MIGRATION

Extreme altitudes during diurnal flights in a nocturnal songbird migrant

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Billions of nocturnally migrating songbirds fly across oceans and deserts on their annual journeys. Using multisensor data loggers, we show that great reed warblers (*Acrocephalus arundinaceus*) regularly prolong their otherwise strictly nocturnal flights into daytime when crossing the Mediterranean Sea and the Sahara Desert. Unexpectedly, when prolonging their flights, they climbed steeply at dawn, from a mean of 2394 meters above sea level to reach extreme cruising altitudes (mean 5367 and maximum 6267 meters above sea level) during daytime flights. This previously unknown behavior of using exceedingly high flight altitudes when migrating during daytime could be caused by diel variation in ambient temperature, winds, predation, vision range, and solar radiation. Our finding of this notable behavior provides new perspectives on constraints in bird flight and might help to explain the evolution of nocturnal migration.

Most songbird migrants are known to preferably fly at night throughout their entire migratory journeys. However, recent geolocator studies have shown that some individuals of several songbird species sometimes prolong nighttime flights into daytime, or even change to a nonstop flight strategy, when crossing the inhospitable Sahara Desert (*1*, *2*).

Current knowledge suggests that songbirds typically migrate below 2000 m above ground level (*3*). By selecting altitudes with favorable winds, birds can substantially increase the flight range and thus reduce energy expenditure and water loss (*4*, *5*). However, knowledge of how birds regulate altitude throughout their flights is limited because of previous difficulties in quantifying individual flight characteristics over longer distances. Recent studies have revealed a more complex altitudinal pattern than previously assumed (*6*, *7*), suggesting that migrants may change flight altitude to gain wind support and avoid warm ambient temperatures (*8*). Flights as high as 5000 m above sea level (m asl) or higher have been observed in songbirds crossing ecological barriers [e.g., (*3, 9*)] but have hitherto been interpreted as rare extreme cases.

To provide more insights into flight behavior of migrants crossing barriers, we equipped great reed warblers (*Acrocephalus arundinaceus*) with custom-made multisensor data loggers. The great reed warbler is a medium-sized songbird (~30 g) that performs solitary nocturnal migratory flights between breeding sites in Europe (in this case, Sweden) and wintering areas in tropical Africa (*10*). This migratory cycle includes crossings of barriers, i.e., the Mediterranean Sea and the Sahara Desert, twice a year. The data loggers recorded physical data on light period and sensor temperature and behavioral data on altitude [obtained from barometer data (*7*)] and activity [exact timing of continuous flapping flight and resting and movements on the ground based on accelerometer data (*11*)]. We obtained such data for 23 barrier crossings of 14 individuals (nine in autumn, 14 in spring). Each individual made at least one prolonged flight during the barrier crossing (i.e., flights starting in the nighttime and continuing during daytime after 6:30 Coordinated Universal Time). In total, we recorded 29 prolonged flights ranging from 12.1 to 34.2 hours (table S1). For 14 of these prolonged flights (involving seven individuals), it was also possible to determine the approximate geographic location of the associated flight sessions from light data (Fig. 1B and table S2), allowing us to extract relevant data on air temperature and geopotential height from the National Centers for Environmental Predictions (NCEP) data.

An unexpected pattern emerged when we analyzed the prolonged flights [which only occurred during barrier crossings (*1*)]. The birds consistently made a substantial climb at dawn (Fig. 1A). Accordingly, whereas the overall nighttime mean flight altitude was relatively high (mean ± SD: 2394 ± 1270 m asl; N = 29 prolonged flights), cruising altitude in the daytime was consistently extremely high (mean ± SD: 5367 ± 589 m asl; N = 13 full day flights; maximum altitude range 5445 to 6267 m asl; Fig. 1A and table S1). The birds climbed and descended relatively steeply immediately before or at sunrise and at or immediately after sunset, respectively (Fig. 1C). Although the birds were flying at ambient temperatures of 13.8 ± 9.0°C at night (mean ± SD for times, altitudes, and locations of seven birds with available light data), the climb at dawn left them flying in much colder ambient temperatures of −9.3 ± 3.9°C during the day (Fig. 1D).

The explanations for the marked increase in flight altitude between night and day are not clear. We will briefly discuss five possible hypotheses related to diel variation in ambient temperature, winds, predation, vision range, and solar radiation. It has been proposed that birds reduce evaporative water loss and risk of dehydration by performing sustained migratory flights at altitudes with cool temperatures [below 15 to 20°C (*5*, *12*)]. Moreover, birds are expected to prefer flight altitudes with the most favorable winds (*4*, *5*, *8*). However, diel variation in ambient temperature and wind speed and/or direction is expected to be small above 1500 m asl in the troposphere [at pressure levels of 850 to 300 hPa; Fig. 1D; (*13, 14*)]. Therefore, for birds that fly above 1500 m asl without changing their flight altitude between night and day, only small differences in air temperature and wind vector would be expected between the diurnal and nocturnal parts of the flight.

Migrating birds are liable to predation on their flights across the Mediterranean Sea and the Sahara Desert, mainly from falcons that hunt from dawn and into the daytime hours. In particular, Eleonora's falcons (*Falco eleonora*), which breed in the Mediterranean region during late summer and early autumn and travel across the Sahara Desert during autumn and spring on their way to and from winter quarters in Madagascar (*15*), constitute a possible threat to songbird migrants. This may have triggered the great reed warblers to climb to altitudes above the falcons' hunting range in the daytime. How high this range may extend is presently unknown, but there are estimates of hunting altitudes up to 3500 m asl (*16*).

By climbing to high altitudes, migrants may extend their vision range when daylight provides full visibility of the landscape below. Because of the Earth's curvature, the theoretical range of vision to an object on ground level will approximately equal $\sqrt{2 \times h \times R}$, where h is the altitude of the observer and R is the radius of Earth (6371 km). Therefore, from altitudes of 0.5, 2, and 5 km, the theoretical range of vision will be ~80, ~160, and ~252 km, respectively. Landmarks protruding above the surface, such as mountains, will theoretically be visible at even longer ranges depending on their height. Even if atmospheric visibility conditions limit long-range vision to large and contrasting features, and the great reed warblers are nocturnal migrants well adapted for flying and navigating during the night, one cannot exclude the possibility that an improved overview of the landscape from higher altitude may be useful, e.g., when searching for suitable stopover and/or landing habitat.

Solar radiation can affect the heat balance of flying birds (*17*), potentially exposing them to

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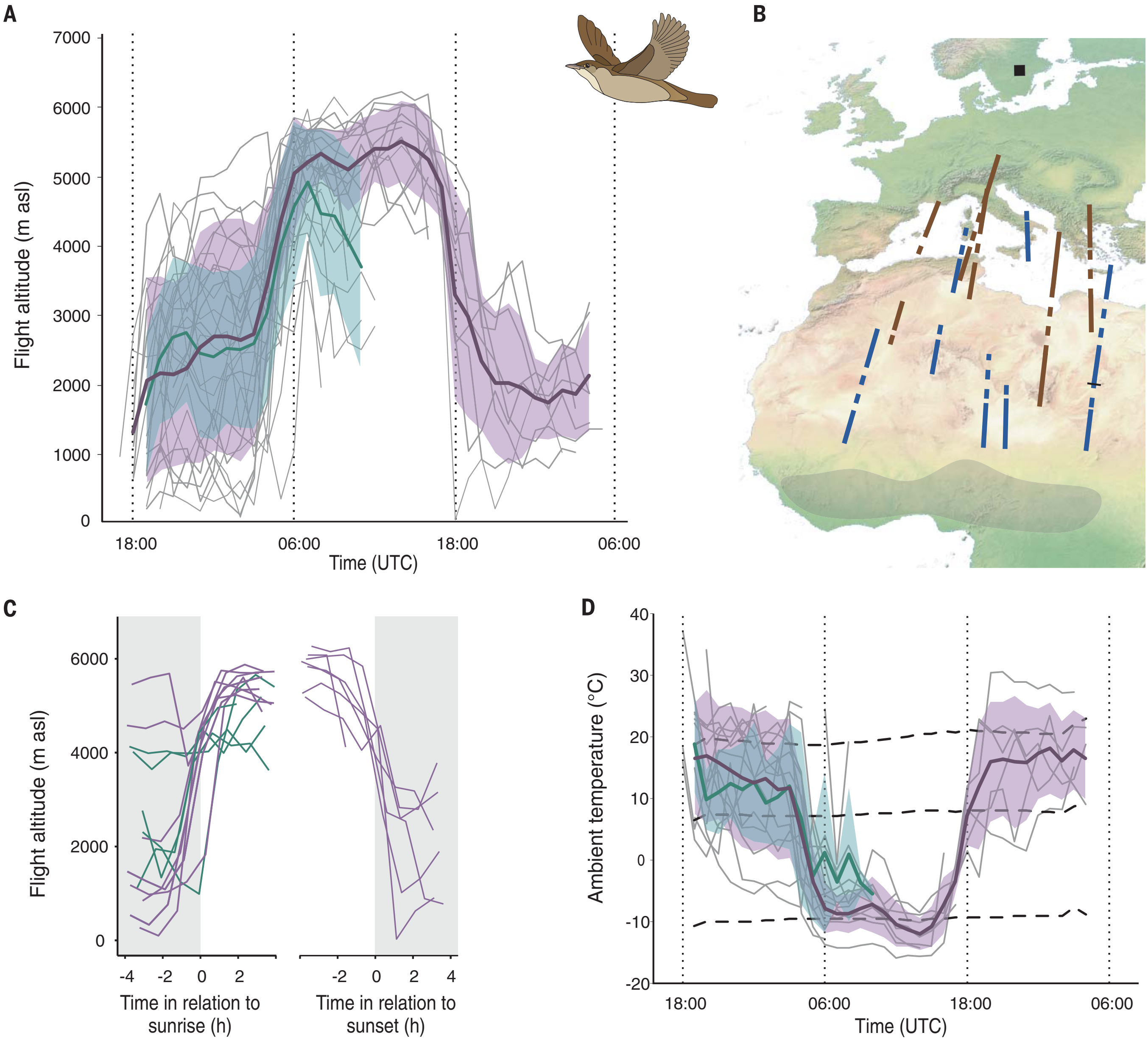

Fig. 1. Flight altitudes and ambient temperatures during prolonged migratory flights by great reed warblers over the Mediterranean Sea and Sahara Desert. (**A**) Altitude profiles in relation to the time of day and night for prolonged flights into the day in otherwise typically nocturnally migrating great reed warblers. Flight altitudes were significantly higher during daytime compared with nighttime hours [colored lines and areas shows the mean ± SD for fully (purple) and partly (green) prolonged flights; gray lines show individual flights; linear mixed-models test of difference in flight altitude between nocturnal and diurnal flights: $df = 342.7$, $t = 25.3$, $P < 0.001$; table S3]. (**B**) Approximate locations of the prolonged flights [$n = 7$ individuals and $n = 14$ flights; spring is shown in blue; autumn is shown in brown; diurnal part of flight indicated by broken lines; wintering areas shadowed; background map was made from Natural Earth, https://naturalearthdata.com, and positions of prolonged flights were generated using QGIS version 3.4.11 (*23*)]. Square shows the breeding site of the population (Lake Kvismaren, Sweden) where the data loggers were attached. (**C**) Ascents and descents in flight altitude in relation to sunset and sunrise for the 14 flights where locations were estimated (gray areas indicate night). (**D**) Ambient temperature profiles in relation to time of day for the prolonged flights [colored lines and areas shows the mean ± SD for fully (purple) and partly (green) prolonged flights; gray lines show individual flights; only flights with an estimated location are included]. The three dashed lines show ambient temperatures (~20°C, ~8°C, and ~−10°C) that would be expected if the fully prolonged flights were at a constant pressure level of 850, 700, and 500 hPa, respectively, during both night and day (corresponding to constant altitudes at 1457, 3011, and 5573 m asl, respectively).

the risk of overheating. Increased body temperature has been shown to limit flight duration in ducks (*18*), and birds in warm tropical regions more often fly with trailing legs when exposed to strong solar radiation, most likely to increase the rate of heat loss (*19*). Risk of hyperthermia caused by solar radiative heat gain may constrain flight activity during daylight in bats (*20*, *21*), which is further supported by elevated flight costs in terms of increased body temperature and metabolic rate in bats flying at day compared with at night (*22*). Thus, we propose the hypothesis that migrating birds climb to extremely high altitudes in the daytime (Fig. 1A) to reach much colder conditions (Fig. 1D) to mitigate the risk of solar radiation–generated heat stress, allowing for a faster crossing of vast ecological barriers. This hypothesis calls for future investigations of the thermal and behavioral consequences of solar radiation on songbird migration.

Here, we demonstrate an unexpected and pronounced pattern in which songbirds, when prolonging their nocturnal migratory flights into daytime, climb steeply at dawn to reach astonishingly high cruising altitudes of 5000 to 6300 m asl. Future studies of differences in the physical and biological conditions encountered by the birds during nocturnal versus diurnal flights are needed to reveal the causes of this behavior. This finding sheds new light on constraints on migratory flights and may help to explain why the overwhelming majority of nonsoaring long-distance migrant birds generally conduct their migratory flights during the night.

REFERENCES AND NOTES

1. G. Malmiga, M. Tarka, T. Alerstam, B. Hansson, D. Hasselquist, *J. Avian Biol.* **52**, e02549 (2021).
2. J. Ouwehand, C. Both, *Biol. Lett.* **12**, 20151060 (2016).
3. B. Bruderer, D. Peter, F. Korner-Nievergelt, *J. Ornithol.* **159**, 315–336 (2018).
4. F. Liechti, B. Bruderer, *J. Avian Biol.* **29**, 561–568 (1998).
5. F. Liechti, M. Klaassen, B. Bruderer, *Auk* **117**, 205–214 (2000).
6. M. S. Bowlin *et al.*, *Auk* **132**, 808–816 (2015).
7. S. Sjöberg *et al.*, *J. Avian Biol.* **49**, e01821 (2018).
8. N. R. Senner *et al.*, *Proc. Biol. Sci.* **285**, 20180569 (2018).
9. F. Liechti *et al.*, *Mov. Ecol.* **6**, 19 (2018).
10. J. Koleček *et al.*, *J. Avian Biol.* **47**, 756–767 (2016).
11. J. Bäckman *et al.*, *J. Avian Biol.* **48**, 309–319 (2017).
12. J. R. Torre-Bueno, *J. Exp. Biol.* **75**, 231–236 (1978).
13. J. M. Wallace, F. R. Hartranft, *Mon. Weather Rev.* **97**, 446–455 (1969).
14. D. J. Seidel, M. Free, J. Wang, *J. Geophys. Res. Atmos.* **110**, D09102 (2005).
15. U. Mellone, P. López-López, R. Limiñana, G. Piasevoli, V. Urios, *J. Avian Biol.* **44**, 417–426 (2013).
16. S. M. Xirouchakis, M. Panuccio, *J. Raptor Res.* **53**, 56 (2019).
17. B. O. Wolf, G. E. Walsberg, *Am. Zool.* **40**, 575–584 (2000).
18. M. Guillemette *et al.*, *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **371**, 20150386 (2016).
19. D. M. Bryant, *Ibis* **125**, 313–323 (1983).
20. J. R. Speakman, E. Król, *J. Anim. Ecol.* **79**, 726–746 (2010).
21. J. Rydell, M. B. Fenton, E. Seamark, P. W. Webala, T. C. Michaelsen, *Can. J. Zool.* **98**, 149–156 (2020).
22. C. C. Voigt, D. Lewanzik, *Proc. Biol. Sci.* **278**, 2311–2317 (2011).
23. QGIS Development Team, "QGIS geographic information system" (QGIS, 2019); https://qgis.org.
24. S. Sjöberg, G. Malmiga, A. Nord, A. Andersson, J. Bäckman, M. Tarka, M. Willemoes, K. Thorup, B. Hansson, T. Alerstam, D. Hasselquist, Data for: Extreme altitudes during diurnal flights in a nocturnal songbird migrant, Dryad (2021); https://doi.org/10.5061/dryad.q2bvq83j9.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Tables S1 to S3
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High fliers

Migrating from hemisphere to hemisphere is a global strategy for many bird species. Despite allowing birds to track productivity, these long-distance movements bring them in contact with inhospitable regions such as deserts and oceans. Sjöberg *et al.* used geolocators to monitor flight in great reed warblers (*Acrocephalus arundinaceus*) and found that when over these types of regions, this normally nocturnal migrating species flew both day and night. During the day, the birds increased the altitudes at which they flew, rising to more than 5000 meters. Such behavior may allow them to avoid heat stress or other daytime threats during migration.

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