Current Biology

Report

Extreme altitude changes between night and day during marathon flights of great snipes

Highlights

- Great snipes follow a diel altitude cycle, flying much higher at day than at night
- Most birds reached above 6,000 m and one bird reached a record height of 8,700 m
- Daytime ascents may relate to orientation, predator avoidance, or need for cooling
- Repeated flight altitude changes may be a common phenomenon among migrating birds

Authors

Åke Lindström, Thomas Alerstam,
Arne Andersson, ..., Michał Korniluk,
Sissel Sjöberg, Julia K.M. Weber

Correspondence

ake.lindstrom@biol.lu.se

In brief

Migrating great snipes regularly make 60–90 h long marathon flights. Lindström et al. show that they regularly fly much higher at day than at night. The most plausible explanations for the daytime ascents are improved orientation by landmarks, predator avoidance, and not least, seeking cold altitudes to avoid over-heating from solar radiation.

Lindström et al., 2021, Current Biology *31*, 3433–3439
August 9, 2021
https://doi.org/10.1016/j.cub.2021.05.047

Current Biology

CellPress
OPEN ACCESS

Report

Extreme altitude changes between night and day during marathon flights of great snipes

Åke Lindström,[1,9,*] Thomas Alerstam,[1] Arne Andersson,[1] Johan Bäckman,[1] Peter Bahlenberg,[2] Roeland Bom,[3] Robert Ekblom,[4,5] Raymond H.G. Klaassen,[6] Michał Korniluk,[7,8] Sissel Sjöberg,[1] and Julia K.M. Weber[1]
[1]Department of Biology, Lund University, Ecology Building, SE-22362 Lund, Sweden
[2]Lake Ånnsjön Bird Observatory, Handöl 563, SE-83015 Duved, Sweden
[3]Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB, Den Burg, Texel, the Netherlands
[4]Department of Ecology and Genetics, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE-75236 Uppsala, Sweden
[5]Swedish Environmental Protection Agency, SE-106 48 Stockholm, Sweden
[6]Conservation Ecology Group, GELIFES, University of Groningen, Groningen, the Netherlands
[7]Museum & Institute of Zoology PAS, Warsaw, Poland
[8]Natura International Polska, Białystok, Poland
[9]Lead contact
*Correspondence: ake.lindstrom@biol.lu.se
https://doi.org/10.1016/j.cub.2021.05.047

SUMMARY

Several factors affect the flight altitude of migratory birds, such as topography, ambient temperature, wind conditions, air humidity, predation avoidance, landmark orientation, and avoiding over-heating from direct sunlight.[1–6] Recent tracking of migratory birds over long distances has shown that migrants change flight altitude more commonly and dramatically than previously thought.[4–8] The reasons behind these altitude changes are not well understood. In their seasonal migrations between Sweden and sub-Saharan Africa, great snipes *Gallinago media* make non-stop flights of 4,000–7,000 km, lasting 60–90 h.[9,10] Activity and air pressure data from multisensor dataloggers showed that great snipes repeatedly changed altitudes around dawn and dusk, between average cruising heights about 2,000 m (above sea level) at night and around 4,000 m during daytime. Frequency and autocorrelation analyses corroborated a conspicuous diel cycle in flight altitude. Most birds regularly flew at 6,000 m and one bird reached 8,700 m, possibly the highest altitude ever recorded for an identified migrating bird. The diel altitude changes took place independently of climate zone, topography, and habitat overflown. Ambient temperature, wind condition, and humidity have no important diel variation at the high altitudes chosen by great snipes. Instead, improved view for orientation by landmarks, predator avoidance, and not least, seeking cold altitudes at day to counteract heating from direct sunlight are the most plausible explanations for the diel altitude cycle. Together with similar recent findings for a small songbird,[6] the great snipes' altitudinal performance sheds new light on the complexity and challenges of migratory flights.

RESULTS

Timing of the long flights

We analyzed flight altitudes (estimated from air pressure readings) from three categories of long flights carried out by great snipes during their annual migration:[10] the Europe-to-Sahel flight in autumn (*Autumn*), the following flight from the Sahel region to the final wintering grounds near the equator (*In-Africa*), and the equator-to-Europe flight in spring (*Spring*; Figure 1). These flights started on average on August 24, September 24, and April 18, respectively, lasting on average 73.4, 23.2, and 82.4 h (Table S1). All birds departed close to dusk, on average at 19:04 in *Autumn*, at 17:21 *In-Africa*, and at 16:18 in *Spring* (UTC; Figure 2; Table S1).

Cyclic flight altitudes

There was an overall strong and consistent diel cycle in the altitudes used by the great snipes, in all three long flights (Figures 2A–2C). After a night at moderate to high altitudes, the birds ascended to very high altitudes in early morning, stayed at these high altitudes during the day, and descended again in late afternoon. They then repeated this cycle for one or two more days.

The mean individual flight altitudes (always given as m above sea level) of individuals were on average 3,348 m in *Autumn*, 2,364 m *In-Africa*, and 2,820 m in *Spring* (n = 13, 9, and 5 individuals, respectively; Table S1). In periods of certain daylight (10:00–16:00 UTC) and darkness (21:00–03:00 UTC), the mean individual daytime flight altitude in *Autumn* was on average 2,423 m higher than at night (4,549 m versus 2,126 m). For the *In-Africa* and *Spring* flights the differences between day and night were 2,014 m (3,874 m versus 1,860 m) and 2,502 m (4,114 m versus 1,612 m), respectively (Table S1). It should be noted that these altitudes were estimated from air pressure readings using standard equations and may to some extent be underestimates (see STAR Methods, Table S2, and below).

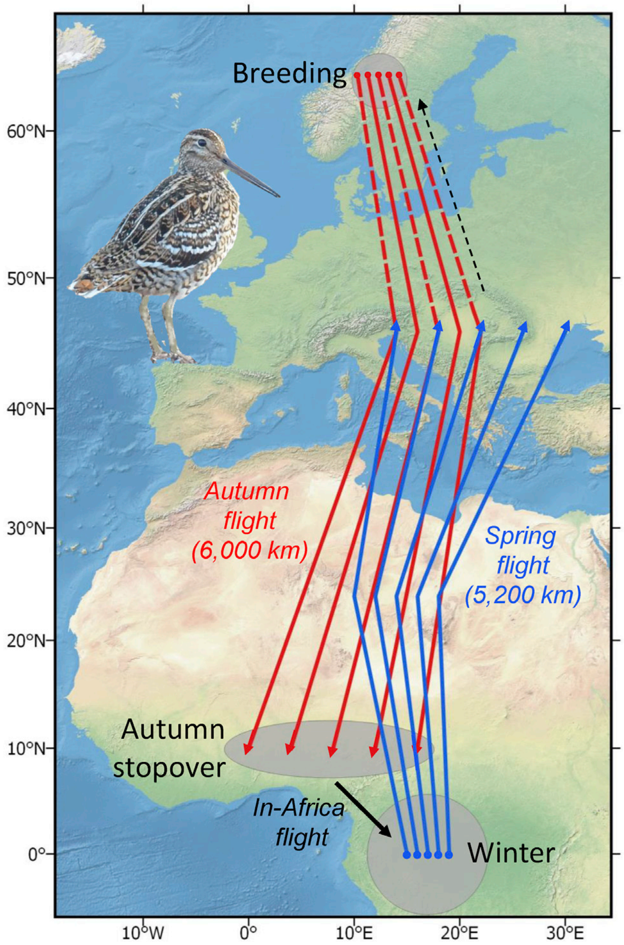

Figure 1. Schematic flight routes of Swedish male great snipes

In *Autumn*, the birds fly either non-stop (red solid lines) from the breeding grounds to the Sahel region (Autumn stopover), or they make one or a few shorter flights in northern Europe before embarking on the trans-Sahara flight from farther south along the route (stippled red lines). After about a month, they make an *In-Africa* flight to the wintering grounds (Winter). In *Spring* they all fly non-stop from the winter grounds to southeast Europe (blue solid lines), from where they make several shorter flights back to the breeding grounds (thin stippled black line). The central of the five *Autumn* and *Spring* tracks approximates the mean route based on geolocator tracks:[10] approximately 6,000 and 5,200 km long, respectively. The four outer tracks of each season were used to estimate the variation in topography and weather variables over an area where most birds are likely to have migrated (map from https://www.naturalearthdata.com). The coordinates for the approximate routes are given in Table S3. See also Figures S1–S3.

A spectral (DFT) analysis confirmed a conspicuous diel cycle in flight altitude, with a prominent peak at one cycle per 24 h for both *Autumn* and *Spring* flights (Figure 2D). A conspicuous 24 h cycle is also apparent from the autocorrelation analysis (Figure 2E), with peaks of negative mean correlation coefficients at time lags around 12 and 36 h. That is, a high altitude in one hour was matched by a low altitude 12 and 36 h later. In contrast, a high altitude in one hour was matched by a high altitude 24 and 48 h later.

The corresponding diel flight altitude cycle was as prominent also in the *In-Africa* flights (Figure 2B), but too few flights longer than 24 h precluded formal analyses.

Peak altitudes

Some great snipes occasionally flew extremely high and then always during daytime. The maximum altitude reached per individual was on average 6,433 m in *Autumn,* 4,579 m *In-Africa*, and 6,364 m in *Spring* (Table S1). Three birds in *Autumn* and two birds in *Spring* reached 7,000 m or more.

The single highest altitude estimate of 8,077 m was reached in *Autumn* and was recorded within a 5 h series between 11:00 and 15:00 UTC on August 18 at estimated altitudes all above 7,600 m. For this particular episode, we calculated a geopotential (“true”) altitude using local weather information (NCEP; STAR Methods). An approximate position was estimated at 22.6°N and 10.8°E (right over the Sahara), assuming that this individual had flown 4,600 km from the breeding grounds (STAR Methods). The air pressure of 351.5 hPa measured by the logger on August 18, 2017, at 12:00 UTC corresponds to a geopotential height of 8,700 m, and an air temperature of -21.3°C. The bird stayed above 8,000 m for 5 h.

Flight altitudes and topography

The flight altitudes of the snipes along the estimated approximate routes (STAR Methods) were on average at least 2,000 m above the highest landmarks and rarely as low as the average topographical profile (Figures 3A and 3B). Thus, topography shows little potential for additional explanation of flight altitude variation, in addition to the diel cycle. It should be noted that in *Spring* the pattern of altitude variation with distance flown along the flight route (Figure 3B) is very similar to the pattern found over time (Figure 2C) as the birds did not perform any pre-flights and were assumed to start from the same place.

Patterns of ambient temperature and wind conditions

Whereas ambient temperatures are higher toward the equator, there is no apparent variation between day and night, especially not at altitudes from 3,000 m and above (Figures 3C and 3D). The example altitudes chosen correspond to the fixed air pressure levels at which these weather variables are measured (~1,500, 3,000, 5,600, and 7,200 m). Nor is there an apparent variation between day and night in wind conditions and air humidity (Figure S1).

DISCUSSION

Changes in flight altitude during migratory flights

All great snipes regularly changed flight altitudes during their long flights, generally following a diel (24 h) cycle. This is the first case for which a regular diel altitude cycle could be demonstrated by frequency analysis of flight altitude data from nonstop flights lasting several successive nights and days. Altitude changes in most cases took place within a few hours at dawn and dusk. The circadian pattern was very similar between *Autumn*, *In-Africa*, and *Spring* flights, suggesting a common cause that is largely independent of climate zone (temperate or tropical), topography, and landscape overflown (forest, savanna, farmland, desert, or water).

Our finding of distinct changes in flight altitude adds to several recent reports of altitude changes in migrants tracked over many hours.[4–8,11,12] In fact, all published tracks we have found from long flights have reported prominent flight altitude changes.

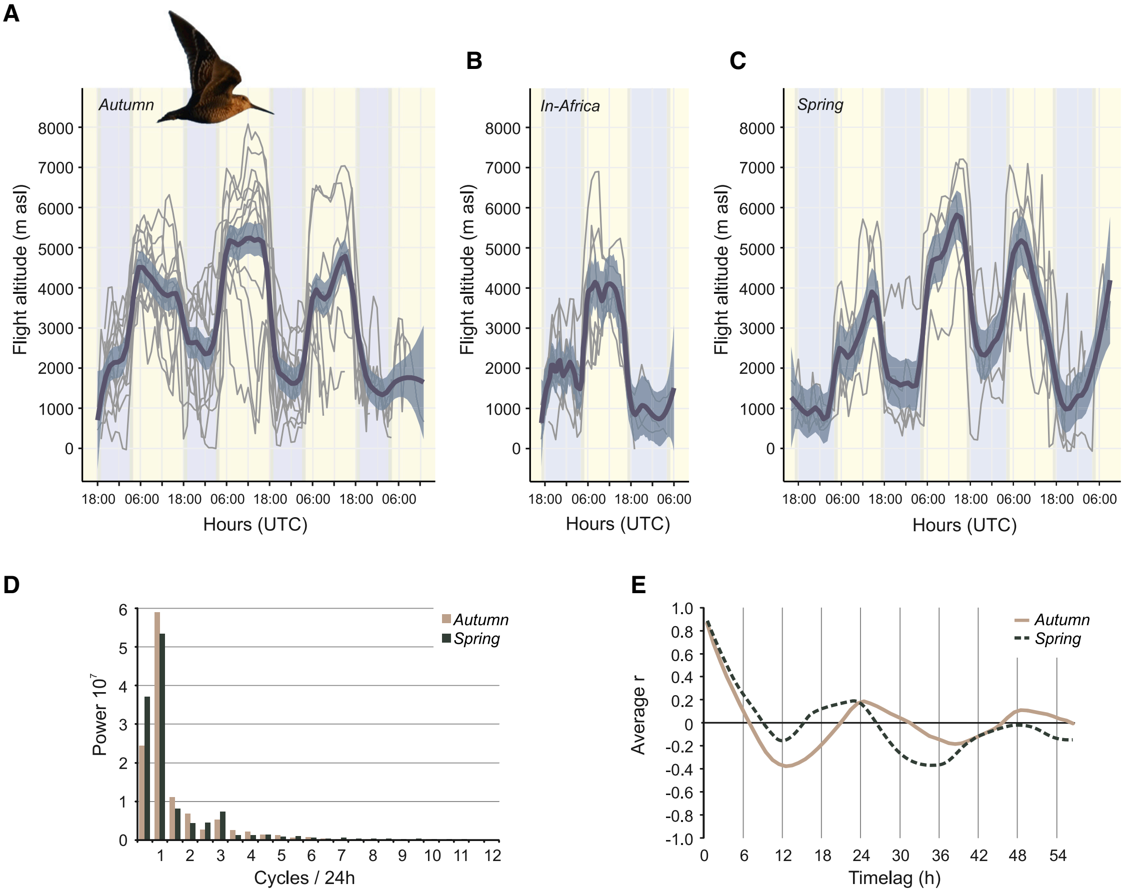

Figure 2. The diel cycle in flight altitudes by great snipes

(A–C) Flight altitudes (m a.s.l.) of great snipes during the *Autumn*, *In-Africa*, and *Spring* flights (Figure 1), in relation to time of day (UTC). The solid dark line and gray shading are the average flight altitude and its 95% CI, as estimated from LOESS. Approximate day (yellow) and night (gray) are shown for the average date and longitude of migration in each season. Thin gray lines denote the individual tracks. When estimating sunrise (03:43) and sunset (18:21) for the *Autumn* flights, we assumed an average estimated starting point for all flights of 700 km south of the breeding grounds (56.8°N, 15.0°E), on August 23. For the *Spring* flight the estimated sunrise (04:48) and sunset (16:55) were based on an average starting point for all flights at 0.00°N, 17.00°E, on April 17. For the *In-Africa* flight the estimated sunrise (05:17) and sunset (17:22) were based on an average starting point for all flights at 10.00°N, 8.00°E, on September 25. See also Figures S1–S4.

(D) Frequency analysis (discrete Fourier transform) with power spectrum of variations in altitude during the long migratory flights of great snipes for *Autumn* (light brown; n = 13) and *Spring* flights (dark green; n = 5). The frequency is presented as number of cycles in altitude per 24 h. Clearly, the strongly dominating regular frequency is one altitude cycle/day. Bars indicate average power components and data are for the same flights as shown in (A) and (C).

(E) Autocorrelations of hourly flight altitudes during the long migratory flights of great snipes. The time series are based on altitudes measured hourly for *Autumn* (solid) and *Spring* flights (dashed). The local correlation maxima, as indicated by the average correlation coefficient (r), that occur after ~24 and ~48 h show that the altitude at any given hour is best matched by the altitude recorded ~24 or ~48 h before (or after) that. The local correlation minima (negative correlation coefficients) that occur after ca. ~12 and ~36 h show that the altitude at any given hour is matched by an altitude at the opposite side of the altitude range ~12 or ~36 h before (or after).

Clearly, significant altitude changes may be more common in migrating birds using flapping flight than previously assumed.

Two recent studies seem particularly relevant to the great snipe behavior. Black-tailed godwits *Limosa limosa* migrating from Europe to West Africa changed flight altitude by several thousand meters within a few hours.[4] The changes were associated with high ambient temperatures at lower altitudes and increasing wind support at higher altitudes. This behavior of a migrating wader is clearly reminiscent of the pattern we found in great snipes, but the flights were of shorter duration and time of day was not presented. In addition, when great reed warblers migrating over the Mediterranean Sea and the Sahara prolonged their regular night-time flights into the day, they on average ascended 3,000 m around dawn (from 2,400 to 5,400 m).[6] Three possible explanations for the differences between nocturnal and diurnal flight altitudes were put forward: avoidance of diurnal predators, improved visibility of the landscape below, and reaching very cold conditions to mitigate the risk of solar radiation-generated heat stress.[6] What factors then can explain the diel altitude cycle in great snipes?

Factors potentially explaining the diel cycle in flight altitudes

Several biotic and abiotic factors have been identified to affect flight altitude of migrating birds (Table 1). One of the earliest studies showing in-flight altitude changes suggested that

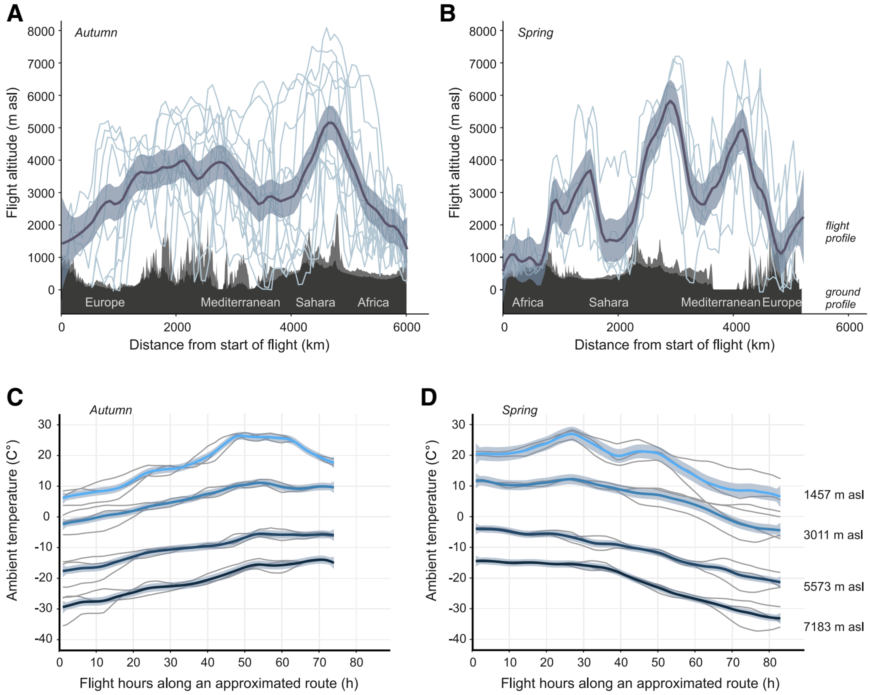

Figure 3. Flight altitudes in relation to topography and air temperature

(A and B) Flight altitudes (m a.s.l.) of great snipes during *Autumn* and *Spring* flights in relation to Earth's topography at estimated distances along five schematic flight routes (Figure 1; Table S3). The solid dark line and gray shading are the average flight altitude and its 95% CI, as estimated from LOESS. Thin gray lines denote the individual tracks. The topography is shown as the average (black) and maximum (gray) altitude along the approximated tracks.

(C and D) Ambient air temperatures in autumn and spring at four different atmospheric pressure levels of 850, 700, 500, and 400 hPa (corresponding to altitudes as indicated in D), along the approximate *Autumn* and *Spring* flight routes #3 (Table S3). The solid dark line and gray shading are the average air temperature and its 95% CI for each pressure level, as estimated from LOESS. Thin gray lines denote the individual temperature profile for an early, average, and late timing at each pressure level.

See also Figure S1.

thrushes that temporarily descend during nocturnal flights may have been attracted to the lights of cities beneath.[8] However, a recent radar study found that night migrating birds generally flew at higher altitudes over urban areas than over non-urban areas.[13] In addition, the low amount of artificial light in the Sahara, where both great snipes and great reed warblers[6] still fly much lower at night, speaks against light attraction as a general explanation for the pattern we found.

It may be beneficial for migratory birds to ascend to higher altitudes at daylight to locate important distant landmarks for orientation or landfall.[20] Conversely, at night, landmarks would be easier to see or hear from lower altitudes.[22] Hence, it is possible that great snipes fly higher at day and lower at night to better find their way. Flying low in general would also make it easier to find good emergency landing sites.[23] However, this is probably not the cause for lower night-time altitudes in great snipes as the birds, at least during the first nights of the longest flights, seem very dedicated to flying and are probably not looking for landing sites.

Great snipes may ascend at dawn to avoid attacks of daytime predators like Eleonora's falcon *Falco elenonorae* and peregrine falcon *Falco peregrinus*. Eleonora's falcons are known to hunt small migrating birds, especially in the first few hours after dawn at altitudes as high as 3,500 m.[18] However, Eleonora's falcons primarily catch birds much smaller than great snipes and occur mainly in the Mediterranean Sea area.[19] The importance of avian predation at high altitudes remains to be investigated.

Most avian migration takes place within the so-called planetary boundary layer,[15] the 2,000 m nearest to the Earth's surface. Within this layer the atmospheric conditions change significantly between night and day: daytime ambient temperatures are much higher.[15] Since high temperatures may force birds to use evaporative cooling potentially leading to dehydration, migrants should avoid flying during daytime or, alternatively, fly higher during the day.[15,24] However, great snipes generally flew well above the planetary boundary layer, where, most importantly, there are only minimal systematic differences between night and day in ambient temperature[25] (Figure 3) and wind conditions[26] (Figure S1). Accordingly, there is no important diel cycle in ambient air temperature or wind conditions at high altitudes that could explain the overall regular diel pattern of flight altitude selection found in great snipes.

The suggestion that birds should fly higher at daytime to minimize evaporative cooling and thereby the risk of dehydration[15] could still be valid if another atmospheric factor is added to the equation: solar radiation. Solar radiation is known to impose heat stress and risk of hyperthermia on flying birds and bats at daytime, not least in tropical areas.[27,28] Sjöberg et al.[6] suggested that great reed warblers ascend to much higher and colder altitudes at dawn to counteract the additional heat stress caused by solar radiation, thereby mitigating the risk of hyperthermia. The same explanation may well hold for great snipes. Clearly, by ascending to higher and colder altitudes, the birds can cool themselves through heat convection. However, the birds must descend again at dusk, since without the warming sun the ambient temperatures may generally be way too cold (down to −25°C at 5,000 m and −35°C at 7,000 m; Figure 3). A complicating factor that needs to be given more attention is that by flying higher, migrants will often experience lower air humidity (Figure S1) and thus become exposed to an increased risk of dehydration.[21,29]

Great reed warblers showed altitude changes between night and day during their crossing of the Sahara and the Mediterranean Sea (they traveled exclusively by night outside this region[6]). The great snipes showed a prominent diel altitude cycle also over continental Europe and south of the Sahara. This shows

Table 1. Evaluation of factors potentially explaining the diel cycle in flight altitudes

Factor	Benefits	Reference	Can it explain diel altitude cycle?
Inability to keep altitude	none		no
Magnetic disturbance	none	[14]	unlikely
The Earth's topography	avoid hitting the ground	[7]	no
Avoid dust storms, thunderstorms	increased safety and comfort		unlikely
Avoid turbulent air	improved transport economy and comfort	[15]	unlikely
Find beneficial horizontal winds	improved transport economy	[2]	unlikely
Find beneficial vertical winds	improved transport economy	[7]	unlikely
Avoid clouds and rain	comfort and good visibility	[16]	unlikely
Temperature regulation	avoid high air ambient temperatures	[4]	unlikely
Temperature regulation	avoid freezing bare parts	[17]	unlikely
Predation risk	escape attacks	[18,19]	possibly
View the Earth's surface	find landmarks and habitats	[7,20]	possibly
Maintain water balance	avoid dehydration	[15,21]	possibly
Temperature regulation	avoid overheating from solar radiation	[6]	possibly

An evaluation of potential factors behind the distinct diel cycle in flight altitude (higher altitudes during day compared to night) during long nonstop flights of migrating great snipe. The factors have been proposed or verified in the cited papers, or can be inferred from them. Each of the factors may well explain altitude selection at any given moment, but here we evaluate whether a factor can help explain a regular circadian pattern of flight altitudes ("no," "unlikely," or "possibly") among birds using flapping (non-soaring) flight.

that the behavior is not limited to barrier crossing, nor to tropical or subtropical regions.

Many more factors are known to affect choice of flight altitude in migrants, but they are unlikely to be the drivers behind the diel pattern found in great snipes (Table 1). Birds are known to change flight altitude over shorter time spans, for example in response to local magnetic anomalies[14] or when crossing coast lines from sea to land or vice versa.[1,15] None of these factors will coincide with a diel pattern along the flight routes. The same is true for sudden strong weather disturbances, such as dust (sand) storms[30,31] and thunderstorms, that migrants may react to.

Birds may need to change altitude because of the Earth's topography, e.g., the Himalayas[5,11] and the Greenland icecap.[32,33] There are only few sites along the main route of great snipes that contain peaks above 2,000 m[10] (Figure 3), suggesting that great snipes will rarely be affected by the Earth's topography.[4]

Migratory birds may avoid flying within clouds or between cloud layers because orientation may be impaired.[16,22,23] Adjustments to clouds and precipitation are probably not the main cause for the circadian regularity in altitude shifts in great snipes but could certainly be a reason behind the occasional divergence from the general pattern (Figure 2). Overall, any of the factors listed in Table 1 could have added to the variation around the overall pattern, as well as caused the few clear exceptions.

Peak flight altitudes

Great snipes repeatedly reached altitudes above 6,000 m, and when correcting for prevailing atmospheric conditions, the true flight altitude was more likely around 8,700 m for the highest flying bird. This may be the highest altitude ever recorded for an identified migrant. The highest altitude to date is 8,200 m, a flock of whooper swans *Cygnus cygnus* flying between Iceland and Scotland.[29,34] In a study of bird migration by radar at the Negev desert in Israel, birds were regularly found migrating 5,000–7,500 m, with a single echo at "almost 9,000 m a.s.l."[2] Based on wingbeat frequencies and direct observations, it was suggested that some of the high-altitude migrants were shorebirds. The highest known altitude of any identified bird is the 11,000 m (37,000 ft) of a Rüppell's vulture *Gyps rueppellii* that collided with an airplane.[29,35]

Not only did one great snipe reach 8,700 m; it stayed above 8,000 m for several hours. With an estimated ambient temperature of −21°C, the additional chilling effect from an air flow proportional to flight speed, the very low oxygen and air pressures (350 hPa), and strong ultraviolet radiation, this is a truly inhospitable environment.[29] Migratory birds are able to carry out flapping flight at such high altitudes due to several physiological adaptations of the heart, lungs, and muscles.[25] Whereas we can add no extra knowledge to how the birds manage to fly at the extreme altitudes, it should be noted that the great snipes spend the complete year, with the exceptions of the long flights, at altitudes below 1,500 m and carry out these exceptional flights without any apparent physical training, "warm-up," or acclimatization.

Concluding remarks

There are still only a few papers reporting altitude data from long-distance tracks of migrating birds, but all of them report more or less distinct altitude changes as well as some surprisingly high flight altitudes. It is likely that with the increasing use of light-weight multisensor dataloggers, dramatic changes in flight altitudes and flights at extreme altitudes may prove to be much more common than hitherto believed, shedding new light on the complexity and challenges of migratory flights. We foresee intensified research to explore how and why migratory birds using flapping flight vary their cruising altitudes in the atmosphere, a so far partly neglected dimension in bird migration research. With more tracks available, it may be possible to support or disprove the potential explanations for a diel altitude cycle given here. It would, for example, be interesting to know if a diel cycle is apparent also in long flights over areas largely lacking bird predators, such as vast oceans, and how birds behave at daytime in overhead cloud cover.

STAR★METHODS

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

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact
  - Materials availability
  - Data and code availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
  - Study site
- METHOD DETAILS
  - Multisensor dataloggers
  - Logger recovery rates and available data
  - Functionality details of the dataloggers
  - Estimating altitude
  - Determining day and night
  - Approximate flight routes and topography
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Diel rhythms in flight altitudes

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.05.047.

ACKNOWLEDGMENTS

We are most grateful to Peter Jonsson for his generous and invaluable help throughout the study. Anna-Carin Bäckman, Amandine Doré, Koos van Ee, Arne Hegemann, Ingela Källén, Ola Olsson, Daniel Piec, Johan Råghall, Tonio Schaub, Anders Tengholm, Johan Tengholm, and Ellinor Wiklund helped in the field. Ånnsjön Bird Observatory most kindly allowed us to use their excellent facilities and Handölsdalens Sami village granted us access to a local road. Financial support was received from the Centre for Animal Movement Research at Lund University, CAnMove, Linnaeus grant 349-2007-8690; the Crafoord Foundation in Lund; Lunds Djurskyddsfond; and Olle Engkvists Stiftelse (to Å.L.). The work was carried out under permits from the Lund/Malmö Ethical Committee for Animal Experiments (M112-09, M27-10, M470-12, M33-13, M72-15, and 5.8.18-6518/2020) and the Swedish Natural History Museum (bird ringing license #418 to Å.L.).

AUTHOR CONTRIBUTIONS

Conceptualization, Å.L., T.A., J.B., and R.H.G.K.; Methodology, A.A. and J.B.; Formal Analysis, Å.L., T.A., A.A., J.B., S.S., and J.K.M.W.; Investigation, Å.L., J.B., P.B., R.B., R.E., R.H.G.K., M.K., S.S., and J.K.M.W.; Writing – Original Draft, Å.L., J.K.M.W., T.A., J.B., and S.S.; Writing – Review & Editing, Å.L., T.A., S.S., J.B., A.A., P.B., R.B., R.E., R.H.G.K., and M.K.; Visualization, Å.L., J.B., R.B., S.S., and J.K.M.W.; Project Administration, Å.L.; Funding Acquisition, Å.L., T.A., and J.B.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: April 6, 2021
Revised: May 17, 2021
Accepted: May 20, 2021
Published: June 30, 2021

REFERENCES

1. Alerstam, T. (1990). Bird Migration (Cambrige University Press).
2. Liechti, F., and Schaller, E. (1999). The use of low-level jets by migrating birds. Naturwissenschaften *86*, 549–551.
3. Shamoun-Baranes, J., Liechti, F., and Vansteelant, W.M.G. (2017). Atmospheric conditions create freeways, detours and tailbacks for migrating birds. J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol. *203*, 509–529.
4. Senner, N.R., Stager, M., Verhoeven, M.A., Cheviron, Z.A., Piersma, T., and Bouten, W. (2018). High-altitude shorebird migration in the absence of topographical barriers: avoiding high air temperatures and searching for profitable winds. Proc. Biol. Sci. *285*, 20180569.
5. Li, D., Davison, G., Lisovski, S., Battley, P.F., Ma, Z., Yang, S., How, C.B., Watkins, D., Round, P., Yee, A., et al. (2020). Shorebirds wintering in Southeast Asia demonstrate trans-Himalayan flights. Sci. Rep. *10*, 21232.
6. Sjöberg, S., Malmiga, G., Nord, A., Andersson, A., Bäckman, J., Tarka, M., Willemoes, M., Thorup, K., Hansson, B., Alerstam, T., and Hasselquist, D. (2021). Extreme altitudes during diurnal flights in a nocturnal songbird migrant. Science *372*, 646–648.
7. Bishop, C.M., Spivey, R.J., Hawkes, L.A., Batbayar, N., Chua, B., Frappell, P.B., Milsom, W.K., Natsagdorj, T., Newman, S.H., Scott, G.R., et al. (2015). The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. Science *347*, 250–254.
8. Bowlin, M.S., Enstrom, D.A., Murphy, B.J., Plaza, E., Jurich, P., and Cochran, J. (2015). Unexplained altitude changes in a migrating thrush: long-flight altitude data from radio-telemetry. Auk *132*, 808–816.
9. Klaassen, R.H.G., Alerstam, T., Carlsson, P., Fox, J.W., and Lindström, A. (2011). Great flights by great snipes: long and fast non-stop migration over benign habitats. Biol. Lett. *7*, 833–835.
10. Lindström, Å., Alerstam, T., Bahlenberg, P., Ekblom, R., Fox, J.W., Råghall, J., and Klaassen, R.H.G. (2016). The migration of the great snipe Gallinago media: intriguing variations on a grand theme. J. Avian Biol. *47*, 321–334.
11. Hawkes, L.A., Balachandran, S., Batbayar, N., Butler, P.J., Chua, B., Douglas, D.C., Frappell, P.B., Hou, Y., Milsom, W.K., Newman, S.H., et al. (2013). The paradox of extreme high-altitude migration in bar-headed geese Anser indicus. Proc. Biol. Sci. *280*, 20122114.
12. Sjöberg, S., Pedersen, L., Malmiga, G., Alerstam, T., Hansson, B., Hasselquist, D., Thorup, K., Tøttrup, A.P., Andersson, A., and Bäckman, J. (2018). Barometer logging reveals new dimensions of individual songbird migration. J. Avian Biol. *49*, e01821.
13. Cabrera-Cruz, S.A., Smolinsky, J.A., McCarthy, K.P., and Buler, J.J. (2019). Urban areas affect flight altitudes of nocturnally migrating birds. J. Anim. Ecol. *88*, 1873–1887.
14. Alerstam, T. (1987). Bird migration across a strong magnetic anomaly. J. Exp. Biol. *130*, 63–86.
15. Kerlinger, P., and Moore, F.R. (1989). Atmospheric structure and avian migration. In Current Ornithology, *Volume 6*, D.M. Power, ed. (Plenum Press), pp. 109–142.
16. Griffin, D. (1973). Oriented bird migration in or between opaque cloud layers. Proc. Am. Philos. Soc. *117*, 117–141.
17. Lindström, Å., and Alerstam, T. (2020). Waders flying with folded legs – which species, when, where and why? Wader Study *127*, 1–8.
18. Xirouchakis, S.M., and Panuccio, M. (2019). Hunting altitude of Eleonora's falcon (Falco eleonorae) over a breeding colony. J. Raptor Res. *53*, 56.
19. Walter, H. (1979). Eleonora's Falcon: Adaptations to Prey and Habitat in a Social Raptor (University of Chicago Press).

20. Myres, M.T. (1964). Dawn ascent and re-orientation of Scandinavian thrushes (Turdus spp.) migrating at night over the northeastern Atlantic Ocean in autumn. Ibis *106*, 7–51.
21. Klaassen, M. (2004). May dehydration risk govern long-distance migratory behaviour? J. Avian Biol. *35*, 4–6.
22. Griffin, D.R., and Hopkins, C.D. (1974). Sounds audible to migrating birds. Anim. Behav. *22*, 672–678.
23. Richardson, W. (1978). Timing and amount of bird migration in relation to weather: a review. Oikos *30*, 224–272.
24. Gauthreaux, S.A. (1972). Behavioral responses of migrating birds to daylight and darkness: a radar and direct visual study. Wilson Bull. *84*, 136–148.
25. Seidel, D.J., Free, M., and Wang, J. (2005). Diurnal cycle of upper-air temperature estimated from radiosondes. J. Geophys. Res. Atmos. *110*, 1–13.
26. Wallace, J.M., and Hartranft, F.R. (1969). Diurnal wind variations, surface to 30 kilometers. Mon. Weather Rev. *97*, 446–455.
27. Bryant, D.M. (1983). Heat stress in tropical birds: behavioural thermoregulation during flight. Ibis *125*, 313–323.
28. Speakman, J.R., and Król, E. (2010). Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. J. Anim. Ecol. *79*, 726–746.
29. Parr, N., Wilkes, M., and Hawkes, L.A. (2019). Natural climbers: insights from avian physiology at high altitude. High Alt. Med. Biol. *20*, 427–437.
30. Wallace, J.M. (1975). Diurnal variations in precipitation and thunderstorm frequency over the conterminous United States. Mon. Weather Rev. *97*, 446–455.
31. Natsagdorj, L., Jugder, D., and Chung, Y.S. (2003). Analysis of dust storms observed in Mongolia during 1937-1999. Atmos. Environ. *37*, 1401–1411.
32. Alerstam, T., Hjort, C., Högstedt, G., Jönsson, P., Karlsson, J., and Larsson, B. (1986). Spring migration of birds across the Greenland Inlandice. Medd. Gronl. Biosci. *21*, 1–38.
33. Kok, E.M.A., Tibbitts, T.L., Douglas, D.C., Howey, P.W., Dekinga, A., Gnep, B., and Piersma, T. (2020). A red knot as a black swan: how a single bird shows navigational abilities during repeat crossings of the Greenland Icecap. J. Avian Biol. *51*, 1–11.
34. Stewart, A.G. (1978). Swans flying at 8000 metres. Br. Birds *71*, 459–460.
35. Laybourne, R. (1974). Collision between a vulture and an aircraft at an altitude of 37,000 feet. Wilson Bull. *86*, 461–462.
36. Aybar, C., Wu, Q., Bautista, L., Yali, R., and Barja, A. (2020). rgee: An R package for interacting with Google Earth Engine. J. Open Source Softw. *5*, 2272.
37. Ekblom, R., and Carlsson, P. (2007). An estimate of the great snipe Gallinago media population in Sweden based on recent surveys at Ånnsjön and Storlien. Ornis Svec. *17*, 37–47.
38. Bäckman, J., Andersson, A., Alerstam, T., Pedersen, L., Sjöberg, S., Thorup, K., and Tøttrup, A.P. (2017). Activity and migratory flights of individual free-flying songbirds throughout the annual cycle: method and first case study. J. Avian Biol. *48*, 309–319.
39. Bäckman, J., Andersson, A., Pedersen, L., Sjöberg, S., Tøttrup, A.P., and Alerstam, T. (2017). Actogram analysis of free-flying migratory birds: new perspectives based on acceleration logging. J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol. *203*, 543–564.
40. Lisovski, S., and Hahn, S. (2012). GeoLight - processing and analysing light-based geolocator data in R. Methods Ecol. Evol. *3*, 1055–1059.
41. Danielson, J.J., and Gesch, D.B. (2011). Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010), Volume 2011-1073. https://www.usgs.gov/centers/eros/science/usgs-eros-archive-digital-elevation-global-multi-resolution-terrain-elevation?qt-science_center_objects=0#qt-science_center_objects.
42. R Development Core Team (2017). R: A language and environment for statistical computing (R Foundation for Statistical Computing).
43. Kemp, M.U., Emiel van Loon, E., Shamoun-Baranes, J., and Bouten, W. (2012). RNCEP: global weather and climate data at your fingertips. Methods Ecol. Evol. *3*, 65–70.
44. Jenkins, G.M., and Watts, D.G. (1968). Spectral Analysis and Its Applications (Holden-Day).

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Flight altitude and activity data from long flights, and example data of year around activity, temperature, air pressure and altitude for one individual	This paper	Mendeley data: https://doi.org/10.17632/k25sxgwgs2.1
Experimental models: Organisms/strains		
Great snipe *Gallinago media*	Wild	N/A
Software and algorithms		
R	[36]	https://cran.r-project.org/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Åke Lindström (ake.lindstrom@biol.lu.se).

Materials availability

This study did not generate any new unique materials.

Data and code availability

Raw data from Figures 2, 3, S2, and S4 and Table S1 were deposited on Mendeley at https://doi.org/10.17632/k25sxgwgs2.1. This study did not generate any new code.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study site

We studied a breeding population of great snipes in the Storulvån area in Jämtland, west central Sweden[10,37] (appr. 63.17°N, 12.38°E, Figure 1). The birds were trapped at night in 2015–2020, at four different leks within a maximum distance of 9 km from each other. Dataloggers were only put on adult males, given that they are more easily trapped and have higher recapture rates than females.[10]

METHOD DETAILS

Multisensor dataloggers

Information about behavior and flights were collected from multisensor dataloggers, consisting of an accelerometer for activity measurements, a barometric pressure sensor with internal temperature sensor, a light-level sensor, a real-time clock, and memory. The dataloggers weighed 1.4–1.7 g (about 1% of the birds' total body mass) and were attached to a plastic ring, which in turn was mounted on the tibia of the bird. This is the same way as geo-locators were attached in our previous studies of this species.[9,10] The dataloggers from 2015–2017 started logging on Aug 1st. The dataloggers from 2018 and 2019 started logging May 31st or June 1st.

The accelerometers were configured to measure along the vertical axis when the logger is hanging under the leg in flight, thereby recording the inevitable up-and-down movement of a bird in flapping flight. Measurements were taken in short sequences every 5 min.[38,39] Each sequence consists of 5 recordings of activity or non-activity, resulting in a score of 0–5 depending on the number of recordings indicating activity, with 0 being no activity and 5 meaning full activity. Twelve scores were stored per h, without mutual order. Scores of 4 and 5 were assumed to reflect flight. For a more detailed presentation of the dataloggers and measurement schemes, see Bäckman et al.[38,39]

Barometric pressure and temperature within the pressure sensor were measured momentarily at the final activity measurement every h using a Bosch Sensortec BMP280 sensor (absolute accuracy ca ± 1 hPa, equivalent to ca ± 8 m). The dataloggers also carried a light sensor that was activated for five days at five different occasions over the year.

Logger recovery rates and available data

In total 107 dataloggers were put on great snipes in 2015–2019 (n = 20, 20, 30, 25 and 12, respectively). Among the birds receiving a datalogger, 36 were retrapped one, two or three years later (but four birds had lost their logger). This is an overall return rate of 34%, which is similar to the return rates of birds with geolocators,[10] and to birds only ringed with a metal ring (31% in both groups). In total 25 out of the 32 retrieved loggers had functioned for some time, and 16 carried information on flight altitude for at least one of the long flights. One datalogger gave information on two autumn trans-Sahara flights (a datalogger put on 2017 and recovered 2019). Five individuals also brought data from two years, but through carrying different dataloggers.

We focused our analysis on three categories of long flights carried out by great snipes, corresponding to different flight segments: the Europe-to-Sahel flight in autumn (*Autumn*), the following flight from the Sahel region to the final wintering grounds near the Equator (*In-Africa*), and the Equator-to-Europe flight in spring (*Spring*, *cf*. Lindström et al.[10] and Figure 1). For the birds with data from two flights of the same category (in different years) we used only one flight of each type per individual to avoid pseudo-replication. In these cases, we used either the one with the most complete dataset, or, as in one case when the same amount of data were available, from the first of the two years. The final dataset included 27 flights (13 *Autumn*, 9 *In-Africa*, and 5 *Spring*), stemming from 14 loggers and 14 individuals (Table S1).

In six out of nine cases the *In-Africa* movement consisted of two or three consecutive flights. We included only the first of these flights in our analyses, which in eight out of nine cases was also the longest flight.

Functionality details of the dataloggers

Of our focal loggers put on in 2017, logger 975 of bird 5154835, stopped logging about a week after the Autumn flight and did not restart until after 3 months, which meant that we lost information for the In-Africa flight of this bird. The 2017 dataloggers were, to save battery power, programmed to stay "asleep" until the start of logging on Aug 1st although mounted on the birds already around June 1st. The program was changed from 2018 onward so that in case of a restart, logging would re-start immediately. Two other loggers (1X5 of individual 5154887 and 985 of individual 5153153) each stopped operating for a few hours, which both could be corrected using time data from the light measurements.

Throughout the flights, there were occasionally some activity sequences scoring lower than 5 (and hence, hourly scores < 60, Figure S4). In most cases this was thought to be caused by the bird gliding for parts of a second, coinciding with the activity recording. In the five instances that an hourly activity dropped below 40 (out of 60), the bird probably aligned its leg in a way that would result in no movement along the Z axis.[17] Since the exact reason for these reductions in activity could not be stated, but to make sure that they did not include landings, the activity data were compared with altitude estimates. If the altitude remained the same over 1-4 h of reduced activity, the bird was assumed to still be flying.

The dataloggers were programmed to measure light for five consecutive days, at five different occasions over the year. Light levels were recorded every minute during these days but only the maximum light levels during 5-min long periods was stored. The dates for the 5-day periods were chosen to maximize the chance of identifying key sites along the migration routes.[10] The distribution of the key sites retrieved from these light recordings using a light-threshold based position estimate[40] matched the general pattern of three long flights previously reported[10] (Figure S3). However, in addition to the malfunctioning of some light sensors, the difficulty of getting precise locations from only five days in a row (not least since some birds moved during these days), suggested that the data could not be used to reconstruct more detailed flight paths of each individual. Hence, they were not included further in the analyses.

Estimating altitude

Periods of continuous flight were easily identified from the annual actograms for each individual (Figure S2). Altitudes were estimated from the barometer readings using the Standard Atmosphere (SA) equation (International Organization for Standardization 1975: ISO 2533:1975; Equation 1)

$$z = -\frac{T_0}{L} * \left(1 - \left(\frac{p}{p_0}\right)^{\frac{-LR_0}{g}}\right), \qquad \text{(Equation 1)}$$

where z is the altitude, T_0 is the temperature at ground level (assumed to be 288.15°K, or 15°C), L is the altitudinal lapse rate of temperature (how much the temperature is assumed to change with altitude: -0.0065 deg K m^{-1}), P_0 is the standard atmospheric pressure at sea level (1013 hPa), P is measured air pressure, g is acceleration due to gravity (9.8 ms^{-2}) and R_0 is the gas constant for air (287.04 J kg^{-1} K^{-1}). All altitude estimates given in this report refer to meters above sea level.

Altitude estimates based on pressure and using the SA model will deviate somewhat from true altitude because of local pressure and temperature variation. As far as the *Autumn* and *Spring* flights are concerned, passing both the Sahara and Mediterranean Sea, they are to a large extent carried out through a system of subtropical high pressures. Therefore, the true altitudes ("geopotential altitude") of the great snipes, would normally be higher than those estimated using Equation 1. For example, for a bird at 3,000 m altitude in Europe, our estimates during *Autumn* are about 80 m too low. For a bird at 7,200 m above Africa during spring, we underestimate true altitude by around 400 m (Table S2). We nevertheless present altitudes derived from Equation 1, except when looking at the details of the highest-flying bird.

Determining day and night

All times reported are UTC (GMT), as recorded by the real-time clock of the datalogger. The birds of our breeding population spend most of their lives between longitudes 0° and 30°E, centered around 15°E[10] (Figure 1). Sunrise and sunset times were retrieved from NOAA Global Monitoring Laboratory (https://www.esrl.noaa.gov/gmd/grad/solcalc/). Since we did not know the exact positions of the birds, but still wanted to compare behavior and conditions at day and night, we assumed approximate times for dawn and dusk along approximate routes (see below). In analyses where it was important to know for sure whether the bird was flying at day or night, we considered 10:00–16:00 UTC to be daytime and 21:00–03:00 UTC to be night.

Approximate flight routes and topography

To get an estimate of the topography and weather variables along the long flights, we constructed a set of five approximate flight routes for the birds, for *Spring* and *Autumn* respectively (Figure 1; Table S3). This is the relatively narrow band within which the migration of Swedish male great snipes takes place, based on 19 tracked individuals,[10] and we feel confident that the assumed approximate flight routes are close enough for the purpose of our analyses.

Approximate *Autumn* and *Spring* flight routes were each drawn as two consecutive great circle segments (Figure 1). In *Autumn* the route extends from the breeding grounds (63.17°N, 12.38°E) to SE Europe (46°N, 18°E), and from there to a stopover site just south of the Sahara (10°N, 8°E). This is a total distance of ~6,000 km. In *Spring*, the approximate route starts at the winter grounds (0°N, 17°E), flexes at a point in the Sahara (24°N, 14°E), from where the birds head for a first European stopover site on the Balkan Peninsula (46°N, 22°E). This is a total distance of about 5,200 km (for more details, see Table S3).

For each *Autumn* flight, the distance of 6,000 km was divided by the total flight time, to find the average flight speed (ground speed, in km h^{-1}). Some birds covered a smaller part of the distance southward from the breeding grounds in one or a few shorter "pre-flights," conducted in early–mid August, i.e., in advance of the long non-stop *Autumn* flight[10] (Figures 1 and S2). In such cases we assumed that the long non-stop flight would start south of the breeding grounds along the approximate track, at a distance corresponding to the time spent on pre-flights at the average flight speed. We could thereby estimate an approximate starting point of the trans-Saharan flight, and where along the approximate track each hourly measurement of the long flight was taken. The corresponding treatment was given to *Spring* flights, but since there were generally no "pre-flights" before the long flight started, we used the duration of the non-stop flight as the time used to cover a total distance of 5,200 km.

We used the approximate routes to investigate the land topography potentially encountered by the migrating great snipes. We calculated elevation over 10 km intervals along each track. Elevation was extracted from the Global Multi-resolution Terrain Data 2010 (GMTED2010) digital elevation model,[41] with a spatial resolution of 7.5 arc-seconds (app. 250 m at the Equator) and elevation calculated according to the 'breakline emphasis product'. Finally, for each 10 km interval the average and maximum elevation was calculated. We used the RGEE package[36] within the R software[42] to extract elevation.

To illustrate the diel cycle in ambient temperature at different altitudes, the approximated *Autumn* and *Spring* routes #3 (Table S3) were divided by average flight duration (autumn: 73 h, spring: 82 h, Table S1). The dates of the earliest, average and latest flights recorded (Table S1) were used for *Autumn* and *Spring* flights, respectively. We used average start time (autumn: 19:04, spring:16:18) as starting h, and used weather data from 2018 and 2019, for *Autumn* and *Spring* flights, respectively. For each of these times and locations, data on ambient temperature were extracted from the National Centers for Environmental Predictions (NCEP) data using the RNCEP package at 850, 700, 500 and 400 hPa, corresponding to SA altitudes of 1457, 3011, 5 573 and 7183 m asl, respectively.[42,43] In addition, NCEP data on winds (u and v wind) and relative humidity was extracted for route #3 (Table S3) at an average flight date (Table S1) and the same locations and pressure levels as the ambient temperature[42,43] (Figure S1).

NCEP data on geopotential height were extracted and used to estimate the difference between true altitude and the calculated SA altitudes. The geopotential height data were extracted at 00:00 and 12:00 UTC for each fifth positions along the approximated routes #3 (for the *Spring* route the last two positions were included to increase the data from Europe) for an early, average and late flight timing (same as for temperature data, Table S1) at 850, 600, 700, 500, 400 and 300 hPa.[42,43] Since weather systems on average differ between regions, the data were grouped according to latitude, where latitudes > 45°N was classified as "Europe," latitudes 30°N–45°N as "Mediterranean," and latitudes < 30°N as "Africa" (Table S2).

QUANTIFICATION AND STATISTICAL ANALYSIS

Basic descriptive statistics on flight altitude can be found in Table S1. All analyses are based on 13 *Autumn*, 9 *In-Africa* and 5 *Spring* flights.

Diel rhythms in flight altitudes

The time-series of flight altitudes were analyzed individually using two different methods. We performed a frequency analysis using discrete Fourier transform (DFT) that produces a power spectrum with the relative frequency content of the series. We also calculated autocorrelation coefficients for each flight altitude series. DFT was estimated with the "spectrum" function and autocorrelation with the "acf" function.[42] The resulting power spectrums for all tracks were used to calculate an average frequency spectrum for *Autumn* and *Spring* flights and tested for significant frequency components using the χ^2-test of sample spectrum estimator.[44] The autocorrelation data were treated in a similar way, where we calculated average autocorrelation values for each time lag by adding all results separately for *Autumn* and *Spring* flights.

Average curves for flight altitude, in relation to time of day and distance flown, were calculated using geom_smooth in package 'ggplot2', with span set to 0.1. Since there is a heavy bias in the number of recordings per season (21 tracks from 2017/2018, 5 from 2016/2017 and 1 from 2019/2020), we did not test for differences between years. We used R[42] for all calculations.