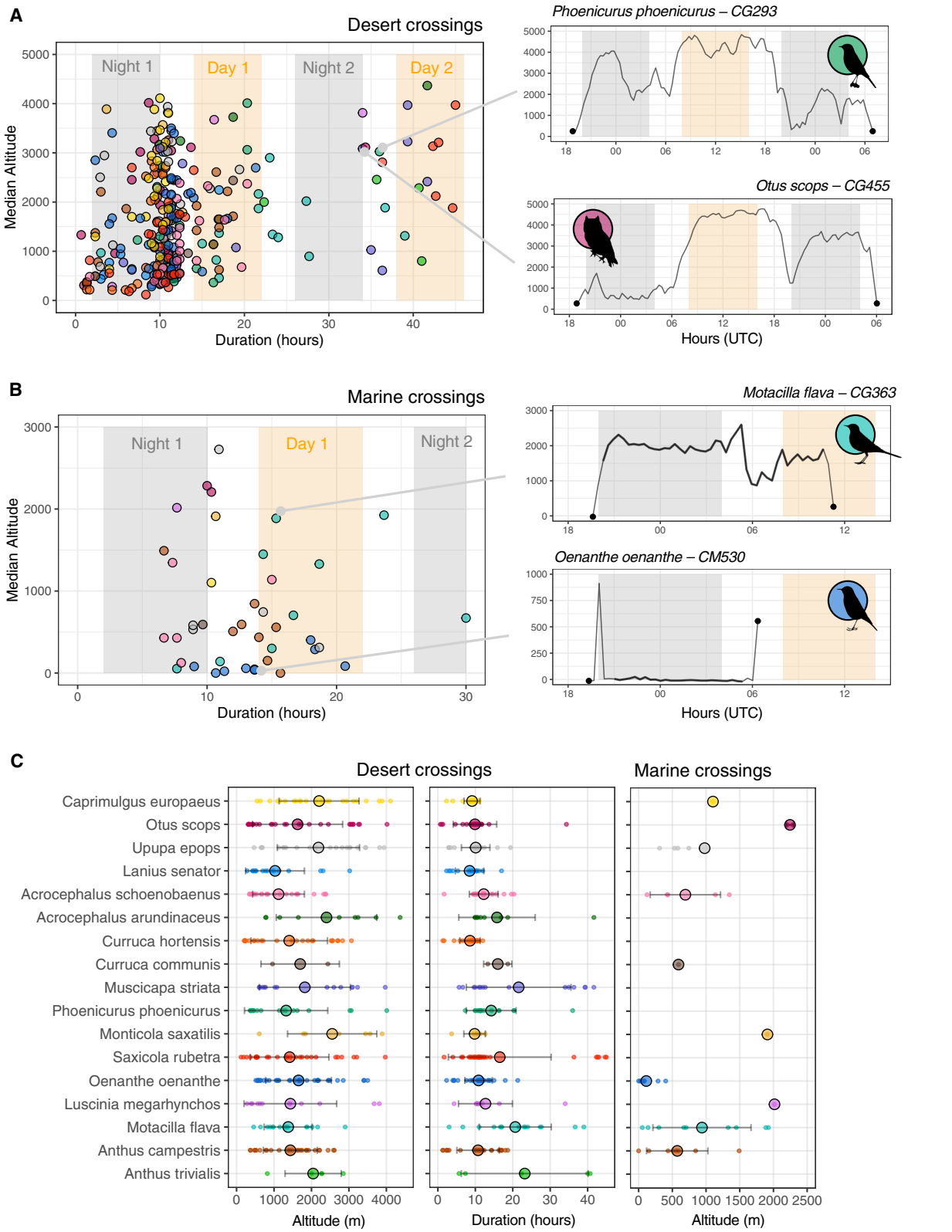
took place at a median altitude of less than 500 m above sea level. In particular, *Oenanthe oenanthe* performed flights at an average altitude of 112 ± 137 m asl (n = 9 flights): during 8 of 9 flights, birds spent more than 30% of the flight time below 50 m, with proportions ranging from 38% to 97%, indicating that a substantial portion of these flights occurred rather close to the sea surface despite occasional high-altitude segments. By comparison, *Anthus campestris* and *Motacilla flava* generally flew at higher altitudes than *Oenanthe oenanthe* and flew less frequently close to the sea surface. When they did, birds also spent a substantial portion of the flight near the water: for example, 1 of 8 *A. campestris* flights spent 71% of the time below 50 m, and 1 of 9 *M. flava* flights spent 50% of the flight below 50 m. When flights extended into daytime, we found that 4 out of 5 species (80%) descended to lower elevations (paired t test for all the flights: t = −3.55, df = 35, p-value = 0.001; Figure 2). Altitude profiles of all prolonged desert and sea crossings are shown in Figures S3 and S4, respectively.

As we found no phylogenetic signal in the PGLS models ($\lambda < 0.001$, Table S2), we focused on linear mixed-effects models, which account for intra-specific variation by including multiple individuals per species and multiple flights per individual (Table 2). For desert crossings, hand wing area was positively associated with median flight altitude during both the entire flight and the night period (Table 2; Figure 3), while aspect ratio and plumage lightness were not significant. During the day period, median flight altitude showed a negative relationship with plumage lightness and a positive one with hand wing area; aspect ratio remained non-significant. Only the hand wing area was significantly and negatively related to flight duration. Median flight altitude showed a negative relationship with the relative length of wing bones but only during daytime (Table 3; Figure 3). Variance partitioning showed substantial contributions from individuals, species, and taxonomy (nested together), and season across most models (Tables 2 and 3). For marine crossings, individuals, species, and taxonomy again contributed substantially to variance, while season had minimal influence. Median flight altitude was significantly associated with all three traits: aspect ratio and hand wing area showed positive relationships, and plumage lightness showed a negative one (Table 2).

DISCUSSION

High altitude flights and overheating avoidance over desert barriers

Our results show that crossing the Sahara varies greatly from one species to another and can vary within species. Firstly, we confirmed that some species often extend flights during the day or over multiple days, while others stop after the first night.[11,12,16,39] For example, *Curruca hortensis* never extends nocturnal flights into the day and likely stops in acacia-filled wadis during spring migration across the western Sahara.[40–43] Species such as *Oenanthe oenanthe* and *Anthus campestris* also make short flights and may be more flexible in habitat use in the Sahara. In contrast, frequent day-flyers such as *Muscicapa striata* may have greater endurance or stricter stopover habitat needs, making desert crossings more challenging. The negative relationship between hand-wing area and flight duration was unexpected, as we initially hypothesized that species with more efficient wing morphologies would sustain longer flights. However, hand-wing area and hand-wing index (a proxy for wing aspect ratio) capture different aerodynamic properties: while



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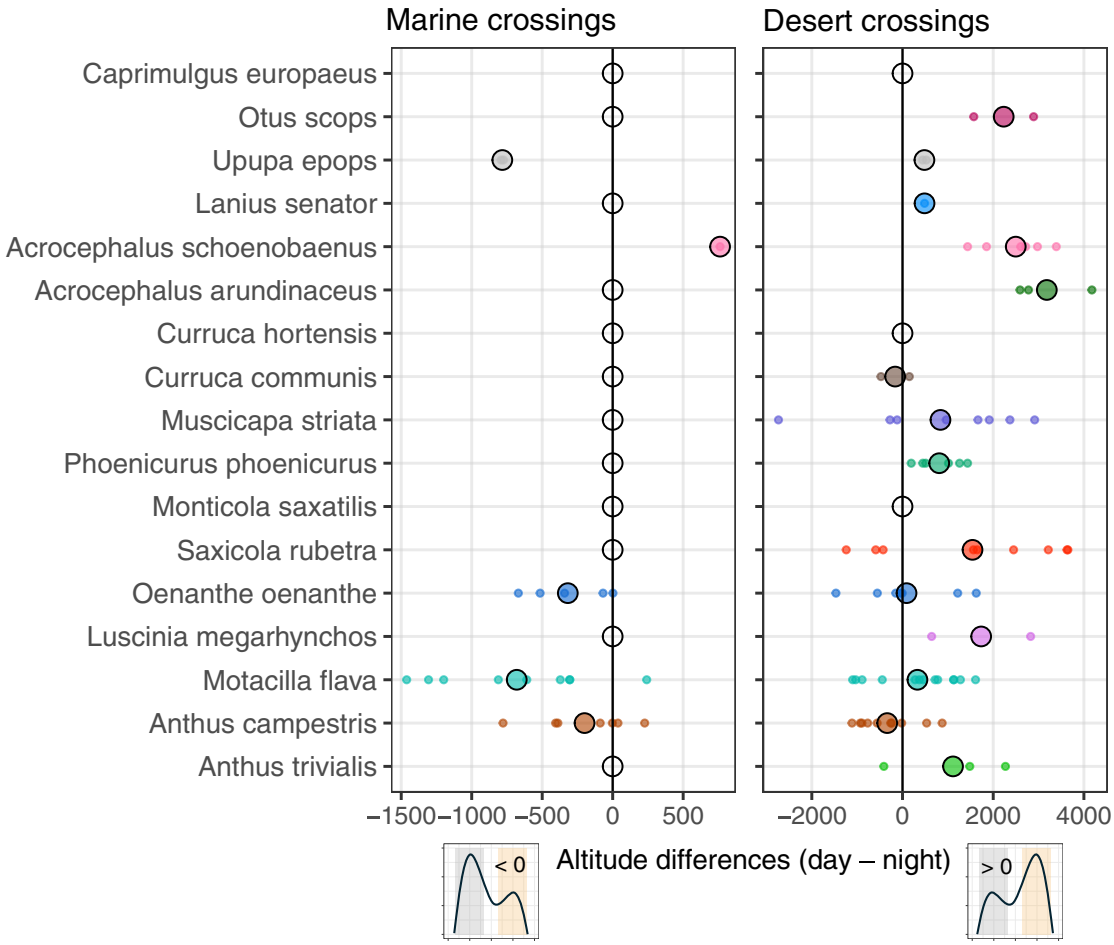


Figure 2. Differences in flight altitude between day and night of small migratory species when crossing marine and desert barriers

The x axis indicates the altitude difference (day minus night), with positive values signifying higher flight altitudes during the day and negative values indicating higher altitudes at night. The colored dots represent mean values. Empty (unfilled) dots denote species that did not engage in prolonged flight during daytime.

larger wing area relative to body mass (lower wing loading) may facilitate lift, higher aspect ratio wings are associated with energy-efficient flight over distance rather than necessarily over time.[25–28] One possible explanation is that environmental conditions during migration may outweigh the effect of wing morphology on flight duration.[44–46] Additionally, species with smaller wing areas may rely on flight styles such as flap-bounding or low-speed cruising that prolong flight time despite higher energetic costs.

Regarding flight altitude, we found important differences among species. Several species reached unexpected high altitudes, such as *Otus scops*, *Acrocephalus schoenobaenus,* or *Saxicola rubetra*, which all flew higher than 4,000 m during daytime. Among species that extend flights into the day, most climb higher than the previous night, but some, such as *Oenanthe oenanthe* and *Anthus campestris*, maintain or even descend to lower altitudes. Our analyses also demonstrate that different aspects of wing morphology and plumage color influence barrier-crossing strategies over the desert. Indeed, we found that hand wing area (rather than hand-wing index/aspect ratio) was positively correlated with flight altitudes, which corroborates the idea that larger winged birds can generate more lift with

Figure 1. Variation in flight altitude and duration across ecological barriers

Variation in durations and altitudes of flights of small migratory species when crossing (A) the desert (Sahara Desert) and (B) the marine barriers (Mediterranean Sea and Bay of Biscay). Flight durations (in hours) are plotted against median altitudes (meters above sea level). Each dot represents a flight, colored by species. Yellow and gray bars represent diurnal (8:00–16:00 UTC) and nocturnal (20:00–4:00 UTC) segments included in analyses. For marine crossings, the thicker lines in the two altitude profiles denote flights over the sea. In (C), average values per species of median altitudes and flight durations are presented for both desert and marine crossings. Flight durations for sea crossings are not plotted because they are largely determined by geographical distance rather than bird behavior. Large dots represent species-averaged values, while small dots represent individual flights. Error bars represent standard deviation across individual flights. Silhouettes were downloaded from phylopic.org.

Table 2. Results of the mixed-effects models analyzing the influence of wing morphology and plumage color on flight behavior across different barriers (desert and marine barriers)

		Fixed effects				Random effects	
Barrier	Response	Variables	Est.	Std. Error	p.value	Variables	Est.
Desert	Median altitude	Intercept	1334,4	488,8	0.192	ind:sp:taxo	104028
		Aspect ratio	54,2	240,9	0.822	Season	432927
		Hand wing area	**658,0**	**229,1**	**0,006**	Residual	736081
		Lightness	118,1	236,6	0.619		
	Median altitude - night	Intercept	1282,8	460,9	0.186	ind:sp:taxo	72731
		Aspect ratio	−111,6	228,1	0.623	Season	384751
		Hand wing area	**825,8**	**214,4**	**<0,001**	Residual	739189
		Lightness	215,7	224,2	0.339		
	Median altitude - day	Intercept	3004,1	590,8	0.011	ind:sp:taxo	374163
		Aspect ratio	748,2	640,7	0.251	Season	335567
		Hand wing area	**2041,2**	**880,6**	**0,023**	Residual	141815
		Lightness	**−2438,4**	**651,1**	**<0,001**		
	Flight duration	Intercept	14,0	2,1	0.004	ind:sp:taxo	17,0
		Aspect ratio	2,8	2,5	0.267	Season	4,4
		Hand wing area	**−6,3**	**2,4**	**0,013**	Residual	49,3
		Lightness	0,2	2,4	0.939		
Marine	Median altitude	Intercept	994,3	244,0	<0.001	ind:sp:taxo	131969
		Aspect ratio	**843,2**	**341,9**	**0,021**	Residual	194347
		Hand wing area	**1431,8**	**334,6**	**<0,001**		
		Lightness	**−1851,8**	**389,8**	**<0,001**		

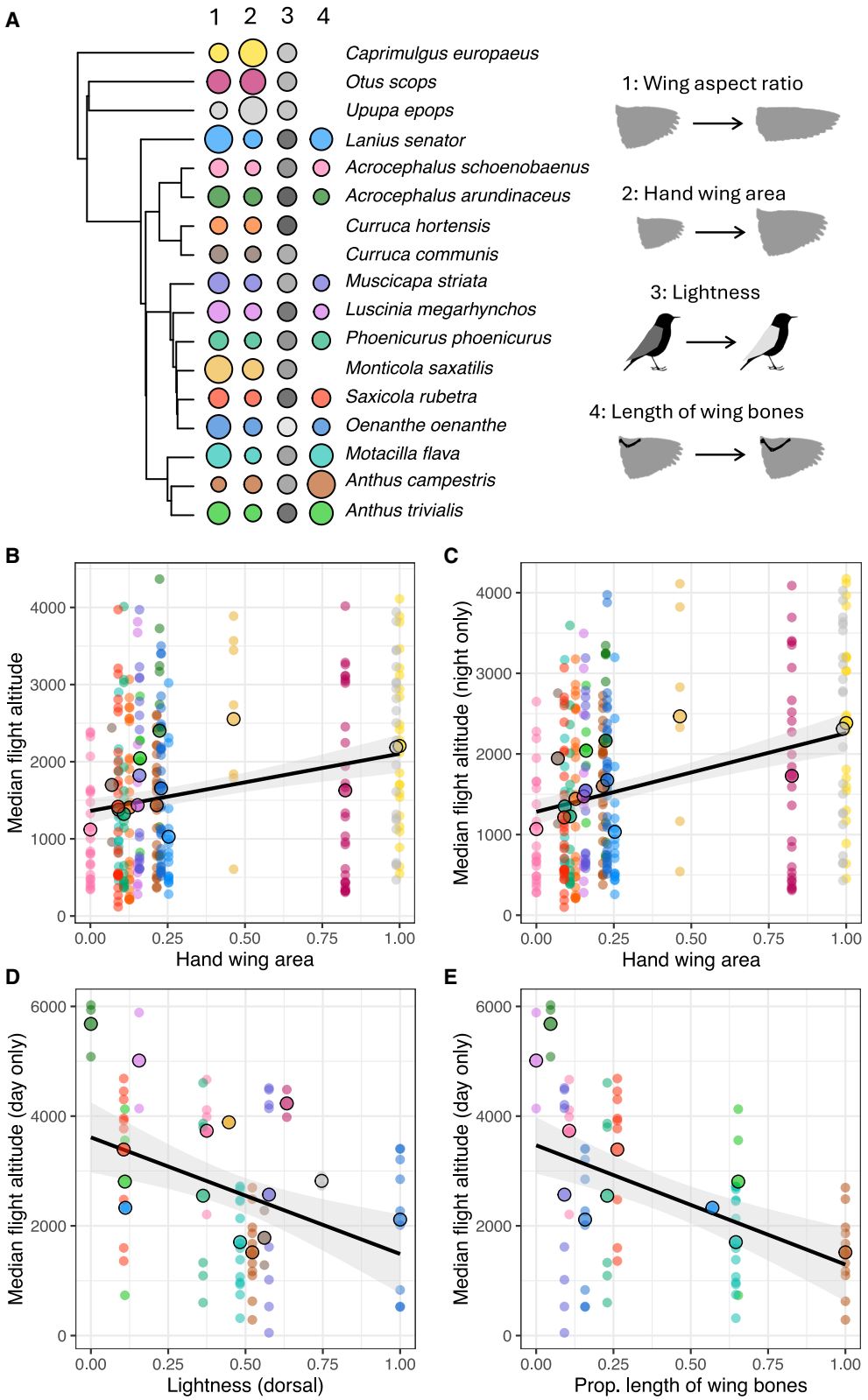
Fixed effects include aspect ratio, hand wing area, and lightness of the plumage, while random effects account for season, individual, species-level, and taxonomic (nested together as ind:sp:taxo) variation. Estimates (Est.), standard errors (Std. Error), and *p*-values (p.value) are reported for fixed effects, along with variance components for random effects. Significant effects ($p < 0.05$) are highlighted in bold.

less effort, enabling them to sustain flight at higher altitudes where the air is thinner.[29,47] Additionally, we found that the lightness of the plumage and the relative length of wing bones were negatively correlated with flight altitudes, considering the daytime period only. The results on plumage color confirm the prediction of Delhey et al.[33] that because darker birds absorb more solar radiation than lighter ones, they would tend to fly at higher altitudes to reach cooler conditions and mitigate excess heat from solar radiation. From another perspective, this may also suggest that plumage coloration in small migration landbirds has evolved in close association with the climatic conditions experienced during migration or outside the breeding season (as observed in *Larus* species[48]). The results on wing structure suggest, as hypothesized, that species with relatively shorter wing bones and potentially less vascularized wings may struggle to dissipate heat during prolonged flight and might compensate by flying at higher altitudes to cool down. It remains to be tested whether species with longer wing bones evolved this trait due to selection associated with barrier-crossing flights, and whether species with shorter bones may have evolved other mechanisms to cope with high-altitude flight. These ideas are highly speculative but suggest that wing structure likely plays a role in overcoming the heat-dissipation challenges that can occur during prolonged flights, as explained in.[32] Note that this relationship is currently based on a relatively small number of species and flight records and should therefore be interpreted with caution. We hope that new data on the wing structure and barrier crossing strategies of additional species will help confirm the generality of these findings. Altogether, these findings are consistent with the hypothesis proposed by Schmaljohann et al.[19] and tested using multi-sensor loggers by Sjöberg et al.,[21] suggesting that birds fly at higher altitudes during the daytime to reduce the thermal load from solar radiation.

Low altitude flights over marine areas

Among the 17 small, nocturnal migratory bird species, no single strategy emerged for crossing marine barriers, but we observed a frequent strategy among some species, in particular in *Oenanthe oenanthe*, to fly at very low altitudes, possibly just above the water's surface, especially during daytime.

Our data show that several birds traveling at these low altitudes quickly reach a constant altitude, which they maintain for most of their crossing. While near-water flights can theoretically save energy, particularly in situations of headwinds or crosswinds, where birds may exploit weaker winds close to the water surface, or by flying in ground effect, which reduces the aerodynamic cost of induced drag,[49] we cannot confirm that the birds were consistently close enough to the surface of the water to fully benefit from energy savings. The uncertainty of our altitude measurements limits how precisely we can determine the birds' proximity to the water. Nevertheless, near-water flights, especially during daytime, have been documented in other species,



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Table 3. Results of the mixed-effects models analyzing the influence of the relative length of wing bones on flight behavior during desert crossings

		Fixed effects				Random effects	
Barrier	Response	Variables	Est.	Std. Error	p.value	Variables	Est.
Desert	Median altitude	Intercept	1591,3	523,5	0.190	ind:sp:taxo	108980
		Length wing bones	−217,3	235,6	0.362	Season	524536
						Residual	585396
	Median altitude - night	Intercept	1431,9	506,6	0.204	ind:sp:taxo	110808
		Length wing bones	34,2	228,1	0.881	Season	491458
						Residual	487390
	Median altitude - day	Intercept	3387,7	500,5	0.039	ind:sp:taxo	345375
		Length wing bones	**−2128,9**	**523,0**	**<0,001**	Season	354813
						Residual	1408336

Random effects account for season, individual, species-level, and taxonomic (nested together as ind:sp:taxo) variation. Estimates (Est.), standard errors (Std. Error), and *p*-values (p.value) are reported for fixed effects, along with variance components for random effects. Significant effects ($p < 0.05$) are highlighted.

such as *Caprimulgus europaeus*,[17] where the authors suggested that flying near the water may be an adaptive strategy to reduce flight costs. Interestingly, we observe this behavior here in species whose flight styles are quite different from that of the nightjar (i.e., wagtails, pipits, or hoopoes). A possible explanation is that this low sea-crossing strategy has been selected, independently of the aerodynamic flight styles, to save energy, thereby also preventing overheating when these migratory birds cross large marine areas. An additional, non-mutually exclusive explanation is that darker-plumaged birds flying closer to the sea surface may experience reduced predation risk, as their plumage could render them more cryptic to raptors or gulls searching for prey from above. These hypotheses are highly putative at this stage and would require targeted testing to be confirmed; likewise, future studies with higher-resolution altitude measurements are needed to directly quantify energy savings from ground effect or wind interactions.

Interestingly, we found that variables included as fixed effects significantly predicted the median flight altitude during marine crossings. Both aspect ratio and hand-wing area (here used as a proxy for wing size) had a positive effect, while plumage lightness had a negative effect: a pattern similar to that observed during desert crossings, despite most marine flights occurring at night (with only some individuals continuing into daylight hours). We believe these results should be interpreted with caution, given the limited sample size (42 flights), and that additional data are needed to better understand the factors driving altitude variation during marine crossings. While we hypothesize that our findings (e.g., low-altitude flight over marine areas) may hold in other geographic contexts, this remains to be tested. Tracking birds crossing the Gulf of Mexico, for instance, would offer a valuable comparison because migratory flights in that region are typically longer and may involve different wind conditions and energetic demands than those over the Mediterranean Sea or the Bay of Biscay.[5]

Limitations of the study

Our study highlights substantial inter- and intra-specific variation in flight strategies across ecological barriers, with flight altitude influenced by wing morphology, wing structure, and plumage color. However, some limitations must be acknowledged. We were unable to directly test other important factors known to shape migration strategies, such as wind conditions and sex. Additionally, sample sizes, especially for marine crossings, were limited. The low-altitude flights observed over the sea, particularly during the day, are of particular interest, but understanding their drivers will require further data. Finally, while the use of multi-sensor geolocators greatly improves trajectory reconstruction, we acknowledge that some uncertainty remains. However, we believe its impact on our results is limited, as barrier crossings were classified based on the crossing of broad polygons rather than precise locations. Despite these limitations, our findings refine current hypotheses on barrier-crossing behavior and underscore the combined role of environmental and morphological drivers. Future studies incorporating broader taxonomic coverage, environmental data, and physiological measurements will be key to deepening our understanding of avian strategies in extreme environments.

Figure 3. Relationship between wing morphology, plumage color, wing structure, and flight altitude

The panel (A) shows a maximum clade credibility tree of the studied species, with colored circles whose size and shading represents variations of three morphological traits: (1) wing aspect ratio, (2) hand wing area, (3) lightness of the dorsal part of the plumage and (4) the relative length of wing bones (the absence of a point indicates a lack of available data). Note that the colors of the circles for wing aspect ratio, hand wing area, and relative length of wing bones indicate species identity (using the same colors as in the previous figures). The lower panels display scatterplots represent significant relationships (see Table 1 for other relationships). They link (B) the median flight altitude to hand wing area, (C) the median flight altitude of the night period to hand wing area, (D) the median flight altitude of the day period to the plumage lightness both, and (E) the median flight altitude of the day period to the relative length of wing bones, all during desert crossings. The black line represents the best-fit linear regression line, and the shaded gray area around the black line represents the confidence interval for the regression line. Large dots represent species-averaged values, while small dots represent individual flights.

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).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All data necessary to reproduce this publication have been deposited on Zenodo.[50] This includes all parameter values as well as labeled pressure, light, and activity data files required to reproduce the geolocator analyses. Additionally, a Supplementary Data file (BARRIERS_Supplementary_Data) is available online, providing details on the individuals equipped for this project, including dates and locations of capture, along with measurements taken at equipment and retrieval times.
- 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

Conceptualization, P.D.; survey and data, G.C., Y.C., P.D., T.D., C.d.F., B.J., F.J., F.R., R.M., S.T., and S.d.G.; methodology, P.D. and R.N.; visualization, P.D.; funding acquisition, P.B., J.C., O.D., and F.J.; writing – original draft, PD; writing – review and editing, all the authors.

DECLARATION OF INTERESTS

Authors declare no competing interests.[50]

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		
Raw and analyzed geolocator data	This paper	[50]
Details on captured and equipped individuals	This paper, supplementary data file	ISCIENCE-D-25-11093R3
Software and algorithms		
Rstudio	RStudio Team https://www.rstudio.com/	Rstudio 4.4.1
R package GeoPressureR	Nussbaumer,[37] Nussbaumer[38]	https://github.com/Rafnuss/GeoPressureR
R package lme4	Bates[51]	https://cran.r-project.org/web/packages/lme4/index.html
R package phylolm	Ho[52]	https://cran.r-project.org/web/packages/phylolm/index.html
Other		
Multi-sensor geolocators	Swiss Ornithological Institute	GDL3-PAM 1.2g
Multi-sensor geolocators	Migrate Technology Ltd, Cambridge, UK	CARP30Z11-7-DIP 0.6g

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Birds were captured and tagged under licenses delivered by the MNHN-CRBPO (reference program PP1190 Migralion and PP1245 Migratlane) and the British Trust for Ornithology, granted by the Special Marks Technical Panel (project code 2728). A Supplementary Data file (BARRIERS_Supplementary_Data), available online, also provides details on the individuals equipped for this project, including dates, locations of capture, along with sex (if determined) and measurements taken at equipment and retrieval times.

METHOD DETAILS

Geolocators and species data

For this study, 318 multi-sensor loggers were fitted on 17 species including 14 passerines and three non-passerines (see the list in Table 1) in different locations of France and the United-Kingdom (Figure S1) between 2021 and 2023. We used two types of loggers: 63 GDL3-PAM manufactured by the Swiss Ornithological Institute (1.2 g with harness) and 255 CARP30Z11-7-DIP manufactured by Migrate Technology (0.6 g with harness). The weight of the species tagged varied between 12 g for the smallest (*Acrocephalus schoenobaenus*) and 90 g for the heaviest (*Otus scops*) and the device always amounted to less than 5% of the body mass of the tagged birds. In the subsequent years, the same individuals have been recaptured to recover the tag. All birds in this study were breeding and experienced individuals that had completed at least one round-trip migration (see details in supplemental information). Previous studies have shown no detectable effects of geolocators on survival or migration performance,[53,54] and we therefore do not expect the loggers used here to have influenced the flight strategies examined in this study. However, it is important to note that our data necessarily come from individuals that successfully completed migration (and crossed ecological barriers), which may bias the sample towards the successful flight strategies and birds less affected by potential tagging costs.

All loggers recorded ambient light intensity, activity data, atmospheric pressure, and temperature. Birds were captured and tagged under licenses delivered by the MNHN-CRBPO (reference program PP1190 Migralion and PP1245 Migratlane) and the British Trust for Ornithology, granted by the Special Marks Technical Panel (project code 2728).

Description of barrier-crossing flights

To determine where, when and how each bird crossed the ecological barriers, we modelled the trajectory of each track following the approach presented in Nussbaumer et al.[38] and using the R package *GeoPressureR* (version 3.2). All steps needed to reproduce these estimates are described in the supplemental information. All data, code, and parameter values, including raw and labelled pressure, light, and activity data for each individual are available in.[50] This includes a *config.yml* file specifying individual settings such as deployment sites, crop dates, map extent and resolution, and the inclusion of wind or light data in movement model estimation.

We considered three barriers: the Sahara as a desert barrier (which can span up to 2,000 km) and the Mediterranean Sea and the Bay of Biscay as two marine barriers (respectively 500 – 800 km and 300 – 500 km). Using the most likely trajectory of each individual, we considered that a flight occurred over an ecological barrier if at least half of its duration happened within the polygon delimiting this barrier (see Figure S1). This threshold was chosen to ensure that most of the flight was meaningfully associated with the barrier environment, while accommodating potential uncertainty in trajectory estimation and barrier boundary delineation. Then, for each crossing flight, we extracted flight duration and median flight altitude, using barometric equation accounting for the pressure and temperature at ground level from the ERA 5 data at the most likely location. Altitude estimation is subject to different sources of uncertainty, including sensor resolution, biases in ERA5 reanalysis fields, and geolocation error. Together, these yield an expected error of approximately ±100 m.[15,38] In most cases, this level of uncertainty does not affect the biological interpretation of flight behavior. However, under certain conditions (e.g., rapidly changing weather systems, complex terrain, and/or flights close to sea level), this can result in implausible negative altitude estimates. Such cases do not reflect actual behavior but rather the propagation of atmospheric and positional uncertainty into the altitude estimates and should not be interpreted literally.

We also calculated the median flight altitude for the night (20:00 – 4:00 UTC) and the day periods only (8:00 – 16:00 UTC). These fixed UTC windows were chosen to standardize comparisons across all flights, since our dataset spans wide geographic ranges where local solar times vary considerably. By focusing on these ''core'' periods, we capture the biologically relevant nighttime and daytime phases of migration excluding twilight periods when birds are known to change their flight altitudes.[16,18] We identified prolonged flights into daytime as those lasting $\geq$14 hours, which almost always extend beyond 8:00 UTC. For prolonged flights, we also compared flight altitudes during night and day to test whether migrating birds tend to change altitudes between these periods. We used paired t-tests to assess whether the differences were statistically significant.

Flight altitude differences among species

To quantify interspecific variation in wing morphology, wing structure, and plumage color related to flight ability and altitude, we selected four explanatory variables: wing aspect ratio, hand-wing area, relative length of wing bones, and plumage lightness. We obtained both wing aspect ratio and hand-wing area data from,[29] wing structure data from[32] and plumage lightness from,[55] specifically focusing on the dorsal part of the bird, as it is the most exposed to solar radiation during migratory flights. For hand-wing area, we chose to use absolute values (and not relative to body size, e.g., wing loading) to capture general patterns in why some species fly higher than others, including the role of body size itself. For relative length of wing bones, we used the sum of humerus and ulna lengths divided by the length of the primary flight feathers (following the approach of[32]) as a proxy for the proportion of the wing that is vascularized. However, because data were available for only 11 of the 17 species included in this study, we analyzed this variable separately (see below). When sex-specific plumage lightness values were reported in,[55] we used the average value for the species to maintain consistency, especially since sex was not always determined for the individuals in our study (for species with no sex plumage dimorphism). Differences between sexes within species were generally small (median absolute difference = 0.107, range 0–0.445) compared with differences between species (median = 4.41, range 0.04–13.61), confirming that averaging sexes captures the dominant interspecific variation. We also verified the absence of collinearity between these variables (wing aspect ratio, hand-wing area, and plumage lightness) by using Variance Inflation Factors (VIFs). We found VIFs of 1.32 for hand-wing area and plumage lightness (i.e., well below the common threshold, $\leq$5), confirming the absence of problematic collinearity among predictors. We also acknowledge that not directly recording wing morphology on captured birds can be seen as a limitation of our study.

Before selecting our modelling approach, we tested for phylogenetic signal in the model residuals using phylogenetic generalized least squares (PGLS[56]). The estimated values of Pagel's λ were consistently low (Table S2), indicating little to no phylogenetic signal in the residual variance (see supplemental information). We therefore fitted linear mixed-effects models using the package *lme4*[57] using all individual flight records and adding season (spring vs. autumn), species, individuals and taxonomy (Passeriformes vs. non-Passeriformes) as random effects. The last three random effects were structured hierarchically, with individuals nested within species and species nested within taxonomic groups. For desert crossings, we tested separate models to assess how variables influenced median flight altitudes during the entire flight, night, and day periods, as well as flight duration, expecting different variables to affect flight behavior depending on the period. For marine crossings, we examined only the relationship between the explanatory variables and the median flight altitude of the entire flight, since flight duration is largely determined by where the crossing occurs, and because few individuals flew during daytime. For the wing structure (i.e., relative length of wing bones), we also fitted linear mixed-effects models to assess how this variable alone influenced median flight altitudes during the entire flight, night, and day periods for desert crossings and by using the same random effects. We limited this test to this variable only because of the limited amount of wing structure data available per species and, consequently, the number of flights to be tested.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses were performed in R (v4.2) using lme4 for linear mixed-effects models, GeoPressureR for trajectory reconstruction, and phylolm for phylogenetic tests. Sample sizes refer to the number of individual barrier-crossing flights (312 desert, 42

marine) and are reported in figure legends, Tables 1, 2, and 3, and Results. Flight altitudes and durations are summarized as median ± SD, and day–night differences were tested with paired t-tests. Predictors of flight altitude (wing morphology, plumage lightness) were assessed using hierarchical mixed-effects models with individuals nested in species and species nested in taxonomic groups. Relative wing bone length was analyzed in separate models due to limited data. Full statistical details, including exact sample sizes, test statistics, effect sizes, and measures of variability, are reported in figure legends, main text, and Tables S1 and S2.