REVIEWS
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# How Bar-Headed Geese Fly Over the Himalayas

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Bar-headed geese cross the Himalayas on one of the most iconic high-altitude migrations in the world. Heart rates and metabolic costs of flight increase with elevation and can be near maximal during steep climbs. Their ability to sustain the high oxygen demands of flight in air that is exceedingly oxygen-thin depends on the unique cardiorespiratory physiology of birds in general along with several evolved specializations across the $O_2$ transport cascade.

> *"On one cold and still night in early April, I stood beside the Barun glacier [near Mount Makalu, the fifth highest mountain in the world at 8,463 m above sea level] . . . 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."*–Lawrence Swan (46)

Since early mountaineers and naturalists first sighted bar-headed geese migrating amidst the Himalayan mountains, the migration of this species has been a fascination to both scientists and the general public. Bar-headed geese can be found anywhere from Mongolia to the Tibetan plateau in the summer, where they raise young before the majority take long flights south to the Indian subcontinent in the autumn, and return again the following spring (24, 47). As the most metabolically intense form of vertebrate locomotion, flight demands an extremely high rate of oxygen consumption (51), yet the air at high altitudes in the Himalayas contains only one-third to one-half of the oxygen that is available in air at sea level. Therein lies the apparent paradox that has intrigued so many scientists: bar-headed geese must be capable of sustaining the high oxygen demands of flight in air that is exceedingly oxygen-thin. What is the evidence that bar-headed geese can in fact accomplish this paradoxical feat? What physiological mechanisms underlie high-altitude flight? Recent efforts to address these questions, from characterizing the physiological ecology of the natural migration to elucidating the unique respiratory and metabolic physiology that underlies it, are shedding new insight into the paradox of high-altitude flight in this species.

## The Challenges of High-Altitude Flight

Bar-headed geese fly at altitudes that are extremely challenging to lowland humans and animals. Geese migrating between India and Mongolia have been tracked by satellite telemetry crossing the Himalayan mountains across a broad front (47) (FIGURE 1). Most birds reach altitudes of 5,000–6,000 m during the migration, where the $P_{O_2}$ is roughly half of that at sea level, and they occasionally fly even higher (e.g., one recorded bird reached 7,290 m) (16, 24, 47). Although the accuracy of auditory and visual observations are questionable (16), there are anecdotal reports of bar-headed geese flying even higher, above the highest peaks in the Himalayas (of which there are 14 above 8,000 m), where the $P_{O_2}$ is only one-third of the sea-level value (46). The level of hypoxia at these elevations, even the lowest at which bar-headed geese cross the mountains, is sufficient to reduce maximal $O_2$ uptake rates in humans substantially (53). In fact, the atmosphere atop the highest peaks in the Himalayas is believed to have scarcely enough oxygen to support basal metabolism in humans (53). Therefore, bar-headed geese face the challenge of sustaining the high rates of $O_2$ consumption needed for flapping flight, which ranges from 10- to 15-fold above resting levels during steady flight in a wind tunnel at sea level (51), in air that can severely limit aerobic metabolism in many lowland animals (49). At the same time, the temperatures at high altitudes can be very low, well below freezing year round in the high Himalayas (56), which could require additional metabolic energy for thermogenesis if the heat production from exercise is not sufficient to maintain body temperature. Maintaining water balance during flight should also be a major challenge in the dry air at high altitudes, given that water loss can constrain flight duration at sea level in some species (11).

As bar-headed geese fly to higher elevations, it becomes progressively more difficult to generate lift in the decreasing air density. Logging of physiological variables during migration has shown that average heart rates during flight increase with rising elevation (FIGURE 2B), and geese spend a greater proportion of time flying with near maximal heart rates when altitude exceeds 4,800 m (4). When possible, geese will offset the metabolic

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power requirements of flight at high altitude (as estimated by logged heart rates) by taking lower altitude routes, such as through riverine valleys, or by taking advantage of the orographic lift or katabatic winds near mountains (4, 16) (FIGURE 2C). Nevertheless, bar-headed geese are flapping fliers that very rarely glide, even during steep descents (4).

Crossing the Himalayas from India onto the Tibetan plateau also requires bar-headed geese to ascend for many hours, sustaining the longest sustained rates of climbing flight recorded to date, and possibly even into headwinds (17). Climbing flight presents a much greater metabolic challenge than level flight and generally requires higher average heart rates and wing-beat frequencies (4). Indeed, heart rates of individual geese have been shown to increase as they ascend and to decrease as they descend (FIGURE 2A), and there is a positive relationship between rate of ascent and heart rate (FIGURE 2C) (4). Therefore, it would be advantageous for bar-headed geese to make use of upslope tailwinds during ascent (7, 9). However, upslope tailwinds predominate only during the day in mountainous regions, and bar-headed geese often migrate at night and in the early morning when the predominant winds travel downslope (17). Although these nighttime flights likely entail a greater metabolic cost than flying later in the day when updrafts predominate, the darkness should lessen predation risk (e.g., from predatory birds), the wind currents are more stable and less turbulent, and the air is cooler and will have a slightly higher density and $P_{O_2}$. These benefits may outweigh the metabolic costs of having to flap harder to climb to high altitudes.

The ecophysiological studies of the natural migration of bar-headed geese emphasize the challenges of high-altitude flight. Although bar-headed geese may

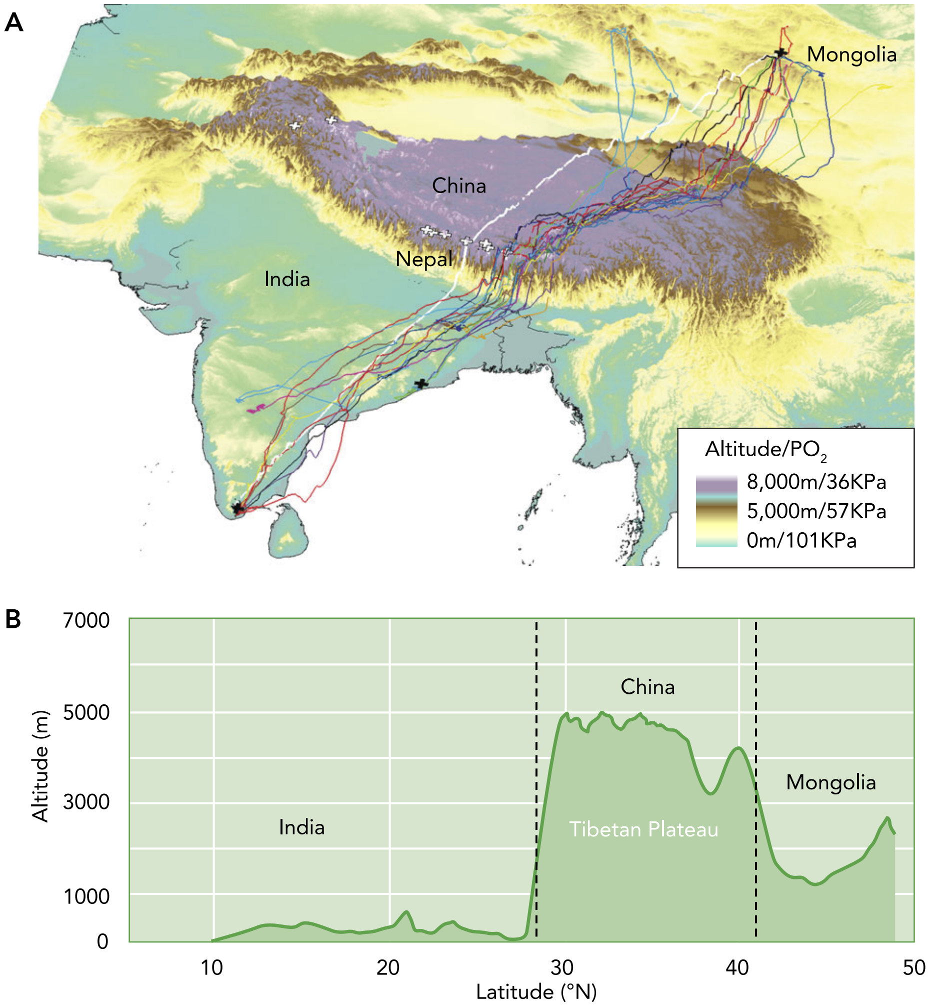


FIGURE 1. **The high-altitude migration of bar-headed geese**
*A*: satellite tracking of migrating bar-headed geese (colored lines are individual geese) shows where individuals from a Mongolian population cross the Himalayas on their southward migration to India. The colored background shading indicates elevation, and the white crosses are the world's highest mountains (all over 8,000-m elevation). *B*: on their northward migration out of India, the ascent over the mountains is very steep (minimum climb rates of 0.8–2.2 km/h) and occurs very quickly (<1 day) (17). Image was modified and reproduced from Ref. 16 with permission.

take help from wind assistance to lessen the metabolic requirements of flight when possible, much like lowland geese (9), they also experience prolonged periods of relatively high heart rates and intense metabolic activity (4). That these periods of intense activity occur in hypoxic air ($P_{O_2}$ of ≤50% of that at sea level) makes this physiological feat all the more impressive. The ability of bar-headed geese to transport enough $O_2$ to the flight muscle and other tissues to sustain the high metabolic requirements of flight appears to require a variety of physiological traits, some of which are general traits of all birds (i.e., high-altitude exaptations, evolved traits that are important at high altitudes but are not considered to be adaptations) and some additional traits that likely evolved during the process of evolutionary adaptation to high altitude (FIGURE 3).

## Avian Physiology as High-Altitude Exaptations

The exceptional hypoxia tolerance of birds in general, which may have arisen with the evolution of increased cardiorespiratory performance to support flight, is likely an important contributor to the ability of bar-headed geese to fly at high altitudes (12, 38). Early work showed that even lowland sparrows can fly in a wind tunnel while breathing air that simulated the $P_{O_2}$ at 6,100 m, which was sufficiently hypoxic to render domestic mice comatose (50). Birds are generally more tolerant of hypoxia than mammals, and bar-headed geese and some other hypoxia-tolerant birds can survive lower $P_{O_2}$ (lowest survivable $P_{O_2}$, ~2.7 kPa) than the most hypoxia-tolerant euthermic mammals (e.g., mole rats, ~4.7 kPa) (49). Several unique features of avian respiratory and cardiovascular physiology, distributed across the oxygen cascade (21, 48) (shown in FIGURE 3), are likely responsible for this heightened hypoxia tolerance of birds. These unique traits probably act as important exaptations that facilitate high-altitude flight.

Birds are thought to be capable of higher ventilation rates than mammals in hypoxia. The decline in arterial $P_{O_2}$ ("hypoxemia") drives the increase in breathing in response to environmental hypoxia, but $CO_2$ excretion increases as a secondary consequence (42). Low $P_{CO_2}$ in the blood ("hypocapnia")

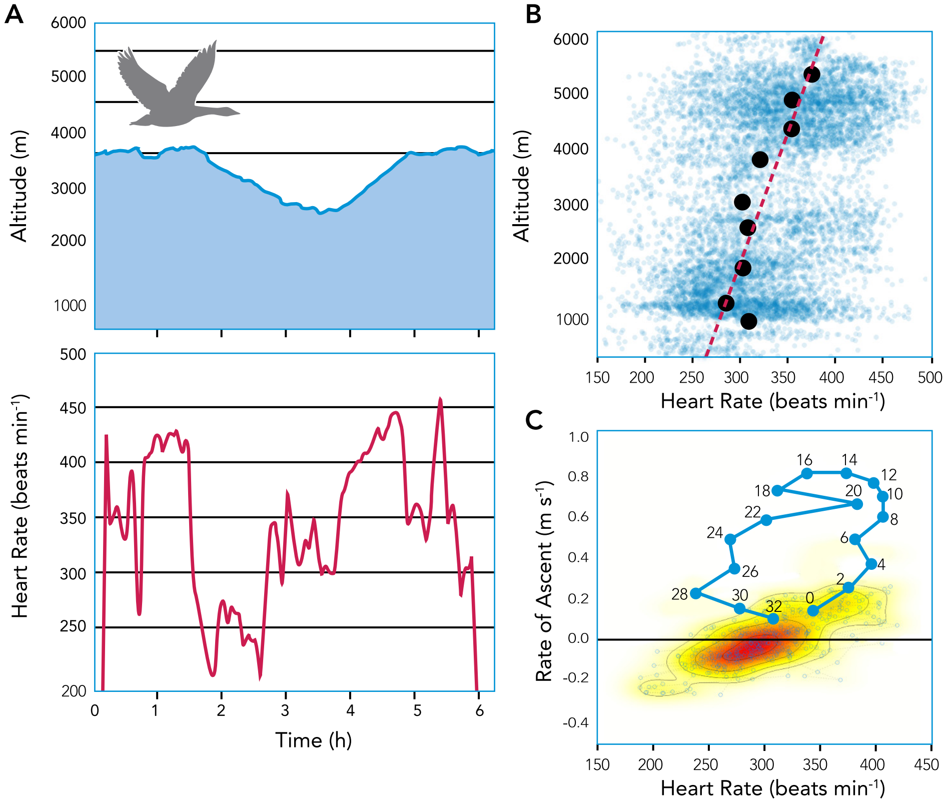
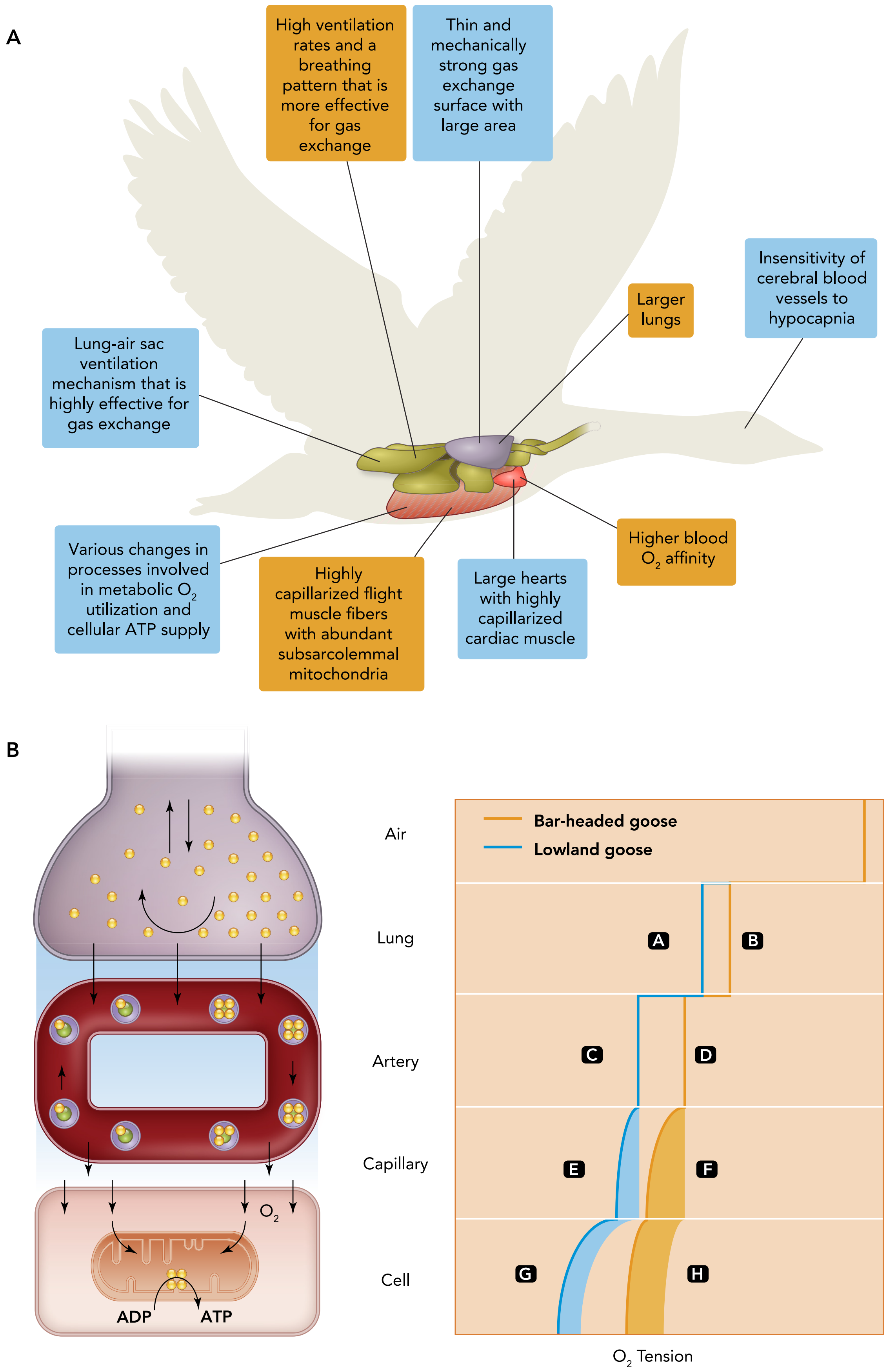


FIGURE 2. **The metabolic cost of high-altitude flight can be substantial, as reflected by heart rates logged during the natural migration**

*A*: altitudes and heart rates of an individual bar-headed goose flying across the Tibetan plateau, showing the changes in heart rate during descent and ascent. *B*: the average heart rates exhibited during flight increase with elevation. *C*: environmental assistance (e.g., uplifting winds) can lessen the heart rates and presumably the metabolic costs of climbing flight when available. An individual goose is shown as an example, with blue lines indicating sequential data points (numbered in minutes) for an event of assisted lift that lies outside the typical relationship between ascent rate and heart rate (red color intensity reflects the overall density of observations). Image modified and reproduced from Ref. 4 with permission.


A
High ventilation rates and a breathing pattern that is more effective for gas exchange
Thin and mechanically strong gas exchange surface with large area
Insensitivity of cerebral blood vessels to hypocapnia
Larger lungs
Lung-air sac ventilation mechanism that is highly effective for gas exchange
Higher blood $O_2$ affinity
Various changes in processes involved in metabolic $O_2$ utilization and cellular ATP supply
Highly capillarized flight muscle fibers with abundant subsarcolemmal mitochondria
Large hearts with highly capillarized cardiac muscle
B
$O_2$
ADP
ATP
Air
Lung
Artery
Capillary
Cell
Bar-headed goose
Lowland goose
A
B
C
D
E
F
G
H
$O_2$ Tension

ensues, which restrains the hypoxic ventilatory response and can lead to an alkalosis of the blood. Based on the extremely low arterial $P_{CO_2}$ (<1 kPa) recorded in birds breathing heavily in severe hypoxia, it has been suggested that birds can ventilate more than mammals in severe hypoxia because they can tolerate a greater depletion of blood $CO_2$ before normal cellular function is impaired (35). This may result from an enhanced capacity to restore blood pH rapidly when blood $P_{CO_2}$ changes (10) or because the brain vasculature is insensitive to hypocapnia (as discussed in more detail below). As a result, $O_2$ transport to the gas-exchange surface in hypoxia may be enhanced in birds compared with mammals.

The structure and function of the avian lung imparts an inherently greater gas-exchange capacity than that of the mammalian lung. Birds possess a system of unidirectional airflow in the lungs, which arose in reptiles (14) and later evolved into a highly effective gas exchanger (36). Blood in the pulmonary capillaries flows perpendicular to the air flowing through the parabronchi, so the bird lung functions as a cross-current gas exchanger (28). Cross-current gas exchange is inherently more effective than the alveolar exchange mechanism of mammalian lungs, such that birds in hypoxia can have an arterial $P_{O_2}$ that exceeds that of the expired gas (33, 35). The capacity for $O_2$ diffusion in the lungs is also very high in birds because the gas-exchange tissue is exceptionally thin (0.1–0.2 μm compared with 0.4–0.8 μm or more in mammals) and generally has a larger surface area (40–100 $cm^2/g$ compared with 15–40 $cm^2/g$ in nonflying mammals) (52, 54).

The unique physiology of the pulmonary vessels in birds may also impart resistance to high-altitude pulmonary edema, a major contributor to acute mountain sickness in mammals (37). The pulmonary vessels of mammals constrict in response to hypoxia, which can result in pulmonary hypertension, impairment of gas exchange, and pulmonary edema (26, 37). In contrast, the pulmonary vasculature does not constrict in response to hypoxia in birds, and pulmonary arterial pressures increase in hypoxia only when cardiac output rises (6, 13, 55). The avian blood-gas barrier is also thought to be mechanically stronger and more resistant to stress failure than that of mammals (54).

There are several differences in the hearts of birds compared with mammals that should help support higher cardiac outputs and greater convective $O_2$ delivery during hypoxia. Birds have ~50% larger hearts and cardiac stroke volumes than mammals of similar body size, and birds can sustain heart rates during free flight that are similar to or greater than those of mammals during maximal exercise (3, 15). Capillary density in the cardiac muscle also appears to be higher in birds compared with mammals (12), which would be associated with higher oxygen diffusion capacity and should presumably make bird hearts more resistant to cardiac oxygen limitation in hypoxia.

The capacity for $O_2$ diffusion into the peripheral tissues appears to be higher in birds than in mammals and other vertebrates. The capillary exchange capacity is higher in the flight muscle of birds (capillary length per fiber volume of 6,015 and ~13,910 $mm^{-2}$ in pigeons and hummingbirds) compared with the locomotory muscles of nonflying mammals (5,700 and 1,890 $mm^{-2}$ in the hindlimb of deer mice and dogs) (29). This distinction exists largely because there is a mesh of branching capillaries that surrounds avian muscle fibers, which are themselves smaller in size compared with nonflying mammals of a similar body size (fiber diameters of 20 and 14 μm in pigeons and hummingbirds, and 29 and 45 μm in the hindlimb of deer mice and dogs) (29).

Several differences in the brain physiology of birds compared with mammals may protect against cerebral dysfunction in hypoxia. In birds, unlike in mammals (1), cerebral blood flow is not inhibited by respiratory hypocapnia (12). This should improve brain oxygenation during environmental hypoxia, although this has not yet been confirmed by direct measurement. Avian neurons also have an inherently higher tolerance of low cellular $O_2$ levels (as reflected by the greater survival of cerebellar slices from ducks and chickens than that from rats in 60 min of anoxia) (25) and therefore appear to be well protected from cellular damage induced by $O_2$ limitation. An intriguing question that has yet to be addressed is whether birds suffer hypoxic cerebral edema, one of the most dangerous consequences of high-altitude exposure in humans (19).

The unique respiratory and cardiovascular physiology of birds enhances hypoxia tolerance and

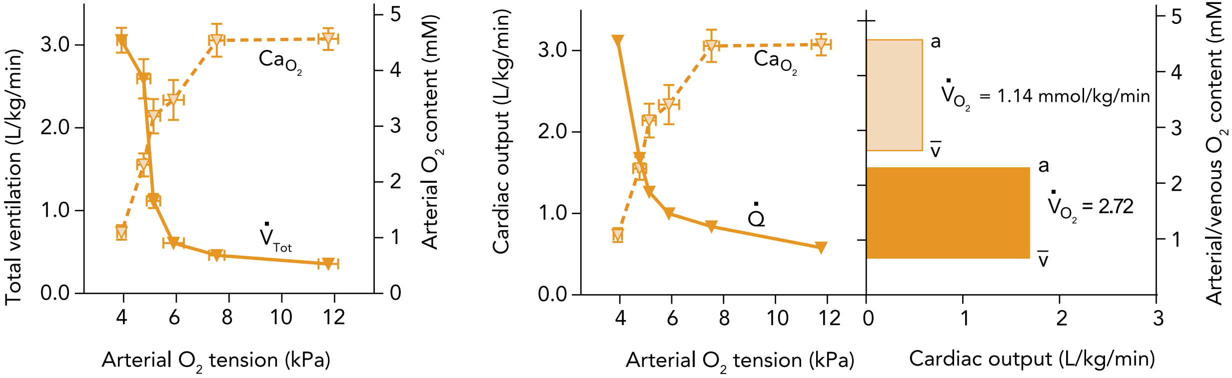
FIGURE 3. **High-altitude flight is facilitated by several general avian traits**
*A*: high-altitude flight is facilitated by several general avian traits (blue) as well as many evolved specializations in bar-headed geese (orange). *B*: the qualitative effects of the evolved specializations increase oxygen tensions ($P_{O_2}$) across the oxygen transport cascade (shown at *left*) compared with lowland geese (with letters added for comparison between bar-headed geese and lowland geese). The capillary $P_{O_2}$ driving diffusion decreases along the length of capillaries as the blood loses $O_2$ to the tissues. The decline in capillary $P_{O_2}$ and decrease in $P_{O_2}$ with distance from capillaries lead to a range of potential cellular $P_{O_2}$. The oxygen transport cascade is adapted from Refs. 21, 48.

exercise capacity by improving the overall capacity for $O_2$ transport, but most birds probably cannot fly at extremely high altitudes. Many species cannot tolerate the levels of hypoxia that exist atop the world's highest mountains (5), and some birds fly exceptionally long distances during their migration to avoid mountain barriers (20). Why bar-headed geese do not do the same is unclear, but it is suggested that the species (or its ancestor) may have begun migrating between South and Central Asia in the late Pliocene or early Pleistocene at a time in geological history when the Himalayas were not nearly as high (46). Because migration routes can be genetically programmed, the species may have slowly evolved to fly higher and higher as they continued along the same migration route over thousands of years. Whatever the evolutionary path that has led to modern day bar-headed geese, it has resulted in the evolution of several specialized traits that set this species apart from most other birds and that allow them to sustain the high $O_2$ requirements of flight in the oxygen-thin air at high altitudes.

## The Specialized Physiology of Bar-Headed Geese

The capacity of bar-headed geese to transport and consume oxygen at high rates in hypoxia distinguishes this species from similar lowland waterfowl. Bar-headed geese can tolerate extreme hypoxia at rest (inspired $P_{O_2}$ tensions as low as ~2.7 kPa, approximating ~12,000 m), which far exceeds the tolerance of many lowland waterfowl (5, 41). Bar-headed geese also maintain body temperature in hypoxia to a lower inspired $P_{O_2}$ (~9 kPa) than lowland waterfowl (~12 kPa), and they depress body temperature less (39). In fact, they elevate metabolic rate two- to threefold in hypoxia (inspired $P_{O_2}$ between ~4 and 9 kPa) at rest, presumably to support the $O_2$ demands of the respiratory and cardiovascular responses to hypoxia (FIGURE 4) (5, 41). Bar-headed geese are also capable of achieving the high metabolic rates needed for flight in a normobaric wind-tunnel and maximal running on a treadmill at comparable levels of

Bar-Headed Goose (Anser indicus)



Greylag Goose (Anser anser)

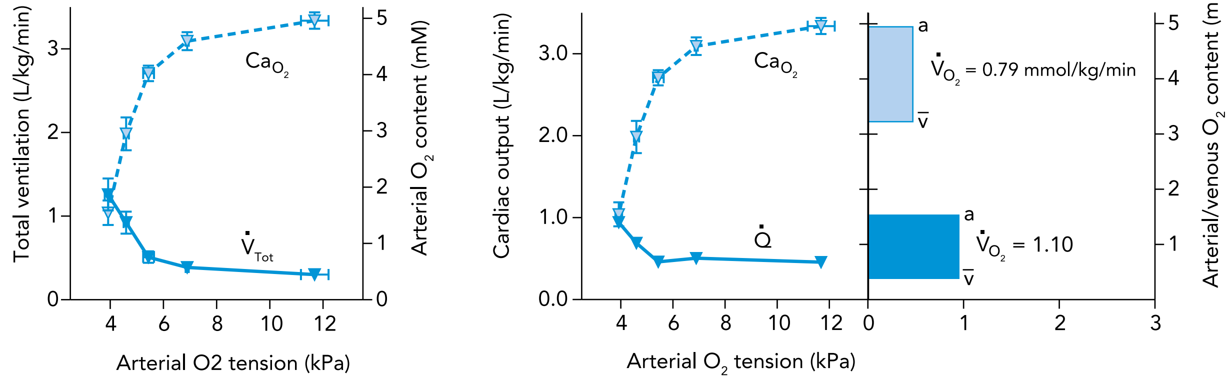


FIGURE 4. **The cardiorespiratory and metabolic responses to hypoxia at rest are enhanced in bar-headed geese compared with lowland waterfowl**

Total ventilation ($\dot{V}_{Tot}$) and cardiac output ($\dot{Q}$) increase in hypoxia below the arterial $O_2$ tension at which the blood begins to desaturate, but this increase is much greater in bar-headed geese than in greylag geese. Associated with this heightened cardiorespiratory response to hypoxia in bar-headed geese is a much larger increase in $O_2$ consumption rate ($\dot{V}O_2$), which is reflected by the area of the bars in the *right* panels for each species in normoxia and in 5% inspired $O_2$ fraction. Data are from Ref. 41, with the exception of cardiac output, which was calculated by the Fick equation ($\dot{V}O_2 = \dot{Q}\,[Ca_{O_2} - Cv_{\bar{V}O_2}]$) from data in Ref. 41. $Ca_{O_2}$, arterial $O_2$ content; $Cv_{\bar{V}O_2}$, mixed venous $O_2$ content; a, arterial; $\bar{V}$, mixed venous.

hypoxia to those on the summit of Mount Everest (~7 kPa) (18, 31a). As discussed below, this impressive ability to sustain high metabolic rates in hypoxia appears to arise from increases in the capacity of several steps in the $O_2$ transport pathway that augment cellular $P_{O_2}$ (FIGURE 3).

The control of breathing has evolved in bar-headed geese to improve $O_2$ uptake into the respiratory system in hypoxia. Bar-headed geese have been shown to exhibit larger increases in total ventilation in response to severe hypoxia (inspired $P_{O_2}$ of ≤6 kPa) than any other bird species studied to date (5, 41, 42). For example, total ventilation in bar-headed geese during severe hypoxia is roughly twice that in the greylag goose, a closely related species that does not generally fly at high altitudes (FIGURE 4). Furthermore, bar-headed geese breathe more deeply (with higher tidal volumes) and less frequently than low-altitude birds at a given level of total ventilation (39, 41), a breathing pattern that is more effective for gas exchange because it reduces dead-space ventilation and produces a higher $P_{O_2}$ at the gas-exchange surface in the lungs (compare FIGURE 3, A AND B). Bar-headed geese also have ~25% larger lungs than lowland waterfowl of comparable body mass (45), which should enhance the area and diffusion capacity of the pulmonary gas-exchange surface. These specializations allow bar-headed geese to maintain higher $P_{O_2}$ in the arterial blood than their lowland counterparts during hypoxia (compare FIGURE 3 C AND D; FIGURE 4).

Circulatory $O_2$ delivery in hypoxia is improved in bar-headed geese by evolved changes in blood physiology. The hemoglobin of bar-headed geese has a higher affinity for $O_2$ (whole-blood $P_{50}$ of 4.0 kPa at pH 7.4 and $CO_2$ tension of ~5 kPa) than that of closely related lowland geese (5.3 kPa in greylag goose under the same conditions) (32), which increases pulmonary $O_2$ loading and peripheral $O_2$ delivery in hypoxia by increasing hemoglobin saturation at a given blood $P_{O_2}$ (43). The genetic basis for this increase in affinity could involve several amino-acid substitutions in the α-subunit of the hemoglobin protein. Birds possess major (HbA) and minor (HbD) forms of hemoglobin, and in bar-headed geese the α-subunits of these forms contain four ($\alpha^A$) and two ($\alpha^D$) derived substitutions, respectively (30). Site-directed mutagenesis has shown that one of the substitutions in $\alpha^A$ (proline-119 → alanine) can account for much of the increase in $O_2$ affinity (23), likely by altering the interaction between α- and β-subunits and destabilizing the deoxygenated state of the protein (57). Hemoglobin-$O_2$ binding is also more sensitive to temperature in bar-headed geese than in other birds and mammals (31). This could have significant implications for $O_2$ transport if there is thermal heterogeneity between the lungs and flight muscle during flight (27, 43). For example, warming of blood in the active flight muscle (8) would transiently decrease hemoglobin $O_2$ affinity and favor $O_2$ unloading. The benefit of this mechanism for $O_2$ transport depends on the magnitude of thermal heterogeneity, which is currently unknown. Theoretical analyses suggest that a 10°C temperature difference between the lungs and flight muscle would increase $O_2$ transport in hypoxia by ~40–60%, and this potential effect will be magnified by the enhanced thermal sensitivity of bar-headed goose hemoglobin (43).

Circulatory $O_2$ delivery in hypoxia may also be improved in bar-headed geese by evolved changes in heart function. Bar-headed geese have a 30–40% higher capillary density in the left ventricle of the heart than closely related lowland geese but similar myoglobin concentration and maximal activity of several metabolic enzymes (e.g., citrate synthase, hydroxyacyl-coA dehydrogenase, lactate dehydrogenase, pyruvate kinase) (34, 45). This should increase the $P_{O_2}$ in cardiac myocytes, improve the hypoxemia tolerance of the heart, and allow bar-headed geese to increase cardiac output during hypoxia (FIGURE 4).

The capillarity of the flight muscle is also higher in bar-headed geese than in lowland waterfowl (40), which increases the capacity for $O_2$ diffusion from the blood in hypoxia. Furthermore, a greater proportion of the mitochondria in oxidative muscle fibers are in a subsarcolemmal location (located next to the cell membrane) in bar-headed geese (~50%) compared with lowland geese (~35%) (40), which reduces intracellular $O_2$ diffusion distances. Each of these evolved specializations will increase the capacity for extracting $O_2$ from the blood (compare FIGURE 3, E AND F) and maintain a high $P_{O_2}$ at the mitochondria (compare FIGURE 3, G AND H) during flight at high altitudes.

The increases in the capacity of bar-headed geese to transport $O_2$ during hypoxia (FIGURE 3) are accompanied by various evolved changes in the properties of metabolic $O_2$ utilization in the flight muscle and heart. The proportional abundance of oxidative fibers in the flight muscle is higher in bar-headed geese than in lowland waterfowl (~70% vs. ~60% by area in the superficial pectoralis) (40). In contrast, the mitochondrial respiratory capacity and $O_2$ kinetics (i.e., sensitivity to low $O_2$ tension) as well as the abundance of mitochondria in oxidative fibers are similar in bar-headed geese and lowland geese (40). The affinity of cytochrome c oxidase (COX; the enzyme that consumes $O_2$ in oxidative phosphorylation) for cytochrome c is also higher in bar-headed geese than in lowland waterfowl (45). This change may have arisen from a single mutation in COX subunit

3 at a site that is otherwise conserved across vertebrates (tryptophan-116 → arginine) and appears to alter inter-subunit interactions (45). The physiological importance of this unique trait is not completely understood, but it may act to reduce the propensity of mitochondria to produce reactive oxygen species (ROS) by allowing the electron transport chain to operate in a less reduced state. If so, this trait could reduce the propensity of bar-headed geese to experience oxidative stress, an underappreciated stressor associated with prolonged migration (22).

There also appear to be mechanisms in place that better match cellular ATP supply and demand in the flight muscle of bar-headed geese. Mitochondrial respiration in situ in permeabilized muscle fibers is more strongly regulated by creatine in bar-headed geese than in low-altitude waterfowl (44). These results suggest that ATP supply and demand is better coupled via the creatine kinase shuttle, a system important for moving ATP-equivalents around the cell (2). This unique trait could even be related to the subsarcolemmal localization of mitochondria in the flight muscle (see above), compensating for the greater distance between these organelles and the contractile elements.

## Conclusions

High-altitude flight is an extremely challenging feat of performance that is underpinned by a number of specialized physiological traits. Bar-headed geese can reach high altitudes during their migration across the Himalayas and Tibetan plateau because they can continue supporting the metabolic costs of flight as the air becomes extremely hypoxic. Like other migrating birds, they may occasionally make use of updraft wind assistance to help offset flight costs. However, they also experience periods of intense flapping flight that require extremely high heart rates, wing-beat frequencies, and metabolic power, such as during level flight at high elevation or during climbs that are not assisted by wind. Physiological specializations have evolved at all steps in the $O_2$ cascade of bar-headed geese that help them accomplish this feat by improving $O_2$ transport in hypoxia. However, most of what is known about the physiology of bar-headed geese comes from comparing this species to lowland birds in a common environment at sea level. It is likely that the evolved specializations that have already been discovered do not entirely explain high-altitude flight. For example, we know much more about how bar-headed geese cope with hypoxia than how they deal with low barometric pressure, cold, and dry air at high altitudes. We also know relatively little about the influence of phenotypic plasticity (i.e., acclimatization) and developmental plasticity on the physiology of this species. We therefore have much yet to learn about the migration of this fascinating species, which will undoubtedly continue to shed light on nature's impressive solutions to oxygen deprivation. ■

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