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Great flights by great snipes: long and fast non-stop migration over benign habitats

Raymond H. G. Klaassen[1,*], Thomas Alerstam[1], Peter Carlsson[2], James W. Fox[3] and Åke Lindström[1]

[1]*Department of Biology, Lund University, Ecology Building, 22362 Lund, Sweden*
[2]*Lake Ånnsjön Bird Observatory, Handöl 563, 83015 Duved, Sweden*
[3]*British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK*
**Author for correspondence* (*raymond.klaassen@biol.lu.se*).

Migratory land birds perform extreme endurance flights when crossing ecological barriers, such as deserts, oceans and ice-caps. When travelling over benign areas, birds are expected to migrate by shorter flight steps, since carrying the heavy fuel loads needed for long non-stop flights comes at considerable cost. Here, we show that great snipes *Gallinago media* made long and fast non-stop flights (4300–6800 km in 48–96 h), not only over deserts and seas but also over wide areas of suitable habitats, which represents a previously unknown migration strategy among land birds. Furthermore, the great snipes achieved very high ground speeds (15–27 m s^{-1}), which was not an effect of strong tailwind support, and we know of no other animal that travels this rapidly over such a long distance. Our results demonstrate that some migratory birds are prepared to accept extreme costs of strenuous exercise and large fuel loads, even when stopover sites are available along the route and there is little tailwind assistance. A strategy of storing a lot of energy before departure, even if migration is over benign habitats, may be advantageous owing to differential conditions of fuel deposition, predation or infection risk along the migration route.

Keywords: avian migration; endurance exercise; geolocators; stopover ecology; wind assistance

1. INTRODUCTION

Many terrestrial birds fly several thousands of kilometres non-stop during migration when crossing ecological barriers, such as deserts, oceans and ice-caps [1–3], where they cannot find food for refuelling. But long non-stop flights come at some cost. In addition to the strenuous exercise itself, the huge fuel stores needed (up to 100 per cent of lean body mass in long-distance migrants [2,4,5]) have a negative effect on transport economy [6,7] and manoeuvrability [8] and may increase predation risk [9]. When flying over hospitable land, terrestrial birds, therefore, generally avoid long flights and migrate by shorter flight steps, carrying only small to moderate fuel loads [4].

Still, our understanding of the migration strategies of birds is rather limited because for the majority of species we cannot follow the annual movements of individuals. With minute geolocators [10], allowing the tracking of small individual birds [11], a new and exciting picture of avian flight capacity and migration strategies is emerging [11–14]. We used geolocators to unravel the complete annual migration of the great snipe *Gallinago media*, an enigmatic and endangered Eurasian inland shorebird with an unknown migration strategy.

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2. MATERIAL AND METHODS

(a) *Fieldwork*

In May 2009, 10 male great snipes (159–169 g) were captured in mistnets at a lek in Jämtland, Sweden (63° N, 12° E) and equipped with geolocators (Mk10, 1.1 g, British Antarctic Survey (BAS); electronic supplementary material, figure S1). In May 2010, three of the birds were recaptured.

(b) *Data analysis*

Times of sunrise and sunset were extracted (TransEdit, BAS) using a single light threshold value of 2. We calculated locations (BirdTracker, v. 1.0, BAS) using the length of the solar day (or night) to determine latitude and the time of local solar noon (or midnight) to determine longitude. For these calculations, we used a sun angle that minimized the difference in latitude between pre- and post-equinox periods when the birds were stationary (−4.0, −3.5 and −3.0 for individuals 1, 2 and 3, respectively). This procedure is based on the observation that the latitude error increases with increasing mismatch between light threshold value and inferred sun angle [15]. For the non-stop flights, data were smoothed twice [16] giving estimates for noon and midnight positions, which defined 12 h-segments. Travel distance is the sum of the length of individual segments, and the mean ground speed is the travel distance divided by the duration of the flight.

(c) *Environmental data*

Wind data were obtained from the NCEP/NCAR reanalysis project (NOAA/OAR/ESRL PSD, Boulder, CO, USA, http://www.esrl.noaa.gov/psd/). For every 12 h-segment, wind data were extracted for the start, mid- and endpoint, in which the midpoint was given twice as much weight during averaging. The airspeed and heading of the bird were calculated by subtracting the wind vector from the track vector. Subsequently, we calculated, for each long non-stop flight, the total distance the birds flew through the air and the corresponding mean airspeed. Flight altitudes of the birds were not recorded, so these calculations were repeated for different altitudes (750, 1500, 3000 and 5000 m). We also considered the scenario where the bird always chose the altitude with most profitable winds ('min' in figure 1*c*,*d*).

(d) *Wind drift analysis*

The effect of wind on the direction of movement was analysed by relating track direction (direction of a 12 h-segment) to the angle between track and heading direction. This angular difference is the angle of drift or compensation caused by wind. A value of 0 indicates no relationship between wind and course changes (complete compensation). Positive values indicate that the track direction is a function of the wind direction, i.e. the track direction is affected by the wind (wind drift). A value of 1 is the special case where the bird keeps a constant heading and is fully affected by wind (full drift). Negative values mean that the flight paths are directed into the crosswind component.

3. RESULTS

In late August, three birds flew 6170, 6800 and 4620 km non-stop from the breeding area to tropical Africa (figure 1*a*,*c*). These flights lasted for 72, 84 and 48 h, respectively (electronic supplementary material, table S1). In spring, the birds flew 4980, 5180 and 4280 km non-stop (during 72, 96 and 48 h, respectively) from the equatorial winter quarters to the Balkan region (figure 1*b*,*c*). From there onwards, the birds made several short flights

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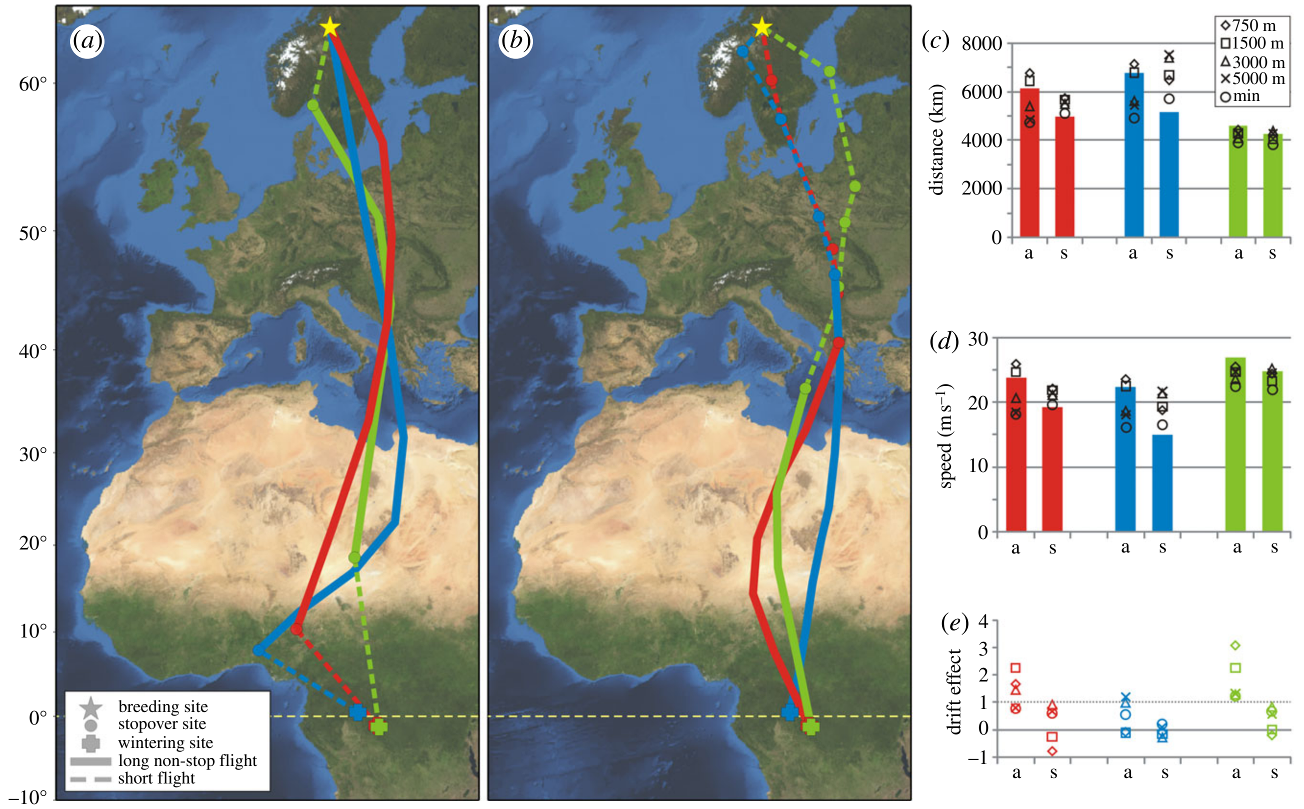

Figure 1. (*a*) The autumn and (*b*) spring migration of three great snipes travelling between the breeding site in Sweden (63° N, 12° E) and winter quarters in central Africa (1° S, 20° E). Bar graphs show (*c*) the distance and (*d*) ground speed for non-stop flights. Symbols depict distance and speed in relation to surrounding air, should the bird have flown at a given altitude. 'min' reflects the conditions for a bird that always selects the most profitable altitude. (*e*) Relationship between wind and directional changes (see main text). a, autumn; s, spring.

interspersed with short stopovers, until reaching the breeding grounds (figure 1*b*).

Travel speeds were very high for the non-stop flights: ground speeds were 22–27 $\mathrm{m\,s^{-1}}$ in autumn and 15–25 $\mathrm{m\,s^{-1}}$ in spring (figure 1*d*). Meteorological data indicated that in autumn tailwind support existed at high altitudes (3000–5000 m a.s.l.). However, for these altitudes calculated airspeeds were only 12–22% lower than corresponding ground speeds (figure 1*d*) indicating only a limited effect of wind. In spring, two birds even faced net headwinds at all altitudes. For high altitudes (where the birds had most tailwind support), and for the scenario where the bird always chooses the altitude with the most profitable winds, a positive relationship existed between the wind effect and the track direction, indicating lateral wind drift (figure 1*e*).

4. DISCUSSION

Great snipe flights are remarkable for two reasons. First, it is surprising that the flights are very long. In autumn, the non-stop flights cover the whole temperate zone and part of the savannah, including 2500 km across areas where numerous other migrants with similar ecology (e.g. ruff *Philomachus pugnax*, wood sandpiper *Tringa glareola*) are known to stop and refuel in autumn [1,17]. Moreover, the great snipes we tracked made stopovers in these areas in spring (figure 1*b*), indicating that the temperate zone generally offers suitable stopover habitats for them. Also, in the spring a substantial part of the non-stop flights was over potential feeding habitat (at least 1300 km of savannah). To our knowledge, the flights of the great snipes are the longest non-stop flights ever recorded where a substantial part of the distance (especially in autumn) is over potentially benign areas (green areas in figure 1*a*,*b*).

Second, the non-stop flights were notably fast, and the ground speeds of great snipes (15–27 $\mathrm{m\,s^{-1}}$) were substantially higher than those recorded for three other shorebird species during similar non-stop flights for 3–8 days over 2500–11 700 km (7.4–18 $\mathrm{m\,s^{-1}}$) [2,18,19]. Winds were not or only slightly favourable during non-stop flights, and thus the high ground speeds of the great snipes are accounted for by high airspeeds (16–26 $\mathrm{m\,s^{-1}}$) rather than strong tailwinds. The great snipes presumably had high airspeeds because of a high wing loading (up to 77 $\mathrm{N\,m^{-2}}$ at the onset of the flight; electronic supplementary material, table S2) and flying at relatively high altitudes. Great snipes do not seem to be specifically adapted for long flights as they have relatively rounded wings, whereas pointed wings are associated with energy efficient flight (electronic supplementary material, figure S2 and table S2). However, the aspect ratio of great snipes' wings is somewhat higher than for the closely related, and less-migratory, common snipe *Gallinago gallinago* [20]. The curved shape of the flight courses (figure 1*a*,*b*) may be explained by lateral wind drift from a rather constant heading by varying high-altitude winds (figure 1*e*). Wind drift generally increases travel distance [21] and thus will contribute to high speeds.

Our results show that some migrants are prepared to carry out long-distance flights, even when stopover sites are available and there is little tailwind assistance, in spite of the costs of strenuous exercise [22] and carrying large fuel stores [4]. That great snipes deposit large fat stores in autumn is well exemplified by a historic report: '*great snipes are so fat and heavy in autumn that their skin sometimes ruptures when the shot bird hits the ground*' ([23], pp. 266–269). The over-flying of potential staging sites implies that great snipes minimize the time rather than the energy spent on migration [24], and that conditions in late summer are very favourable at the northerly latitudes in comparison with potential stopover sites further south in Europe with respect to fuel deposition, predation and/or infection risk [2,24–26]. In spring, the great snipes used several stopover sites in eastern Europe. This would allow them not only to refuel for further flights, but also to optimize the timing of arrival at the breeding grounds and to add extra stores for the start of the breeding period [2,27]. The long and fast flights of the great snipes across ecological barriers as well as benign habitats represent an unexpected and previously unknown strategy in bird migration, and indicate that we have not yet grasped the full range of variability in bird migration strategies.

The study was approved by the ethical committee in Malmö/Lund (M112-09).

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