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High-altitude shorebird migration in the absence of topographical barriers: avoiding high air temperatures and searching for profitable winds

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Nearly 20% of all bird species migrate between breeding and nonbreeding sites annually. Their migrations include storied feats of endurance and physiology, from non-stop trans-Pacific crossings to flights at the cruising altitudes of jetliners. Despite intense interest in these performances, there remains great uncertainty about which factors most directly influence bird behaviour during migratory flights. We used GPS trackers that measure an individual's altitude and wingbeat frequency to track the migration of black-tailed godwits (*Limosa limosa*) and identify the abiotic factors influencing their in-flight migratory behaviour. We found that godwits flew at altitudes above 5000 m during 21% of all migratory flights, and reached maximum flight altitudes of nearly 6000 m. The partial pressure of oxygen at these altitudes is less than 50% of that at sea level, yet these extremely high flights occurred in the absence of topographical barriers. Instead, they were associated with high air temperatures at lower altitudes and increasing wind support at higher altitudes. Our results therefore suggest that wind, temperature and topography all play a role in determining migratory behaviour, but that their relative importance is context dependent. Extremely high-altitude flights may thus not be especially rare, but they may only occur in very specific environmental contexts.

1. Introduction

Radar observations have documented a number of bird species flying at extremely high altitudes (e.g. greater than 5000 m), but these flights are generally thought to be rare [1–3] (but see [4]). For instance, fewer than 5% of individual birds passing over northeastern Canada during autumn migration fly at heights greater than 4400 m [2]. Moreover, the factors driving these impressive feats have remained elusive, and understanding how birds behave during their migratory flights is one of the final frontiers in the study of bird migration [5,6]. As a result, it was not until recent studies of bar-headed geese (*Anser indicus*) migrating over the Himalayan Mountains that the remarkably dynamic nature of individual flight behaviour began to be revealed. Those studies have shown that bar-headed geese employ a 'mountain-hugging' migration strategy that follows the terrain of the ground below them, forcing them to climb to altitudes greater than 7000 m for some portions of their flight, but allowing them to spend much of their time below 4000 m [7,8]. However, small passerines migrating over lowland areas have also recently been observed displaying

rapid changes in altitude mid-flight, but for seemingly inexplicable reasons [9]. These findings, combined with the continued difficulty of tracking many species for the duration of their migratory flights, indicate that much remains to be learned about the factors that influence in-flight behaviour.

Long-distance migration is energetically expensive. During their migratory flights, birds may sustain metabolic rates over nine times greater than their basal metabolic rate for more than a week [10]. These energetic costs suggest that, once in flight, migrants should strive to find an 'optimal' flight altitude in order to minimize energy expenditure [11]. However, this optimal altitude may fluctuate in response to changes in an individual's body condition and physiological capacities, as well as external environmental conditions. For instance, wind commonly influences migratory flight height and speed, and is frequently thought to be the strongest abiotic driver of migratory behaviour in long-distance migrants [12]. Accordingly, bar-tailed godwits (*Limosa lapponica baueri*) flying non-stop from Alaska to New Zealand only depart on their epic migrations with the aid of low-pressure weather systems that provide sustained wind assistance, and are subsequently thought to dynamically optimize their flight altitude to maintain maximum wind support [13]. Additionally, temperature and humidity can also play a role, with high temperatures and low humidity potentially leading to hyperthermia and increased water loss via evaporative cooling [14,15], which can minimize flight distances [16] and force migrants to make desert crossings at night to avoid heat stress [17]. Other factors, such as topography [7,8], an individual's aerobic capacity at high altitude [18,19] and its body size (which determines the cost of climbing flight [20]), can be important as well. Thus, at any point in time, several different variables can influence decisions about how high to fly and whether or not to stop.

Here we present data collected from GPS trackers that measured the altitude, ground speed and wingbeat frequency of black-tailed godwits (*Limosa limosa limosa*; hereafter, 'godwits') during their migrations from the Netherlands to sub-Saharan West Africa. Using these data, we asked which abiotic factors—wind support, air temperature, relative humidity and topography—best explain an individual's flight altitude and decision to change altitudes mid-flight, as well as how the relative influence of these factors changes over the course of a flight. Based on optimal migration theory and previous studies in other migratory birds [13,21], we predicted that godwits would alter their flight altitude over the course of a flight to optimize the amount of wind assistance received. However, because previous work has also suggested that rates of water loss should increase above 3000 m due to reductions in air temperature, humidity, and air density [15,16,22], we predicted that godwits would predominantly fly at altitudes below 3000 m. Our study thus provides some of the first empirical data to directly test these predictions, and can enable a reassessment of what should be considered both normal and possible for migratory species.

2. Material and methods

(a) Study species and field methods

Continental black-tailed godwits breed primarily in the Netherlands and have a disjunct nonbreeding range, with some individuals wintering on the Iberian Peninsula, but most

crossing the Sahara Desert to spend the winter in West Africa [23]. In 2013, we deployed 7.5 g solar-powered UvA-BiTS GPS trackers [24] on 20 female godwits breeding in the Haanmeer Nature Reserve (52.9226° N, 5.4336° E) in southwest Friesland, the Netherlands [25]. In accordance with Dutch Welfare License 6350A and C, we attached the trackers with a leg-loop harness using 2 mm nylon rope for a total attachment weighing approximately 9 g and an average loading factor of $2.88 \pm 0.19\%$ ($n = 20$) at the time of capture. The trackers—data from which can be remotely downloaded—were programmed to record an individual's location and altitude once every 5 min when the battery was fully charged and once every 15–30 min in all other instances. Battery-charging issues caused by long periods of low light conditions or by feathers covering the trackers' solar panels occasionally meant that the trackers were unable to collect any data for extended periods of time; we present here only data from flights with no gaps longer than 30 min.

(b) Tracking and weather data

For each fix, along with an individual's location, the trackers measured an individual's ground speed—using instantaneous Doppler shift measurements from the GPS—and altitude. On wild birds, UvA-BiTS trackers estimate location and altitude with errors of ± 2.45 m (0.34–7.14 m, 95% CI) and ± 2.77 m (0.38–7.61 m, 95% CI), respectively, meaning that they are well suited for efforts to pinpoint the relationship between weather variables and changes in in-flight behaviour [24]. In addition, our trackers were also outfitted with accelerometers, which measured an individual's acceleration at 20 Hz along three spatial axes (e.g. its surge (x), sway (y) and heave (z)) for a 1 s period following each GPS measurement. From this accelerometer data we calculated an individual's wingbeat frequency using a fast Fourier transformation of the heave [26].

We considered a migratory flight any non-stop movement longer than 200 km. Throughout these migratory flights, we obtained measures of wind speed, wind direction, relative humidity and temperature from the ERA-Interim dataset produced by the European Centre for Medium-Range Weather Forecasts (ECMWF) [27] at an individual's flight altitude, as well as at the following pressure levels: 1000, 975, 950, 925, 900, 875, 850, 800, 750, 700, 600 and 550 mbar. Because the ECMWF dataset presents weather data for $0.75 \times 0.75^\circ$ grid cells every 3 h, we used a linear interpolation among data from four positions, two pressure levels, and two consecutive points in time from the ECMWF dataset in order to estimate the weather conditions occurring at each GPS location from our tracking dataset. Using this interpolated weather data, we estimated the level of wind support at each pressure level at each time point using an individual's flight direction between consecutive time points along their migratory path, as individuals may compensate, over-compensate, or drift with the wind depending on their location and the direction of the wind. Models with wind support calculated in this manner were qualitatively the same, but outperformed those in which we calculated wind support based on an individual's flight direction over the entire course of a migratory flight. Additionally, for each GPS location taken during a migratory flight, we calculated an individual's airspeed—by subtracting the estimated horizontal wind vector at an individual's flight altitude from its measured ground speed vector [28]—and rate of change in altitude (m s^{-1}) since its last location.

(c) Statistical analyses

We separately tested the influence of abiotic conditions on flight altitude and rate of change in altitude. To do this, we used generalized linear mixed-effect models (GLMMs) and a two-step process. First, we developed a global model for each dependent variable that included flight segment and individual as random effects. However, to reduce the number of random

effects included in our candidate model sets (see below), we compared among all possible combinations of these two variables as random effects (e.g. flight only, individual only, flight and individual, and flight nested within individual; see electronic supplementary material, table S1) using AIC_c values and our global models. Those random effects included in the model with the lowest AIC_c score were then included in our overall candidate model set.

Second, with our reduced set of random effects, we used a candidate model approach in which we standardized all predictor variables [29], then tested the effects of each of them separately, as well as all potential combinations among them. We also compared among models using an AIC framework, choosing the model with the lowest AIC_c score as the most well supported model. If no model had a model weight (w_i) greater than 0.90, we used model averaging to identify the most important predictor variables [30]. We considered predictor variables that had model-averaged 95% CIs that did not cross zero to be biologically relevant. For ease of interpretation, we also ran our top models with unstandardized predictor variables. We present these unstandardized results in the electronic supplementary material tables only, while the Results section refers to the standardized coefficients. We ran all models using the R packages 'lme4' [31] and 'MuMIn' [32].

To assess the conditions that affect an individual's flight altitude, we only considered the effects of ground conditions and the altitude with maximum wind support on flight altitude because godwits may change altitudes in order to experience relatively constant conditions throughout their flights [13], and because temperature and humidity, in general, scale linearly with altitude [33]. Thus, our GLMM included flight altitude as the dependent variable; flight as a random effect; and time since departure, ground elevation, altitude with maximum wind support, and ground wind support, temperature and relative humidity as predictor variables.

The conditions that influence an individual's decision to change altitude mid-flight, however, may be separate from the conditions that helped determine their previous flight altitude. We therefore tested whether the conditions an individual experienced at their flight altitude at a given time point influenced their rate of altitudinal change to the subsequent time point. For this, we again used a GLMM, but with an individual's rate of altitudinal change between consecutive time points as the dependent variable; flight as a random effect; and the previous temperature, relative humidity and level of wind support at an individual's flight altitude, previous altitude with maximum wind support, previous ground elevation, and time since an individual's departure as predictor variables.

Additionally, to test for differences in flight speeds and determine whether godwits employed different modes of flight (e.g. soaring or gliding) at different altitudes, we used GLMMs with wingbeat frequency, ground speed or air speed as the dependent variables; individual and flight as potential random effects (see above); and flight altitude or rate of change in flight altitude between consecutive time points as the predictor variables.

3. Results

Fourteen of the 20 godwits outfitted with trackers in 2013 returned to their breeding grounds in 2014. Of those returning individuals, four had working trackers, and one individual ultimately provided migratory tracks from two consecutive years. Because godwits stop to refuel in wetlands and agricultural fields along their migratory route [23], we obtained data on a total of 24 migratory flights from the four individuals—16 during southward migration and 8 during northward migration (figure 1; table 1). Individuals

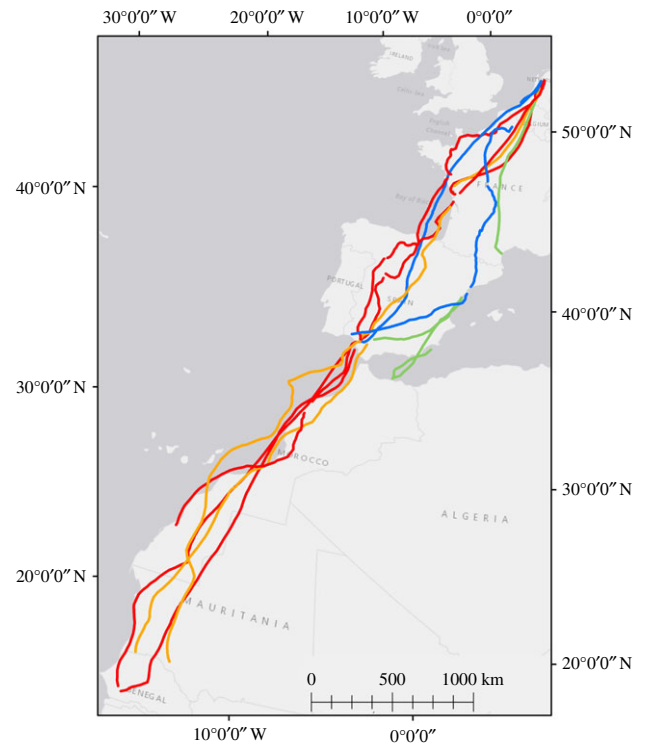


Figure 1. Migratory tracks of four female continental black-tailed godwits captured at a breeding site in southwest Friesland, the Netherlands, carrying GPS trackers. Each line represents a flight segment connecting two stopover sites ($n = 24$ flights). Colours indicate individuals A (red), B (orange), C (green), and D (blue).

were tracked for 3, 4, 5 and 12 flights, respectively, and on average we recorded locations every 22 ± 14 min during those flights for a total of 1128 in-flight locations.

We found that flights differed in duration, with a range of 3.52–48.32 h ($\mu = 17.34 \pm 10.96$ h; all results \pm s.d.), covering 214–2687 km ($\mu = 1080 \pm 845$ km; table 1). Ground speeds also varied tremendously, averaging 64.98 ± 21.63 km h⁻¹, but ranging as high as 145 km h⁻¹. At no point did godwits employ soaring or gliding during their migratory flights: wingbeat frequencies averaged 6.30 ± 0.85 Hz ($n = 903$ locations) and were higher during climbing flight, but did not approach zero during descents ($\beta = 0.52$, s.e. = 0.04, CI = 0.44, 0.61; electronic supplementary material, figure S2, tables S2 and S3). Additionally, we found that flight altitudes reached as high as 5956 metres above sea level (m.a.s.l.; $\mu = 3607 \pm 1573$ m.a.s.l.). However, rather than remaining at a constant altitude, flight patterns were dynamic, with individuals frequently changing their altitude throughout a flight (figure 2; electronic supplementary material, figure S1). In total, all individuals were recorded flying above 5000 m during at least one flight, with 42% of all flights reaching above 4000 m.a.s.l. and 21% above 5000 m.a.s.l. (figure 3; table 1).

Ground elevation was a significant predictor of flight altitude ($\beta = 1214.30$, s.e. = 79.60, CI = 1058.14, 1370.53; electronic supplementary material, tables S1–S3), but it failed to explain the majority of the variation in flight altitudes exhibited by godwits (electronic supplementary material, figure S1). Thus, flight altitudes above ground level were only slightly lower than flight altitudes above sea level ($\mu = 1317 \pm 1316$ m.a.g.l. versus $\mu = 1549 \pm 1383$ m.a.s.l., $n = 1128$ locations), reflecting the fact that

Table 1. Summary statistics of the migratory flights of four female continental black-tailed godwits captured at a breeding site in southwest Friesland, the Netherlands, carrying GPS trackers. Flight numbers correspond to those presented in electronic supplementary material, figure S1. Averages are presented \pm s.d.

ind.	flight	season	flight duration (h)	distance covered (km)	maximum altitude (m.a.s.l.)	average altitude (m.a.s.l.)
A	1	autumn	13.42	527	3539	1791 \pm 994
A	2	autumn	9.29	298	1669	614 \pm 461
A	3	autumn	11.04	636	1797	773 \pm 482
A	4	autumn	8.99	521	3802	1952 \pm 861
A	5	autumn	31.74	2643	4351	1726 \pm 1460
A	6	spring	22.61	2524	5231	2463 \pm 1405
A	7	spring	12.75	493	2622	390 \pm 818
A	8	spring	9.36	894	2116	751 \pm 552
A	9	autumn	13.27	883	3974	1887 \pm 1245
A	10	autumn	13.30	637	3102	1687 \pm 799
A	11	autumn	8.98	422	2101	998 \pm 511
A	12	autumn	32.18	2687	3309	1489 \pm 1016
B	1	autumn	10.53	835	4071	1755 \pm 1336
B	2	autumn	19.07	1050	2422	1150 \pm 729
B	3	autumn	38.63	2484	4147	891 \pm 919
B	4	spring	48.32	2385	5956	2003 \pm 1578
C	1	autumn	12.85	995	5630	3566 \pm 1724
C	2	autumn	15.30	361	5582	1984 \pm 1635
C	3	autumn	13.84	613	2197	1095 \pm 572
D	1	autumn	29.76	1997	5139	1637 \pm 1644
D	2	spring	12.71	788	4481	919 \pm 1122
D	3	spring	14.98	642	2424	1047 \pm 730
D	4	spring	9.75	384	533	305 \pm 92
D	5	spring	3.52	214	730	370 \pm 267

ground elevations were generally low and did not vary dramatically along much of the godwit migration route ($\mu = 232 \pm 327$ m).

Instead, weather conditions were the strongest correlates of variation in flight altitude. In accordance with previous studies [12,13], we found that wind conditions influenced godwit flight altitudes and, in some circumstances, were correlated with periods of extreme high-altitude flight (altitude with maximum wind support: $\beta = 689.91$, s.e. = 82.43, CI = 528.18, 851.65; electronic supplementary material, tables S1–S3). However, the movement of godwits to higher altitudes was not correlated with the occurrence of headwinds, but rather with tailwinds (wind support: $\beta = 0.06$, s.e. = 0.02, CI = 0.02, 0.11, electronic supplementary material, tables S1–S3), and this was especially true when wind support was higher later in flights (ground wind support \times time since departure interaction: $\beta = 475.40$, s.e. = 152.53, CI = 175.73, 775.05; electronic supplementary material, tables S1–S3). Correspondingly, godwits achieved faster ground speeds at higher altitudes ($\beta = 1.62$, s.e. = 0.33, CI = 0.98, 2.27; electronic supplementary material, figure S2, tables S1–S3).

Nonetheless, in none of our models was the level of wind support or altitude with maximum wind support the

strongest factor explaining variation in either godwit flight altitudes or the rate of change in altitude (electronic supplementary material, tables S2 and S3). Rather, high ground temperatures were a stronger correlate of high above ground flight altitudes ($\beta = 953.84$, s.e. = 216.89, CI = 525.43, 1386.78; figure 2; electronic supplementary material, tables S2 and S3), and godwits moved to higher altitudes in association with the occurrence of high temperatures at their previous flight altitude ($\beta = 0.10$, s.e. = 0.03, CI = 0.04, 0.16; figure 4; electronic supplementary material, tables S2 and S3). Thus, although ground temperatures averaged $18.75 \pm 6.29^\circ\text{C}$ and occasionally exceeded 40°C along godwit flight paths, temperatures at their flight altitudes averaged $10.20 \pm 9.12^\circ\text{C}$ ($n = 1128$ locations). Furthermore, we found that godwits spent less than 30% of their migratory flights at altitudes with temperatures that are likely to incur high rates of evaporative water loss (greater than 15°C [34]).

Temperature and wind thus both significantly influenced godwit in-flight behaviour. Accordingly, we found that the factor that had the single largest effect on changes in altitude mid-flight was an interaction between temperature and wind support ($\beta = -0.14$, s.e. = 0.05, CI = -0.24 , -0.05 ; electronic supplementary material, tables S2 and S3), such that godwits

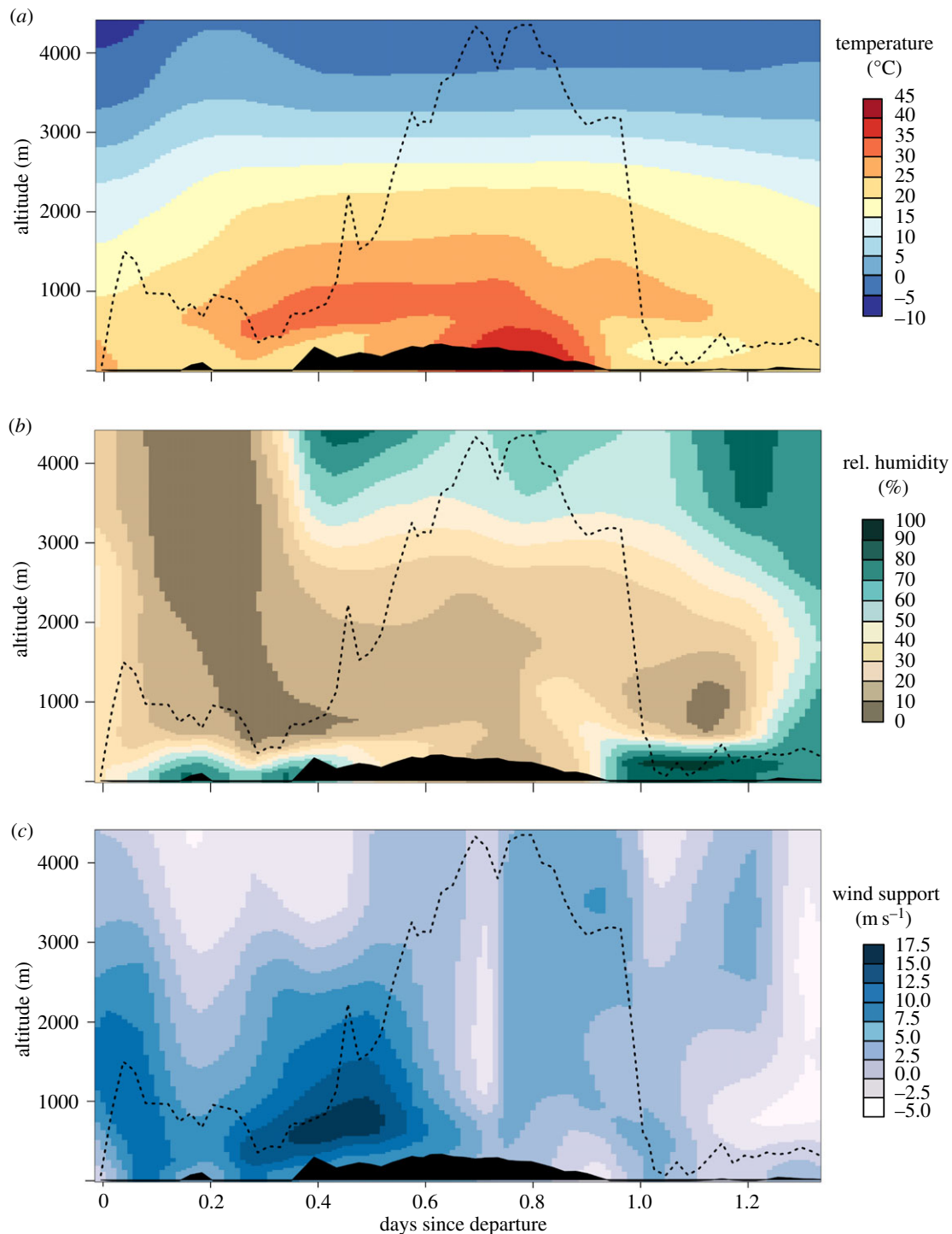


Figure 2. Flight conditions during a migratory flight undertaken by a female continental black-tailed godwit (individual A; flight A4) carrying a GPS tracker. The flight lasted 31.74 h between 28 and 29 June, and spanned from Spain (36.86799° N, 6.38873° W) to Senegal (14.36518° N, 16.2296° W). For each panel, black polygons denote the ground elevation and dotted lines depict the flight path. Colours indicate (a) temperature, (b) relative humidity and (c) wind support at 12 pressure levels from the ECMWF dataset.

gained altitude most quickly when they encountered high temperatures and low wind support or, vice versa, low temperatures and high wind support; low temperatures and low wind support caused them to lose altitude (figure 4).

Flight segment was a significant random effect in all models (electronic supplementary material, table S1). However, individual was only a significant random effect in two models: those modelling the relationships between wingbeat frequency and flight altitude, and wingbeat frequency and rate of change in altitude.

4. Discussion

We successfully tracked four continental black-tailed godwits along their migrations from the Netherlands to sub-Saharan West Africa using GPS trackers that enabled the estimation of their geographical location, flight altitude, wingbeat frequency and ground speed. We found that godwits flew at altitudes up to nearly 6000 m above sea level on migratory flights that ranged in duration from 3–48 h. An individual's flight altitude at a given point in time was influenced by interactions among a

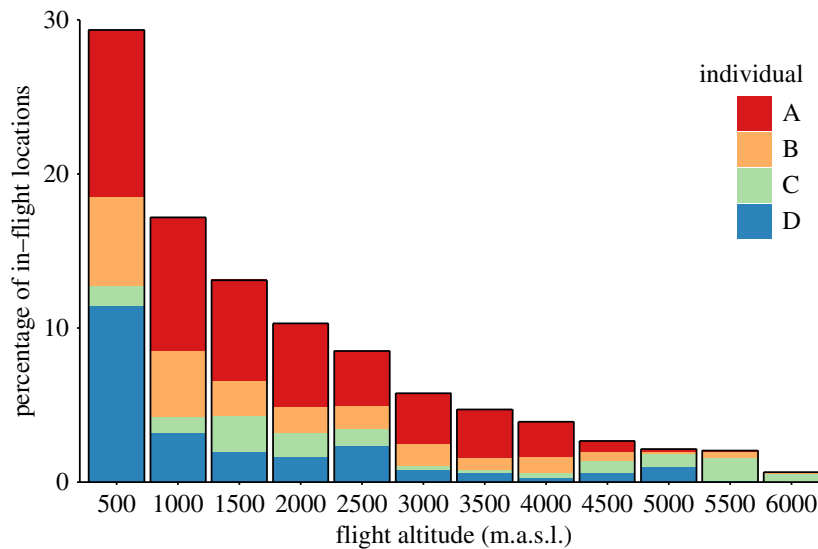


Figure 3. Percentage of recorded flight altitudes (m.a.s.l.) during migratory flights undertaken by female continental black-tailed godwits carrying GPS trackers. Each flight altitude category on the x-axis represents a 500 m increment such that all flights below 500 m fall under '500', flights from 500 to 1000 m fall under '1000', etc. Colours indicate individuals A (red), B (orange), C (green) and D (blue).

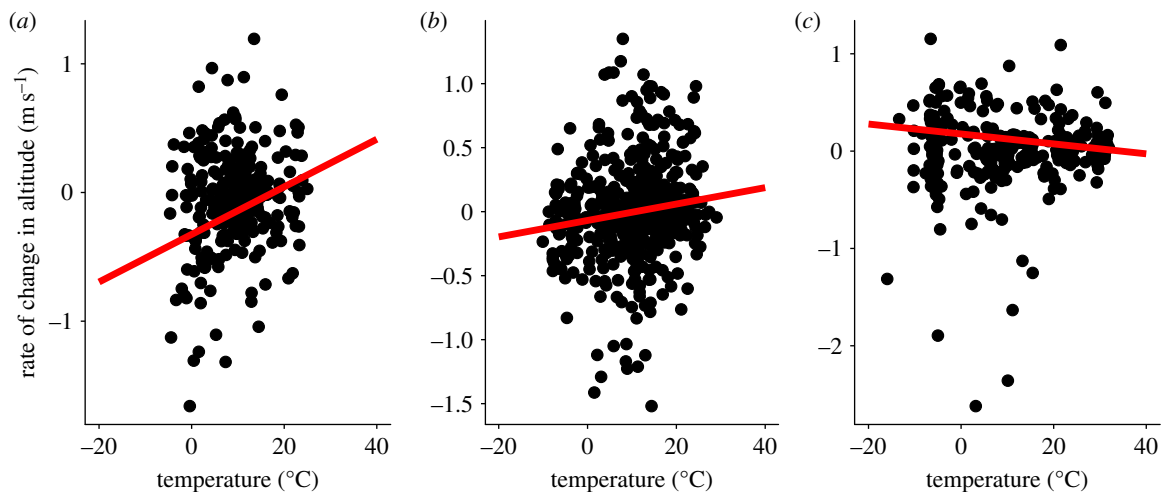


Figure 4. Relationship between temperature at an individual's flight altitude and their rate of altitudinal change leading up to the next time point. Regression lines reflect this relationship when wind support was (a) low (-14.24 – 0.78 km h $^{-1}$), (b) medium (0.78 – 4.73 km h $^{-1}$) or (c) high (4.74 – 18.13 km h $^{-1}$) based on an interaction term between temperature and wind support. Estimates were taken from the generalized linear mixed-effect model described in the electronic supplementary material, tables S2 and S3.

number of abiotic factors, and its response to those abiotic factors differed depending on when they were encountered during a flight. In general, however, periods of migratory flight at extremely high altitudes were associated with high ground temperatures and strong tailwinds. These findings imply that high-altitude flight may not be especially rare and that the in-flight behaviour of migratory birds is determined by a complex set of decisions.

(a) Why do godwits fly so high?

Unlike other species [7,8,35,36], neither ground elevation nor the use of soaring flight explained the extremely high flight altitudes exhibited by godwits. Furthermore, contrary to our expectations, temperatures were a stronger predictor of flight altitudes than were levels of wind support. The factor that had the single largest effect on changes in altitude mid-flight, however, was an interaction between temperature and wind

support. Godwits thus gained altitude most quickly when they encountered either high temperatures and low wind support or, vice versa, low temperatures and high wind support. This interaction suggests a potential hierarchical decision-making process, whereby high temperatures are avoided irrespective of the level of wind support, but strong tailwinds can induce a godwit to move to higher altitudes in search of even more profitable wind conditions. In contrast, when godwits encountered low temperatures and strong headwinds they moved to lower altitudes, possibly enabling them to rapidly end a migratory flight if they depleted their fuel stores or conditions became truly inclement.

High temperatures can potentially impact flight physiology, and thus in-flight behaviour, in a number of ways. First, high temperatures can induce hyperthermia, which in some migratory species constrains flight distances and causes individuals to frequently stop and dissipate excess heat [14]. Second, in an effort to avoid hyperthermia,

migratory birds increasingly attempt to dissipate heat through evaporative cooling at high temperatures, potentially making it difficult to maintain water balance over the course of a long migratory flight [22]. For instance, rock pigeons—which are similar in size to godwits—flying in experimental wind tunnels can sustain constant rates of evaporative water loss at temperatures below 10–15°C, while at higher temperatures they lose water at an increasingly rapid rate [34]. Intriguingly, we found that godwits spent little time flying at altitudes experiencing these high temperatures and, when they did encounter such temperatures, tended to move to higher altitudes. In general, godwits may thus fly at high altitudes in order to minimize the potential for hyperthermia and, ultimately, water loss during their long, non-stop flights.

Nonetheless, the higher wingbeat frequencies characterizing periods of extreme high-altitude and climbing flight could also increase water loss [37]. High levels of wind support, however, can potentially offset some of these costs [16]. Accordingly, we found that godwits experienced greater wind support and flew at faster ground speeds at higher altitudes. Moreover, the effects of tailwinds on godwit flight altitudes were strongest later in flights, which suggests two possibilities that are not mutually exclusive: (1) because individuals lose mass as migratory flights progress, the costs of climbing flight become progressively smaller and individuals may be more inclined to move to higher altitudes later during flights [38]; and (2) as an individual's energy stores become depleted, the relative benefits of wind support are increased and may outweigh the costs of short periods of climbing flight. In either case, although wind support was not the strongest correlate of flight altitudes in godwits, it was probably an important component of their in-flight decision-making process and potentially aided their ability to fly at extremely high altitudes.

A complex array of interacting factors is thus related to how high an individual flies and for how long it is able to migrate before needing to stop. This complexity may help explain the difficulty that previous studies have had in determining the factors most strongly affecting in-flight migratory behaviour. For instance, a recent study found that Swainson's thrushes (*Catharus ustulatus*) make frequent mid-flight altitudinal changes of over 100 m for no discernable reason [9]. Similarly, although previous theory had predicted that evaporative water loss could minimize flight distances and limit high-altitude flight [16], few studies have been able to find direct empirical evidence to support these predictions [14].

The difficulty in pinpointing those factors most directly affecting in-flight behaviour is further demonstrated by the fact that flight segment was a significant random effect in all of our models. This suggests that there is additional variation in migratory behaviour related to other aspects of either the preparation leading up to or conditions encountered during flights that we did not directly capture in our models. For instance, the fuel stores carried by an individual at the onset of a flight could determine both the duration of a flight and an individual's response to conditions encountered during that flight [39]. Similarly, flights over inhospitable regions with few stopover sites may lead to different behaviours than in those flights over regions offering frequent stopover opportunities [40]. Future studies should therefore focus on isolating the potential effects of these factors on in-flight behaviour irrespective of weather conditions.

Tracking data are also challenging to obtain and, as a result, sample sizes from tracking studies are often quite small. We aimed to have a robust sample size of 20 individuals, but loss of transmitters combined with equipment malfunctions resulted in data from only four individuals in our study. Nonetheless, these four individuals provided data on the migratory behaviour of godwits in unprecedented detail and our results suggest that our sample size was large enough to accurately identify those factors affecting in-flight behaviour. For instance, individual was only a significant random effect in two models—both related to wingbeat frequency—indicating that there was little variation among individuals in relation to most aspects of in-flight behaviour. Additionally, we found that flights at extremely high altitudes were not limited to a subset of individuals, with all individuals flying above 5000 m during at least one flight. Finally, we were able to document at least three flights for each individual, as well as flights during both spring and autumn migration for all but one individual.

We thus believe that our results provide an adequate characterization of godwit in-flight behaviour, and therefore offer three novel insights into avian migratory behaviour more generally. First, temperature may be as important a driver of in-flight behaviour as either wind conditions or topography. Second, the relative importance of any single abiotic factor probably changes over the course of a flight and depends on the interaction among a suite of other abiotic and biotic factors. Third, the ability to fly at extremely high altitudes and flexibly alter their flight altitude may mean that, for some species, the abiotic conditions encountered in flight more strongly determine an individual's flight altitude than they do its flight duration.

(b) The costs of extreme high-altitude flight

A growing number of birds have been observed flying at extremely high altitudes, including a number of shorebird and passerine species that radar studies have documented flying above 5000 m over lowland environments [1–4]. However, few of these flights have been put into a behavioural or physiological context [19,36]. The most well-documented example involves bar-headed geese that fly as high as 7200 m over the Himalayan Mountains on their migrations between India and their breeding sites in Mongolia and on the Tibetan Plateau of China [7,8]. Recent studies have found that bar-headed geese exhibit a number of traits that appear to be specifically adapted to aid this high-altitude lifestyle and which confer significant aerobic advantages [18,19]. Nonetheless, bar-headed geese do not undertake long flights at continuously high altitudes. Instead, they employ a mountain-hugging strategy that minimizes their flight altitude and follows the topography of the landscape over which they are migrating, meaning they spend less than half of their migratory flights at altitudes greater than 4000 m [7,8]. These findings have been interpreted to suggest that high-altitude flight must represent significant costs to migratory birds and should therefore generally be minimized or avoided [18].

In contrast to bar-headed geese, godwits face few topographic barriers along their migration route. In fact, the highest topographic barrier encountered by any of our individuals was only 2049 m in northern Spain. Thus, while godwits spend less time at high altitudes during their migratory flights than do bar-headed geese, they fly at high altitudes even in the absence of topographical barriers. Indeed, a number of flights

over lowland Europe exhibited extended periods at high altitudes, including some flights during which individuals spent more than 30% of their time above 5000 m. Moreover, with the exception of their migratory flights, godwits occupy lowland environments throughout the entirety of their lives—they breed exclusively in low-elevation agricultural grasslands in Western Europe and spend the nonbreeding season in coastal wetlands and inland river deltas [23].

Unlike bar-headed geese, godwits therefore face no obvious selection pressure that might lead to the evolution of greater aerobic capabilities than other lowland species that migrate long distances. Additionally, many of the high-altitude adaptations displayed by bar-headed geese would probably be disadvantageous at low elevations, where maintaining ancestral responses to hypoxia may be beneficial to the performance of some activities (e.g. predator avoidance or territorial displays [41,42]). This then raises the question: are godwits better adapted than other long-distance migrants for high-altitude flight solely because of the selection pressures imposed by temperature and wind during migration? Or is high-altitude flight simply common, but rarely observed, among long-distance migrants?

A number of factors suggest that the latter hypothesis is more likely. For instance, although resident bird species living at elevations as low as 2900 m exhibit physiological adaptations for improved aerobic performance at high elevations [43], even resident lowland bird species have some ability to perform intense aerobic activities at high elevations [18,44]. Furthermore, while godwits have proportionally larger hearts than do the majority of other birds [45], and other godwit species undertake the longest non-stop flights of any landbird species [46,47], they are not known to exhibit any other adaptations to aid flights at high altitudes. Instead, anecdotal evidence suggests that their basal metabolic rates [48] and pre-migratory haematocrit levels ($Hct = 52.61 \pm 3.84$, $n = 49$; N.R.S. *et al.* 2015, unpublished data.) are similar to those of other lowland species [49,50]. It therefore would not be surprising if most, if not all, migratory birds are capable of migrating at altitudes up to 6000 m.

The general paucity of reports of birds flying at extremely high altitudes over lowland environments may thus stem from the relatively small range of environmental conditions under which most studies have attempted to characterize

migratory flight altitudes. The majority of radar studies, for example, have been performed either at northerly latitudes or at night, situations in which temperatures do not regularly approach those that our results suggest should induce high-altitude flights. Accordingly, these studies have found fewer than 5% of individuals flying at extremely high altitudes [2,3,50–53]. In contrast, a radar study taking place in a south temperate desert—the Negev Desert in Israel, where average daytime temperatures during spring migration exceed 30°C [51]—found remarkably similar variation in the flight altitudes of diurnal migrants to those exhibited by godwits in our study [4]. Our findings therefore indicate that we need to integrate a systems-based approach to the study of broad-scale migratory patterns that encompasses a wide array of environmental circumstances [6] with studies that can identify the selection pressures influencing individual-level behaviours in order to document the full gamut of migratory strategies and their physiological underpinnings.

Ethics. All fieldwork was done in accordance with the ethical standards of the University of Groningen and following the Dutch Animal Welfare Act Articles 9 and 11 under licence numbers 6350A and C.

Data accessibility. The data used in this manuscript is available at <http://www.uva-bits.nl>.

Authors' contributions. N.R.S., M.A.V. and T.P. designed the study; N.R.S. and M.A.V. carried out the fieldwork; N.R.S., M.S. and W.B. performed the analyses; Z.A.C. contributed physiological expertise; N.R.S. and M.S. wrote the manuscript; and all authors discussed the manuscript and contributed edits.

Competing interests. We declare we have no competing interests.

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References

- Richardson WJ. 1976 Autumn migration over Puerto Rico and the western Atlantic: a radar study. *Ibis* **118**, 309–332. (doi:10.1111/j.1474-919X.1976.tb02023.x)
- Richardson WJ. 1979 Southeastward shorebird migration over Nova Scotia and New Brunswick in autumn: a radar study. *Can. J. Zool.* **57**, 107–124. (doi:10.1139/z79-009)
- Alerstam T, Gudmundsson GA. 1999 Migration patterns of tundra birds: tracking radar observations along the Northeast Passage. *Arctic* **52**, 346–371. (doi:10.14430/arctic941)
- Liechti F, Schaller E. 1999 The use of low-level jets by migrating birds. *Naturwissenschaften* **86**, 549–551. (doi:10.1007/s001140050673)
- Alerstam T. 2011 Optimal bird migration revisited. *J. Ornithol.* **152**(Suppl. 1), S5–S23. (doi:10.1007/s10336-011-0694-1)
- Kelly JF, Horton KG. 2016 Toward a predictive macrosystems framework for migration ecology. *Global Ecol. Biogeogr.* **25**, 1159–1165. (doi:10.1111/geb.12473)
- Hawkes LA *et al.* 2013 The paradox of extreme high-altitude migration in bar-headed geese *Anser indicus*. *Proc. R. Soc. B* **280**, 20122114. (doi:10.1098/rspb.2012.2114)
- Bishop CM *et al.* 2015 The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. *Science* **347**, 250–254. (doi:10.1126/science.1258732)
- Bowlin MS, Enstrom DA, Murphy BJ, Plaza E, Jurich P, Cochran J. 2015 Unexplained altitude changes in a migrating thrush: long-flight altitude data from radio-telemetry. *Auk* **132**, 808–816. (doi:10.1642/AUK-15-33.1)
- Piersma T. 2011 Why marathon migrants get away with high metabolic ceilings: towards an ecology of physiological restraint. *J. Exp. Biol.* **214**, 295–302. (doi:10.1242/jeb.046748)
- Liechti F, Klaassen M, Bruderer B. 2000 Predicting migratory flight altitudes by physiological migration models. *Auk* **117**, 205–214. (doi:10.1642/0004-8038(2000)117[0205:PMFABP]2.0.CO;2)
- Kranstauber B, Weinzierl R, Wikelski M, Safi K. 2015 Global aerial flyways allow efficient

- travelling. *Ecol. Letts.* **18**, 1338–1345. (doi:10.1111/ele.12528)
13. Gill Jr RE, Douglas DC, Handel CM, Tibbitts TL, Hufford G, Piersma T. 2014 Hemispheric-scale wind selection facilitates bar-tailed godwit circum-migration of the Pacific. *Anim. Behav.* **90**, 117–130. (doi:10.1016/j.anbehav.2014.01.020)
 14. Guillemette M, Woakes AJ, Larochelle J, Polymeropolulos ET, Granbois J-M, Butler PJ, Pelletier D, Frappell PB, Portugal SJ. 2016 Does hyperthermia constrain flight duration in a short-distance migrant? *Phil. Trans. R. Soc. B* **371**, 20150386. (doi:10.1098/rstb.2015.0386)
 15. Carmi N, Pinshow B, Porter WP, Jaeger J. 1992 Water and energy limitations on flight duration in small migrating birds. *Auk* **109**, 268–276. (doi:10.2307/4088195)
 16. Klaassen M, Kvist A, Lindström Å. 1999 How body water and fuel stores affect long distance flight in migrating birds. In *Proc. of the 22nd Int. Ornithological Congress* (eds NJ Adams, RH Slotow), pp. 1450–1467. Durban, South Africa: BirdLife South Africa.
 17. Schmaljohann H, Liechti F, Bruderer B. 2007 Songbird migration across the Sahara: the non-stop hypothesis rejected! *Proc. R. Soc. B* **274**, 735–739. (doi:10.1098/rspb.2006.0011)
 18. Scott GR. 2011 Elevated performance: the unique physiology of birds that fly at high altitudes. *J. Exp. Biol.* **214**, 2455–2462. (doi:10.1242/jeb.052548)
 19. Scott GR, Hawkes LA, Frappell PB, Butler PJ, Bishop CM, Milsom WK. 2015 How bar-headed geese fly over the Himalayas. *Physiology* **30**, 107–115. (doi:10.1152/physiol.00050.2014)
 20. Hedenström A, Ålerstam T. 1992 Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. *J. Exp. Biol.* **164**, 19–38.
 21. Ålerstam T. 1979 Optimal use of wind by migrating birds: combined drift and overcompensation. *J. Theor. Biol.* **79**, 341–353. (doi:10.1016/0022-5193(79)90351-5)
 22. Landys MM, Piersma T, Visser GH, Jukema J, Wijkker A. 2000 Water balance during real and simulated long-distance migratory flight in the bar-tailed godwit. *Condor* **102**, 645–652. (doi:10.1650/0010-5422(2000)102[0645:WBDRAS]2.0.CO;2)
 23. Hooijmeijer JCEW, Senner NR, Tibbitts TL, Gill Jr RE, Douglas DC, Bruinzeel LW, Wymenga E, Piersma T. 2013 Post-breeding migration of Dutch-breeding black-tailed godwits: timing, routes, use of stopovers, and nonbreeding destinations. *Ardea* **101**, 141–152. (doi:10.5253/078.101.0209)
 24. Bouten W, Baaij EW, Shamoun-Baranes J, Camphuysen KCJ. 2013 A flexible GPS tracking system for studying bird behaviour at multiple scales. *J. Ornithol.* **154**, 571–580. (doi:10.1007/s10336-012-0908-1)
 25. Senner NR, Verhoeven MA, Abad-Gomez JM, Gutierrez JS, Hooijmeijer JCEW, Kentie R, Masero JA, Tibbitts TL, Piersma T. 2015 When Siberia came to The Netherlands: the response of continental black-tailed godwits to a rare spring weather event. *J. Anim. Ecol.* **84**, 1164–1176. (doi:10.1111/1365-2656.12381)
 26. Shamoun-Baranes J, Bouten W, van Loon EE, Meijer C, Camphuysen CJ. 2016 Flap or soar? How a flight generalist responds to its aerial environment. *Phil. Trans. R. Soc. B* **371**, 20150395. (doi:10.1098/rstb.2015.0395)
 27. Dee DP *et al.* 2011 The ERA-Interim reanalysis: configuration and performance of the data assimilation system. *Q. J. R. Meteor. Soc.* **137**, 553–597. (doi:10.1002/qj.828)
 28. McLaren JD, Shamoun-Baranes J, Camphuysen CJ, Bouten W. 2016 Directed flight and optimal airspeeds: homeward-bound gulls react flexibly to wind yet fly slower than predicted. *J. Avian Biol.* **47**, 476–490. (doi:10.1111/jav.00828)
 29. Gelman A. 2008 Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* **27**, 2865–2873. (doi:10.1002/sim.3107)
 30. Grueber CE, Nakagawa S, Laws RJ, Jamieson IG. 2011 Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* **24**, 699–711. (doi:10.1111/j.1420-9101.2010.02210.x)
 31. Bates D, Maechler M, Bolker B, Walker S. 2015 Fitting linear mixed-effect models using lme4. *J. Stat. Soft.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
 32. Barton K. 2015 MuMIn: multi-model inference. See <https://cran.r-project.org/package=MuMIn>.
 33. Shamoun-Baranes J, Bouten W, van Loon EE. 2010 Integrating meteorology into research on migration. *Soc. Int. Comp. Biol.* **50**, 280–292. (doi:10.1093/icb/icq011)
 34. Giladi I, Pinshow B. 1999 Evaporative and excretory water loss during free flight in pigeons. *J. Comp. Physiol. B* **169**, 311–318. (doi:10.1007/s003600050226)
 35. Parr N *et al.* 2017 High altitude flights by ruddy shelduck (*Tadorna ferruginea*) during trans-Himalayan migrations. *J. Avian Biol.* **48**, 1310–1315. (doi:10.1111/jav.01443)
 36. Sherub S, Bohrer G, Wikelski M, Weinzierl R. 2016 Behavioural adaptations to flight into thin air. *Biol. Letts.* **12**, 20160432. (doi:10.1098/rsbl.2016.0432)
 37. Schmaljohann H, Liechti F. 2009 Adjustments of wingbeat frequency and air speed to air density in free-flying migratory birds. *J. Exp. Biol.* **212**, 3633–3642. (doi:10.1242/jeb.031435)
 38. Pennycuik CJ, Battley PF. 2003 Burning the engine: a time-marching computation of fat and protein consumption in a 5420-km non-stop flight by great knots, *Calidris tenuirostris*. *Oikos* **103**, 323–332. (doi:10.1034/j.1600-0706.2003.12124.x)
 39. Hedenström A. 2010 Extreme endurance migration: what is the limit to non-stop flight? *PLoS Biol.* **8**, e1000362. (doi:10.1371/journal.pbio.1000362)
 40. Klaassen RHG, Strandberg R, Hake M, Ålerstam T. 2008 Flexibility in daily travel routines causes regional variation in bird migration speed. *Behav. Ecol. Sociobiol.* **62**, 1427–1432. (doi:10.1007/s00265-008-0572-x)
 41. Cheviron ZA, Brumfield RT. 2012 Genomic insights into adaptation to high-altitude environments. *Heredity* **108**, 354–361. (doi:10.1038/hdy.2011.85)
 42. Storz JF, Scott GR, Cheviron ZA. 2010 Phenotypic plasticity and genetic adaptation to high-altitude hypoxia in vertebrates. *J. Exp. Biol.* **213**, 4125–4136. (doi:10.1242/jeb.048181)
 43. Cheviron ZA, Brumfield RT. 2009 Migration-selection balance and local adaptation of mitochondrial haplotypes in rufous-collared sparrows (*Zonotrichia capensis*) along an elevation gradient. *Evolution* **63**, 1593–1605. (doi:10.1111/j.1558-5646.2009.00644.x)
 44. Tucker VA. 1968 Respiratory physiology of house sparrows in relation to high-altitude flight. *J. Exp. Biol.* **48**, 55–66.
 45. Nespolo RF, González-Lagos C, Solano-Igüaran JJ, Elfving M, Garitano-Zavala A, Mañosa S, Alonso JC, Altamiras J. 2018 Aerobic power and flight capacity in birds: a phylogenetic test of the heart-size hypothesis. *J. Exp. Biol.* **221**, jeb162693. (doi:10.1242/jeb.162693)
 46. Gill Jr RE *et al.* 2009 Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proc. R. Soc. B* **276**, 447–457. (doi:10.1098/rspb.2008.1142)
 47. Senner NR, Hochachka WM, Fox JW, Afanasyev V. 2014 An exception to the rule: carry-over effects do not accumulate in a long-distance migratory bird. *PLoS ONE* **9**, e86588. (doi:10.1371/journal.pone.0086588)
 48. Gutiérrez JS, Abad-Gómez JM, Sánchez-Guzmán JM, Navedo JG, Masero JA. 2012 Avian BMR in marine and non-marine habitats: a test using shorebirds. *PLoS ONE* **7**, e42206. (doi:10.1371/journal.pone.0042206)
 49. Carey C, Morton ML. 1976 Aspects of circulatory physiology of montane and lowland birds. *Comp. Biochem. Physiol.* **54**, 61–74. (doi:10.1016/S0300-9629(76)80073-4)
 50. Landys-Giannelli MM, Jukema J, Piersma T. 2002 Blood parameter changes during stopover in a long-distance migratory shorebird, the bar-tailed godwit *Limosa lapponica taymyrensis*. *J. Avian Biol.* **33**, 451–455. (doi:10.1034/j.1600-048X.2002.03051.x)
 51. Bruderer B, Underhill LG, Liechti F. 1995 Altitude choice by night migrants in a desert area predicted by meteorological factors. *Ibis* **137**, 44–55. (doi:10.1111/j.1474-919X.1995.tb03218.x)
 52. Kemp MU, Shamoun-Baranes J, Dokter AM, van Loon E, Bouten W. 2012 The influence of weather on the flight altitude of nocturnal migrants in mid-latitudes. *Ibis* **155**, 734–749. (doi:10.1111/ibi.12064)
 53. Dokter AM, Shamoun-Baranes J, Kemp MU, Tijm S, Holleman I. 2013 High altitude bird migration at temperate latitudes: a synoptic perspective on wind assistance. *PLoS ONE* **8**, e52300. (doi:10.1371/journal.pone.0052300)