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High-Altitude Avian Migration across the Himalayas: Challenges, Fly Strategy and Physiological Adaptation

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Abstract. Migrants that fly across the Himalayas, one of the highest geographical blocks in the world, must overcome severe challenges of the extreme high-altitude environment. Supported by evolved specifically adapted physiological performance, migrants such as geese, ducks, shorebirds, cranes, raptors, passerines, take diverse strategies, which is a balance of complex factors, as a result of evolution. This review draws an overall picture of high-altitude avian migration specifying findings in: fly strategies including routes, heights, stopovers, wind use patterns; physiological adaptions including special hypoxia tolerance of birds and unique adaptions of high-altitude migrators; evolution explanations; threats including impact caused by climate change on wetland and phenological mismatch; conservation. Enhanced unclarified questions on: avoid-barrier strategies; wind use patterns; predation pressure; phenomenon of lowland species flying at high altitudes; and most importantly, climate change and conservation. This study on avian high-altitude migration provides a relatively comprehensive summary of relevant findings, helps to understand the complex behaviors of migrants, and arranged various prospects for future studies.

Keywords: bird, high-altitude migration, Himalayas, physiology, conservation

1. Introduction

Migrants undertake their great journey every spring and autumn, traveling between certain breeding site and winter site, for suitable habitats with sufficient food and warm condition for better survival. Sometimes, geographical barriers block the way, and migrants have to fly to cross them, or fly around, to reach their destinations [1]. The Himalayas, one of the three highest regions in the world, blocks the Central Asian Flyway, spanning 2,400 km from east to west approximately, with an average elevation of 6,100 m, junctioning parts of China, Bhutan, Nepal, Indian and Pakistan [2, 3]. At a high altitude above sea level 2,000 m, partial pressure of oxygen (PO_2) drops 1% per 100 m, and halves at 5,000 m a.s.l. approximately [4]. Migrators crossing geographical barriers must survive several challenges in this harsh environment: extreme cold temperature; lack of O_2, and corresponding hypoxia response; water loss; low density of air, which leads to high metabolism requirements, compelling birds to flap harder, for staying lift and keeping body warm [5, 6].

Studies of many birds, mainly including geese, ducks, shorebirds, cranes, raptors, passerines, that migrate across the Himalayas will be discussed in this study: some studies on particularly species mainly covered fly strategy [3, 5, 7-12]. Some studies basically did records on species and discussed possible routes (without much detail on fly strategy and physiology) [3]. Besides, physiological adaptation is typically a research highlight [2-4, 6, 9, 13-17]. The best-known model species flying at high altitudes is Bar-headed Geese. Special physiological adaptions made their miraculous trans-Himalayas flight possible [1]. However, to date, no overall review had provided a comprehensive view of interacting factors on high-altitude migration (across the Himalayas).

In this review, high-altitude migration will be discussed in three parts: fly strategy, which includes fly routes, fly height, stopovers, wind usage, and other possible affecting factors; physiological adaption, which explains physiological changes caused by migration, avian tolerance to hypoxia environment, and special adaption of extreme high-altitude migrants; evolutionary explanations, which provides explanations in evolution, and some interesting exceptions. At last, the author will mention the alarming current climate change and its possible effects on including wetlands and phenological mismatch on high-altitude migrants, and give some advice on conservation. The author also proposes perspectives for future study throughout the article. This study would help with understanding and explaining complex behaviors of high-altitude fliers during migrations.

2. Fly strategy

2.1. Routes

Migration routes diversify in avian species, determined by overall energy and time dispensation, and the safety of the migration [1, 18]. Obligate migrators travel between particularly breeding and wintering sites year-round, with some species flying directly to their destination, while some take a winding route. For one species, different populations may choose different routes. Also, routes of many species vary by season [1]. For species that have to fly across one of the greatest geographical barriers – the Himalayas, migrators choose relatively lower routes. Many of them fly over the mountain regions directly, instead of taking a long journey around them [3, 5]. Researchers suppose this as a more cost-effective strategy, under a limit of time and energy costs [3].

Bar-headed Geese populations that migrate across the Himalayas and Qinghai-Tibet Plateau, travel between the Indian Subcontinent and Mongolia. Most ducks fly over the Himalayas to Central Asia and Siberia in spring, and back to the Indian Subcontinent in the autumn annually [3]. Demoiselle Cranes in East Asia take vastly different seasonal routes: they fly across the Himalayas in spring, and take a loop route from the north in autumn [7, 11]. Some Shorebirds fly directly over the Himalayas from their wintering site in Singapore, with some of them avoiding the Himalayas through valleys of Yunnan and Sichuan province, China, heading to breeding sites in the Qinghai-Tibet Plateau or North-Central Russia [8]. Although many passerines are resident altitudinal migrators, abounding species do migrate long distances, by taking an indirect route, or flying directly across the barriers using passageways. Many passerines visit the Tibetan-Himalayas region in the summer, and migrate to Indian lowlands in winter. Most raptors fly across the Himalayas, using valleys or rivers as short-distance passageways, while some avoid the barriers in autumn (Figure 1.) [3].

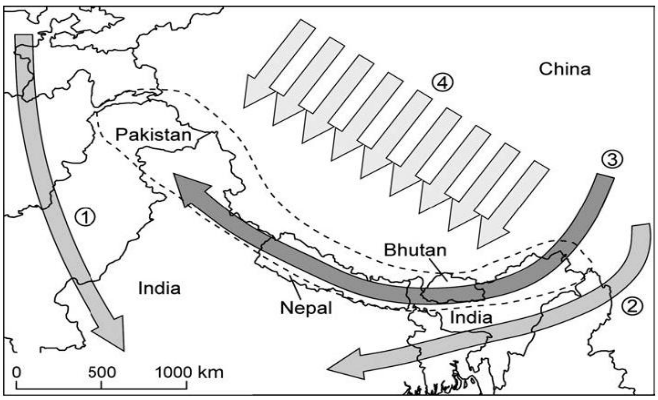

Figure 1. Autumn corridors of raptors migrate across and around the Himalayas: (1) Western Circum-Himalayan Corridor, (2) Eastern Circum-Himalayan Corridor (3) East-to-West Southern Corridor, (4) Broad-Frontal Trans-Himalayan Corridor [3].

2.2. Stopovers

Many wetlands, offer crucial stopovers for birds crossing the Himalayas, locating on either side of the Himalayas (with seasonal wetlands especially rich on the southern slopes), and along their routes, including numerous lakes, rivers, and adjacent marshes, mudflats, meadows [3]. Some migrants frequently rest at stopovers along migration routes, while long-distance non-stop migrants occasionally stop to rest and refuel, sometimes the stop is brief, and may be longer at other times [1]. Some shorebirds recorded in the study of Li David et al. (2020) do stop (over 3 days) and others seemed to fly directly to their destination. Migrants basically take preparation before crossing the barriers: Common Redshanks meanly spent about 13–32 days at 1–2 stopovers; Whimbrels spent about 14–31 days at 1–2 stopovers in spring, and they markedly spent more time at stopovers in winter migration [8]. Demoiselle cranes mainly stop on herbaceous land cover when they fly above the Qinghai-Tibet Plateau [7]. For Bar-headed Goose, duration at stopovers and the speed of migration varied by population. Fig. 2 shows the main stopovers of different populations. Populations that mentioned in "Routes" travel between western Mongolia and India take a 3,400–4,850 km route, they fly 62 days on average with 2–5 stopovers in spring migration, and 80 days on average with 2–7 stopovers in autumn migration, which suggest Bar-headed Geese relatively need to stop more [3].

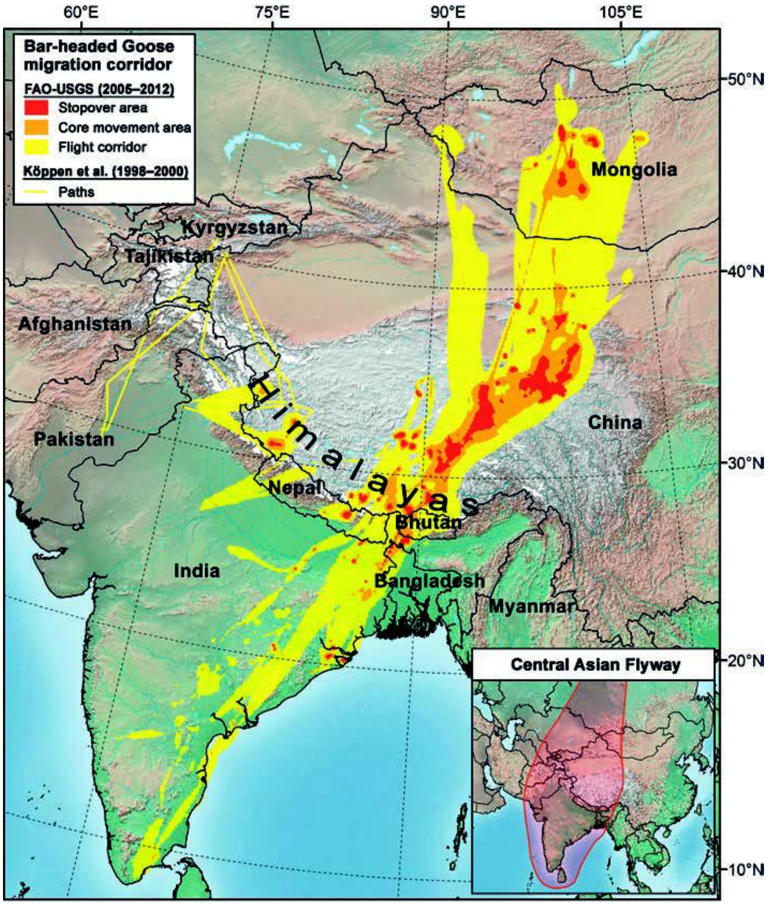

Figure 2. Central Asian flyway: fly extent, migration routes and related stopover areas for 44 satellite-marked Bar-headed Geese. Colors from darkest to lightest represent 50%, 75% and 99% cumulative probability contours from a dynamic Brownian Bridge movement model [3].

2.3. Height of flights

Birds that migrate across the Himalayas must face the challenge of flying over the averaged 6,000 m a.s.l. high barrier [3]. They tend to fly lower as possible, and usually cross the Himalayas by using some low passes (over 4,000 m a.s.l.): Sela Pass (4,225 m a.s.l.) and Nathu Pass (4,310 m a.s.l); the single lowest pass between central and central west Himalayas – Shiphi La (4,720 m a.s.l.) [8]. Most ducks tracked in the study of Tsewang Namgail et al. (2017) crossed the Himalayas by relatively low passes, such as Niti Pas-s (5,070 m a.s.l.) and Nathu Pass [3]. Ruddy shelducks takes a more circuitous route avoiding peaks, with a mean fly height of 4,755–6,800 m, but basically remain below 5,590 m [12]. Shorebirds such as Common Redshanks likely reach 4,800–5,800 m during their migrations, and Whimbrels have to fly at 5,500–6,000 m a.s.l to cross the barriers [8]. Most Bar-headed Geese fly at altitude about 5,000 m during the migration and basically remain below 6,000 m [5, 6]. Although they can fly even higher as one individual recorded reached altitude 7,290 m in autumn migration, they tend to remain as low as possible, and frequently give up the height they gained [5, 10]. This strategy is effective in reducing flying costs, benefiting from higher-density air at lower altitudes [5].

2.4. Use of wind

Migratory flights are accompanied by wind, of which migrants choose the appropriate departure time and flight altitude to make better use [18]. Migrants generally depart from staging and stopover sites on days with favorable winds [1]. An appropriate wind condition provides powerful support that makes the flight much easier: flight costs can be negligible while tailwind, while can also be easily doubled in headwind [18]. In spring, the prevailing southwesterly winds are beneficial for migrants heading north [3]. However, migrants do not always gain help from wind, that they usually have to compensate wind drift for displacements to reach certain distance. Demoiselle cranes had been observed flying with tailwinds in spring across the Himalayas, and headwinds in autumn migration heading south. In both seasons, they frequently fly through strong crosswinds, which means that they need to compensate for wind instead of being supported [7]. Ruddy shelducks were observed not gaining benefits from favorable wind conditions (with 20% of tailwinds and 25% of headwinds during flights) [12]. Whereas Bar-headed Geese also hardly glade, instead, they are typical flapping fliers [6]. Generally, wind speeds increase with altitude, which makes high-altitude migrations even more challenging [18].

On mountains, wind condition varies by many microscales weather patterns (small-scale local, isolated thermal events) and mesoscale weather patterns (groups of thermals and strong valley breezes) at different times of a day, as mountain wind flows down at night, and valley wind lifts up in the afternoons [3]. Soaring birds (vultures, eagles, large hawks, buzzards, storks, pelicans, etc.) are talented wind users, through climbing and gliding, using thermals rising along heated ridges, these birds could move hundred kilometers each day expending quite little energy under a favorable wind condition [1, 3]. Adversely to them, weather conditions across the Himalayas are often unfavorable for soaring [3].

Exceptionally, Bar-headed Geese do not select favorable weather conditions as other birds [10]. While climbing southern face of the Himalayas, they prefer less windy and cooler conditions with slight downdrafts overnight and early morning, instead of flying in the afternoons when upslope tailwinds take place [10, 13]. This habit can be explained by physiological adaptions that they are adapted to flapping flight and hardly glade, also by a requirements of avoiding predation during the day [13]. Advantages of migrating at night also include taking advantage of cooler, denser air with reduced turbulence, especially over mountains [3]. Whether this could explain conditions of other migrants is uncertain.

2.5. Other considerable factors

Migratory time and route are based on a comprehensive strategy of many interactive factors. What exactly caused the difference in migration route – flying over directly or avoiding the barriers – among species is not yet well explained, either. As Demoiselle cranes fly in a quite different loop route under headwind in autumn, for better foraging conditions along the inbound route should be one possible explanation [11]. The safety (predation pressure) may also be a considerable risk to migrants, as they usually migrate before raptors [1]. However, the degree of anti-predator behavior and how it reduces the risk is still unclear [3]. Moreover, physiological limitations are also considerable, because some birds are not able to fly such high as Bar-headed Geese to cross the barriers.

3. Physiological adaption

3.1. Preparation for migration

Birds prepare for migration forage 2 or 3 times more food than normal food intake, by increased stomach and intestine capacity, to store fat as primary energy for the extremely high energy requirement during migration (as flapping flight costs about 8 or 9 times more energy than resting metabolic) [1]. Lipid metabolism is used as main metabolism, which actually costs more O_2 than carbohydrate metabolism, and makes the metabolism more stressed [13]. They also enlarge the flight musculature, and shrink organs such as gut and liver that is unproductive during the flight the last days before migration, which helps to reduce the weight burden. Bar-headed Geese preparing for migration produce more hemoglobin, more red blood cells, and more myoglobin [1].

3.2. Avian tolerance to hypoxia

Birds are extraordinarily adapted to hypoxia environment. Early work suggested lowland house sparrows are able to act normally and fly for short periods at an altitude of 6,100 m in wind tunnel simulation, which also indicates that even resident lowland birds have physiological adaptations to hypoxia at high elevations [6, 19]. Birds are capable of presenting high ventilation rates under hypoxemia (i.e., low partial pressure of O2 in blood), and high tolerance to hypocapnia (i.e., low partial pressure of CO2 in blood), which they can keep lung and brain functioning while mammals may have to suffer from dysfunction of cerebral and lung under hypoxia [6]. Birds are unique in cardiorespiratory, respiratory and cardiovascular physiological performance.

Heart of birds is twice larger as that of mammals (in same body mass), with less frequent heart rates, and greater cardiac output, which increases sevenfold to eightfold during flight, and threefold or more during rest at hypoxia conditions. Lung of birds is two or three times larger in surface areas than mammals [3, 4], and is unique in structure, which helps them exchange gas more efficiently (comparison of avian lung and mammal lung described by cross-current model of gas exchange, see Scott et al., 2011) [13]. Avian lung is relatively inflexible, less ultra-structural stresses would take place as the volume only slightly changes when inspiration [3]. Blood-gas barrier in lung, which has large surface area and an extraordinarily thin and uniform structure, generates greater O_2 diffusion ability [13, 17]. Capillary density in cardiac muscle and brain is high in densities [4, 13]. And In the flight muscle of birds, capillaries tightly surround the fibers as a mesh, aerobic fibers are also smaller than mammals. These features of capillary density increase oxygen diffusion capacity in birds, trans more O_2 from blood to mitochondria in different tissues [13].

3.3. Unique physiological adaption of high-altitude migrators

Although birds are adapted to hypoxia environment, the challenging long flights at high altitudes require exceptional physiological adaptations, as discussed in "Introduction" [1]. Studies on some high-altitude adapted birds (including resident and migrant) certify their physiological adapting characteristics. Generally, their higher haemoglobin-O_2 affinity (than that of lowland populations) increases the saturation of haemoglobin, then brings greater pulmonary O_2 loading and O_2 delivery amount [6, 13, 20, 21]. Other high-altitude birds also harbor much more O_2 diffusing from blood to mitochondria in their flight muscle. A comparison of characteristics of normal birds and high fliers is shown in Fig. 3, which also illustrates a pathway of O_2 transportation: when breathing, although high fliers retain low oxygen gradients, O_2 flow rapidly along from air to mitochondria: beginning with ventilation, which provides air to gas exchange surface; followed by O_2 diffusing into blood; O_2 circulate with blood, diffuse to tissues; and finally, to mitochondria, ATP are produced [22].

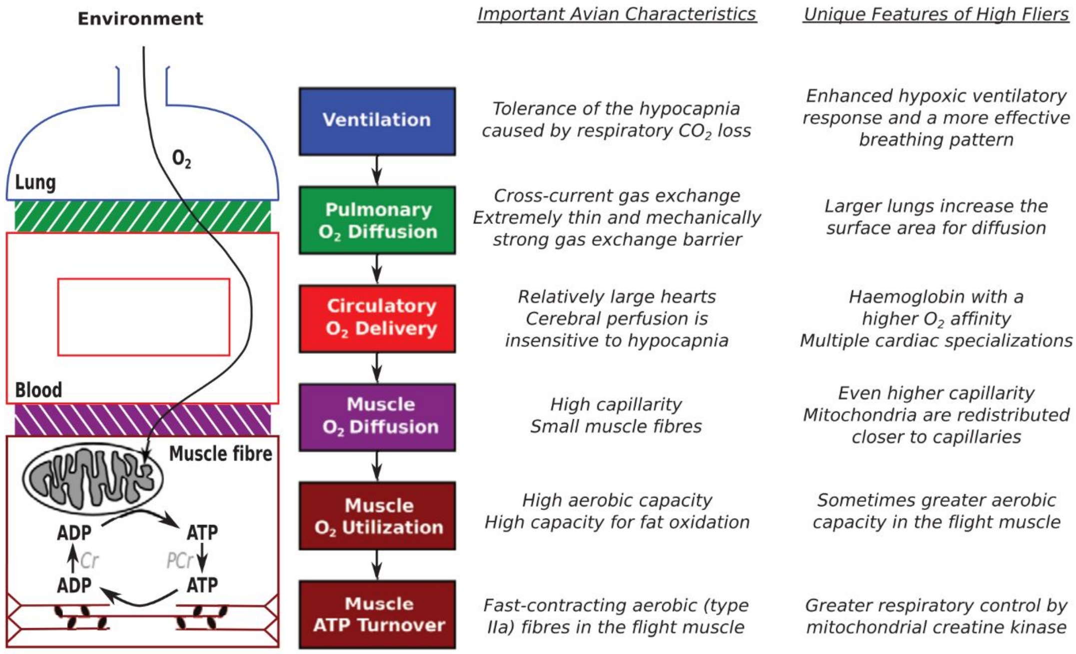

Figure 3. Several effective physiological pathways of transporting atmospheric O_2 from air to the tissue cell mitochondria (e.g., muscle fibers), illustrate striking properties in use of O_2 and turnover of ATP in flight muscle during hypoxia [13].

Bar-headed Geese are proven specifically adapted to high altitudes and have more significant physiological advantages than other birds including some high-altitude migrants [6, 13]. Compared with two lowland geese (Pink-footed Geese and Barnacle Geese), Bar-headed Geese have stronger hearts, with denser capillaries in left ventricle, which may help them to maintain heart function under hypoxaemia. And in reduced state of a special-form enzyme in heart – the cytochrome c oxidase (COX) – shows more affinity for cytochrome c, allowing geese to minimize oxidative damage [1, 13]. The strong cardiovascular allows bar-headed geese to fly above 5,000 m a.s.l. with a heart rate rising linearly with altitude to reach almost 400 beats per minute [5]. Larger lungs (25% larger than the other two geese) should enlarge the pulmonary gas-exchange surface and strengthen the diffusion capacity of O_2. With a more effective gas exchange respiratory, Bar-headed Geese have twice ventilation totally than that in lowland-geese Greylag Geese, and a deeper and less frequently breathing pattern than other lowland birds. Aforesaid lung and respiratory features maintain higher PO_2 in their arterial blood. In blood, their hemoglobin has higher O_2 affinity, and the binging of hemoglobin-O_2 has higher sensitivity to temperature [6, 14]. In the flight muscle, more capillary increases O_2 diffusion. Muscle has higher proportion of oxidative fibers, in which mitochondria distribute close to the cell membrane, which reduces O_2 diffusion distances in cell [6, 13]. In mitochondria, produce of ATP is stronger regulated by creatine kinase in Bar-headed Geese [13].

Remarkably, physiological adaptions vary in species and migratory patterns. In the Andes, another remarkable high-altitude region in the world, migrant Andean Geese and resident Crested Ducks substantially increase stroke volume and lung oxygen extraction, which helps to maintain oxygenation under hypoxia, in contrast to Bar-headed Geese, who superior on O_2 transportation, relying upon sturdy reinforcement of heart rate and ventilation [2, 15]. Another resident bird, Andean Coot, has more capillarities and smaller fibers in flight muscles, than that of lowland populations, which increases the O_2 diffuse ability [13]. High-altitude migrant Demoiselle crane have typically strong pectoral muscles, which is specialized for facilitating circulatory innervations, and enhancing blood flow [1]. Adaptation differences among species are still deficient in description and comparison. In addition, it is worth mentioning that, the phenotype may be presented differently among high-altitude elevational migrants, elevational niche-shift migrants, and high-altitude resident species, which is not clarified in this study ("resident" in this study only represents birds resident in particular regions, excluding elevational resident birds) [4, 16].

3.4. Evolutionary explanation

3.4.1. As a result of evolution. The uplift of the Himalayas was a result of the collision of the plate of Indian and Asia tectonic about 50 million years ago, enormously influenced the climate of Asia (e.g., helped formed Asian monsoon), and presumably created a significant geographical barrier to birds during the Oligocene–Early Miocene period (34–15 million years ago). In the past 2 million years, under the impact of fluvial erosion and glacial erosion (more recently), the Himalayas formed the diverse climatic, hydrological system, and the corresponding distinct vegetation, attracting a large number of migrants [3].

Migration is suggested as a result of enduring evolution, regulated by genetic mechanism, an adaption under the survival demand to changing environments for many millions of years, with individuals whose movements obtained better opportunities to survive natural selection [1]. In geological history, as the Himalayas was relatively low, Bar-headed Geese may have beguinn migrating between South and Central Asia from the Late Pliocene or Early Pleistocene (about 2.58 million years ago) [6, 23]. Hence, they may have slowly evolved their migration routes, and physiological adaption to high-altitude flight during this long period of time [6]. Among high-altitude species, some phenotypes emerged during the long-period evolution. High-altitude animals seem first evolved physiological adaptions that adjust the metabolic pathways, thenceforth evolved increment in tissue capillarity enhanced mitochondrial O_2 supply. Common strategies in response to the challenges of high altitudes are the work of beta oxidation, and changes in capacity of glycolysis and mitochondrial function. In the same region (the Andes), convergent evolution changes occurred in many metabolism pathways of high-altitude waterfowls [21].

3.4.2. Flights at High altitudes without Geographical Barriers. Strikingly, instead of taking an avoid-flying-high strategy, a few studies find that even lowland birds not facing geographical barriers and lacking a physiological evolution history fly at high altitudes for some time while migrating. Black-tailed Godwits did not undertake selection pressure as Bar-headed Geese, they spend entire life in lowlands, and have similar basal metabolic rates and pre-migratory haematocrit levels as other lowland species. However, they were observed flying at altitudes above 5,000 m during 21% of the migration [19]. Great snipe is another lowland shorebird species (spend most of their lifetime at altitudes below 1,500 m a.s.l.) who repeatedly reached altitudes above 6,000 m during migration. Their flying altitudes presented as a strong diel cycle: climbed up to extreme high altitudes in early morning, and descended again in late afternoon [24]. While migrating above lowlands, Great Reed Warbler regularly fly into daytime unlike most other songbirds (only fly at night during migration), and they were observed climbing at dawn from a mean of 2,394 m a.s.l. to extremely high altitudes (mean 5,367 and maximum 6,267 m a.s.l.) [25].

The reason why these birds fly so high without clear necessity is not yet clarified. This kind of phenomenon can be interpreted by requirements of avoiding the risk of overheating [19, 24, 25], keeping water balance, reducing predation risk, and for a better view of land [24, 25]. Wind support is also a considerable factor that affects fly height, but cannot explain why some birds regularly ascend [19, 24, 25]. Also, higher wingbeat frequencies and climbing flights during high-altitude migration increase water loss and other physiological pressures [19]. This seems a complex strategy, which still needs more explanations. Probably, high-altitude flights may be much more common than prospected in the past [19, 24].

4. The changing climate and conservation

4.1. Impact on migrants of climate change

4.1.1. Climate change and habitat. The IPCC (Intergovernmental Panel on Climate Change) alarmed that global warming will reach 1.5°C between 2030 and 2052, which will cause higher climate-related risks to natural and human systems the extent is depending on warming rate, geographic location, vulnerability, development level, and on the implementation of related mitigation options by policymakers [26]. High-altitude mountain regions are proven to be highly sensitive to climate change and human activities [3]. Under impact of global warming, Himalayan temperature increases 1.5–1.75 times that of global rate in the 21st century, with the precipitation increasing and becoming more variable and extreme [27]. Along the migration flyways, the Qinghai-Tibet Plateau (QTP), bordering on the westeast of the Himalayas, harbors wetlands comprising lakes, rivers, swamps, reservoirs, etc., with an estimated total area of 139,900 km2 which provides crucial habitat and stopovers for birds [28]. However, as a region with an average elevation above 4,000 meters, the average temperature in the QTP is estimated (predicted in 2020) to rise 1.6 °C–2.0 °C by 2050 remarkably [29].

Glaciers in the Himalayas and the QTP have been losing rapidly as a result of warming temperature [3]. This brings more snowmelt water and larger annual runoff in the river for now, but would cause a loss in long term, and further greatly affect the hydrological cycle [30]. The hydrological changes would affect wetlands – the critical stopovers for migrants along the flyway. In the Himalayas, wetlands distribute in the western and northwestern part (mainly at high elevations), and depend heavily on seasonal water storage from snow and ice, not heavily influenced by rainfall, while wetlands distribute in the central and eastern part (mainly at low elevations) depend mostly on seasonal monsoon rainfall [3]. Climate changes lead to earlier supply of snowmelt waters, which may reduce runoff during the summer season (wetland ecosystems are most active in summer), and bring more extreme weather (extreme rainfall and an increasing dry duration in the Indian monsoon domain) [3]. Some studies had discussed how climate change affects wetland ecosystem, however, how would the changes affect the resident organisms and obligate migrants, especially in the most vulnerable high-altitude regions, still lacks assessment.

4.1.2. Phenological mismatch. Warmer temperature frequently generates earlier arrival of migrants in both spring and autumn, although departure dates in autumn may also be influenced by some other factors such as age and success of breeding [31, 32]. The advance of migration contributes to more positive population trends, however, this kind of adaption vary among species, as some species do not advance their migration [32]. In spring, the phenological responses of the resource of food also vary, which may lead to a mismatch between arriving date of birds and peak supply of food resources. Changes at stopovers along the flyways may allow migrants to adjust their pace by available resources, however, resources may shift to a time before their arrival [31]. Since a noticeable shift in temperature that the QTP is having warmer winter, and the Mongolia is having warmer autumn and colder winter, it can be expected that Bar-headed Geese may also advance their departure time [33]. A mismatch between high may also exist among high altitudes and lowlands as temperature rise at a different speed. Broader perspectives on spatial, temporal or taxonomic scales, etc., are also essential for clarifying the impact of climate change on entire ecosystems [31].

4.2. Conservation

Human activity act as the most serious factor that greatly impacts bird populations, with direct impact including legal or illegal capture, and indirect impact on habitats including tourism, grazing, land utilization expansion (reclamation, development), pollution, global warming, etc [3]. Migrant populations are also threatened by disease, for example, the H5N1 global outbreak derived from QTP in 2005, as a consequence caused by social and environmental factors [34]. The immediate approach of protecting migrants is to protect the popular intersect stopovers (the wetlands) along flyways and their breeding and winter sites (as described in “Stopovers”). For conservation in China, an analysis in 2015 of protected areas showed the decline of waterbirds in conservation zones, with a more severe loss in provincial status zones than at of national level, indicating that besides creating more conservation zone, the corresponding fund support and management need to be improved. Related conservation policies and evaluating frameworks are also essential. It is also important to hold periodic bird surveys to investigate the population dynamics [35]. Enhance popularization and education of natural conservation and mobilize the public to take part in conservation activities. As the Himalayan region locates at junctions of national boundaries (as narrated in “Introduction”), it is also important to facilitate international cooperation.

5. Conclusion

Special physiological adaptation against hypoxia as a result of long-term evolution made the incredible avian migration possible, crossing the highest geographical barriers, and overcoming severe challenges of the extreme high-altitude environment. Migrants take quite diverse strategies along their journey, with different routes, fly heights, wind use patterns, and refuel frequency balancing time, safety and physiological utmost. Unique adaptions make birds adapted to hypoxia while flyi¬ng at high altitudes, which is more typical in extreme high-altitude fliers as Bar-headed Geese, and varies among species. Alarming climate change may cause effects on these wildlife, by affecting hydrological system changing wetland ecosystem, and causing phenological mismatch.

Future studies should further evaluate the impact of climate change and foster conservation. Some other questions are left for further discussion. The exact role of wind use pattern in avian migration seems conflictive, and lacks data support. Strategy of whether to fly over or avoid the barriers had not been well explained. How migrants respond to predation pressure needs more explanations. The physiological studies can move on to contrast different adaptions among species. Remarkably, as many lowland species migrate at high altitudes, whether more migrants have potential ability to fly high, and the mechanism hiding behind needs further attention. This study overall interpreted the avian migratory flight across the Himalayas, discussed the challenges, fly strategies, physiological adaptations and evolutionary explanations, provided references for conservation, and perspectives for future study.

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