

The trans-Himalayan flights of bar-headed geese (*Anser indicus*)

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Edited by Robert E. Ricklefs, University of Missouri, St. Louis, MO, and approved April 27, 2011 (received for review November 18, 2010)

Birds that fly over mountain barriers must be capable of meeting the increased energetic cost of climbing in low-density air, even though less oxygen may be available to support their metabolism. This challenge is magnified by the reduction in maximum sustained climbing rates in large birds. Bar-headed geese (*Anser indicus*) make one of the highest and most iconic transmountain migrations in the world. We show that those populations of geese that winter at sea level in India are capable of passing over the Himalayas in 1 d, typically climbing between 4,000 and 6,000 m in 7–8 h. Surprisingly, these birds do not rely on the assistance of upslope tailwinds that usually occur during the day and can support minimum climb rates of 0.8–2.2 km·h⁻¹, even in the relative stillness of the night. They appear to strategically avoid higher speed winds during the afternoon, thus maximizing safety and control during flight. It would seem, therefore, that bar-headed geese are capable of sustained climbing flight over the passes of the Himalaya under their own aerobic power.

exercise physiology | high altitude | satellite tracking | vertebrate migration | climbing flight

Mountains and high plateaus present formidable obstacles to the migratory flights of a number of bird species. Large birds, such as cranes and geese, may find such barriers particularly challenging as the sustained climbing rates of birds scale negatively with increasing body mass (1). For example, brent geese (*Branta bernicla*) are unable to sustain climbing flights over the Greenland icecap (summit elevation 3,207 m, mean elevation >2,000 m) and make regular stops to recover, possibly from partly anaerobic flights (2). Nevertheless, populations of bar-headed geese (*Anser indicus*) that spend the winter at sea level in India and the summer in central Asia must perform the world's steepest migratory flight north over the highest mountain range on earth, the Himalaya (3). There, most passes are at altitudes greater than 5,000 m, where the air density and partial pressure of oxygen are only about half of those at sea level. As a consequence, the partial pressure of oxygen (PO₂) in the arterial blood may begin to limit maximum performance (4, 5), although negative effects on the rate of oxygen diffusion may be partially ameliorated by an increase in the gas diffusion coefficient (6). The thinner air at these higher altitudes will also reduce lift generation during flapping flight for any given air speed, thus increasing the energy costs of flying by around 30% (7, 8).

However, bar-headed geese have adapted in a variety of ways for living and flying at high altitudes (4, 5). Their skeletal and cardiac muscles are better supplied with oxygen, having greater capillary density, more homogenous capillary spacing, a higher proportion of mitochondria in a subsarcolemmal location, and a greater proportion of oxidative fibers than other waterfowl (9, 10). Bar-headed goose hemoglobin is also highly effective at oxygen loading (11), compared with many other bird species, largely as a result of a single amino acid point mutation (12–14).

Bar-headed geese also have proportionally larger lungs than those of other species of waterfowl (15) and can hyperventilate at up to seven times the normoxic resting rate when exposed to severe hypoxia (11, 16). These adaptations should significantly improve O₂ uptake and transport at high altitudes, and may contribute to this species' ability to climb thousands of meters of elevation without acclimatization. This feat is particularly impressive when considering that humans could suffer dizziness, altitude sickness, high-altitude pulmonary edema (HAPE) (17), and possibly even death when faced with a similarly extreme change in elevation. In the present study, we detail how the trans-Himalayan migration of bar-headed geese is achieved and provide insights into their aerobic flight capacity.

On the basis of a growing body of literature showing associations between bird flight and wind conditions, an additional possibility is that bar-headed geese could enhance their climb rates and/or flight speeds by selecting favorable wind conditions in which to migrate (8, 18). Large mountainous areas are characterized by daily slope winds that occur due to predictable changes in daily solar radiation and thermal conditions [e.g., the Alps (19, 20), the Andes (21), the Himalaya (22, 23), and mountainous areas in the United States (24, 25)]. These winds reach an upslope “anabatic” maximum during the warmest part of the day, and a downslope, “katabatic” maximum in the evening and overnight (19, 20). In the Eastern Himalaya, near Mount Everest, these winds start to blow upslope (from a southerly direction) at ~09:00 h local time, reaching their maximum of around 22 km·h⁻¹ by 12:45 h and reversing overnight to blow southward (Fig. 1A). By flying in the midmorning through to early afternoon, therefore, geese could take advantage of these updrafts and tailwinds to maximize climb rates and/or forward ground speeds during their migration (18). We set out to describe the detailed timings and altitudinal profiles of bar-headed geese during climbing flights over the Himalaya and to investigate whether they make strategic use of potentially favorable wind conditions.

Results and Discussion

Movement Over the Himalayas. Our data show that bar-headed geese travel north, from sea level over the Himalayas, in a single day (median date March 24, range March 15 to May 6). The median crossing time was 8 h ($n = 5$ geese tracked for the complete crossing, Fig. 1A and B) and the shortest flights were ~7 h long. Minimum 3D transit speeds (median 53.2 km·h⁻¹, calcu-

Author contributions: P.J.B., J.Y.T., M.W., and C.M.B. designed research; L.A.H., S.B., N.B., P.J.B., P.B.F., W.K.M., N.T., S.H.N., G.R.S., P.S., J.Y.T., and C.M.B. performed research; L.A.H. analyzed data; and L.A.H. and C.M.B. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

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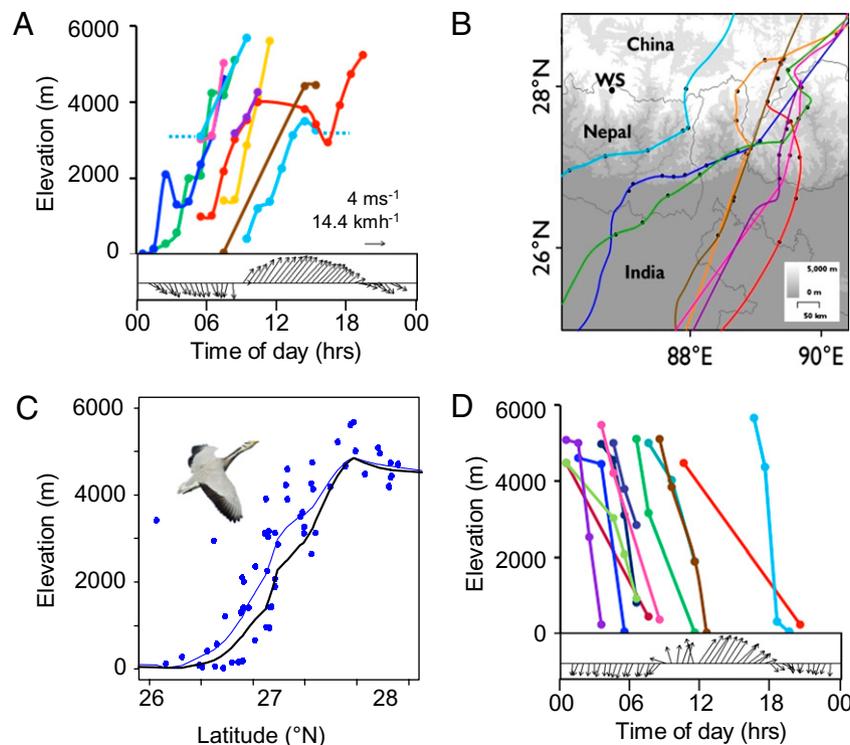


Fig. 1. Timing of migrations with 30-min average wind speed and direction from the Nepal Climate Observatory at Pyramid station for geese migrating (A) northward ($n = 8$) and (D) southward ($n = 12$) over the Himalaya. Arrows show cardinal direction (north pointing up to 0°) in which the wind was blowing and arrow length (indicated in A) is proportional to wind speed in A and D. (B) Map showing the northward migration routes; weather station (WS) location is indicated. (C) Elevation of the mean northward track across the Himalaya (for all crossing locations from all eight geese), blue circles show individual data points and blue line shows Lowess smoother for mean ground elevation under the track (black line).

lated from the straight line distance and altitude traveled between successive hourly locations ($n = 18$ locations) were correlated with instantaneous speeds transmitted by the satellite tags (here after referred to as “tags,” see *Methods*; median $64.5 \text{ km}\cdot\text{h}^{-1}$, Spearman’s $\rho = 0.71$, $P < 0.01$), indicating that the geese were flying aerobically and could not have stopped for prolonged periods (i.e., >15 min) during the climb. These median speeds are close to the predicted minimum power speed ($61.2 \text{ km}\cdot\text{h}^{-1}$) (8), thus minimizing forward flight costs and maximizing additional power available for climbing. The range of speeds recorded are also similar to those previously published for captive bar-headed geese flying in a wind tunnel (26), suggesting that the geese flew in the absence of strongly assisting tailwinds, which would have increased forward flight speed significantly. Geese did not travel faster in anabatic daytime conditions compared with katabatic nighttime flights (flying at 63.0 versus $59.0 \text{ km}\cdot\text{h}^{-1}$, respectively, Wilcoxon test $P > 0.05$). Flight theory (8) suggests that at higher altitude, where air is less dense, drag (for example profile and parasite drag) is reduced, but the power required to generate lift and thrust increases; minimum speeds required to maintain horizontal flight are faster and, therefore, more expensive. Bar-headed geese in this study did, indeed, travel faster at higher altitude (Wilcoxon test, $P < 0.01$), with geese traveling at $54 \text{ km}\cdot\text{h}^{-1}$ (median value) at lower altitudes compared with $67.0 \text{ km}\cdot\text{h}^{-1}$ at higher altitudes.

Geese climbed northward over the Himalaya (Fig. 1A and B), gaining 1.1 km of altitude per hour (median value, $n = 6$ geese, range 0.8 – $2.2 \text{ km}\cdot\text{h}^{-1}$, calculated from the 18 steepest climbs reported at successive hourly locations). The three highest climb rates of 1-h duration were 1.88 , 1.94 , and $2.15 \text{ km}\cdot\text{h}^{-1}$, along with transit speeds of 43.2 , 45.8 , and $68.2 \text{ km}\cdot\text{h}^{-1}$, respectively. In addition, three geese averaged climb rates of 1.4 , 1.2 , and $1.1 \text{ km}\cdot\text{h}^{-1}$, along with transit speeds of 31.1 , 41.0 , and $63.5 \text{ km}\cdot\text{h}^{-1}$,

respectively, over 3 h. These observations represent the longest continuous climbing rates ever recorded. Climb rates were not affected significantly by altitude, flight speed, or wind conditions (with geese climbing at 1.04 versus $1.40 \text{ km}\cdot\text{h}^{-1}$ in anabatic versus katabatic conditions). Geese generally matched the underlying terrain during their climbs (median height 130 m ; Fig. 1C) and were most frequently located within 340 m of the ground (containing 80% of locations) and thus avoided climbing any steeper than was necessary. Rates of climb reported for similarly sized Greylag geese ($1.15 \text{ km}\cdot\text{h}^{-1}$ sustained for 20 min at sea level) (1) were similar to our values. However, bar-headed geese sustained their climb rates over much longer periods and at much higher altitudes.

We also tracked 13 geese during autumn southward flights into India, after breeding in Mongolia (median crossing date November 20, range November 10 to December 19). Bar-headed geese cross the Himalaya southward in 4.5 h (median value, $n = 8$ geese), and in as little as 3 h ($n = 2$ geese). Geese traveled significantly faster than the predicted minimum power speed (Mann–Whitney $U = 108$, $P < 0.05$) but on average, neither their descent rate (median 1.3 km of elevation per hour, range 0.9 – $4.1 \text{ km}\cdot\text{h}^{-1}$) nor their speed ($64 \text{ km}\cdot\text{h}^{-1}$) were significantly steeper than their 18 steepest climb rates and speed over the Himalaya when going northward (descent rate: Mann–Whitney $U = 93$, $P > 0.05$, speed: $U = 481$, $P > 0.05$, excluding stopovers). Southward migrating geese neither traveled nor descended significantly faster in anabatic versus katabatic wind conditions. However, instantaneous speeds transmitted from geese flying southward (median $64.0 \text{ km}\cdot\text{h}^{-1}$) were significantly faster than minimum transit speeds (mean $55.8 \text{ km}\cdot\text{h}^{-1}$, Wilcoxon test, $P < 0.05$), indicating that the geese may have undertaken short stops en route (of 8 min or less) or, more likely, did not travel in a straight line.

Role of Weather. In contrast to expectation, the majority of northward-flying geese began climbing during the night or early morning in what were, on the basis of conditions at the Pyramid station and the known prevalence of mountain-valley wind systems in the Himalaya (22, 23), likely to be light headwind (katabatic) conditions, and two geese completed their entire climb before anabatic conditions should have begun. The majority of climbing flights took place before 10:00 h and the four highest climb rates were recorded before 07:00 h (range 1.5–2.2 km·h⁻¹). The last goose to begin its crossing of the Himalaya did not complete its climb in 1 d and landed during the afternoon during what were likely to be peak afternoon tailwinds. This goose did not complete its climb until early the next morning. Another bird stopped climbing before midday and completed the climb during the late afternoon, a period when winds should have been slowing (Fig. 1A). Even when geese did fly in the late morning there were no significant increases in ground speeds or minimum climb rates and, thus, no indication of the use (or presence) of assisting wind conditions. Although headwinds may maximize climb rates relative to the ground, they do so at the expense of horizontal gain. The geese in our study did not appear to trade off horizontal ground speed for vertical gain, traveling at median forward transit speeds during the climbs of 51.9 km·h⁻¹ ($n = 18$).

Similar results were obtained for geese that we tracked during their southward autumn migration into India (Fig. 1D): the majority of geese took off during the night or early morning, with all but four arriving in India before the transition to anabatic conditions would have been likely to occur. We recorded three of the four greatest rates of descent between 19:00 h and 02:00 h (range 0.9–2.5 km·h⁻¹).

We suggest that these relatively early flight times, for both southerly and northerly migrating individuals, may be suitable because the air is likely to be colder and with lower wind speeds, which could be beneficial in a number of ways. Firstly, cooler air is denser and could, therefore, reduce the costs of flapping flight. For example, at 6,000 m elevation, the maximum observed variation in air temperature at the Pyramid site (19.8 °C) could reduce the altitude effectively experienced by the geese (the density altitude) by 690 m. This would reduce the flight speed required for minimum power consumption by 0.8 m·sec⁻¹, (a 4% energy saving) while maintaining the same lift–drag ratio. Secondly, cooler and denser conditions will increase the partial pressure of oxygen following the ideal gas law (for example, at 6,000 m the change in density altitude by 690 m would increase inspired PO₂ from ~75–81 mm Hg, or 10–10.8 kPa), increasing the diffusion gradient at the alveoli–blood interface and potentially increasing hemoglobin saturation. This increase may be critical in O₂ uptake, as has been shown for mountaineers attempting to reach the summit of Mount Everest (27) without supplementary oxygen. In addition, early flights would avoid the potential heat load of flying at low altitudes in India during the hottest time of the day, whilst cooler nighttime and early morning temperatures could help dissipate metabolically produced heat from the body (maximum daily temperatures in the Khumbu valley were 23.4 °C at 2,660 m, 17.2 °C at 3,560 m, and –10 °C at 5,585 m). In this regard, if bar-headed geese could directly decrease their pulmonary blood temperature at the air/lung interface (4), or indirectly via dropping core body temperature (28), they could improve the O₂ loading and saturation of hemoglobin by leftward shifting the hemoglobin–O₂ equilibrium curve (29). Finally, these calmer periods during the early morning may also be optimal because they provide the birds with an extra measure of flight safety and aerodynamic control, avoiding turbulent and/or stormy weather more prevalent in the afternoon. Indeed, geese flying in the mountains might choose to avoid tailwinds as they would reduce climb angles with respect to the underlying terrain. Calmer conditions may also facilitate the use of formation flight to further reduce energy costs (30).

We make the surprising observation that the majority of climbing flights occurred during the night and early morning and, more often than not, did not overlap with times predicted to provide tailwinds. Lawrence Swan, a naturalist who accompanied Sir Edmund Hillary on an expedition to the Himalayas observed: “On one such cold and still night in early April, I stood beside the Barun glacier. . . Coming from the south the distant hum became a call. Then, as if from the stars above me, I heard the honking of bar-headed geese” (31). Thus, whether descending or ascending, the bar-headed geese we tracked usually cross the Himalaya when the prevailing wind speeds are likely to be minimal, in a sustained aerobic flight, and flying close to the air speeds that are predicted to maximize power available for the climb. As a consequence, they can maintain maximum safety and control over their flights, while optimizing lift production and oxygen availability. We conclude that bar-headed geese are not reliant on upslope tailwinds to aid flights over the Himalaya and may strategically avoid such conditions while performing these remarkable sustained flights under their own muscular power, even in the relative stillness of the night.

Methods

Bar-headed geese were deployed with satellite transmitters (Microwave Telemetry Solar Argos-global positioning system (GPS) PTT-100 30 g reinforced, high-resolution setting recording up to 20,480 m maximum altitude, with an accuracy of ±10 m) from two sites in India (from where the geese subsequently migrated northward) and from one in Mongolia (from where they subsequently migrated southward), attached using Teflon tape or braided elastic harnesses. Wintering geese were captured at Chilika Lake (19.694°N, 85.307°E) in eastern India, Koonthankulum bird sanctuary (8.472°N, 77.705°E) in southern India, and at Terkhiin Tsagaan Lake (48.147°N, 99.576°E), Mongolia.

Data were received and managed using the Satellite Tracking and Analysis Tool (32) and hosted on Movebank (<http://www.movebank.org>) (33). Transmitters report GPS location (±18 m horizontal accuracy) and altitude (±22 m vertical accuracy) as well as instantaneous airspeed (±0.27 m·s⁻¹, reported as forward flight speeds in this study). Altitude (from GPS) is reported at 10 m increments to a maximum of 20,480 m above sea level. We calculated minimum straight-line ground speed (transit speed) using great circle distance between successive locations (using the “oce” package for R) and compared them with instantaneous GPS airspeeds. Thus, calculated transit speeds may be underestimated, as geese probably did not fly in completely straight lines and/or may have made short stops between locations. We calculated the maximum time between reported hourly climbing locations (defined as >700 m altitudinal gain) that birds could have stopped by dividing the transit distance traveled in each hourly leg by the reported instantaneous GPS speed. We also calculated the ratio between the instantaneous transmitted speed and the transit speed to derive a tortuosity value (1.32 for northward birds and 1.15 for southward birds) to further describe the likelihood of geese stopping during the climb. Land elevation data coincident to bird tracks were obtained by mapping tracks over the National Aeronautics and Space Administration/National Geospatial-Intelligence Agency 90 m shuttle radar topography mission (SRTM) (<http://www2.jpl.nasa.gov/srtm/>) topography data product. We extracted the climb for each goose by plotting displacement from original deployment site to obtain the stopover locations just before and after the flight across the Himalayas. We report minimum climb rates (defined as >0.72 km·h⁻¹ vertical change) as altitudinal gain per hour between each location. However, climb rates may be underestimated, as geese were unlikely to have climbed linearly throughout the hour and/or may have made short stops between locations (although see *Results and Discussion* above).

Wind data for the eastern Himalaya were obtained from the SHARE Everest CAMP/Himalayas (<http://www.share-everest.org>) Pyramid station, in the Khumbu valley at 5,035 m (34, 35), ~250 km west of the crossing site, representing the closest available dataset. Although there were radiosonde releases closer to the site where geese crossed the Himalaya (<http://badc.nerc.ac.uk/data/radiosonde/radhelp.html>), the data were not temporally coincident and, therefore, did not improve our interpretation of wind patterns for the satellite tracks. Although topographic features such as valleys and slope angle will undoubtedly affect local wind conditions, anabatic/katabatic wind phenomena are common in every terrestrial mountain range on earth (19–25) and operate at the scale of mountain ranges, relevant to the migratory distance traveled by the geese. The Pyramid station data describe wind speed and direction at 30-min intervals for the year and cover the period over

which we tracked birds migrating. Wind data were extracted for the days between the first and the last goose to migrate across the Himalayas (northward range: March 15 to May 6, southward range November 10 to December 16) and used to make a composite plot for northward and southward movements, respectively, in R.

We estimated minimum power speed using Flight 1.20 (8). In the absence of exact data describing premigratory bird masses, we used 120% of the mean bird's body masses ($2.41 \text{ kg} \times 1.2$) recorded at deployment in India and Mongolia to account for migratory fattening and report values as kilometres per hour throughout. We used a mean wing span value of 1.45 m^2 and wing area (in m^2) of 0.22 (36). Tests of differences and correlations were carried out using nonparametric statistics (Wilcoxon matched pairs and Spearman's rank correlation coefficient).

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