Variations in flight strategy of small migratory birds crossing major ecological barriers

Paul Dufour[1,2], Raphaël Nussbaumer[3], Pierrick Bocher[4], Martins Briedis[3,5], Yannig Coulomb[3], Rose Delacroix[4], Thomas Dagonet[2], Christophe de Franceschi[1], Sophie de Grissac[6], Bastien Jeannin[2], Robin Monchatre[2], Fanny Rey[4], Stephan Tillo[2], Jocelyn Champagnon[2*], Olivier Duriez[1*], Frédéric Jiguet[6*]

[1]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[2]Tour du Valat, Research Institute for the Conservation of Mediterranean Wetlands, Le Sambuc, Arles, France
[3]Bird Migration Unit, Swiss Ornithological Institute, Sempach, Switzerland
[4]Laboratory Littoral Environnement Et Sociétés, UMR LIENSs 7266, CNRS-La Rochelle University, La Rochelle, France
[5]Lab of Ornithology, Institute of Biology, University of Latvia, Riga, Latvia
[6]CESCO, UMR7204 MNHN-CNRS-Sorbonne Université, France
[*]co-last authors

Corresponding author: Paul Dufour[1,2] paul.dufour80@gmail.com

Keywords: migration – birds – ecological barrier – flight dynamics – Sahara Desert – sea crossing – nocturnal migrants

Abstract

The recent development of tracking technologies has allowed to discover how small migratory birds cope with large ecological barriers such as seas and deserts, displaying remarkable behaviors like extreme diel flight altitude changes when crossing the Sahara Desert. However, the drivers and the prevalence of such behaviors among terrestrial migrants remain understudied. By deploying multi-sensor loggers on 59 individuals from 16 species in southern Europe, and using methods of geo-positioning integrating light, pressure, and activity data, we investigated where, when, and how small, nocturnal, migratory birds crossed two types of ecological barriers: two marine areas (the Bay of Biscay and the Mediterranean Sea) and one desert (the Sahara Desert). We found that sea crossings were often performed at very low altitude, close to sea level. Conversely, flights over the Sahara Desert typically reached median altitudes of 3000-4000 meters above sea level. These flights often lasted throughout the entire night (50% of the time) or extended up to 45 hours. Species with longer wings tended to cross the Sahara at higher altitudes. We also highlighted changes of flight altitudes between night and day in prolonged flights over the Sahara Desert in 13 species and showed that these changes do not correspond to the search for constant temperature conditions nor supporting winds. Nevertheless, during these flights, we found that birds tend to take advantage of supporting winds by flying at higher altitudes and make more significant changes of altitude when the air temperature is warmer. These changes in altitude, which coincide with sunrise, support the hypothesis that birds reach high altitudes during daytime to mitigate the effect of extra heating from solar radiation. Our study describes the flight strategies of several species crossing different types of ecological barriers and offers new insights into the dynamics of flight altitudes of small migratory birds crossing the Sahara Desert. It also confirms that the heat balance of a flying bird is complex, with several factors interacting, and calls for further research, including experimental studies, to unravel the role of each of these factors.

Introduction

Birds undertake some of the most spectacular annual migrations in the animal kingdom, with several billions of birds travelling twice a year, sometimes over tens of thousands of kilometers between their breeding and wintering grounds (Dokter *et al.* 2018). In the Palearctic-African migration system, it has been estimated that 2.1 billion of songbirds and near-passerines migrate each season between Europe and sub-Saharan Africa (Hahn et al. 2009), 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 (see Loonstra et al. 2019). Between Western Europe and sub-Saharan Africa, migratory birds can face the sea crossings of the Mediterranean Sea and/or the Bay of Biscay, and the crossing of the Sahara Desert which locally extends over 2000 kilometers. In some cases, birds can avoid and bypass these barriers, but under certain circumstances, they either choose or are forced to cross them.

How small migratory birds cross such large ecological barriers has long remained a mystery. 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 and that a fraction of these nocturnal migrants regularly extend their flight into the day when crossing large barriers such as the Sahara Desert (Biebach et al. 2000; Bruderer et al. 2018; Schmaljohann et al. 2007; Weisshaupt et al. 2018). Light patterns recorded by light-level geolocators then confirmed that prolonged flights extended during daytime are a common strategy among small migratory species when crossing large barriers (Adamík et al. 2016). Finally, the use of multi-sensor loggers, including temperature and pressure sensors, recently allowed to describe the duration of these flights as well as the flight altitudes more accurately (Briedis et al. 2020; Jiguet et al. 2019; Sjöberg et al. 2018). They revealed extremely high-altitude flights and diel cycles of flight dynamics during the Sahara crossing for different species (in *Acrocephalus arundinaceus* and *Upupa epops*; Liechti et al. 2018; Sjöberg et al. 2021) and conversely, flights near-water during the Mediterranean crossing (in *Caprimulgus europaeus*; Norevik et al. 2023).

To explain these crossing strategies, which involve extended flights during the day and changes in altitude during desert crossings, several hypotheses have been proposed. These hypotheses are related to factors such as predation, vision range, solar radiation, diel variation in ambient temperature, and wind support (Lindström et al. 2021; Sjöberg et al. 2021). Yet, few of them have been properly tested. In the context of landscape of fear (Gaynor et al. 2019), the predation hypothesis suggests that because migratory birds can face the predation of, e.g., *Falco eleonorae* when crossing the Mediterranean Sea and the Sahara Desert, it may have triggered changes of flight altitudes, above the hunting range of the falcons during daytime (Sjöberg et al. 2021; Xirouchakis & Panuccio 2019). The vision range hypothesis suggests flying higher during daytime may improve the search for suitable stop-over habitats (Sjöberg et al. 2021). Regarding solar radiation, Sjöberg et al. (2023) 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, they found that birds flying at the same altitude were warmer during the day that at night, suggesting that climbing during the day to colder altitudes might counterbalance the heating from solar radiation. In the same perspective, since birds seek

optimal temperature conditions during their migratory flight to maintain a constant body temperature (Liechti et al. 2000), it might be expected that variations of altitudes correspond to the tracking of the same temperature during their prolonged flight. Finally, it has been shown that migratory birds choose their flight altitudes according to the most favorable winds (Alerstam 1979; Liechti 2006; Senner et al. 2018) and we can therefore expect variations in altitudes during extended flight to correspond to the search for favorable wind conditions. These two hypotheses have not yet been tested. However, it has been suggested that because wind and temperature variations are supposedly small above 2000 meters (Wallace & Hartranft 1969), it is unlikely that these two factors are primary causes for the observed regular diel cycle in flight altitude (Sjöberg et al. 2023).

Given the complexity of flying birds, many factors and their interactions must still be understood to achieve an accurate heat balance for this model (Wolf & Walsberg 2000). Additionally, several other factors, such as wind, temperature, and plumage, may play a secondary role but have yet to be tested. In addition, our understanding is also limited by the difficulty of tracking small species and therefore of knowing their precise position during their migratory journey. Uncertainties of geolocation obtained from light-level geolocators are of the order of several hundreds of kilometers during migration (e.g., Cooper et al. 2017; Dufour et al. 2021), which make it difficult to assess the meteorological conditions encountered. Finally, our understanding is currently based on the study of a few species, and we can assume that physiological and morphometric variations between species may affect the species or even individual strategies to cross barriers (see Jiguet et al. 2019).

In this study, we analyzed data collected by multi-sensor loggers tracking sea and desert crossings by 59 individuals of 16 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. To do so, we used a recently developed method of geo-positioning integrating activity, light, and pressure data (Nussbaumer et al. 2023b, a) to accurately estimate where, when and how each individual crossed the different ecological barriers. Then, we tested whether differences in flight altitude recorded between species are related to morphometric differences (i.e., wing length, mass, wings aspect ratio). Third, we investigated the extreme diel flight altitude changes when crossing the Sahara Desert and especially those of prolonged flights over daytime. We extracted local meteorological conditions (i.e., windspeed, wind support, temperature) to question their influence on the observed variations in flight altitudes. We tested whether diel cycle of altitudes might correspond to a search of constant conditions of ambient air temperature or a search for optimal wind conditions and assessed whether the moment when the birds change altitude corresponds with the time of sunrise, i.e., when solar radiation can start affecting the bird's heat balance.

Materials and methods

Geolocators and species data

For this study, 290 multi-sensor loggers were fitted on 17 species including 14 passerines (*Lanius senator, Acrocephalus schoenobaenus, Acrocephalus arundinaceus, Curruca hortensis, Curruca communis, Muscicapa striata, Phoenicurus phoenicurus, Monticola*

saxatilis, Saxicola rubetra, Oenanthe Oenanthe, Luscina megarhynchos, Motacilla flava, Anthus trivialis, Anthus campestris) and three non-passerines (*Caprimulgus europaeus*, *Upupa epops*, and *Otus scops*) in different locations of southern and western France 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 227 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. Most devices were mounted using a leg-loop harness made with a stretchy elastic thread with a diameter depending on the size of the species (0.7 to 1.0 mm). Note that we used a tressed UV-proof thread for *Otus scops*, *Lanius senator*, *Caprimulgus europaeus,* and *Upupa epops*. All loggers recorded ambient light intensity, activity data, atmospheric pressure, and temperature. The GDL3-PAM loggers recorded pressure data at 5-minutes intervals and activity data every 30 minutes (Liechti et al. 2018). The CARP30Z11-7-DIP loggers recorded both pressure and activity data every 20 minutes. All birds were individually marked with a metal ring (mandatory) and an engraved color ring to facilitate their detection for recapture the following year. Different techniques, either spring traps or vertical mist nets, were used to catch the birds. All captured birds were equipped, measured (mass, wing length, tarsus length) before being released after ca. 10 min of handling. In the subsequent years, the same individuals have been recaptured to recover the tag. All details regarding the individuals equipped for this project, the location of capture, the dates and biometry (at equipment and retrieval time, if retrieved) are available in Supplementary Information. Birds were captured and handled with permission from the MNHN-CRBPO of France (reference program PP1190 Migralion and PP1245 Migratlane).

For comparative analysis, we collected from the literature, for each species, averaged morphometric data for four variables. Body mass, wing length and secondary length (i.e., length from the carpal joint to the tip of the first secondary) were extracted from AVONET (Tobias et al. 2022). Mean wingspan was obtained from Birds of the World (Billerman et al. 2022). Using the model proposed in (Howard et al. 2018), we calculated the total wing area and the wings aspect ratio, as the ratio between the square of the wingspan and the total wing area. To apply a phylogenetic correction, we constructed a phylogeny of the 16 species with a composite of bird phylogeny established by Prum et al. (2015) and a maximum clade credibility tree computed from 10,000 iterations of the Hackett backbone (Jetz et al. 2012), following the method of Cooney et al. (2017).

Geolocators data analyses

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. (2023b) and using the R package *GeoPressureR* (version 3.2; Nussbaumer & Gravey 2024). We briefly describe the main steps of the approach and refer the readers to Nussbaumer et al. (2023b) for further details regarding the implementation of the method.

First, we separated stationary and flight periods by manually labelling the geolocator pressure and activity measurements. Stationary periods were characterized by a limited variation in consecutive pressure measurements indicating an absence of change in altitude associated with a limited variation in consecutive activity measurements. Migratory flights

typically displayed a clear drop in atmospheric pressure, corresponding to altitude gain in-flight associated with consecutive high activity measurements (which forms a plateau of the same duration as the variation in pressure).

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. Note that we did not use light intensity data (and only atmospheric pressure) for the nocturnal species *Otus scops* and *Caprimulgus europaeus* due to poor quality data (individuals spending most of daytime under cover). 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 reanalysis dataset (spatial resolution: 0.5×0.5°) to produce a likelihood map of the geolocator's position (following the method of Nussbaumer et al. 2023a). 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. For the light-based maps, we calculated likelihood estimates following Nussbaumer et al. (2023a). We used an "in-habitat" calibration from the equipment and retrieval periods (as described in Lisovski et al. 2012; Lisovski & Hahn 2012) fitting the distribution of zenith angle with a kernel density estimation. The likelihood maps of twilights belonging to the same stationary period were aggregated with a log-linear pooling.

Finally, we constructed the trajectories of each bird following a Hidden Markov Model presented in Nussbaumer et al. (2023b). The observation model consisted of the likelihood maps generated from pressure and light 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. For all individuals, a low (flight) airspeed threshold of 20 km/h was used to account for potential short local or exploratory flights. Using this model, we generated (1) the marginal probability map of the position of each stationary period and (2) the most likely migration trajectory of the birds. All the data, code, and parameter values, including the labelled pressure, light and activity data of each individual, are available in Dufour & Nussbaumer (2024).

Description of barrier-crossing flights

In this study, we considered three barriers: the Sahara as a desert barrier and the Mediterranean Sea and the Bay of Biscay as two marine barriers. 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. For the limits of the Sahara Desert, we adopted the limits described in Brito et al. (2016) (see Figure 1). For crossings of the Mediterranean Sea, we considered both direct crossings from the south of France or the north of the Iberian Peninsula to the African continent, as well as crossings that included a stopover in the Balearic Islands. Both, autumn and spring, flights were considered in the study.

Then, for each crossing flights, 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. For the crossing of the Sahara Desert, we tested whether these two parameters varied between spring and autumn migration. We identified prolonged flight into daytime as flights lasting at least 14 hours (which generally corresponds to flights

extending after 8:00 UTC). For these prolonged flights, we also extracted the maximum flight altitude defined as the quantile 90 of altitude values and the amplitude of flight altitude defined as the difference between the quantile 10 and quantile 90 of altitude values. This amplitude value represents the typical extent of altitude variations, providing a particularly suitable metric to assess the change of flight altitude between day and night.

Flight differences among species

To explain differences of flight altitudes between species, we selected three variables potentially affecting flight altitude: 1) the wing length, 2) the body mass and 3) the wing aspect ratio. Aerodynamic theory showed that longer wings are more efficient for longer flights (Pennycuick 2008; see also Hedenström 2002; Weeks et al. 2020). Besides, the aspect ratio of the wing is also often considered as the single most important morphological predictor of the efficiency of long-distance flight (Pennycuick 2008; Taylor & Thomas 2014). Higher wing loading is associated with higher airspeeds in migratory birds, whereas low wing loading, and broad wings generate more lift (Alerstam et al. 2007). The mass and the wing length were highly correlated for our species (Correlation coefficient, r= 0.92) while the wing length and the aspect ratio were moderately correlated (r= 0.74) and we therefore kept only the wing length and the aspect ratio as explanatory variables in two separate models. Using the package *phylolm* (Tung Ho & Ané 2014), we fitted two different phylogenetic generalized least square (PGLS) models to test how the two explanatory variables were associated with the median flight altitudes (averaged per species), while controlling for phylogenetic relatedness with Pagel's λ lambda (Pagel 1999). Because some species never prolonged their flights during daytime and those which do, tend to fly higher during daytime (i.e., diel flight altitude changes), we repeated the analysis with two different variables: (1) the median flight altitudes for the entire flight and (2) the median flight altitudes only for the night-time part (20:00-4:00 UTC). As our sampling included Passeriformes and non-Passeriformes which have longer wings, we also repeated these tests excluding the three non-Passeriformes species.

Flight altitude dynamics in prolonged flights

Our second aim was to go further in understanding the diel flight altitude changes observed when crossing the Sahara Desert. Focusing on prolonged flights, we wanted to test three hypotheses: whether diel cycle of altitudes might correspond to 1) a search of constant conditions of ambient air temperature or 2) a search for optimal wind conditions; 3) whether changes of altitude correspond with the time of sunrise when solar radiation can start affecting the bird's heat balance. To do so, we extended the GeoPressureR package (version 3.2 and above) with the function *edge_add_wind* (https://raphaelnussbaumer.com/GeoPressureR/reference/edge_add_wind.html) to be able to retrieve environmental variable from ERA5 pressure level along a flight trajectory. More precisely this function interpolates the environmental variable (e.g., wind speed with *u* east-west and *v* north-south components, air temperature) from the original 4D ERA-5 grid (0.1° x 0.1° x 1h x 37 pre-defined pressure level) at the exact position (lat-lon-pressure level) of the most-likely trajectory. Note that the operation is similar to the existing retrieval of wind speed already implemented (Nussbaumer et al. 2023b) but allows for a most efficient and precise computation of the interpolation.

To test the first hypothesis, we compared the variance of temperature experienced by the bird with the variance of temperature if the bird had flown at a constant altitude (here using the median altitude of the first night; 20:00-4:00 UTC) and the variance of temperature at ground level. If birds seek for constant conditions of ambient air temperature during their prolonged flight, we expected the variance of the temperature experienced to be lower than the other two temperature variables (ground level and night-altitude level). We first compared the variance of these three temperature values and then performed simple linear regression models to test for correlations between the median temperature at ground level and the variance of temperature experienced, the maximum altitudes and the amplitude. Doing so, we tested whether the variation of altitude or altitude reached during prolonged flights was higher when the air is warmer.

To test for the second hypothesis, we compared the median wind support experienced by the bird with the median wind support at a constant altitude (again using the median altitude of the first night; 20:00-4:00 UTC) and at ground level. We computed the wind support from groundspeed and airspeed using the *windsupport* function in the GeoPressureR package. If bird adjust their altitude to optimize the use of windspeed, we expected the wind support to be stronger than the two other wind support. We also performed linear regression models to test if birds flying at higher altitudes or at more varying altitudes (using respectively the maximum altitude and the amplitude) tend to experience more wind support.

Finally, to test for the third hypothesis, we visually inspected the altitude profiles to filter out flights where there was a clear change in altitude between day and night. We estimated the time of sunrise with two values of solar depression angle (0° for sunrise/sunset, and -6° for civil twilight) at the exact location of the birds, using the *path2twilight* function in the GeoPressureR package. Hence, we calculated the difference of time between the time of sunrise (at 0° and -6°) and the time corresponding to the change of altitude (which we recorded manually from the data inspection). If bird change their altitude in response to solar radiation, we expected that this time difference would be centered around 0.

Results

A total of 59 multi-sensor loggers (6 GDL3-PAM and 53 CARP30Z11-7-DIP) were retrieved on 16 different species. None of the loggers were recovered for *Anthus trivialis*; one bird returned but was not recaptured. For the other species, number of loggers retrieved per species were variable (minimum of one logger retrieved for *Curruca communis*, *Monticola saxatilis* and *Caprimulgus europaeus*; maximum of 7 loggers for *Oenanthe oenanthe*) as well as retrieving rates (minimum of 7.1% in *Curruca communis*; maximum of 57.1% in *Otus scops*; 22.2% in average; see Supplementary Information for details with returning rates including birds seen with loggers but not recaptured). All retrieved loggers contained data but three stopped during the wintering period and only contained data for the autumnal migration period.

Analysis of the trajectories of all these individuals revealed 270 flights over the Sahara Desert and 39 flights over the Mediterranean Sea or the Bay of Biscay. The number of flights recorded per species over each of these barriers is presented in Figure 1. The distribution of these flights suggests that the migratory birds breeding in the west and south of France crossed the Sahara Desert exclusively in its western part. Twenty-eight of the tracked individuals have

crossed one of the two marine barriers, with three individuals making a stop in the Balearic Islands during their crossing of the Mediterranean Sea (Figure 1).

We found that both in spring and autumn, flights over the Sahara most frequently lasted the duration of the night, i.e., between 10 and 14 hours (50%; Figure 2A). Less frequently, flights were shorter (<10 hours; 30%) or extended beyond the first night for up to 45 hours (20%). No birds stopped during the second day, i.e. if the flight was extended beyond one night and one day, birds continued until at least the morning following the second night. We found that spring flights were performed on average at higher altitudes (2068 ± 979 meters above sea level, m asl) than autumn flights (1117 ± 896 m asl) and were more frequently prolonged during daytime, i.e., beyond 14 flight hours (35, 13%, flights in spring compared with 20, 7%, flights in autumn; Figure 2A), showing important diel flight altitude changes. The altitude profiles of all the extended flights (beyond 14 hours) when crossing the Sahara Desert are shown in Figure S1. For sea crossings, flights generally lasted between 10 and 20 hours, depending on the sea extent to cross (Figure 2B). In addition, several individuals performed flights at very low altitudes, close to the sea surface. We found that 21 of the 39 flights (54%) identified as sea crossing took place at a median altitude of less than 500 meters above sea level. In particular, *Oenanthe oenanthe* performed flights at an average altitude of 112 ± 137 m asl (n = 9 flights) and *Anthus campestris* at an average altitude of 572 ± 455 m asl (n = 8 flights). Furthermore, we found that crossing the Mediterranean Sea was a regular strategy for *Anthus campestris* or *Motacilla flava* (4 individuals out of the 5 *Anthus campestris* tracked and 3 individuals out of the 3 *Motacilla flava* tracked) while other species, like *Phoenicurus phoenicurus* breeding in same locations seem to never perform marine crossing. Note that two *Motacilla flava* performed a sea crossing flight which started in early morning (1:00 and 2:00 UTC; see Figure S2). The altitude profiles of all sea crossing flights when crossing the Mediterranean Sea or the Bay of Biscay are shown in Figure S2.

We found significant differences in flight altitudes between species when crossing the Sahara. For example, during nighttime, *Lanius senator* flew at lower altitudes (1033 ± 796 m asl, n = 17 flights) than *Otus scops* (1730 ± 1246 m asl, n = 26 flights), which also flew at lower altitudes than *Acrocephalus arundinaceus* or *Monticola saxatilis* (2165 ± 1231 m asl, n = 9 flights and 2466 ± 1420 m asl, n = 6 flights respectively). The median flight altitude per species during the night was significantly correlated with wing length (Figure 3, Table 1), but not with the wing's aspect ratio (Table 1). By reproducing this test (1) with the flights in their entirety (i.e., including night and day altitudes) and (2) excluding the non-Passeriformes species, we found the same positive significant relationship between flight altitudes and wing length (see Table 1).

Focusing on the 55 extended flights identified, we found important differences between species in maximum altitudes and amplitude of flight altitudes variations between night and day (Figure 4). Some species reached very high altitudes during these prolonged flights (maximum recorded of 5910 m asl in *Luscinia megarhynchos*, 6638 m asl in *Acrocephalus arundinaceus*) but variations between night and day varied between species (2308 m of difference on average in *Luscinia megarhynchos* vs. 4274 m in *Acrocephalus arundinaceus*).

We found a significant difference between the variance of experienced temperature and the variance of temperatures at constant altitude and at ground level (Figure 4E), suggesting that birds performing diel flight altitude changes do not seek for constant conditions of ambient

air temperature (Figure 4E). In fact, birds changing altitudes experienced important changes in temperatures, and apparently experienced more important changes in temperatures (i.e., higher values of variance of temperature experienced) when the ground air temperature is higher (estimate, est. = 0.03; standard error, SE = 0.01; p-value = 0.003; Figure 4F). We also found a positive albeit less-significant relationship between the temperature at ground level and the maximum altitude (est. = 0.001; SE= <0.001; p = 0.037) or amplitude (est. = 54.6; SE = 28.74; p = 0.063). Similarly, birds did not experience better wind support conditions with their changes of altitudes than if they had remained at a constant altitude. However, they experienced more favorable wind conditions than if they had been flying at ground level (Figure 4G). We found no relationship between experienced wind support and maximum flight altitude (est. = -6.34; SE = 48.23; p = 0.89) or amplitude (est. = -23.88; SE = 39.50; p = 0.54). Finally, we found that changes in altitude between night and day generally started at sunrise (Figure 5). Of the 25 flights identified, we found that the change in altitude occurred on average 20 ± 91 minutes before sunrise when considering a depression angle of 6 degrees (i.e., corresponding to civil twilight), and on average 43 ± 91 minutes before sunrise when considering an angle of 0° (Figure S3).

Discussion

Small migratory birds crossing marine areas

We did not identify a common strategy for crossing marine areas across the 16 studied bird species. Our findings highlight two main points. First, there is significant variation in the duration of sea crossings, likely influenced by the distance to be covered and adverse weather conditions during the flight, although we do not have enough precision in the geopositioning to disentangle these two hypotheses. Second, small migratory birds exhibit variability in their flight altitudes when crossing marine areas. However, we observed a consistent strategy among several species to fly at very low altitudes, often near the water surface. This low-altitude flight strategy is particularly common in species such as *Anthus campestris* and *Oenanthe oenanthe*, which systematically flew near the water surface. In contrast, *Acrocephalus schoenobaenus* demonstrated more variable flight altitudes, ranging from low over the water to heights up to 2000 meters above sea level. Within the Motacillidae family, we found that *Motacilla flava* tends to fly at higher altitudes above water compared to *Anthus campestris*, despite both species having similar morphometrics and employing a similar bounding and undulating flight style.

Unlike larger migratory species, especially soaring species that gain altitude before crossing and gradually lose altitude during their crossing (see Santos et al. 2020), our data show that small migrants traveling at low altitudes quickly reach a constant altitude near the water, which they maintain for most of their crossing. Norevik et al. (2023) found a similar behavior of very low altitude flight during the daytime in *Caprimulgus europaeus* and suggested that this behavior could substantially reduce flight costs. They explained that near-water flights could save energy, particularly in situations of headwinds or crosswinds, where birds can mitigate these effects by flying in weaker winds close to the water surface (Finn et al. 2012) or by flying in ground effect, where the aerodynamic cost associated with induced drag is considerably reduced (Johansson et al. 2018). As the authors noted, these low-altitude flights are the opposite of the very high-altitude flights observed over land or desert, indicating that the hypotheses of improved vision or escape from predation do not apply here. Furthermore, it is interesting to

note that we observed this behavior in several passerine species that use different flight techniques (constant flapping or bounding flight) compared to *Caprimulgus europaeus*, which can alternate flapping phases with less costly phases of gliding. It is thus possible that this behavior has been selected to save energy, thereby preventing overheating when these migratory birds cross large marine expanses. However, further research is needed to understand why there are marked differences in flight strategies between species of the same family (e.g., *Anthus campestris* vs. *Motacilla flava*) and to explore why some species more regularly adopt marine crossings than others, even within the same family (e.g., *Oenanthe oenanthe* vs. *Phoenicurus phoenicurus*).

Interspecific variation of crossing strategies of the Sahara Desert

Our results show that crossing the Sahara varies greatly from one species to another. Firstly, in terms of the duration of the flights: some species frequently extend their flights during the day (and even over multiple days), while others systematically stop after (or during) the first night (see Adamík et al. 2016; Jiguet et al. 2019; Ouwehand & Both 2016; Sjöberg et al. 2021). Some species might be less strict in terms of their stopover habitats. For example, *Curruca hortensis* never prolongs nocturnal flights during the day and might be keen on stopping in wadis with acacia trees, which it frequents extensively during spring migration in the western part of the Sahara (Zwarts et al. 2023). This is also the case for species like *Acrocephalus schoenobaenus* or *Lanius senator*, which migrate close to the Atlantic coast during their autumn migration. Other species, such as *Oenanthe oenanthe*, *Monticola saxatilis*, and *Anthus campestris*, also make relatively short flights during the crossing. We can assume that these species, adapted to open, dry environments, are more flexible in coping with the conditions they encounter in the Sahara. In contrast, species that frequently extend their flights, such as *Acrocephalus arundinaceus* or *Muscicapa striata*, might either have physiological capacities for long endurance flights or face more restrictive stopover habitat requirements, making it difficult to find suitable habitats when crossing the desert.

Regarding flight altitude, we found important differences in the median altitude among species. Several species reached unsuspected altitudes, such as *Otus scops*, *Acrocephalus schoenobaenus* or *Saxicola rubetra*, which all flew higher than 4,000 m during their daytime crossing of the Sahara. In addition, among the species that prolong their flights during the day, there are major differences in maximum altitude and amplitude. *Anthus campestris* and *Motacilla flava*, for example, frequently extended their flights but remained at altitudes of around 2,000-3,000 m during the day, which are slightly higher than the flight altitudes at night. Conversely, both *Acrocephalus arundinaceus* and *A. schoenobaenus* climb to high altitudes during daytime, between 3,000-4,000 m higher than during night. Our results also show that species with the longest wings fly higher on average than others and did not show any significant relationship with aspect ratio, suggesting that species with greater flight abilities can also reach higher altitudes more easily (Alerstam et al. 2007). We expected species with low wing loading and broad wings, such as *Upupa epops*, to have higher climb rates and therefore fly at higher altitudes on average (see Liechti et al. 2018). However, our species sampling and the low number of individuals for some species may not be sufficient to properly test this hypothesis.

Diel flight altitude changes over the Sahara Desert

We found that many species extend their flights into the daytime when crossing the Sahara and that in most cases, a significant change in altitude occurs between night and day as showed in Sjöberg et al. (2021). Our results show that birds would experience more constant temperatures if they flew at a constant altitude (the same as at night) or if they stayed near the ground, suggesting that they do not seek constant temperature conditions by varying their altitude between night and day. Similarly, birds did not experience better wind support conditions with their altitude changes compared to remaining at a constant altitude. However, they benefit from favorable winds by flying higher than at ground level. We also demonstrated that birds tend to vary their altitudes more when the ground-level air temperature is higher, suggesting that their flight behavior might be influenced by air temperature. A possible explanation is that higher radiation is associated with higher temperature on the ground, so the bird moves more in the air column to compensate. Finally, we showed that significant altitude changes between day and night occur near dawn, suggesting that these changes correspond with the time when solar radiation starts to affect the birds' heat balance. All these findings support the general idea proposed by Sjöberg et al. (2023) that birds fly at higher altitudes during the daytime to mitigate the effects of additional heating from solar radiation. Nonetheless, our results suggest that other secondary factors likely influence flight strategies during the Sahara crossing, and there is no single hypothesis to explain these varying behaviors. It is possible that birds seek favorable wind conditions over short periods, even if these altitude variations are negligible compared to the overall pattern of diel altitude change. Similarly, altitude variations between night and day may be more pronounced if birds migrate during hotter periods. Our understanding of ecological barrier crossing strategies in small migratory birds remains incomplete, but these findings suggest that the different hypotheses are not necessarily mutually exclusive. Further research involving more species and integrating experimental studies should help to identify the limiting factors of bird flight and determine if trade-offs are sought by individuals, likely varying according to species and morphometrics.

Perspectives and conclusions

In this study, we focused on crossings occurring in the western part of the Sahara Desert. Sokolovskis et al. (2023) demonstrated, using light-level loggers, that the diurnal migration patterns of *Phylloscopus trochilus* differ between their western and eastern flyways across the Sahara. It is therefore possible that the crossing strategies identified here in small nocturnal migrants vary between different parts of the Sahara and that our results only apply to the western regions. In the same perspective, it has been suggested that *Cuculus canorus* crossing the western Sahara have better survival rates than those crossing the central parts (Hewson et al. 2016). Likewise, extremely few migrants are observed in the interior of the Sahara in Chad, specifically in the wadis of the Tibesti mountains (Guichard 1955). This may suggest that certain areas are avoided by migrants or that birds more systematically prolong their flights when crossing specific parts of the Sahara.

The loggers we used for this study also have a temperature sensor, but we chose not to use or interpret these data. As also discussed in Jiguet et al. (2019), we suspected that the temperature measured by the loggers is a combination of air temperature and bird body temperature. The temperatures recorded were most often between 30 and 40 degrees Celsius,

with significant variations between and within species. Yet, the body temperature of birds is supposed to be around 40 degrees Celsius (Schmidt-Nielsen 1994), and the ambient air temperature above 3000 meters is usually negative. Additionally, the significant differences we found between individuals of the same species suggest that the way the sensor is attached on the back—whether more or less covered by feathers, and before or after molting of the body feathers—affects the data collected. We believe that experimental tests comparing the bird's body temperature with that measured by the logger need to be conducted before these data can be interpreted, even in terms of relative variations. This is particularly important in the context of comparative analyses involving a large number of different species.

To conclude, our study describes the flight strategies of several species crossing different types of ecological barriers. Our results show that both the low-altitude flight near water and the very high-altitude flight with diel flight altitude changes above the Sahara Desert are regular strategies among small nocturnal migratory birds. They also provide new insights into the dynamics of flight altitudes of small migratory birds crossing the Sahara Desert and confirm that the heat balance of a flying bird is complex, with several factors interacting. Finally, our study calls for further research integrating new taxonomic groups, new migration strategies (mostly diurnal migrants such as swallows) and experimental studies to enhance our understanding of the evolution of migration strategies over ecological barriers.

Acknowledgements:

Barbara Helm, Felix Liechti and Steffen Hahn for discussions in earlier stages of the project development. Mathieu Gravey for his help developing the GeoPressureR package for the analysis of this study. Thibaut Lacombe for his help to deploy and retrieve the loggers. This study is part of the Migralion and Migratlane projects, which are founded by the Office Français de la Biodiversité (OFB).

References:

Adamík, P., Emmenegger, T., Briedis, M., Gustafsson, L., Henshaw, I., Krist, M., *et al.* (2016). Barrier crossing in small avian migrants: individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy. *Sci Rep*, 6, 21560.

Alerstam, T. (1979). Optimal use of wind by migrating birds: Combined drift and overcompensation. *J Theor Biol*, 79, 341–353.

Alerstam, T., Rosén, M., Bäckman, J., Ericson, P.G.P. & Hellgren, O. (2007). Flight Speeds among Bird Species: Allometric and Phylogenetic Effects. *PLoS Biol*, 5, e197.

Biebach, H., Biebach, I., Friedrich, W., Heine, G., Partecke, J. & Schmidl, D. (2000). Strategies of passerine migration across the Mediterranean Sea and the Sahara Desert: a radar study. *Ibis*, 142, 623–634.

Billerman, S.M., Keeney, B.K., Rodewald, P.G. & Schulenberg, T.S. (2022). *Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA.*

Briedis, M., Beran, V., Adamík, P. & Hahn, S. (2020). Integrating light-level geolocation with activity tracking reveals unexpected nocturnal migration patterns of the tawny pipit. *J Avian Biol*, 51.

Brito, J.C., Tarroso, P., Vale, C.G., Martínez-Freiría, F., Boratyński, Z., Campos, J.C., *et al.* (2016). Conservation Biogeography of the Sahara-Sahel: additional protected areas are needed to secure unique biodiversity. *Divers Distrib*, 22, 371–384.

Bruderer, B., Peter, D. & Korner-Nievergelt, F. (2018). Vertical distribution of bird migration between the Baltic Sea and the Sahara. *J Ornithol*, 159, 315–336.

Cooney, C.R., Bright, J.A., Capp, E.J.R., Chira, A.M., Hughes, E.C., Moody, C.J.A., *et al.* (2017). Mega-evolutionary dynamics of the adaptive radiation of birds. *Nature*, 542, 344–347.

Cooper, N.W., Hallworth, M.T. & Marra, P.P. (2017). Light-level geolocation reveals wintering distribution, migration routes, and primary stopover locations of an endangered long-distance migratory songbird. *J Avian Biol*, 48, 209–219.

Dokter, A.M., Farnsworth, A., Fink, D., Ruiz-Gutierrez, V., Hochachka, W.M., La Sorte, F.A., *et al.* (2018). Seasonal abundance and survival of North America's migratory avifauna determined by weather radar. *Nat Ecol Evol*, 2, 1603–1609.

Dufour, P., de Franceschi, C., Doniol-Valcroze, P., Jiguet, F., Guéguen, M., Renaud, J., *et al.* (2021). A new westward migration route in an Asian passerine bird. *Current Biology*, 31, 5590-5596.e4.

Dufour, P. & Nussbaumer, R. (2024). Data and codes from: Variations in flight strategy of small migratory birds crossing major ecological barriers [Data set].

Finn, J., Carlsson, J., Kelly, T. & Davenport, J. (2012). Avoidance of headwinds or exploitation of ground effect-why do birds fly low? *J Field Ornithol*, 83, 192–202.

Gaynor, K.M., Brown, J.S., Middleton, A.D., Power, M.E. & Brashares, J.S. (2019). Landscapes of Fear: Spatial Patterns of Risk Perception and Response. *Trends Ecol Evol*, 34, 355–368.

Guichard, K.M. (1955). The birds of Fezzan and Tibesti. *Ibis*, 97, 393–424.

Hahn, S., Bauer, S. & Liechti, F. (2009). The natural link between Europe and Africa – 2.1 billion birds on migration. *Oikos*, 118, 624–626.

Hedenström, A. (2002). Aerodynamics, evolution and ecology of avian flight. *Trends Ecol Evol*, 17, 415–422.

Hewson, C.M., Thorup, K., Pearce-Higgins, J.W. & Atkinson, P.W. (2016). Population decline is linked to migration route in the Common Cuckoo. *Nat Commun*, 7, 12296.

Howard, C., Stephens, P.A., Tobias, J.A., Sheard, C., Butchart, S.H.M. & Willis, S.G. (2018). Flight range, fuel load and the impact of climate change on the journeys of migrant birds. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20172329.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012). The global diversity of birds in space and time. *Nature*, 491, 444–448.

Jiguet, F., Burgess, M., Thorup, K., Conway, G., Arroyo Matos, J.L., Barber, L., *et al.* (2019). Desert crossing strategies of migrant songbirds vary between and within species. *Sci Rep*, 9, 20248.

Johansson, L.C., Jakobsen, L. & Hedenström, A. (2018). Flight in Ground Effect Dramatically Reduces Aerodynamic Costs in Bats. *Current Biology*, 28, 3502-3507.e4.

Liechti, F. (2006). Birds: blowin' by the wind? *J Ornithol*, 147, 202–211.

Liechti, F., Bauer, S., Dhanjal-Adams, K.L., Emmenegger, T., Zehtindjiev, P. & Hahn, S. (2018). Miniaturized multi-sensor loggers provide new insight into year-round flight behaviour of small trans-Sahara avian migrants. *Mov Ecol*, 6, 19.

Liechti, F., Klaassen, M. & Bruderer, B. (2000). Predicting Migratory Flight Altitudes by Physiological Migration Models. *Auk*, 117, 205–214.

Lindström, Å., Alerstam, T., Andersson, A., Bäckman, J., Bahlenberg, P., Bom, R., *et al.* (2021). Extreme altitude changes between night and day during marathon flights of great snipes. *Current Biology*, 31, 3433-3439.e3.

Lisovski, S. & Hahn, S. (2012). G eo L ight - processing and analysing light-based geolocator data in R. *Methods Ecol Evol*, 3, 1055–1059.

Lisovski, S., Hewson, C.M., Klaassen, R.H.G., Korner-Nievergelt, F., Kristensen, M.W. & Hahn, S. (2012). Geolocation by light: accuracy and precision affected by environmental factors. *Methods Ecol Evol*, 3, 603–612.

Loonstra, A.H.J., Verhoeven, M.A., Senner, N.R., Both, C. & Piersma, T. (2019). Adverse wind conditions during northward Sahara crossings increase the in-flight mortality of Black-tailed Godwits. *Ecol Lett*, 22, 2060–2066.

Norevik, G., Åkesson, S. & Hedenström, A. (2023). Extremely low daylight sea-crossing flights of a nocturnal migrant. *PNAS Nexus*, 2, pgad225.

Nussbaumer, R. & Gravey, M. (2024). GeoPressureR: Global Positioning by Atmospheric Pressure (v3.2.0).

Nussbaumer, R., Gravey, M., Briedis, M. & Liechti, F. (2023a). Global positioning with animal-borne pressure sensors. *Methods Ecol Evol*, 14, 1104–1117.

Nussbaumer, R., Gravey, M., Briedis, M., Liechti, F. & Sheldon, D. (2023b). Reconstructing bird trajectories from pressure and wind data using a highly optimized hidden Markov model. *Methods Ecol Evol*, 14, 1118–1129.

Ouwehand, J. & Both, C. (2016). Alternate non-stop migration strategies of pied flycatchers to cross the Sahara desert. *Biol Lett*, 12, 20151060.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884.

Pennycuick, C.J. (2008). *Modelling the Flying Bird.* . Elsevier Academic Press, Amsterdam and London.

Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Lemmon, E.M., *et al.* (2015). A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature*, 526, 569–573.

Santos, C.D., Silva, J.P., Muñoz, A., Onrubia, A. & Wikelski, M. (2020). The gateway to Africa: What determines sea crossing performance of a migratory soaring bird at the Strait of Gibraltar? *Journal of Animal Ecology*, 89, 1317–1328.

Schmaljohann, H., Liechti, F. & Bruderer, B. (2007). Daytime passerine migrants over the Sahara — are these diurnal migrants or prolonged flights of nocturnal migrants? *Ostrich*, 78, 357–362.

Schmidt-Nielsen, K. (1994). *Animal Physiology: adaptation and environment.* . Cambridge University Press, Cambridge.

Senner, N.R., Stager, M., Verhoeven, M.A., Cheviron, Z.A., Piersma, T. & Bouten, W. (2018). High-altitude shorebird migration in the absence of topographical barriers: avoiding high air temperatures and searching for profitable winds. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20180569.

Sjöberg, S., Andersson, A., Bäckman, J., Hansson, B., Malmiga, G., Tarka, M., *et al.* (2023). Solar heating may explain extreme diel flight altitude changes in migrating birds. *Current Biology*, 33, 4232-4237.e2.

Sjöberg, S., Malmiga, G., Nord, A., Andersson, A., Bäckman, J., Tarka, M., *et al.* (2021). Extreme altitudes during diurnal flights in a nocturnal songbird migrant. *Science (1979)*, 372, 646–648.

Sjöberg, S., Pedersen, L., Malmiga, G., Alerstam, T., Hansson, B., Hasselquist, D., *et al.* (2018). Barometer logging reveals new dimensions of individual songbird migration. *J Avian Biol*, 49.

Sokolovskis, K., Caballero-Lopez, V., Åkesson, S., Lundberg, M., Willemoes, M., Zhao, T., *et al.* (2023). Diurnal migration patterns in willow warblers differ between the western and eastern flyways. *Mov Ecol*, 11, 58.

Taylor, G. & Thomas, A. (2014). *Evolutionary biomechanics: Selection, phylogeny and constraint. Oxford Series in Ecology and Evolution.* Oxford University Pres.

Tung Ho, L. si & Ané, C. (2014). A Linear-Time Algorithm for Gaussian and Non-Gaussian Trait Evolution Models. *Syst Biol*, 63, 397–408.

Wallace, J.M. & Hartranft, F.R. (1969). Diurnal wind variations, surface to 30 km. *Mon Weather Rev*, 97, 446–455.

Weeks, B.C., Willard, D.E., Zimova, M., Ellis, A.A., Witynski, M.L., Hennen, M., *et al.* (2020). Shared morphological consequences of global warming in North American migratory birds. *Ecol Lett*, 23, 316–325.

Weisshaupt, N., Dokter, A.M., Arizaga, J. & Maruri, M. (2018). Effects of a sea barrier on large-scale migration patterns studied by a network of weather radars. *Bird Study*, 65, 232–240.

Wolf, B.O. & Walsberg, G.E. (2000). The Role of the Plumage in Heat Transfer Processes of Birds. *Am Zool*, 40, 575–584.

Xirouchakis, S.M. & Panuccio, M. (2019). Hunting Altitude of Eleonora's Falcon (Falco eleonorae) Over a Breeding Colony. *Journal of Raptor Research*, 53, 56.

Zwarts, L., Bijlsma, R.G. & Kamp, J. van der. (2023). Savannah Trees Attract More Migratory Bird Species Than Residents, But Why? *Ardea*, 111.

Tables

Table 1.

Results of Phylogenetic Generalized Least Squares (PGLS) analyses modelling the effect of wing length and wings aspect ratio with the average median altitude per species (during nighttime or during night and daytime). Variables with significant p-values at $p < 0.05$ are indicated in bold.

Model	Response	Variables	Est.	Std Error	p.value	lambda
All species	Median altitude (night only)	Intercept	325.8	886.3	0.719	<0.001
		Aspect ratio	203.3	133.4	0.150	
		Intercept	599.7	294.3	0.061	<0.001
		Wing length	**10.7**	**2.8**	**0.002**	
	Median altitude	Intercept	461.4	890.9	0.612	<0.001
		Aspect ratio	186.2	134.9	0.187	
		Intercept	743.7	321.6	0.036	<0.001
		Wing length	**9.3**	**3.8**	**0.008**	
Passeriformes only	Median altitude (night only)	Intercept	423.4	2207.2	0.851	<0.001
		Aspect ratio	177.2	348.6	0.621	
		Intercept	-669.5	522.7	0.226	0.75
		Wing length	**24.5**	**5.2**	**0.001**	
	Median altitude	Intercept	-21.1	2331.5	0.992	<0.001
		Aspect ratio	255.3	368.0	0.501	
		Intercept	-650.4	569.3	0.277	0.70
		Wing length	**28.7**	**6.9**	**0.002**	

Figure captions

Figure 1.
Total number of flights recorded per species when crossing (A) the Sahara Desert and (B) the Mediterranean Sea and the Bay of Biscay. The number of loggers retrieved per species is indicated between brackets. Each flight is represented on the maps by a gray line and a colored dot indicating the previous stop-over location. The color indicates the species. On the right panels, the orange polygon represents the limits of the Sahara Desert, while the blue polygons represent the limits of the Mediterranean Sea and the Bay of Biscay. We considered that a flight occurred over an ecological barrier if at least half of it occurs within the polygon delimiting this barrier (see Methods for details).

Figure 2.
Flight durations against flight median altitudes (in meters above sea-level) during the crossing of two types of ecological barriers: (A) the Sahara Desert as a desert barrier and (B) the Mediterranean Sea and the Bay of Biscay as two marine barriers. Each dot represents a flight, and the color indicates the species (the same colors as in Figure 1). Several examples illustrate the variation of altitude recorded in individuals of different species when crossing the barrier. In (A), we distinguished between flights during autumn and spring migration. The dotted line highlights flights prolonged beyond 14 hours. In (B), thicker lines delimit the flight over the marine barrier. Flights across the Mediterranean Sea can be full crossing or interrupted crossing with a stop-over in the Balearic Islands. On each panel, yellow and gray bars indicate parts of the flights that are included in the analyses as diurnal (8:00-16:00 UTC) or nocturnal (20:00-4:00 UTC). Silhouettes were downloaded from phylopic.org.

Figure 3.
(A) A maximum clade credibility tree of the 16 species tracked in this study with their wing length and wings aspect ratio measurements. Values were log-transformed to highlight differences between species. (B) Relationship between wing length and median flight altitude at night only (20:00-4:00 UTC) averaged per species. (C) Relationship between wing length and median flight altitude averaged per species. In both scatter plots, each dot represents a species, the black line represents the best-fit linear regression line and the shaded grey area around the black line represents the confidence interval for the regression line. P-values are indicated in both plots.

Figure 4.
Diel flight altitude changes when crossing the Sahara Desert during prolonged flights. The panel (A) represents an example of prolonged flights showing important diel flight altitude changes between night and day, here for an individual of *Luscinia megarhynchos*. The blue line indicates the median altitude of the first night and the red line schematizes the altitude at ground-level. In (B), the black line represents the temperature experienced along the flight by this individual, while the blue line represents the temperature that the bird would have experienced if it had flown at a constant altitude (i.e., the median altitude of the first night, 20:00-4:00 UTC). The red line represents the temperature that the bird would have experienced if it had flown at

ground level. The panel (C) is the same representation than in (B) but with wind support instead of temperature. In (D), we summarized the maximum altitude and the amplitude value (see Methods for details about these variables) for all individuals which performed prolonged flights. In (E), we compared for all flights the variance between the temperature experienced by the bird along the flight, with the variance of temperature if the bird had flown at a constant altitude and or at ground level. Asterisks denotes significant differences from pairwise comparison against all groups (p-value < 0.001). Panel (F) represents the relationship between the variance experienced by each individual along their flight and the median temperature at ground level. Each dot represents a flight, the black line represents the best-fit linear regression line and the shaded grey area around the black line represents the confidence interval for the regression line. In (G), we compared for all flights the median wind support experienced with the wind support that the bird would have experienced if it had flown at constant altitude or at ground level. Asterisks denotes significant differences from pairwise comparison against the first group (here WS exp; p-value < 0.01). "ns" means non-significant.

Figure 5.

Analyses of diel flight altitude changes in relation to sunrise. The panel (A) represents the same example of prolonged flights showing important diel flight altitude changes between night and day. The zoomed panel highlights the time of change of altitude, here estimated from the point of lowest altitude, and the sunrise (at civil twilight), estimated at the location of the bird with the function *path2twilight.* The panel (B) represents a histogram with the difference of time in minutes between the sunrise estimation and the change of altitude for 25 different prolonged flights showing a clear change in altitude between day and night.

Fig. 1

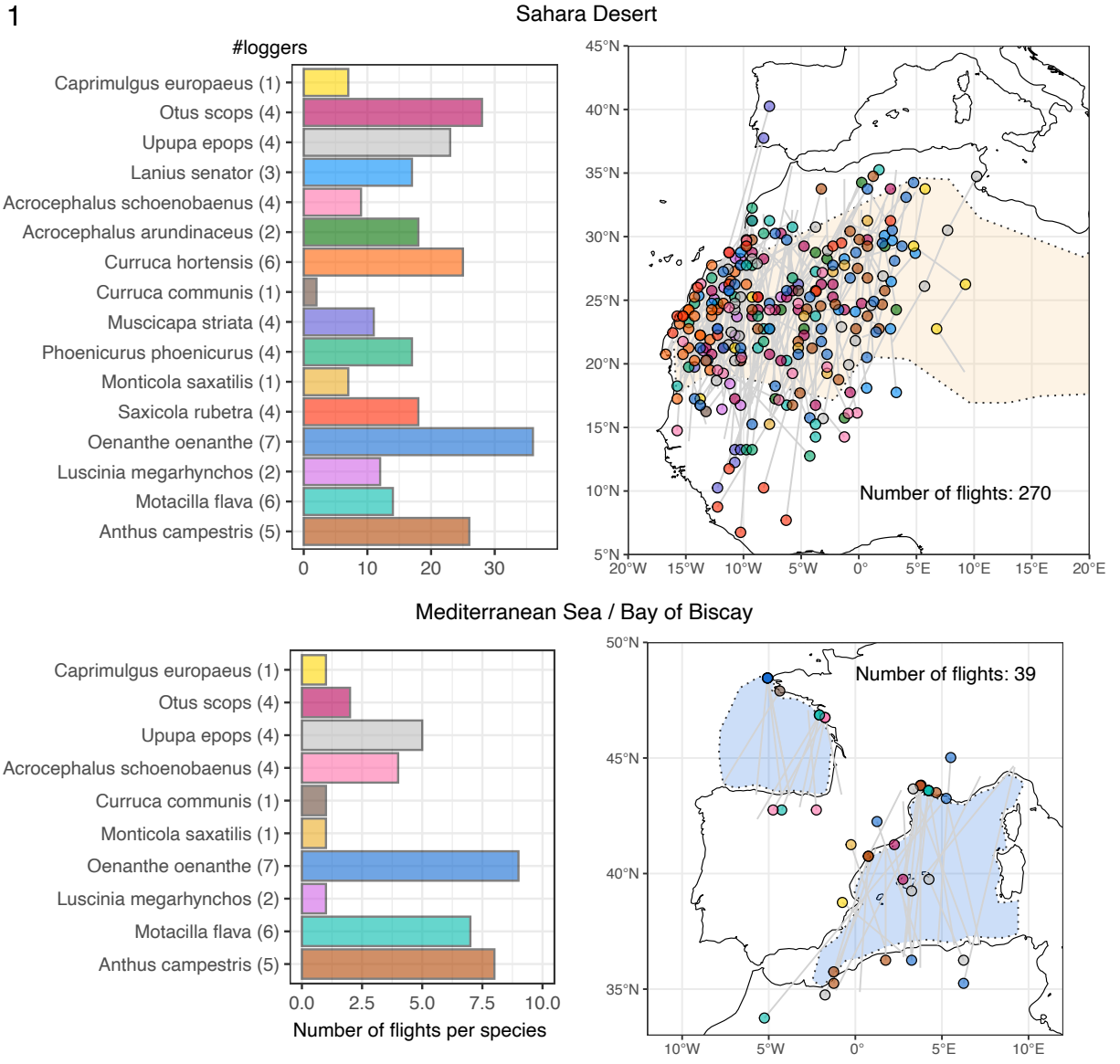

Sahara Desert
#loggers
Caprimulgus europaeus (1)
Otus scops (4)
Upupa epops (4)
Lanius senator (3)
Acrocephalus schoenobaenus (4)
Acrocephalus arundinaceus (2)
Curruca hortensis (6)
Curruca communis (1)
Muscicapa striata (4)
Phoenicurus phoenicurus (4)
Monticola saxatilis (1)
Saxicola rubetra (4)
Oenanthe oenanthe (7)
Luscinia megarhynchos (2)
Motacilla flava (6)
Anthus campestris (5)
0
10
20
30
45°N
40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
20°W
15°W
10°W
5°W
0°
5°E
10°E
15°E
20°E
Number of flights: 270
Mediterranean Sea / Bay of Biscay
Caprimulgus europaeus (1)
Otus scops (4)
Upupa epops (4)
Acrocephalus schoenobaenus (4)
Curruca communis (1)
Monticola saxatilis (1)
Oenanthe oenanthe (7)
Luscinia megarhynchos (2)
Motacilla flava (6)
Anthus campestris (5)
0.0
2.5
5.0
7.5
10.0
Number of flights per species
50°N
45°N
40°N
35°N
10°W
5°W
0°
5°E
10°E
Number of flights: 39

Fig. 2

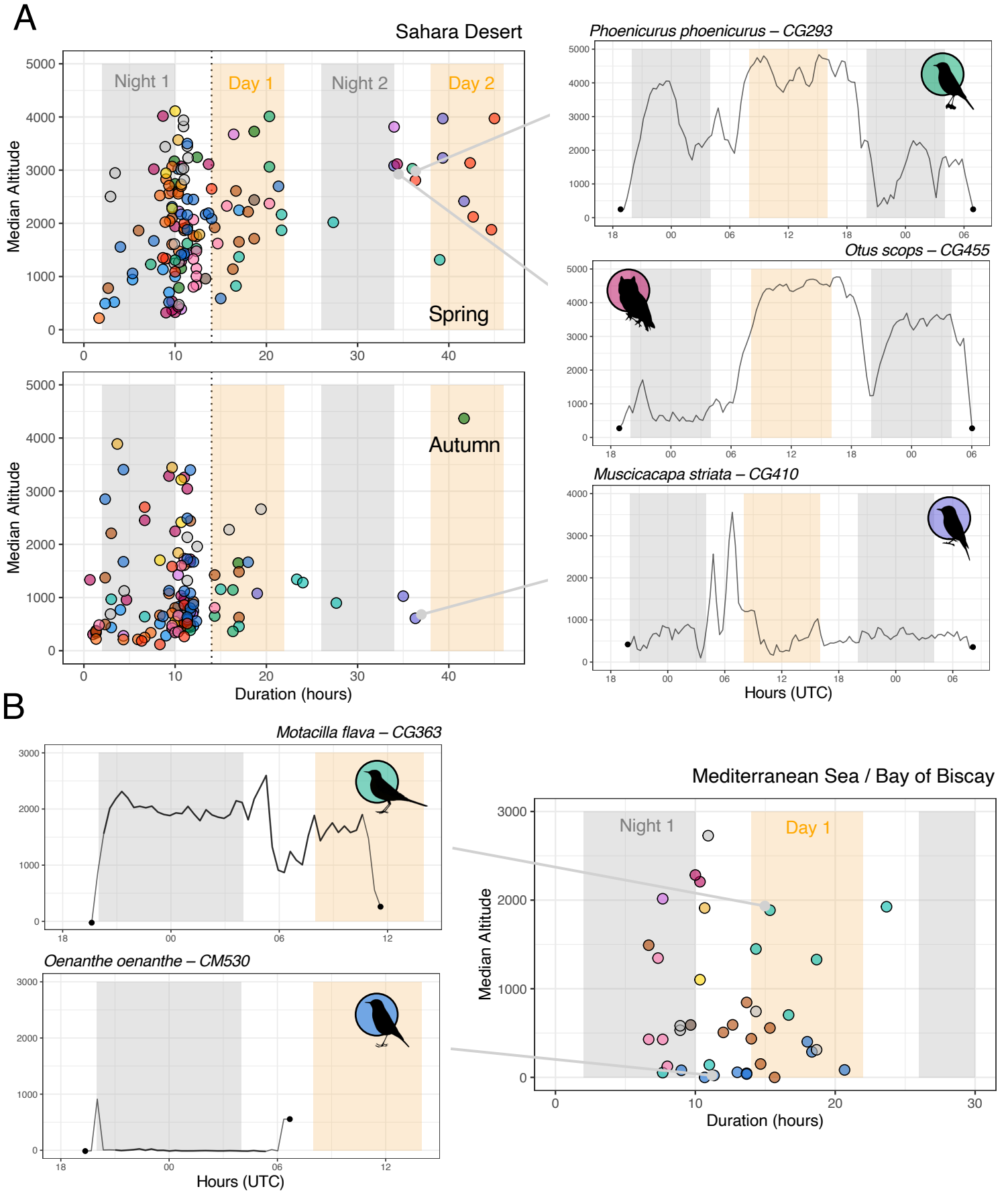
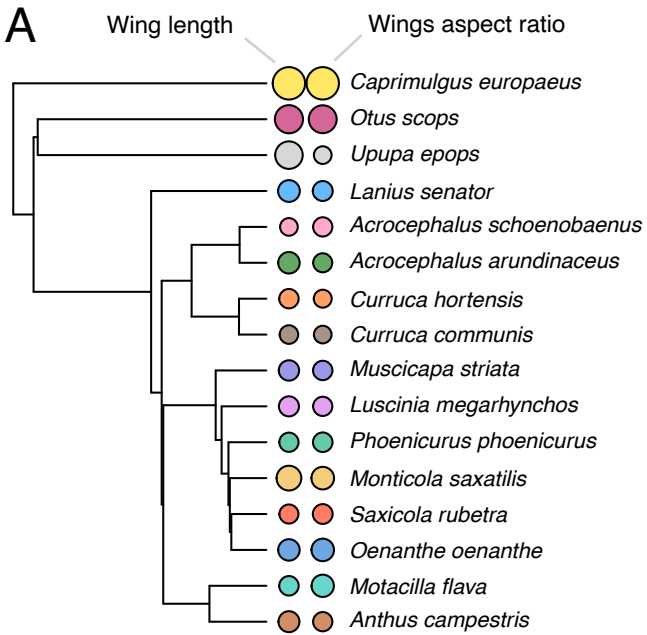
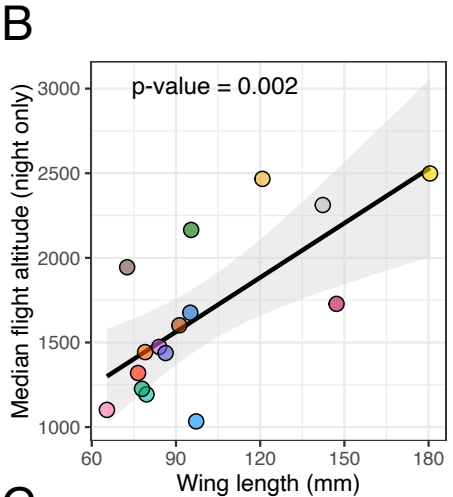

A
Sahara Desert
Night 1
Day 1
Night 2
Day 2
Spring
Autumn
Median Altitude
Duration (hours)
Phoenicurus phoenicurus – CG293
Otus scops – CG455
Muscicapa striata – CG410
Hours (UTC)
B
Motacilla flava – CG363
Oenanthe oenanthe – CM530
Hours (UTC)
Mediterranean Sea / Bay of Biscay
Night 1
Day 1
Median Altitude
Duration (hours)

Fig. 3


A
Wing length
Wings aspect ratio
Caprimulgus europaeus
Otus scops
Upupa epops
Lanius senator
Acrocephalus schoenobaenus
Acrocephalus arundinaceus
Curruca hortensis
Curruca communis
Muscicapa striata
Luscinia megarhynchos
Phoenicurus phoenicurus
Monticola saxatilis
Saxicola rubetra
Oenanthe oenanthe
Motacilla flava
Anthus campestris


B
p-value = 0.002
Median flight altitude (night only)
3000
2500
2000
1500
1000
60
90
120
150
180
Wing length (mm)

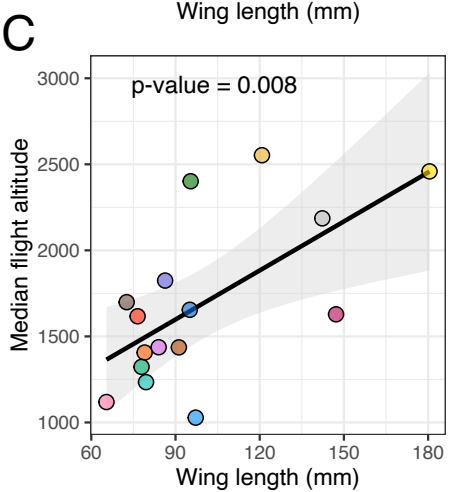

C
p-value = 0.008
Median flight altitude
3000
2500
2000
1500
1000
60
90
120
150
180
Wing length (mm)

Fig. 4

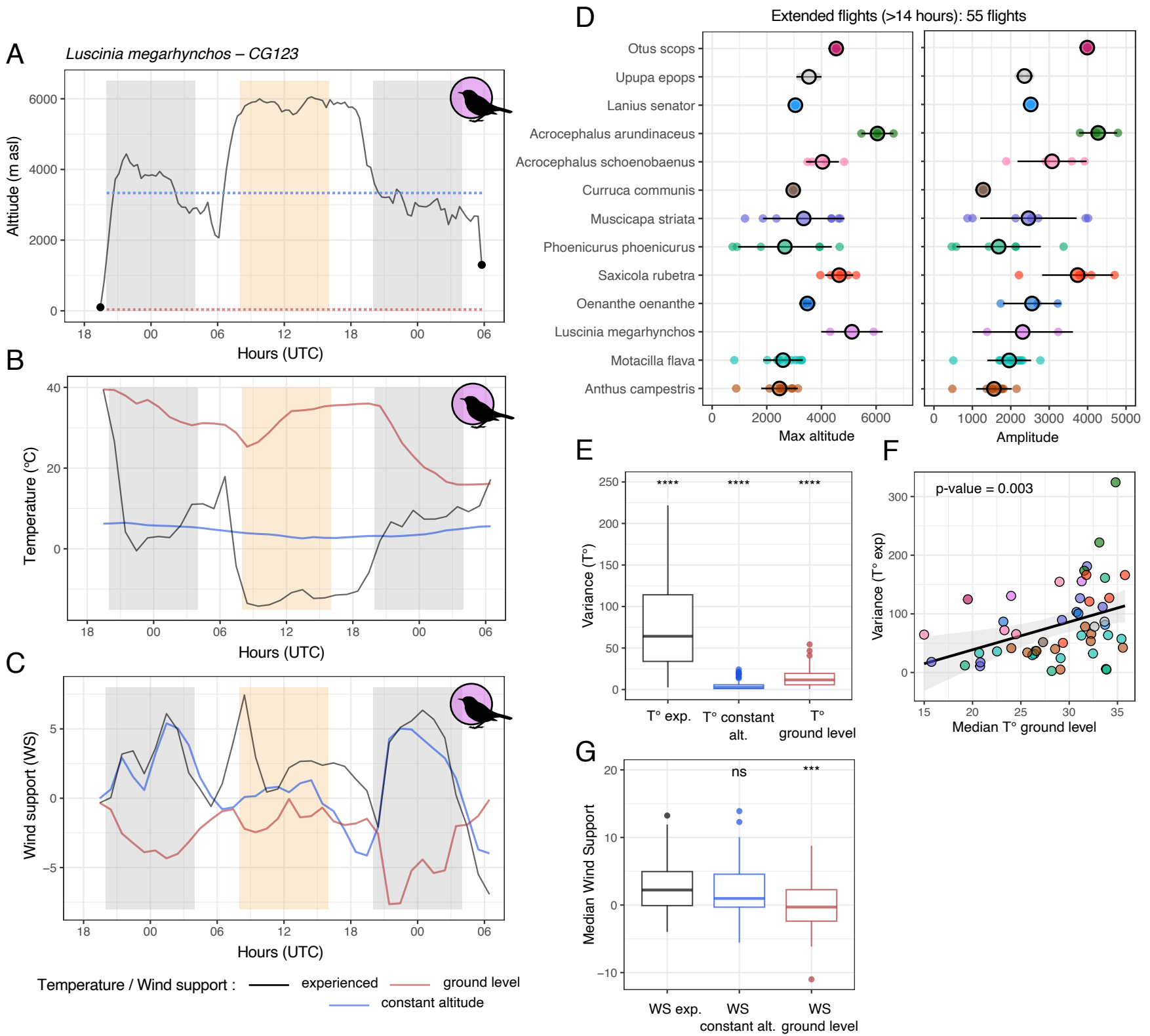
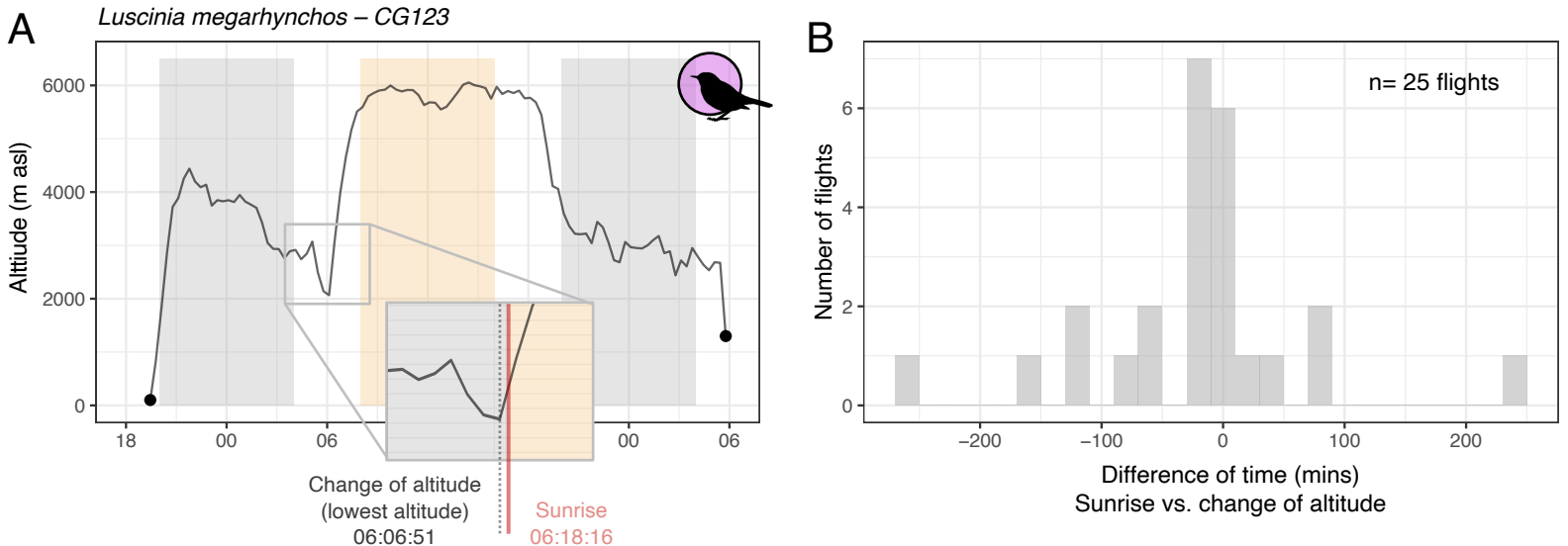

A
Luscinia megarhynchos – CG123
Altitude (m asl)
Hours (UTC)
B
Temperature (°C)
Hours (UTC)
C
Wind support (WS)
Hours (UTC)
Temperature / Wind support :
experienced
ground level
constant altitude
D
Extended flights (>14 hours): 55 flights
Otus scops
Upupa epops
Lanius senator
Acrocephalus arundinaceus
Acrocephalus schoenobaenus
Curruca communis
Muscicapa striata
Phoenicurus phoenicurus
Saxicola rubetra
Oenanthe oenanthe
Luscinia megarhynchos
Motacilla flava
Anthus campestris
Max altitude
Amplitude
E
Variance (T°)
T° exp.
T° constant alt.
T° ground level
F
p-value = 0.003
Variance (T° exp)
Median T° ground level
G
Median Wind Support
ns
***
WS exp.
WS constant alt.
WS ground level

Fig. 5


A
Luscinia megarhynchos – CG123
Alttiude (m asl)
6000
4000
2000
0
18
00
06
00
06
Change of altitude
(lowest altitude)
06:06:51
Sunrise
06:18:16
B
n= 25 flights
Number of flights
6
4
2
0
−200
−100
0
100
200
Difference of time (mins)
Sunrise vs. change of altitude

Supporting Information for: Variations in flight strategy of small migratory birds crossing major ecological barriers

Authors:
Paul Dufour[1,2], Raphaël Nussbaumer[3], Pierrick Bocher[4], Martins Briedis[3,4], Yannig Coulomb[3], Rose Delacroix[5], Thomas Dagonet[2], Christophe de Franceschi[1], Sophie de Grissac[6], Bastien Jeannin[2], Robin Monchatre[2], Fanny Rey[5], Stephan Tillo[2], Jocelyn Champagnon[2*], Olivier Duriez[1*], Frédéric Jiguet[6*]

Affiliations:
[1]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[2]Tour du Valat, Research Institute for the Conservation of Mediterranean Wetlands, Le Sambuc, Arles, France
[3]Bird Migration Unit, Swiss Ornithological Institute, Sempach, Switzerland
[4]Lab of Ornithology, Institute of Biology, University of Latvia, Riga, Latvia
[5]LIENSs, Université La Rochelle-CNRS, France
[6]CESCO, UMR7204 MNHN-CNRS-Sorbonne Université, France
[*]co-last authors

Corresponding author: Paul Dufour, paul.dufour80@gmail.com

This PDF file includes:

Supporting text

Figures S1 to S3

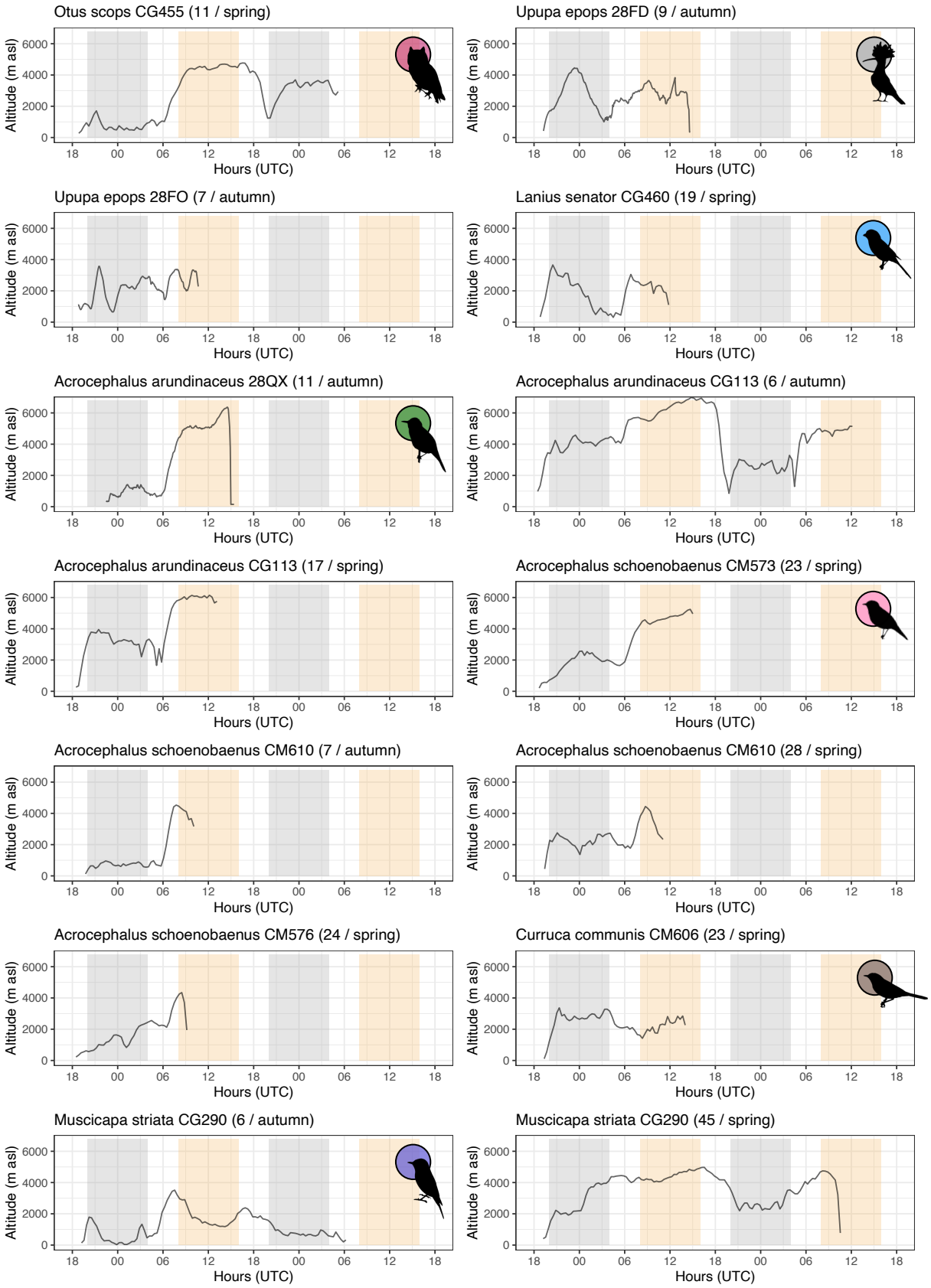
Supporting Text

Results

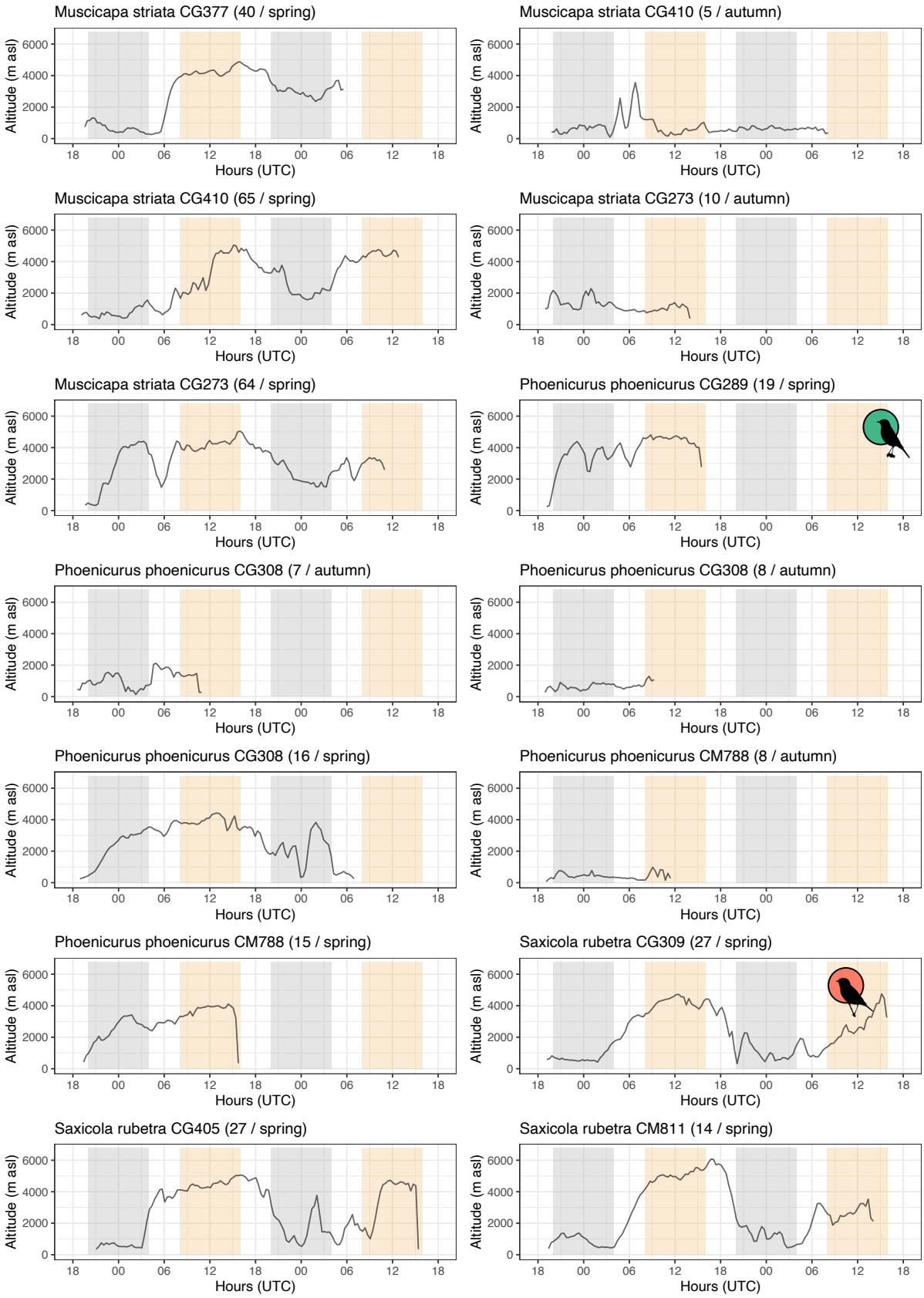
A total of 59 multi-sensor loggers (6 GDL3-PAM and 53 CARP30Z11-7-DIP) were retrieved on 16 different species. None of the loggers were recovered for *Anthus trivialis*; one bird returned but was not recaptured. Retrieving rates thus varied between 0% in *Anthus trivialis* and 57.1% in *Otus scops* (22.2% on average). Specifically, we retrieved for example: 2 out of 21 tagged *Acrocephalus arundinaceus* (9.5%); 1 out of 3 *Monticola saxatilis* (33.3%); 5 out of 21 tagged *Anthus campestris* (23.8%); 3 out of 21 tagged *Lanius senator* (14.3%); 4 out of 9 tagged *Muscicapa striata* (44.4%) and 4 out of 20 tagged *Phoenicurus phoenicurus*. Returning rates, including individuals that returned but were not recaptured or lost their loggers, varied between 7.1% for *Curruca communis* and 57.1% for *Otus scops* (24.7% on average). Specifically, we had 1 *Anthus trivialis*, 1 *Lanius senator*, 2 *Motacilla flava*, and 1 *Upupa epops* that returned but were not recaptured, as well as 2 *Upupa epops* and 1 *Oenanthe oenanthe* that returned but without their logger. A table detailing all the individuals equipped for this project, with the location of capture, the dates and biometry (at equipment and retrieval time, if retrieved) is available in Supplementary Information.

Figure S1. Variation in altitudes recorded among individuals of different species during prolonged flights (over 14 hours) across the Sahara Desert. On each panel, yellow and gray bars indicate parts of the flights that are included in the analyses as diurnal (8:00-16:00 UTC) or nocturnal (20:00-4:00 UTC). Silhouettes were downloaded from phylopic.org.

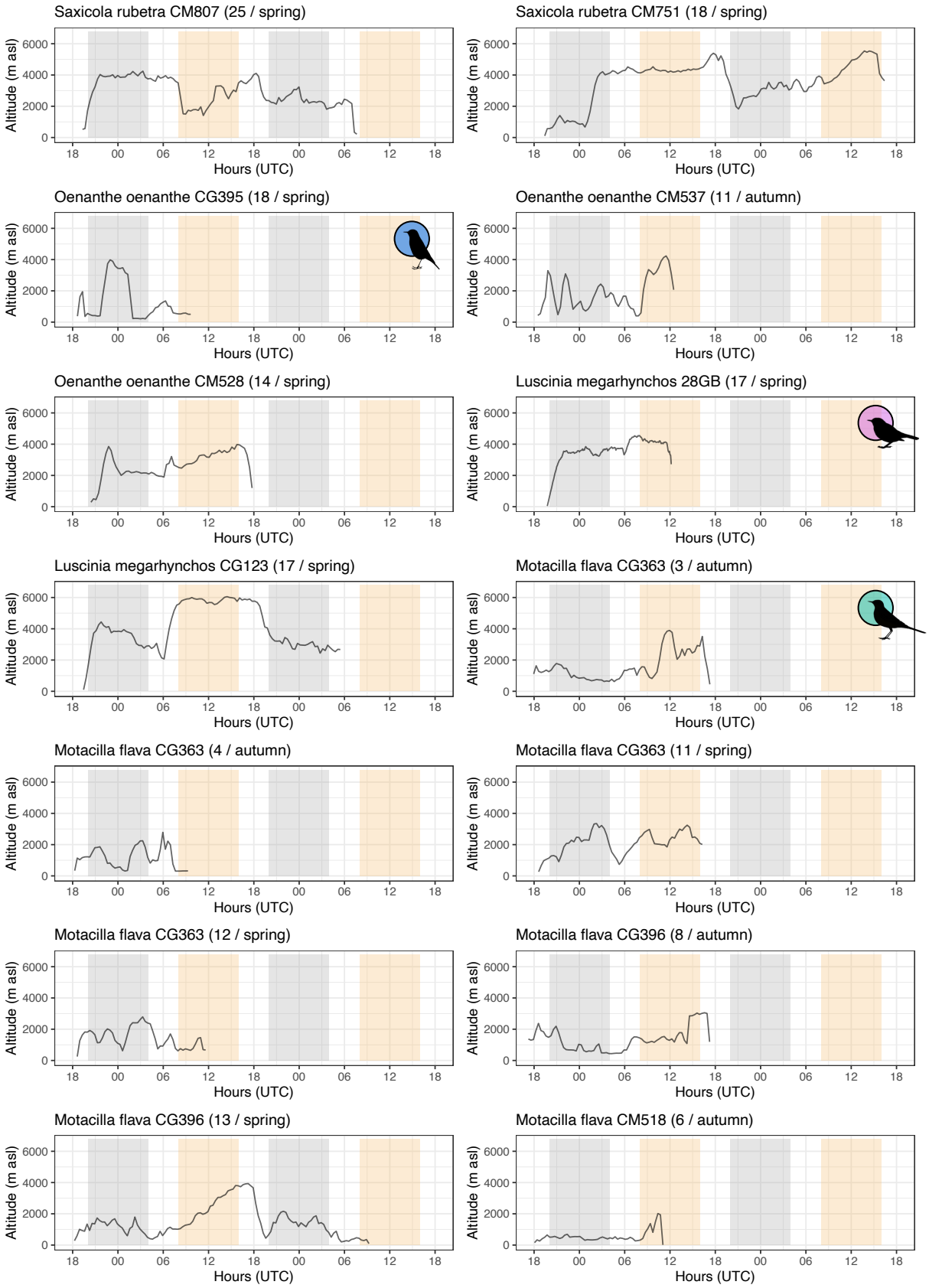
Sahara Desert (1)



Sahara Desert (2)



Sahara Desert (3)



Sahara Desert (4)

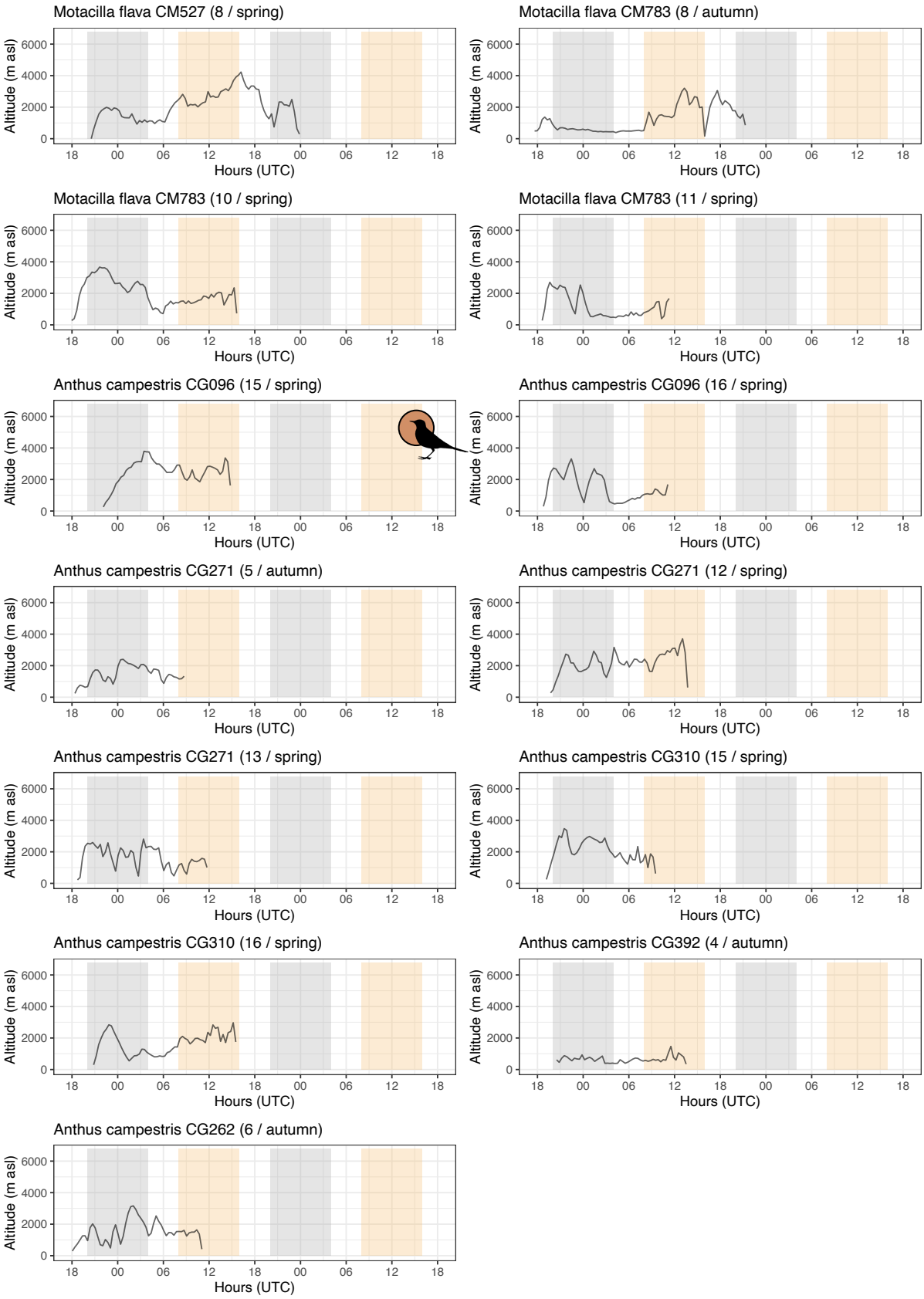
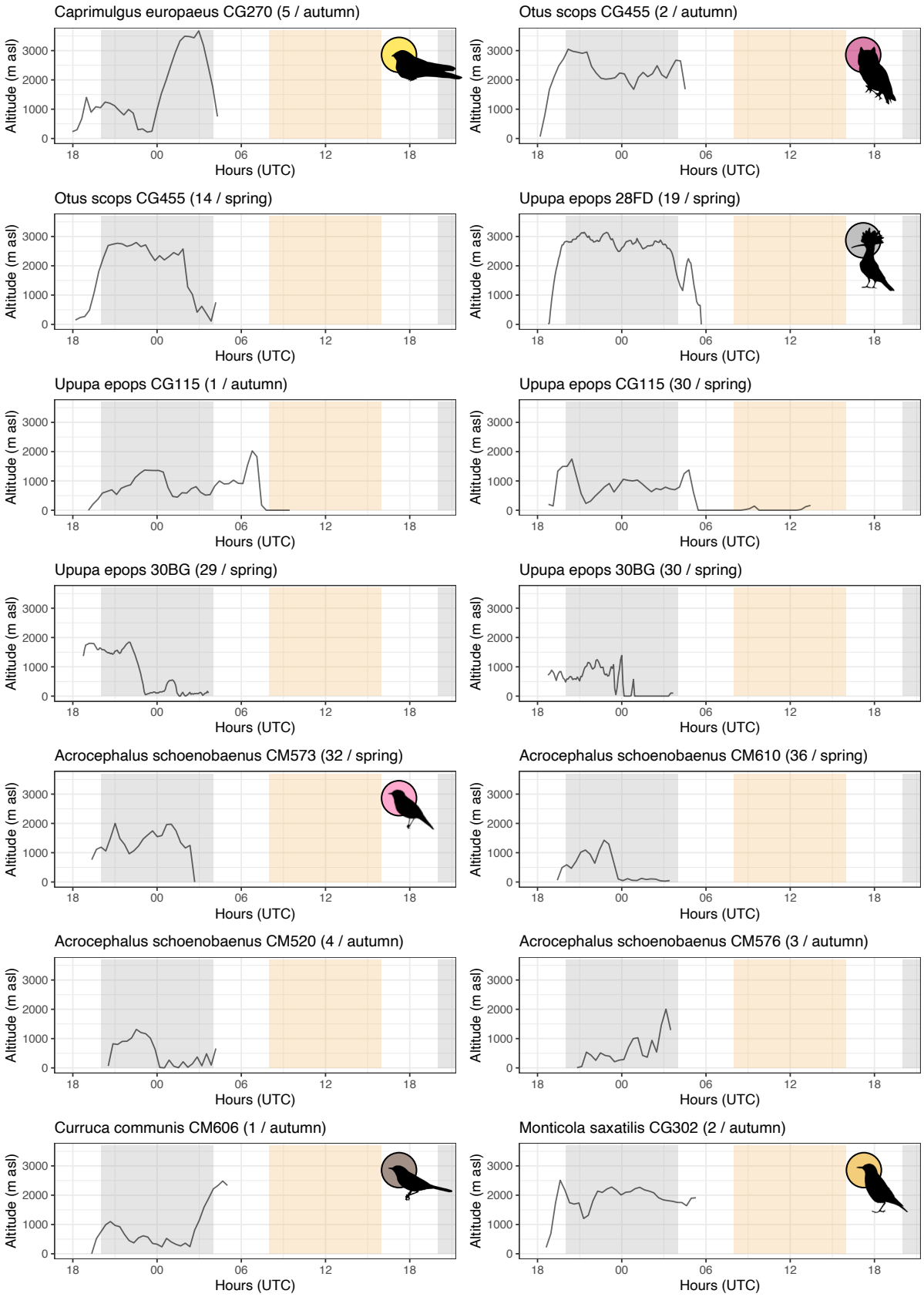
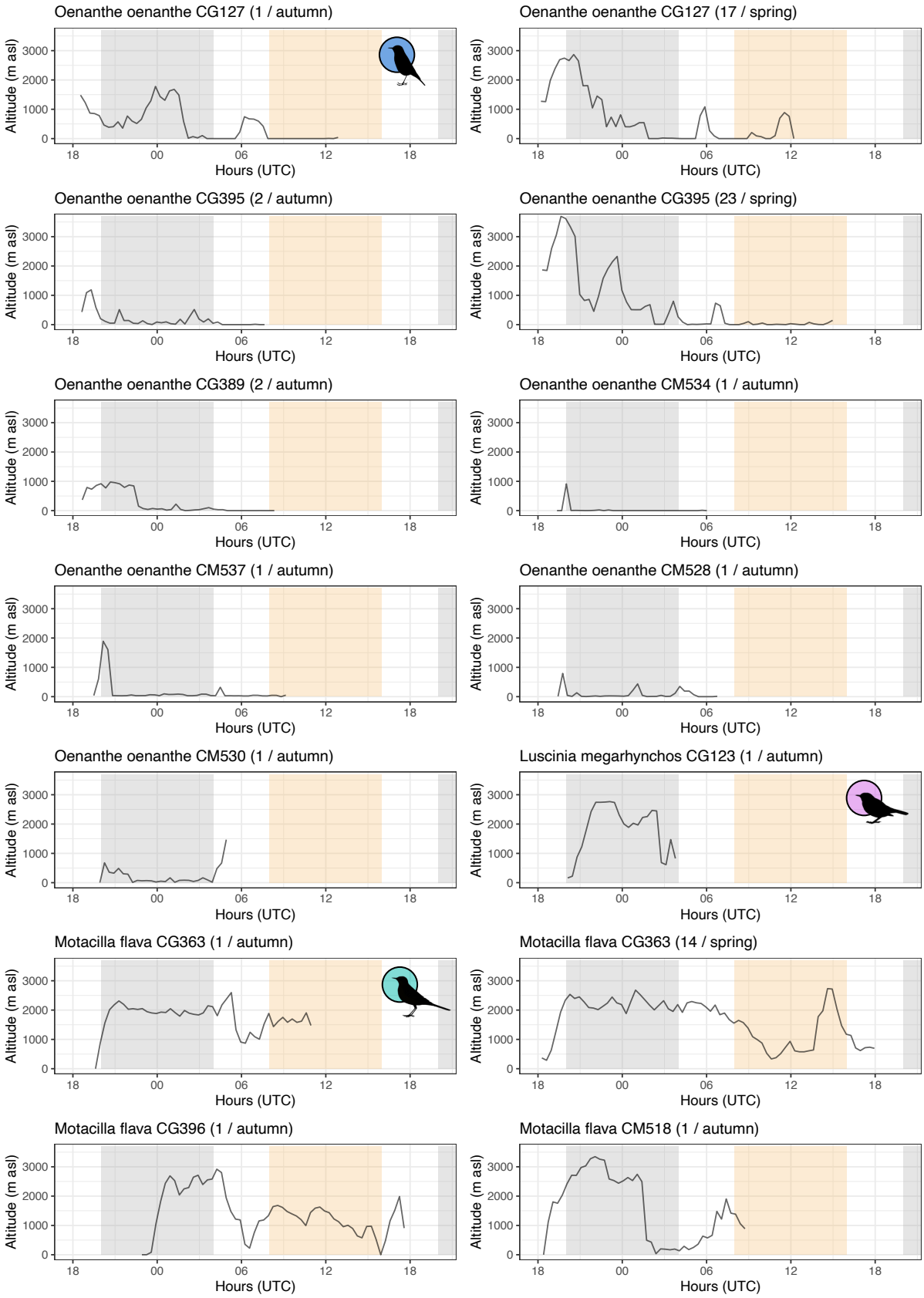


Figure S2. Variation in altitudes recorded among individuals of different species during marine crossing flights across the Mediterranean Sea and the Bay of Biscay. Flights across the Mediterranean Sea can be full crossing or interrupted crossing with a stop-over in the Balearic Islands. On each panel, yellow and gray bars indicate parts of the flights that are included in the analyses as diurnal (8:00-16:00 UTC) or nocturnal (20:00-4:00 UTC). Silhouettes were downloaded from phylopic.org.

Mediterranean Sea / Bay of Biscay (1)



Mediterranean Sea / Bay of Biscay (2)



Mediterranean Sea / Bay of Biscay (3)

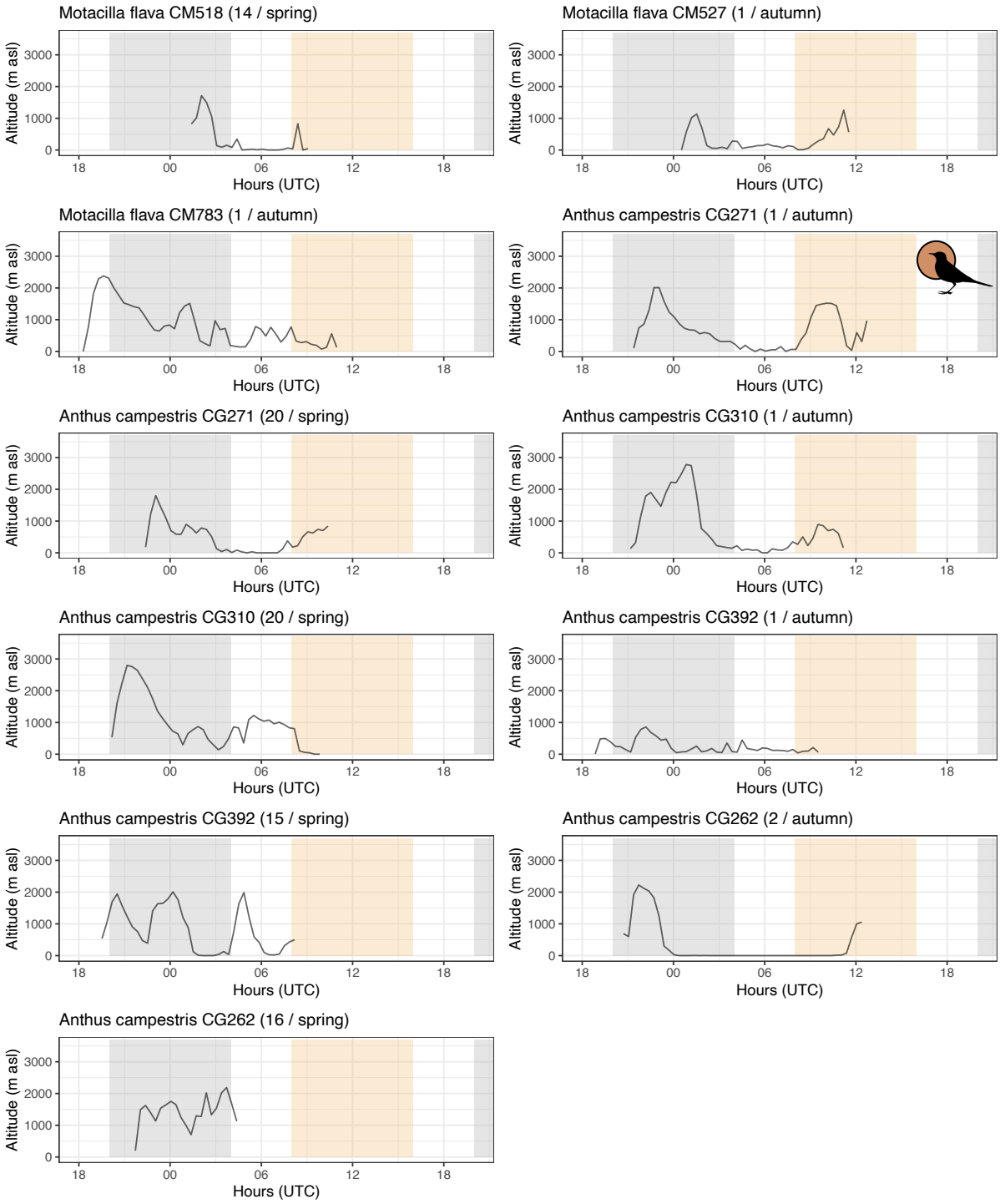
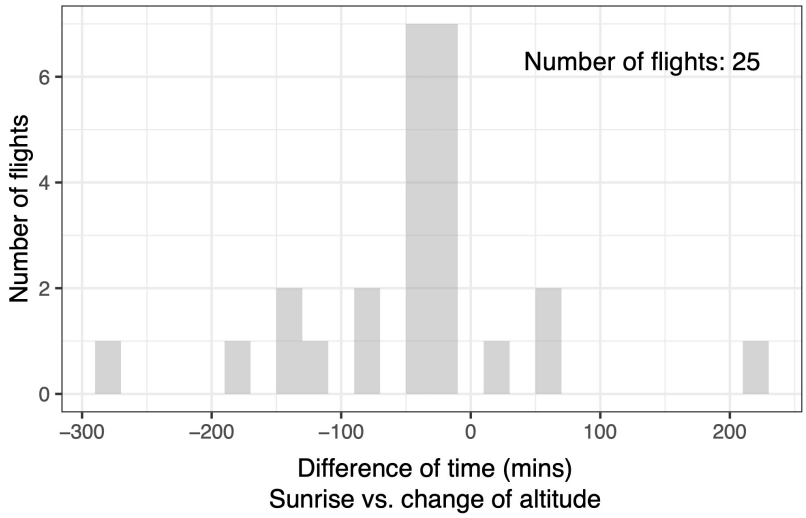



Figure S3. Analyses of diel flight altitude changes in relation to sunrise. Unlike Figure 5B we here estimated the time of sunrise with a value of solar depression angle of 0° for sunrise/sunset (instead of -6° for civil twilight). The figure represents a histogram with the difference of time in minutes between the sunrise estimation and the change of altitude for 25 different prolonged flights showing a clear change in altitude between day and night.