essential crop repertoire, buffered against temperature change with the significant addition of cold-hardy barley. That same combination of crops additionally enabled the establishment of farms at altitudes hitherto uncultivated, taking farming in some places to elevations above 4000 masl.

Several features of this high-altitude farming prompt further questions about adaptive response. As indicated at the outset, these may include genetic resistance in humans to altitude sickness (*27*); genetic response in crop plants that is observable in the genetics of barley, in relation to such attributes as grain vernalization, flowering time response, and ultraviolet radiation tolerance (*28*); and the identity, genetic and ethnic, of the human communities themselves (*1*, *29*). Such genetic outcomes are all consequent upon the ecological trajectories of cross-continental crop movement. Elsewhere in Europe, Asia, and Africa, that movement has been seen to have a wide variety of outcomes. In the NETP, the data presented here document its facilitation of cultivating the "roof of the world."

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SUPPLEMENTARY MATERIALS

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ANIMAL PHYSIOLOGY

The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations

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The physiological and biomechanical requirements of flight at high altitude have been the subject of much interest. Here, we uncover a steep relation between heart rate and wingbeat frequency (raised to the exponent 3.5) and estimated metabolic power and wingbeat frequency (exponent 7) of migratory bar-headed geese. Flight costs increase more rapidly than anticipated as air density declines, which overturns prevailing expectations that this species should maintain high-altitude flight when traversing the Himalayas. Instead, a "roller coaster" strategy, of tracking the underlying terrain and discarding large altitude gains only to recoup them later in the flight with occasional benefits from orographic lift, is shown to be energetically advantageous for flights over the Himalayas.

Migrating birds must overcome many challenging environmental obstacles, such as arid deserts (*1*, *2*) and featureless oceans (*3*–*5*), but few are capable of negotiating the formidably high mountains separating the Indian subcontinent from central Asia. Famously, one species that manages this feat is the bar-headed goose (*Anser indicus*), which biannually traverses the high passes of the Tibetan massif and snow-capped Himalayan mountains (*6*–*8*). Over the years, there has been much debate as to how high these birds might fly and what physiological mechanisms could be involved at the highest altitudes (*8*–*12*), but, although one goose has been directly tracked as high as 7290 m for a brief period (*12*), no measurements of their physiological or biomechanical flight performance have been made in the wild.

To investigate the flight dynamics and energetics of migratory bar-headed geese, we used custom-designed implantable instruments (*13*) to measure abdominal temperature and pressure (every 30 s), tri-axial acceleration (100 Hz in 18-s bursts every 2 min), and electrocardiography (180 Hz in the same 18-s period) from seven birds, collecting data totaling 391 hours of migratory flight (Fig. 1). The data loggers weighed 32 g and were housed in biocompatible tubing (dimensions 7 × 2 cm) capped by titanium electrodes.

Abdominal body temperature during flight (40.2°C ± 1.2 SD) tended to increase in tandem with flight activity, especially during times of

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intense effort (Fig. 1) but was generally insensitive to changes in altitude (fig. S1). The frequency distribution of all pressure-determined altitude measurements recorded during the migratory flights is shown in Fig. 2A. The median altitude while traversing the Tibetan plateau was 4707 m (maximum 6443 m, 90% of observations <5600 m). Thus, pressure-derived altitudes do not provide evidence for a general paradigm of extreme high-altitude (>8000 m) migratory flight in this species (*12*).

In order to estimate rate of oxygen consumption ($\dot{V}_{O_2}$, ml min^{-1}) during flight from measures of heart rate (f_h, beats min^{-1}) (*14–17*), we apply an allometric proportionality derived for 12 species of birds during flight (*14*) to data obtained from bar-headed geese flying in a wind tunnel (*17*) (fig. S2), and obtain the calibration relationship:

$$\dot{V}_{O_2} = 0.07 \pm 0.002 M_b^{0.24\pm0.01} M_h f_h^2 \quad (1)$$

For wild migratory geese, we substitute values for body mass (M_b) of 2.8 kg and heart mass (M_h) of 1% of body mass (*18*). We then converted estimates of $\dot{V}_{O_2}$ to estimates of metabolic flight power (P_m, W kg^{-1}) by assuming 1 ml $O_2 \cong 20.9$ J. Additionally, we estimate biomechanical body power (P_b, W kg^{-1}) during flight, using measures of dynamic body acceleration (*19–22*). Here, we show that a single P_b component is dominant when empirically correlating several theoretical terms (*22*) for P_b against our estimates of P_m, which determines that time-averaged body power during the flapping flight of geese could be predicted by

$$P_b = \frac{\ddot{Z}^2_{rms}}{2p^2 f_w} \quad (2)$$

where $\ddot{Z}^2_{rms}$ is root-mean-square dorsoventral acceleration (z axis) and f_w is wingbeat frequency.

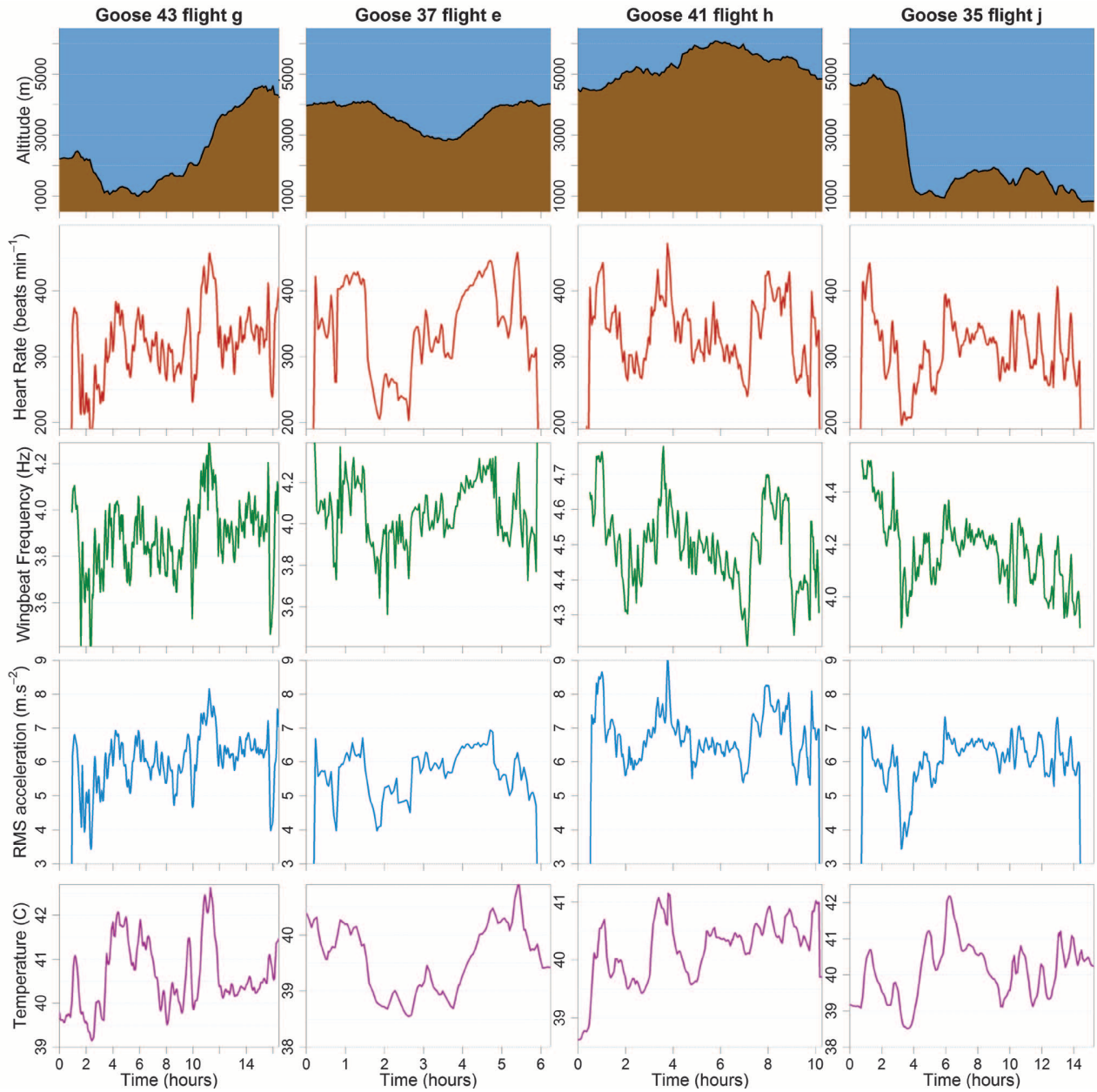

Fig. 1. Examples of autumn migratory flights. Bar-headed goose (*Anser indicus*) P43 travelled South from Mongolia and ascended onto the Tibetan Plateau (column 1); goose P37 (column 2) and goose P41 (column 3) were traversing the Tibetan Plateau; goose P35 (column 4) crossed the Himalayas and descended into India. Pressure altitude (row 1), f_h (row 2), f_w (row 3), $\ddot{Z}^2_{rms}$ (row 4), abdominal body temperature (row 5).

This simple term maximized correlations between the independently derived biomechanical P_b and metabolic P_m (mean r^2 = 0.91 ± 0.05 SD) (Fig. 2B).

During flight, heart rate and wingbeat frequency were significantly correlated (mean r^2 > 0.86 ± 0.11 SD) (Fig. 2, C and D, and fig. S3A), as well as heart rate and $\ddot{Z}^2_{rms}$ (mean r^2 = 0.91 ± 0.05 SD) (Fig. 2C and fig. S3B) and wingbeat frequency and $\ddot{Z}^2_{rms}$ (mean r^2= 0.89 ± 0.09 SD) (fig. S3C). Median wingbeat frequency increased with pressure-derived altitude as air density declined (median f_w = 3.94 Hz at altitude < 2300 m; f_w = 4.35 Hz at altitude >4800 m) (Fig. 2E). Similarly, median heart rate during flight increased with altitude and was generally higher on the Tibetan plateau (f_h = 364 beats min^{-1} at altitude >4800 m) (Fig. 2F) than at lower altitudes (f_h = 300 beats min^{-1} at altitude <2300 m). Although the partial pressure of oxygen decreases with increasing altitude, up to around 5000 m, any potential desaturation of oxygen-bound hemoglobin in the blood of bar-headed geese should still be relatively small, at around 10% (*18*, *23*). Indeed, captive bar-headed geese are able to run for 15 min at similar maximum speeds, whether exposed to atmospheres of 21, 10.5, or 7% oxygen, the last-mentioned condition resulting in a desaturation of between 20 and 23% (*18*).

Our data show that median heart rate during flight scales with air density (ρ) as $f_h \propto \rho^{-0.64}$ (Fig. 2G) and, therefore, that estimated P_m should scale approximately as $P_m \propto \rho^{-0.91}$ (if one assumes that $P_m \propto f_h^2$ but allowing for a 10% additional increase of f_h for a given value of $\dot{V}_{O_2}$ at 5500 m due to a hemoglobin desaturation of 10%). Thus, the relative metabolic flight power of the geese at 5000 m compared with that at sea level is estimated to be around 1.7-fold. This is higher than the anticipated sensitivity of flight power to air density of $P_m \propto \rho^{-0.54}$ predicted by aerodynamic theory (*24*). Similarly, flight theory predicts that wingbeat frequency should be $\propto \rho^{-0.38}$, whereas the present results for bar-headed geese show median $f_w \propto \rho^{-0.23}$ (Fig. 2H). This is at the lower end of the predicted range but in keeping with the observations of large Ciconiiformes (herons, spoonbill, ibis) migrating high above the Negev Desert in Israel (*25*).

Bar-headed geese exhibit an extreme sensitivity of heart rate and, therefore, metabolic flight power to small changes in wingbeat frequency, when a precise method is used for extracting values of f_w (*26*). For example, a 5% increase in f_w from 4.0 to 4.2 Hz equates to a 19% increase in f_h and, therefore, a 41% increase in estimated P_m. Across all migratory flights, f_h correlated in the range of $f_h \propto f_w^{1.95 \text{ to } 6.65}$ and estimated P_m as $P_m \propto f_w^{3.9 \text{ to } 13.3}$, the latter exponent exceeding 3 in every case (median exponent 6.96) (Fig. 2I). For steady horizontal flight, the inertial

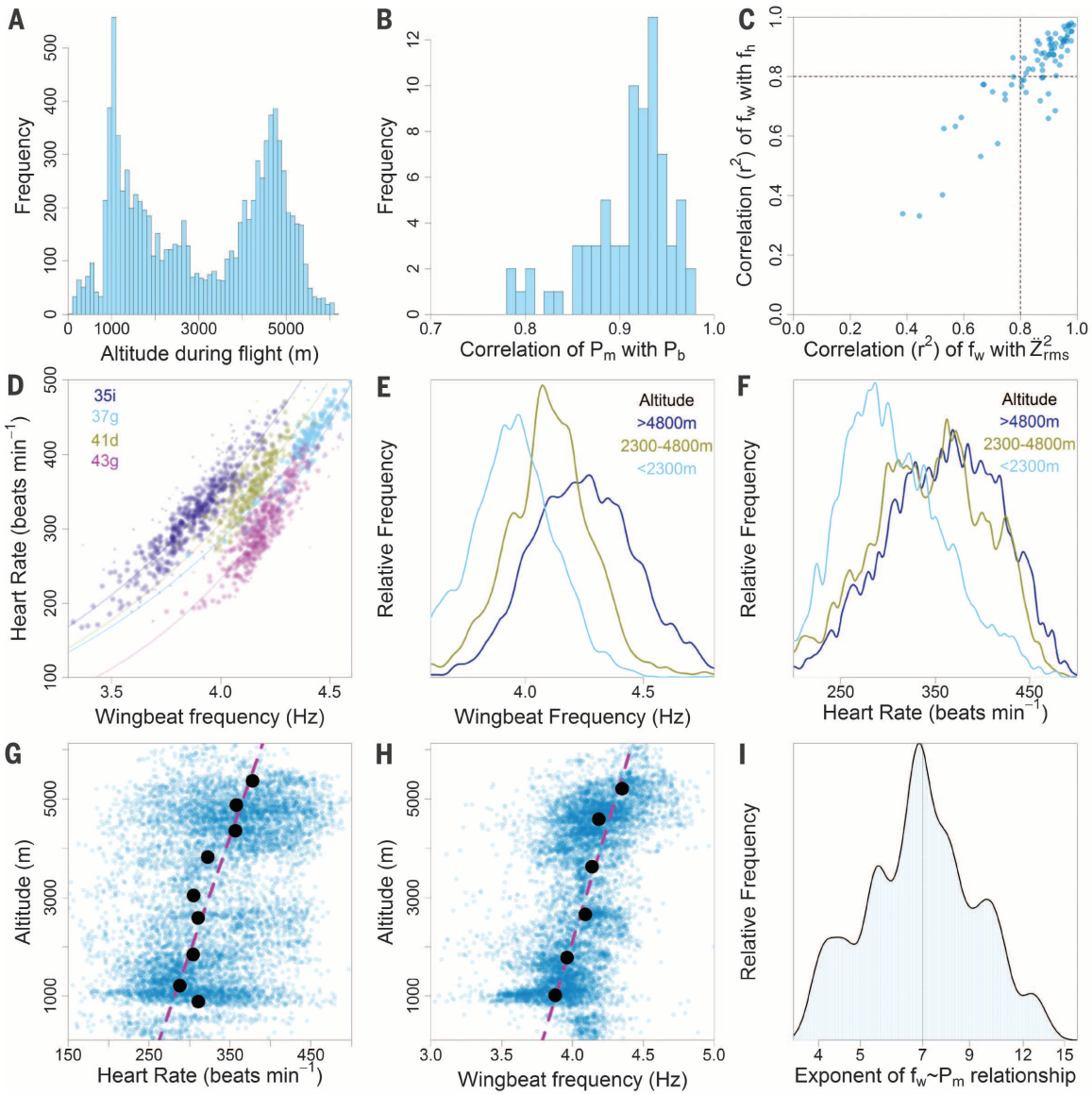

Fig. 2. Descriptive flight statistics. Frequency histograms of (**A**) altitude reported during migratory flights of bar-headed geese (*Anser indicus*) and (**B**) correlation of estimated P_m versus estimated P_b. (**C**) Correlation of f_h versus f_w plotted against correlation of $\ddot{Z}^2_{rms}$ versus f_w. (**D**) Examples of f_h against f_w for four individual flights. Frequency distribution of (**E**) f_w and (**F**) f_h within three altitude zones. Scatter plots of (**G**) f_h and (**H**) f_w plotted against altitude. (**I**) Frequency distribution of power exponents for f_w against estimated P_m.

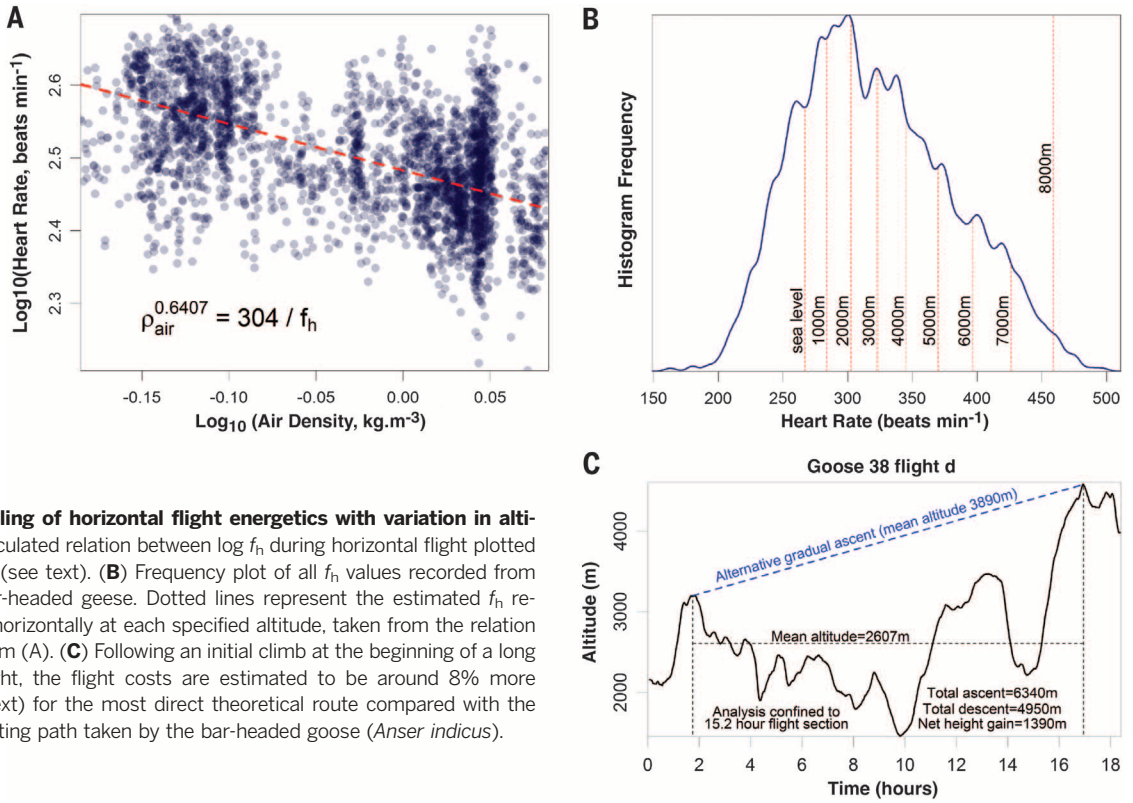

Fig. 3. Modeling of horizontal flight energetics with variation in altitude. (**A**) Calculated relation between log f_h during horizontal flight plotted against log ρ (see text). (**B**) Frequency plot of all f_h values recorded from the same bar-headed geese. Dotted lines represent the estimated f_h required to fly horizontally at each specified altitude, taken from the relation calculated from (A). (**C**) Following an initial climb at the beginning of a long migratory flight, the flight costs are estimated to be around 8% more costly (see text) for the most direct theoretical route compared with the actual undulating path taken by the bar-headed goose (*Anser indicus*).

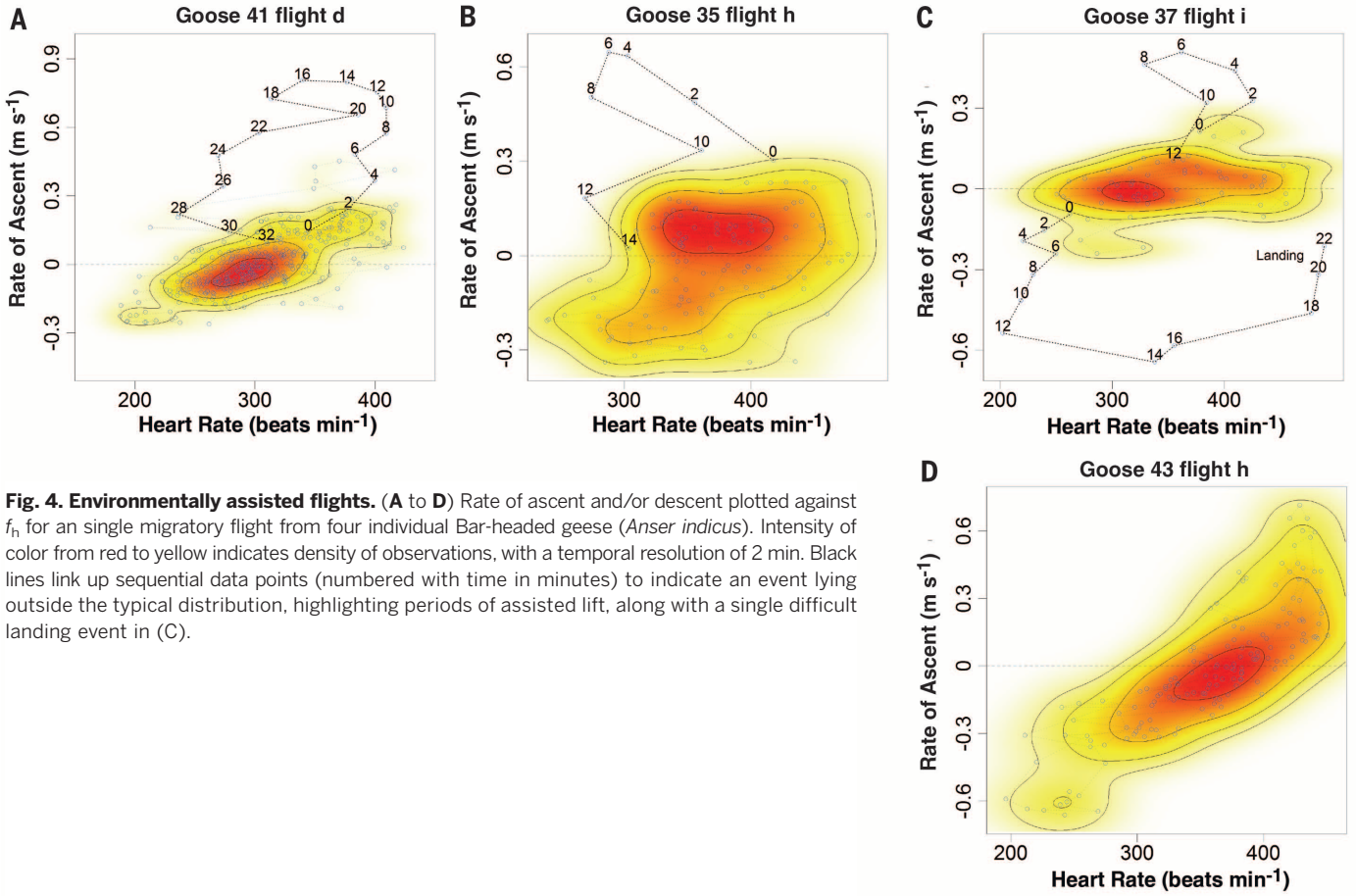

Fig. 4. Environmentally assisted flights. (**A** to **D**) Rate of ascent and/or descent plotted against f_h for an single migratory flight from four individual Bar-headed geese (*Anser indicus*). Intensity of color from red to yellow indicates density of observations, with a temporal resolution of 2 min. Black lines link up sequential data points (numbered with time in minutes) to indicate an event lying outside the typical distribution, highlighting periods of assisted lift, along with a single difficult landing event in (C).

costs of flapping the wings should be proportional to the product of wingbeat frequency cubed and the wing amplitude squared. If the body of the bird undergoes sinusoidal amplitude displacements on the vertical axis (B) then $\ddot{Z}^2_{rms} = 2\sqrt{2}\pi^2 B f_w^2$ (*22*) and so Eq. 2 can be rewritten

$$P_b = 4\pi^2 B^2 f_w^3 \quad (3). \qquad (3)$$

Because B should be positively correlated with wingbeat amplitude, the implication of our experimental data, showing that $P_m \propto f_w^{6.96}$, is that the angular travel of the wing increases with higher f_w. Thus, the exquisite sensitivity of P_m to f_w in geese stems from wingbeat amplitude that is positively correlated with changes in wingbeat frequency.

In the present study, there was no evidence of gliding behavior in bar-headed geese, even when descending rapidly from the Himalayas into India (fig. S4). During the steepest descent phases, f_w remained above 3.6 Hz for 98% of observations, whereas f_h decreased to between 150 and 200 beats min^{-1}. Indeed, f_h was surprisingly low in general throughout the entire migration (overall mean f_h = 328 ± 64 beats min^{-1}) (Fig. 2F), with geese only spending 2.3% of their flight time at altitudes above 4800 m with a f_h greater than 455 beats min^{-1} (and 0.37% of their flight time when below 2300 m altitude). A simple extrapolation of the relations between heart rate and air density (Fig. 3A), with data filtered so that only rates of ascent or descent lying between ±0.1 m s^{-1} are included (an approximation of horizontal flight), demonstrates that a minimum heart rate of around 460 beats min^{-1} might just suffice at around 8000 m in still air conditions (Fig. 3B). However, even this assessment might seem unduly optimistic, given that it ignores the energetics and time required to make the climb itself and the steepness of the relation for hemoglobin desaturation once the partial pressures of oxygen fall below a critical value (*18*, *23*). Thus, unaided horizontal flights over 8000 m are likely to be approaching the limit for sustained aerobic capacity in this species.

Previous low temporal-resolution global positioning system altitude data (*12*) indicated that bar-headed geese tend to fly closest to the ground when traversing the Tibetan massif, with a median height of only 62 m. This is consistent with the high-resolution pressure altitude results of the present study, which imply that geese opt repeatedly to shed hard-won altitude only subsequently to regain height later in the same flight. An example of this tactic can be seen in a 15.2-hour section of a 17-hour flight (Fig. 3C) in which, after an initial climb to 3200 m, the goose followed an undulating profile involving a total ascent of 6340 m with a total descent of 4950 m for a net altitude gain of only 1390 m. Revealingly, calculations show that steadily ascending in a straight line would have increased the journey cost by around 8%. As even horizontal flapping flight is relatively expensive, the increase in energy consumption due to occasional climbs is not as important as the effect of reducing the general costs of flying by seeking higher-density air at lower altitudes.

Rates of ascent and descent during four migratory flights are plotted against f_h (Fig. 4) and against f_w (fig. S5), with maximum ascent rates of up to at least 0.8 m s^{-1}, lasting for several minutes. However, such extreme ascent rates were generally not associated with increases in f_h and f_w. A particularly clear example of such an episode that occurred during a 13-hour migratory flight is shown in Fig. 4A. The central cluster of Fig. 4A exhibits a sloping relation between f_h and rate of ascent (typical of a number of flights), but there was a dramatic departure from this pattern lasting ~30 min involving unusually high rates of ascent despite "normal" values of heart rate. Although the degree of central clustering varied between flights, presumably according to the prevailing wind conditions and underlying terrain, similar unusually high ascent rates occurred on other flights (Fig. 4, B to D). These unique results are interpreted as evidence of sustained assistance from updrafts due to orographic lift (*27*, *28*), presumably indicative of geese flying along the windward side of a ridge. Thus, it is logical to conclude that weaker vertical updrafts could also provide more gentle assistance during other phases of the migratory flights, perhaps comparable in magnitude to the assistance geese might at times receive from V-formation flight (*29*, *30*).

When traversing mountainous areas, a terrain-tracking strategy or flying in the cool of the night (*12*) can reduce the cost of flight in bar-headed geese through exposure to higher air density. Ground-hugging flight may also confer additional advantages including maximizing the potential of any available updrafts of air, reduced exposure to crosswinds and headwinds, greater safety through improved ground visibility, and increased landing opportunities. The atmospheric challenges encountered at the very highest altitudes, coupled with the need for near-maximal physical performance in such conditions, likely explains why bar-headed geese rarely fly close to their altitude ceiling, typically remaining below 6000 m. Given that aerodynamic mass-specific flight costs are thought to increase with body mass and that bar-headed geese are heavier than 98% of avian species, it is particularly impressive that these birds are able to migrate across the world's highest land massif while remaining comfortably within their physiological capabilities.

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The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations

C. M. Bishop *et al.*

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