The physiology and biomechanics of avian flight at high altitude

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Synopsis Many birds fly at high altitude, either during long-distance flights or by virtue of residence in high-elevation habitats. Among the many environmental features that vary systematically with altitude, five have significant consequences for avian flight performance: ambient wind speeds, air temperature, humidity, oxygen availability, and air density. During migratory flights, birds select flight altitudes that minimize energy expenditure via selection of advantageous tail- and cross-winds. Oxygen partial pressure decreases substantially to as little as 26% of sea-level values for the highest altitudes at which birds migrate, whereas many taxa reside above 3000 meters in hypoxic air. Birds exhibit numerous adaptations in pulmonary, cardiovascular, and muscular systems to alleviate such hypoxia. The systematic decrease in air density with altitude can lead to a benefit for forward flight through reduced drag but imposes an increased aerodynamic demand for hovering by degrading lift production and simultaneously elevating the induced power requirements of flight. This effect has been well-studied in the hovering flight of hummingbirds, which occur throughout high-elevation habitats in the western hemisphere. Phylogenetically controlled studies have shown that hummingbirds compensate morphologically for such hypodense air through relative increases in wing size, and kinematically via increased stroke amplitude during the wingbeat. Such compensatory mechanisms result in fairly constant power requirements for hovering at different elevations, but decrease the margin of excess power available for other flight behaviors.

Environmental effects of high altitude on flight

Even casual human visitors to montane habitats are aware of a substantially different physical environment relative to lowland conditions. Lower temperatures, increased winds, and reduced oxygen availability are perhaps the most obvious features of high mountains. Secondarily evident to bipedal mammals might be such features as the low humidity and a reduced air density. For volant animals such as birds, however, all such physical factors may substantially influence the biomechanics and physiology of flight. Research on avian flight has, for anthropogenic reasons deriving from contemporary altitudinal distribution of modern humans (Cohen and Small, 1998), typically been conducted at or near sea-level conditions. Nonetheless, many bird taxa are high-elevation specialists, and a large number of migrants fly at substantial altitude. Here we review existing data on the physiology and biomechanics of flight at high elevations, and demonstrate with ongoing research on montane hummingbirds the advantage of an integrative perspective to studying patterns of adaptation to such physically variable and often demanding conditions.

From a metabolic perspective, primary among the physical changes occurring across elevational gradients is the systematic change in oxygen partial pressure. This reduction in oxygen is, to some extent, offset by an increase in the gaseous diffusion coefficient, which varies in inverse proportion to total pressure (Reid *et al.*, 1987). The diffusion constant is, however, also proportional to gas temperature to the power 1.5, and the lower air temperatures of higher altitudes (see below) will also somewhat diminish diffusive oxygen flux. The high aerobic demands of flight thus lie at odds with reduced oxygen availability at high altitude. Associated responses of the avian respiratory system during flight in hypobaric hypoxia represent an important arena for understanding the limits to aerobic capacity of the vertebrate respiratory system, albeit one substantially understudied relative to flight in normobaria.

Several additional factors that influence avian physiology also change systematically with elevation,

such as solar radiation, air temperature, and absolute humidity, the last deriving directly from reduced ambient temperatures. The environmental lapse rate in air temperature through adiabatic cooling and increase in water content is about $0.65°C/100$ m, and remains linearly so within the troposphere, so that an approximately $26°C$ difference characterizes air at 4000 m relative to that at sea level. Reduced temperatures at high elevations may be important for resident species, particularly when they are not active and generating substantial metabolic heat. Two of the most general ecological principles known as Bergmann's and Allen's rules would predict that, at high elevations, body size would be greater and limb lengths would be smaller, respectively. However, changes in body and wing size will also influence the power requirements for flight, and several conflicting demands should be considered for volant organisms.

For migrating birds, one general suggestion in the avian flight literature is that water loss is reduced at higher elevations because of the large altitudinal temperature gradient (e.g., Torre-Bueno, 1978). However, responses to either alpine or high-elevation thermal regimes may be complex. Desiccation may result from the reduced water content of air at high elevation, an effect that is well-known to mountaineers particularly when ventilation rates increase with exertion. Heat loss via convection will decrease in hypobaria, in approximate proportion to air density raised to the power $-1/3$. Increased metabolic power required by lower air densities (see below) yields increased heat production, and the reduced thickness of the atmosphere typically yields increased solar radiation, although variable cloud cover also pertains. Overall, the net outcome of such varied thermal effects is impossible to predict without quantitative knowledge of the energy balance during flight.

As with oxygen partial pressure, air density systematically declines with elevation in proportion to the concomitant change in total pressure. Sea-level density of air at $20°C$ is about 1.21 kg/m³, decreasing to 0.95 kg/m³ at 2000 m elevation and 0.74 kg/m³ at 4000 m, the latter being a 40% reduction relative to the sea-level value. By contrast, temperature-dependent variation in air density and viscosity is small, as is that associated with changes in relative humidity (see Denny, 1993). Because aerodynamic forces typically vary in linear proportion to air density, morphological and kinematic compensation is necessary to effect flight at different elevations. Behavioral changes in wing and body kinematics must characterize individual birds transiting across elevations, whereas species-level adaptation to residence at different elevations likely involves concerted changes both in wing morphology

and in wingbeat kinematics. Changes in air density also alter the mechanical power requirements of flight. In particular, the cost of supporting body weight (i.e., the induced power requirements) increase at lower air density, whereas profile drag (on the wings) and parasite drag (on the body), together with their associated power expenditures, will concomitantly decrease (Pennycuick, 1975; Norberg, 1990; Rayner, 1990).

A second feature of aerodynamic significance is the general trend of increasing ambient wind speed with altitude. For resident taxa, high wind speeds may influence numerous behaviors including foraging, sexual displays, nest defense and roosting (Fisher et al., 2004). Migrating birds, on the other hand, may be alternatively impeded or aided by higher wind speeds if the wind direction is against or in the direction of desired forward progress, respectively (Green et al., 2004). The overall aerodynamic consequences of flight at high elevation are therefore context-specific and likely depend on both taxon and the particular flight behavior in question. In this review, we examine the evidence for altitudinal effects on three aspects of avian physiology (respiration, temperature regulation, and water balance) and two aspects of avian flight performance (forward flight and hovering).

Respiratory physiology

Birds exhibit numerous adaptations for enhanced oxygen delivery from the pulmonary system to the circulatory system to the muscle fibers, and are highly tolerant of hypoxia at levels that are deleterious to most mammals. The anatomical and physiological features of avian respiratory pathways have been reviewed extensively, with several authors focusing on specific adaptations for high-elevation residence and performance (Fedde, 1990; Faraci, 1991; Maina, 2000). In this section, we briefly highlight the most general features of avian respiratory physiology in rarefied air, giving specific attention to our own work on hummingbird flight performance.

Gas exchange between the avian pulmonary and circulatory systems is particularly efficient due to a suite of anatomical adaptations distinguishing avian gas exchange from mammalian counterparts. Of particular importance is the convoluted and tubular arrangement of the gas exchange components that are very unlike the spherical alveoli of mammals, together with the high oxygen affinity of avian hemoglobin. Combined with other anatomical features of the pulmonary and circulatory systems, avian gas exchange is ultimately enhanced by large lung-to-blood volume ratios, multiple exchanges per inspiration, high gas exchange surface area, and maximal thinning of the air/blood

tissue barrier (Dubach, 1981). The net result of these adaptations is that blood leaving the lung interface can have the same oxygen partial pressure as inspired air, indicating that oxygen delivery in birds is not limited by the pulmonary system (Fedde, 1990). During deep hypoxia, however, respiration is ultimately limited by blood perfusion (Fedde *et al.*, 1989; Shams and Scheid, 1989).

Avian taxa inhabiting high elevations demonstrate further anatomical and physiological adaptations for oxygen delivery, of which some components can arise through acclimation or conditioning whereas others are constrained phylogenetically. As an anatomical example, adaptive changes in muscle ultrastructure have been demonstrated both within and among species and across elevations. Specifically, muscle capillary-per-fiber number is higher for birds at high elevations in both highly aerobic pectoral muscles and less aerobic leg muscles (Hepple *et al.*, 1998; Mathieu-Costello *et al.*, 1998). With respect to physiology, oxygen affinities of avian hemoglobins change in response to experimentally-controlled barometric pressure (Tucker, 1968*b*), but high-elevation taxa such as the bar-headed goose possess hemoglobin with higher baseline affinity for oxygen (Black and Tenney, 1980). These geese also increase oxygen flux to mitochondria as a result of physical conditioning (Saunders and Fedde, 1991).

In contrast with many mammals, birds subjected experimentally to low barometric pressures do not exhibit some of the most maladaptive responses. One pertinent example concerns the impaired cognitive functioning experienced by mountain climbers when exposed to low oxygen partial pressures. The ensuing hyperventilation lowers the partial pressures of arterial carbon dioxide. Whereas this condition leads to arterial constriction and decreased blood flow in many mammals, arterial hypocapnia does not result in vasoconstriction in birds (Faraci, 1991), and both low- and high-elevation taxa exhibit normally cognitive function at elevations well above terrestrial habitation (Black and Tenney, 1980). Similarly in response to hypobaria, birds increase overall rates of oxygen consumption and respiratory rates, whereas these parameters decrease for mice (Tucker, 1968*b*). In summary, the oxygen delivery systems of birds function well across a broad range of oxygen partial pressures and exhibits considerable adaptive plasticity when rapidly exposed to deep hypoxia (Shams and Scheid, 1993). We hypothesize that the ultimate explanation for such respiratory flexibility is associated with evolutionary exposure to varying oxygen partial pressures over geological time (Graham *et al.*, 1995). Because flight is one of the most metabolically-demanding forms of locomotion, birds may be preadapted for performance in deep hypoxia.

Hummingbird flight requires the highest mass-specific oxygen consumption of any vertebrate locomotor mode (Suarez, 1992), but these birds nevertheless inhabit high elevations throughout the New World (Schuchmann, 1999), with some taxa residing up to 5000 m (Carpenter, 1976; Rahbek and Graves, 2000). This observation presents an intriguing problem of how such a metabolically-demanding form of locomotion can thrive in a metabolically-challenging environment. Because it is possible to experimentally decouple air density and oxygen partial pressure in laboratory contexts (Dudley and Chai, 1996), we can examine the physiological and aerodynamic consequences of high-altitude flight both separately and in concert. Under laboratory conditions, rates of oxygen consumption by hovering hummingbirds increases under reduced total pressure (Berger, 1974*a*,*b*) and under hypodense but normoxic conditions (Chai and Dudley, 1995). Oxygen availability may also limit metabolic capacity in hovering flight. Chai and Dudley (1996) replaced normal air with pure helium, thus reducing air density as well as the partial pressure of oxygen. Hummingbirds failed in hovering flight at air densities well above those characteristic of failure in normoxic hypobaria, clearly illustrating a constraint of oxygen delivery. Altshuler and Dudley (2003) replaced normal air with pure nitrogen in similar hovering experiments, thereby reducing partial pressure of oxygen but maintaining near-constant air density. Hummingbirds also failed at a lower oxygen-equivalent rather than density-equivalent elevation. Providing supplemental oxygen does not increase aerodynamic performance in hypodense gas (Chai *et al.*, 1996), but does allow for longer hovering durations when challenged aerodynamically (Altshuler *et al.*, 2001). However, it is important to note that in all hypoxic and hypodense air experiments to date, hummingbirds failed to hover at equivalent elevations over 5000 m (Table 1), which is a distributional limit most likely determined by ecological rather than physiological features.

Thermoregulation and water balance

During prolonged migratory flights, birds face other physiological challenges, and in this section we discuss associated mechanisms that regulate body temperature and minimize water loss across altitudes. For birds, theses processes have been studied with theoretical models, in wind tunnels, and in a limited number of field studies, and it has been generally suggested that altitude selection may aid in thermoregulation and

Table 1 Oxygen- or density-equivalent elevations at which hummingbirds failed to perform sustained hovering during density- and oxygen-reduction trials*

Hummingbird Species/Gender	Normoxic heliox	Nitrogen
Archilochus colubris ♀	6700	
A. colubris ♂	6700	
Selasphorus platycercus ♂	8800	7900
S. rufus ♀	7000	6300
S. rufus ♂	6400	6300

*Replacing normal air with normoxic heliox systematically lowered air density while keeping oxygen concentrations constant. Infusion of nitrogen systematically lowered oxygen concentration while keeping air density close to constant. Experiments with *Archilochus colubris* were performed by Chai and Dudley (1995) and experiments with *Selasphorus platycercus* and *S. rufus* were performed by Altshuler and Dudley (2003).

water balance. However, some authors have suggested that water loss is minimized at lower elevations where relative humidity is higher (*e.g.*, Carmi *et al.*, 1992), whereas others claim that water loss is minimized at high elevations where ambient temperatures are lower (*e.g.*, Torre-Bueno, 1978). These differences illustrate two particularly important pathways for water loss: respiration and evaporative cooling. Of lesser importance is excretory water loss, which represents approximately 10% of total loss and, more importantly, is less dependent on both ambient temperature and humidity (Giladi and Pinshow, 1999). Considering the more important avenues of respiratory and evaporative water loss, these processes are affected differently by changes in altitude.

Water loss via respiration increases with altitude due to systematic decrease in relative humidity. As air is inspired, it becomes saturated with water and although some of this water will be reabsorbed prior to exhalation, the expired air still contains more moisture than ambient air, resulting in a net loss. In a computer-simulation model, Carmi *et al.* (1992) concluded that respiratory dehydration would ultimately limit flight duration and distance, particularly in birds with sufficient fat stores to energetically fuel their flight. Consequently, they predicted that birds should fly at low elevations in more humid air to increase flight distance. Although many birds fly at low elevations, there have not yet been convincing field studies that demonstrate selection of low altitudes to minimize respiratory water loss (see Klaassen, 2004).

When heat-stressed, evaporative cooling is one mechanism by which birds can regulate temperature, albeit one leading to rapid dehydration (*e.g.*, Giladi and

Pinshow, 1999). During active flight, considerable metabolic heat is generated, although much of this may actually enhance muscle contractile activity (Torre-Bueno, 1976). Across a broad range of temperatures, it has been demonstrated in both wind tunnel and free-flight studies that birds can regulate body temperature (Torre-Bueno, 1976; Adams *et al.*, 1999), and that evaporative cooling may be the major pathway for heat dissipation. In wind tunnel studies, budgerigars (Tucker, 1968*a*) and starlings (Torre-Bueno, 1978) exhibited higher rates of evaporative water loss as air temperature increased. Birds are most likely to suffer from overheating in direct sunlight and at low elevations, but several behavioral options are available to mitigate thermal load. Actively flying migrants exhibit a greater tendency to fly at night than passive gliders (Kerlinger and Moore, 1989), and desert migrants will seek shade during the middle of the day to keep temperatures low. It has also been predicted that birds will fly at higher altitudes to keep cool (Torre-Bueno, 1978).

Despite such constraints on thermoregulation and water balance, there are few data supporting hypotheses that these physiological processes are regulated through altitude selection. Instead, benefits derived from wind assistance are likely to motivate migrants to a greater extent (Liechti *et al.*, 2000), although this depends on the importance attributed to maintaining water balance (Klaassen and Biebach, 2000). Currently, there is equivocal evidence that birds actually dehydrate during migratory flights. Most laboratory studies have described considerable water loss during flight, and many reports of incoming migrants suggest they are dehydrated (*e.g.*, Odum *et al.*, 1964). However, other records from incoming migrants at stopover sites suggest these birds have surprisingly high body water content. In the most controlled study, Landys *et al.* (2000) captured incoming godwits after a three-day migration. Comparing incoming migrants to birds that had already refueled revealed no difference in water content as a percentage of body weight. However, Klaassen (2004) has pointed out that body water content can remain constant even as both birds and mammals undergo critical water stress, and thus may be a poor predictor of dehydration state.

The strongest evidence for altitude selection in water balance comes not from migrating birds, but from the nocturnal flights of otherwise diurnally active swifts, sometimes called "roosting flights". During these flights, swifts can reach altitudes as high as 3000 m, even thought the birds are not flying to gain any ground distance, and even orient into headwinds to prevent displacement. Instead, flight altitudes are selected according to temperature, with swifts flying

at higher altitudes on warmer nights (Backman and Alerstam, 2001). In summary, several lines of evidence do suggest that environmental changes with altitude can influence temperature regulation and water balance, but logistical constraints have prevented coherent tests of these effects in all but a few cases.

Forward flight

Aerodynamic performance during forward flight at high altitude can be influenced substantially by low barometric pressure and varying wind speeds. For logistical reasons, studies of forward flight in hypobaria are limited, but reductions in pressure should substantially decrease drag forces. Specifically, aerodynamic models predict an increase in cruising flight speed with altitude at the approximate rate of 5% per 1000 m, primarily because of the reduction in wing and body drag, and because of the relatively small magnitude of induced power in forward flight relative to other components of energetic expenditure (Pennycuick, 1978; Hedenström, 2003). Migrating birds commonly encounter wind speeds ranging from 50–100% of their normal airspeed, and winds are highly variable in time and altitude. Theoretical analysis also predicts that by accounting for wind conditions, birds could double their ground speed and accordingly save as much as half of the energy required for migratory flights (Liechti and Bruderer, 1998). Given the difficulty of determining the actual airspeeds of free-flying birds, as distinct from groundspeed, direct tests of both hypotheses have only recently become possible through use of multiple technologies.

Radar tracking has proven particularly useful for recording flight speeds, and has been recently used to test the prediction that lower air density at high altitude is advantageous during forward flight. Hedenström et al. (2002) tracked the flight speeds of migrating birds at multiple sites along the Northwest Passage in the Canadian Arctic, which flew up to 4,000 meters above sea level. Along this altitudinal cline, flight speed increased by the predicted amount after accounting for the effects of wind speed and direction.

Several lines of evidence now strongly suggest that birds can also minimize aerodynamic costs of flight through wind assistance. One indirect example comes from Western Sandpipers (Calidris mauri) during their spring migration along the Pacific coast of North America to their breeding grounds in Siberia and Alaska (Iverson et al., 1996). By compiling several sources of data, Butler et al. (1997) calculated that the large body masses measured at stopover sites were only possible by accounting for wind-assisted flight. Departure flights from stopover sites have also been

studied in several taxa. In some cases, departure probabilities are strongly correlated with the presence of favorable tailwinds (e.g., Åkesson and Hedenström, 2000; Klaassen et al., 2004), whereas other taxa only depart when winds are absent or weak regardless of wind direction (e.g., Schaub et al., 2004).

As a general trend, wind speed increases with altitude up through the highest elevations where birds have been recorded. This relationship is, however, composed of several interrelated components. The planetary boundary layer extends up for approximately 1–2 kilometers above the earth's surface and within this region, wind speeds increase up to free stream velocities with increasing altitude. Global wind speeds are correlated with differences in air temperature across altitudes, and are thus influenced by latitude as well as the time of the year (Stull, 2000).

Most studies of migrating birds report flights at altitudes within the planetary boundary layer (e.g., Cooper and Ritchie, 1995; Klaassen and Biebach, 2000; Klaassen et al., 2004), and estimates of mechanical power performance suggest that ascending to high altitudes can be prohibitively expensive without wind assistance (Pennycuick et al., 1996). However, high-altitude flights have occasionally been documented through chance observations by mountaineers and pilots (Stewart, 1978), as well as from airplane collisions (Manville, 1963; Laybourne, 1974). More recently, flight elevations have been tracked through onboard altimeters (Weimerskirch et al., 2003) and radar (Bruderer et al., 1995; Klaassen and Biebach, 2000).

Bruno Bruderer, Felix Liechti, and their colleagues have studied migratory flights over the Negev desert in southern Israel, simultaneously recording the altitude and wingbeat frequency of individual birds as well as the altitudinal profile of wind speed using radar measurements. They also obtained altitudinal profiles of barometric pressure, temperature, and relative humidity. Of all meteorological variables, Bruderer et al. (1995) found that only tailwind velocity was significantly correlated with the altitude of migratory flights. Furthermore, some migrants would ascend up to 9000 m to encounter air jets in which they could fly with groundspeeds greater than 45 meters/second (Liechti and Schaller, 1999).

Logistical considerations have precluded systematic use of hypobaric wind tunnels, although Tucker (1968b) studied forward flight behavior in budgerigars up to pressures equivalent to an altitude of 6100 m. Endurance in the wind tunnel decreased substantially with decreasing pressure, although one bird provided with supplemental oxygen apparently flew better than the birds breathing rarefied air (Tucker, 1968b). To our

knowledge, no one else has used a hypobaric wind tunnel to study forward flight in birds, although this would represent another compelling test of Pennycuick's (1978) hypothesis. Also unstudied are the effects of hypobaria on more diverse features of the avian flight envelope, including takeoff performance and maneuverability. Given their small size and logistical tractability for laboratory manipulations, hummingbirds would seem ideally suited for such studies. The systematic decline in hummingbird power reserves with elevation (Altshuler *et al.*, 2004*b*, see below) suggests that the physically imposed consequences of high-elevation residence impinge on a diversity of flight behaviors.

Hovering flight

The systematic decline in air density with increased elevation must adversely affect the aerodynamics of hovering flight. Lower air density yields reduced forces on wings if kinematics are unchanged, and the concomitant reduction in the Reynolds number of the wings may also reduce their effective lift:drag ratio (Ellington, 1984*a*; Vogel, 1988; Dudley, 2000). The precise magnitude of this effect, however, will vary with the particular aerodynamic mechanisms and wing morphologies under consideration (see Usherwood and Ellington, 2002; Altshuler *et al.*, 2004*a*). Also at high altitude, energetic costs may increase substantially depending on the relative magnitude of the induced and profile power components of total mechanical power expenditure (Ellington, 1984*a*; Norberg, 1990). Morphological, behavioral, and physiological adaptations to altitude must correspondingly pertain. One immediate biomechanical prediction is that relative wing size will increase at higher altitudes to offset the increased induced power requirements associated with lower air densities (Ellington, 1984*b*). Intra- and interspecific comparisons of bird taxa suggest relatively larger wings at higher altitudes (*e.g.*, Traylor, 1950; Hamilton, 1961; Mayr, 1963), an effect systematically demonstrated among hummingbird species (Feinsinger *et al.*, 1979; Altshuler and Dudley, 2002). Behavioral means of compensation to the adverse energetics of high-altitude flight are also possible. High-altitude hummingbirds, for example, often perch while feeding, whereas their lowland counterparts almost never do so.

Physical constraints imposed by low-density high-elevation air are most evident aerodynamically during hovering flight, during which lift and power requirements of the flight motor are extreme (Ellington, 1984*a*). Studies of flight aerodynamics in hypodense air have been, with the exception of the

aforementioned work by Tucker (1968*b*), limited to hovering hummingbirds. Hummingbirds (family Trochilidae) represent an ideal taxon with which to evaluate such questions of physiological and biomechanical adaptation to high elevation. Trochilid species diversity, with over 320 taxa, is greatest over the altitudinal range of 1500–2500 m (see Schuchmann, 1999; Dudley, 2001). Some of the larger species are, somewhat paradoxically, most common at high altitudes, exacerbating the demands of hovering flight. For example, the 20–26 g Giant Hummingbird (*Patagona gigas*) is resident at elevations up to 4000 m (Ortiz-Crespo, 1974), and is an ideal candidate for focal studies of flight biomechanics and physiology. Body size systematically increases among hummingbird species at higher elevations (Altshuler *et al.*, 2004*b*; Fig. 1), and the adverse effects of air density on lift and power production will be systematically more pronounced at greater body mass (see Norberg, 1995). By contrast, the relative mechanical and metabolic capacities of flying animals tend to decline with increasing size (Norberg, 1990; Bishop, 1997, 1999; Dudley, 2000). Large hummingbirds hovering at high elevations thus represent a fascinating target for biomechanical
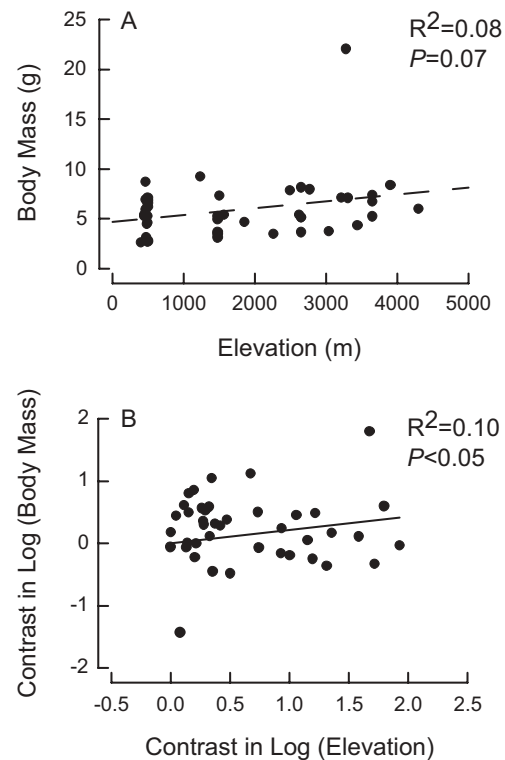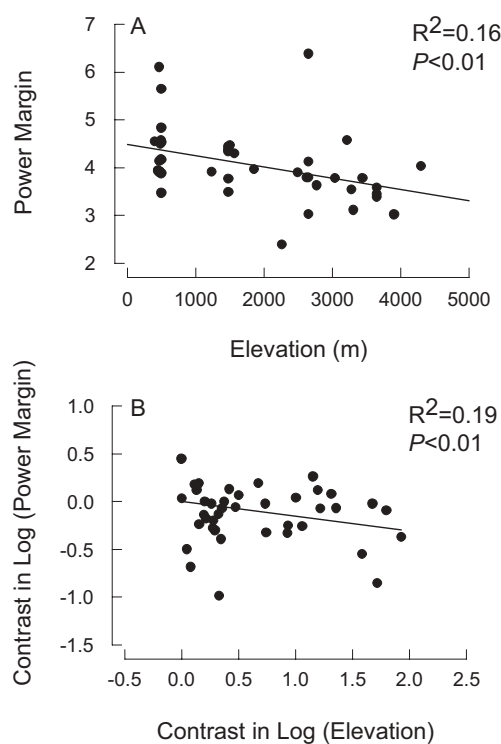

Fig. 1 Hummingbird body mass increases with elevation. Raw species data are presented in panel A and phylogenetically-controlled independent contrasts are presented in panel B. Data points represent species means (or their contrasts) and the statistics for regression equations are given in the figure.

and physiological investigation of the limits to flight performance.

Kinematic and aerodynamic mechanisms of compensation for hypodense air have been studied under both laboratory and field conditions. Berger (1974a) experimentally imposed hypobaria on two species of montane hummingbirds, and elicited systematic increases in stroke amplitude and wing angle of attack, the latter parameter being estimated from horizontal projections of the wing chord. Manipulations of hovering flight in hummingbirds using hypodense helium mixtures under both normoxic and hypoxic conditions (Chai and Dudley, 1995, 1996; Altshuler and Dudley, 2003) similarly revealed that low-density air elicits a systematic increase in stroke amplitude but essentially unchanged wingbeat frequencies. A similar response is seen for hovering in hyperoxic but hypodense gas mixtures (Chai et al., 1996; Altshuler et al., 2001). Under field conditions, we made comparable measurements for 43 hummingbird species across a 4000 m gradient in Peru (Altshuler and Dudley, 2003; Altshuler et al., 2004b). Stroke amplitude during hovering exhibited a systematic increase among species at higher elevations, indicating that kinematic responses by individual birds to hypodense air are mirrored on evolutionary timescales among species. Wingbeat frequency, by contrast, declined as predicted on allometric grounds with body mass but was uncorrelated with elevation. Overall, such a systematic increase in stroke amplitude at constant wingbeat frequency increase relative wing speed to overcome otherwise declining lift production, and simultaneously mitigate the enhanced induced power expenditure associated with hypodense air (see Ellington, 1984b). With the notable exception of Berger (1974a), effects of hypobaria on more detailed wingbeat kinematics such as angle of attack and rotational velocities at the ends of half-strokes are unstudied. Wingbeat kinematics of the Giant Andean Hummingbird are noticeably different at half-stroke transitions relative to those of other hummingbirds (M.-J. Fernandez, pers. comm.), and deserve further study.

The interspecific increase in stroke amplitude of hovering hummingbirds at higher elevations, when coupled with the geometrical constraint on wing motions to amplitudes of approximately 180° on either side of the body (Chai and Dudley, 1995), has important implications for aerodynamic and energetic reserves during flight. Altshuler et al. (2004b) compared normal hovering to maximum load-lifting performance across elevations for the aforementioned set of Peruvian hummingbirds. Among species, the mass-specific aerodynamic power requirements for hovering flight are approximately constant with respect

to altitude, because of systematic interspecific increases in relative wing size and in stroke amplitude at higher elevations. High-elevation hummingbirds are thus not limited in their capacity for normal hovering flight despite the challenges imposed by hypobaric environments. However, load-lifting elicits maximum stroke amplitudes in all taxa, and given that higher-elevation hummingbirds already hover with increased stroke amplitudes, they correspondingly possess less reserve capacity in wing motions and related power production supplemental to that required for normal hovering. The power reserve thus systematically declines at higher elevation (Fig. 2), possibly compromising performance in varied contexts of both natural and sexual selection. A range of compensatory morphological, physiological, and biomechanical adaptations may have permitted larger hummingbirds to progressively colonize higher elevations in South America, but this outcome has not been entirely without cost. Such diminished reserves should also be evident in individual birds that migrate seasonally to higher elevations.

Fig. 2 Hummingbird power margin decreases with elevation. Power margins are calculated as the maximum aerodynamic power that can be produced during load-lifting divided by the minimum aerodynamic power requirements for hovering. Raw species data are presented in panel A and phylogenetically-controlled independent contrasts are presented in panel B. Data points represent species means (or their contrasts) and the statistics for regression equations are given in the figure.

Conclusions

Reductions in oxygen partial pressure, air density, and air temperature all potentially exert major influences on avian flight physiology. Birds in turn can respond on behavioral, ecological, and evolutionary timescales. Respiratory physiology has been the best studied type of such responses, and diverse adaptations are evident in the design of respiratory systems, oxygen-blood transport, and overall hypoxia resistance. Altitudinal gradients in ambient winds are often used by avian migrants to enhance groundspeeds and overall energetic efficiency of migration. Low-density air at high altitudes will affect forward flight and hovering differently. For the former, hypodense air reduces drag forces on the wings and body, which can result in faster flight speeds. During hovering, drag forces on the body are, by definition, nonexistent and induced power requirements to offset gravity are a dominant avenue of energy expenditure. Accordingly, reduced air density at high elevation imposes aerodynamic and energetic costs on hovering, but a number of compensatory responses in flight-related morphology and biomechanics have now been demonstrated among different hummingbird species across elevational gradients. Additional features of flight performance such as maneuverability and forward flight, however, require further study under hypobaric conditions.

Biotic factors also vary with elevation, although their influence on flight performance has received less attention than physical factors. Clearly, ecosystem composition, predators, nutritional resources, and vegetational structure all change dramatically across elevational gradients. These effects are likely to be of secondary importance for long-distance avian migrants, but must impinge substantially on the flight biology of high-altitude residents as well as of altitudinal migrants. For example, sucrose concentrations of hummingbird-pollinated flowers decreases across elevations for sites in the southwestern USA (Pyke and Waser, 1981; Cruden *et al.*, 1983) and in Costa Rica (Hainsworth and Wolf, 1972; Baker, 1975; Pyke and Waser, 1981). This systematic change in nectar availability with altitude could well alter the foraging ecology of hummingbirds, given increases in thermoregulatory demand and costs of hovering flight at higher elevations. Second-order interaction effects in foraging physiology may also be expected. For example, lower nectar temperatures will impose additional energetic costs on meal acquisition by hummingbirds (Lotz *et al.*, 2003). The interaction between foragers and nutritional resources across elevational gradients represents a fascinating field of research in that physical variables and associated constraints potentially impinge on all participants in such interactions. Relevant data are however extremely limited, and overall the variation in wind velocity, oxygen partial pressure and in air density with altitude are of primary relevance to the mechanics and physiology of avian flight.

Acknowledgments

References

Adams, N. J., B. Pinshow, L. Z. Gannes, and H. Biebach. 1999. Body temperatures in free-flying pigeons. *J. Comp. Physiol. B-Biochem. Syst. Environ. Physiol.* **169**:195–199.

Åkesson, S. and A. Hedenström. 2000. Wind selectivity of migratory flight departures in birds. *Behav. Ecol. Sociobiol.* **47**:140–144.

Altshuler, D. L., P. Chai, and J. S. P. Chen. 2001. Hovering performance of hummingbirds in hyperoxic gas mixtures. *J. Exp. Biol.* **204**:2021–2027.

Altshuler, D. L. and R. Dudley. 2002. The ecological and evolutionary interface of hummingbird flight physiology. *J. Exp. Biol.* **205**:2325–2336.

Altshuler, D. L. and R. Dudley. 2003. Kinematics of hovering hummingbird flight along simulated and natural elevational gradients. *J. Exp. Biol.* **206**:3139–3147.

Altshuler, D. L., R. Dudley, and C. P. Ellington. 2004*a*. Aerodynamic forces of revolving hummingbird wings and wing models. *J. Zool.* **264**:327–332.

Altshuler, D. L., R. Dudley, and J. A. McGuire. 2004*b*. Resolution of a paradox: Hummingbird flight at high elevation does not come without a cost. *Proc. Natl. Acad. Sci. USA* **101**:17731–17736.

Backman, J. and T. Alerstam. 2001. Confronting the winds: Orientation and flight behaviour of roosting swifts, *Apus apus. Proc. Roy. Soc. Lond. B-Biol. Sci.* **268**:1081–1087.

Baker, H. G. 1975. Sugar concentrations in nectars from hummingbird flowers. *Biotropica* **71**:37–41.

Berger, M. 1974*a*. Energiewechsel von Kolibris beim Schwirrflug unter Höhenbedingungen. *J. Orn.* **115**:273–288.

Berger, M. 1974*b*. Oxygen consumption and power of hovering hummingbirds at varying barometric and oxygen pressures. *Naturwissenschaften* **61**:407.

Bishop, C. M. 1997. Heart mass and the maximum cardiac output of birds and mammals: implications for estimating the maximum aerobic power input of flying animals. *Phil. Trans. Roy. Soc. Lond B* **352**:447–456.

Bishop, C. M. 1999. The maximum oxygen consumption and aerobic scope of birds and mammals: Getting to the heart of the matter. *Proc. Roy. Soc. Lond. B-Biol. Sci.* **266**:2275–2281.

Black, C. P. and S. M. Tenney. 1980. Oxygen transport during progressive hypoxia in high-altitude and sea-level waterfowl. *Respir. Physiol.* **39**:217–239.

Bruderer, B., L. G. Underhill, and F. Liechti. 1995. Altitude choice by night migrants in a desert area predicted by meteorological factors. *Ibis* **137**:44–55.

Butler, R. W., T. D. Williams, N. Warnock, and M. A. Bishop. 1997. Wind assistance: A requirement for migration of shorebirds? *Auk* **114**:456–466.

Carmi, N., B. Pinshow, W. P. Porter, and J. Jaeger. 1992. Water and energy limitations on flight duration in small migrating birds. *Auk* **109**:268–276.

Carpenter, F. L. 1976. Ecology and evolution of an Andean hummingbird (*Oreotrochilus estella*). *Univ. Calif. Publ. Zool.* **106**:1–74.

Chai, P. and R. Dudley. 1995. Limits to vertebrate locomoter energetics suggested by hummingbirds hovering in heliox. *Nature* **377**:722–725.

Chai, P. and R. Dudley. 1996. Limits to flight energetics of hummingbirds hovering in hypodense and hypoxic gas mixtures. *J. Exp. Biol.* **199**:2285–2295.

Chai, P., R. Harrykissoon, and R. Dudley. 1996. Hummingbird hovering performance in hyperoxic heliox: Effects of body mass and sex. *J. Exp. Biol.* **199**:2745–2755.

Cohen, J. E. and C. Small. 1998. Hypsographic demography: The distribution of human population by altitude. *Proc. Natl. Acad. Sci. USA* **95**:14009–14014.

Cooper, B. A. and R. J. Ritchie. 1995. The altitude of bird migration in east-central Alaska: A radar and visual study. *J. Field Ornithol.* **66**:590–608.

Cruden, R. W., S. M. Hermann, and S. Peterson. 1983. Patterns of nectar production and plant-pollinator coevolution. In B. Bentey and T. Elias (eds), *The biology of nectaries*, pp. 80–125. Columbia University Press, New York.

Denny, M. W. 1993. *Air and water: The biology and physics of life's media*. Princeton University Press, Princeton.

Dubach, M. 1981. Quantitative analysis of the respiratory system of the house sparrow, budgerigar and violet-eared hummingbird. *Respir. Physiol.* **46**:43–60.

Dudley, R. 2000. *The biomechanics of insect flight: Form, function, evolution*. Princeton University Press, Princeton.

Dudley, R. 2001. Limits to human locomotor performance: Phylogenetic origins and comparative perspectives. *J. Exp. Biol.* **204**:3235–3240.

Dudley, R. and P. Chai. 1996. Animal flight mechanics in physically variable gas mixtures. *J. Exp. Biol.* **199**:1881–1885.

Ellington, C. P. 1984a. The aerodynamics of hovering insect flight. IV. Aerodynamic mechanisms. *Philos. Trans. R. Soc. Lond* B **305**:79–113.

Ellington, C. P. 1984b. The aerodynamics of hovering insect flight. VI. Lift and power requirements. *Philos. Trans. R. Soc. Lond* B **305**:145–181.

Faraci, F. M. 1991. Adaptations to hypoxia in birds: How to fly high. *Ann. Rev. Physiol.* **53**:59–70.

Fedde, M. R. 1990. High-altitude bird flight: Exercise in a hostile environment. *News Physiol. Sci.* **5**:191–193.

Fedde, M. R., J. A. Orr, H. Shams, and P. Scheid. 1989. Cardiopulmonary function in exercising bar-headed geese during normoxia and hypoxia. *Respir. Physiol.* **77**:239–262.

Feinsinger, P., R. K. Colwell, J. Terborgh, and S. B. Chaplin. 1979. Elevation and the morphology, flight energetics, and foraging ecology of tropical hummingbirds. *Am. Nat.* **113**:481–497.

Fisher, R. J., R. G. Poulin, L. D. Todd, and R. M. Brigham. 2004. Nest stage, wind speed, and air temperature affect the nest defence behaviours of burrowing owls. *Can. J. Zool.* **82**:707–713.

Giladi, I. and B. Pinshow. 1999. Evaporative and excretory water loss during free flight in pigeons. *J. Comp. Physiol.* B-*Biochem. Syst. Environ. Physiol.* **169**:311–318.

Graham, J. B., R. Dudley, N. M. Aguilar, and C. Gans. 1995. Implications of the late Palaeozoic oxygen pulse for physiology and evolution. *Nature* **375**:117–120.

Green, M., T. Alerstam, G. A. Gudmundsson, A. Hedenström, and T. Piersma. 2004. Do Arctic waders use adaptive wind drift? *J. Avian Biol.* **35**:305–315.

Hainsworth, F. R. and L. L. Wolf. 1972. Crop volume, nectar concentration, and hummingbird energetics. *Comp. Biochem. Physiol.* **42**:359–366.

Hamilton, T. H. 1961. The adaptive significance of intraspecific trends of variation in wing length and body size among bird species. *Evolution* **15**:180–195.

Hedenström, A. 2003. Twenty-three testable predictions about bird flight. In P. Bertold, E. Gwinner, and E. Sonnenschein (eds), *Avian Migration*, pp. 563–582. Springer-Verlag, Berlin Heidelbert.

Hedenström, A., T. Alerstam, M. Green, and G. A. Gudmundsson. 2002. Adaptive variation of airspeed in relation to wind, altitude and climb rate by migrating birds in the Arctic. *Behav. Ecol. Sociobiol.* **52**:308–317.

Hepple, R. T., P. J. Agey, L. Hazelwood, J. M. Szewczak, R. E. MacMillen, and O. Mathieu-Costello. 1998. Increased capillarity in leg muscle of finches living at altitude. *J. Appl. Physiol.* **85**:1871–1876.

Iverson, G. C., S. E. Warnock, R. W. Butler, M. A. Bishop, and N. Warnock. 1996. Spring migration of western sandpipers along the pacific coast of North America: A telemetry study. *Condor* **98**:10–21.

Kerlinger, P. and F. R. Moore. 1989. Atmospheric Structure and avian migration. *Curr. Ornithol.* **6**:109–141.

Klaassen, M. 2004. May dehydration risk govern long-distance migratory behaviour? *J. Avian Biol.* **35**:4–6.

Klaassen, M., J. H. Beekman, J. Kontiokorpi, R. J. W. Mulder, and B. A. Nolet. 2004. Migrating swans profit from favourable changes in wind conditions at low altitude. *J. Ornithol.* **145**:142–151.

Klaassen, M. and H. Biebach. 2000. Flight altitude of trans-Sahara migrants in autumn: A comparison of radar

observations with predictions from meteorological conditions and water and energy balance models. *J. Avian Biol.* **31**:47–55.

Landys, M. M., T. Piersma, G. H. Visser, J. Jukema, and A. Wijker. 2000. Water balance during real and simulated long-distance migratory flight in the bar-tailed godwit. *Condor* **102**:645–652.

Laybourne, R. C. 1974. Collision between a vulture and an aircraft at an altitude of 37,000 feet. *Wilson Bull.* **86**:461–462.

Liechti, F. and B. Bruderer. 1998. The relevance of wind for optimal migration theory. *J. Avian Biol.* **29**:561–568.

Liechti, F., M. Klaassen, and B. Bruderer. 2000. Predicting migratory flight altitudes by physiological migration models. *Auk* **117**:205–214.

Liechti, F. and E. Schaller. 1999. The use of low-level jets by migrating birds. *Naturwissenschaften* **86**:549–551.

Lotz, C. N., C. Martínez del Rio, and S. W. Nicolson. 2003. Hummingbirds pay a high cost for a warm drink. *J. Comp. Physiol.* B **173**:455–462.

Maina, J. N. 2000. What it takes to fly: The structural and functional respiratory refinements in birds and bats. *J. Exp. Biol.* **203**:3045–3064.

Manville, R. H. 1963. Altitude record for a mallard. *Wilson Bull.* **75**:92.

Mathieu-Costello, O., P. J. Agey, L. Wu, J. M. Szewczak, and R. E. MacMillen. 1998. Increased fiber capillarization in flight muscle of finch at altitude. *Respir. Physiol.* **111**:189–199.

Mayr, E. 1963. *Animal Species and evolution.* Harvard University Press, Cambridge.

Norberg, U. M. 1990. *Vertebrate flight: Mechanics, physiology, morphology, ecology and evolution.* Springer-Verlag, Berlin.

Norberg, U. M. 1995. How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Funct. Ecol.* **9**:48–54.

Odum, E. P., D. T. Rogers, and D. L. Hicks. 1964. Homeostasis of nonfat components of migrating birds. *Science* **143**:1037–1039.

Ortiz-Crespo, F. I. 1974. The giant hummingbird *Patagona gigas* in Ecuador. *Ibis* **116**:347–359.

Pennycuick, C. J. 1975. Mechanics of flight. In D. S. Farner and J. R. King (eds), *Avian biology*, pp. 1–75. Academic Press, London.

Pennycuick, C. J. 1978. Fifteen testable predictions about bird flight. *Oikos* **30**:165–176.

Pennycuick, C. J., O. Einarsson, T. A. M. Bradbury, and M. Owen. 1996. Migrating whooper swans *Cygnus cygnus*: Satellite tracks and flight performance calculations. *J. Avian Biol.* **27**:118–134.

Pyke, G. H. and N. M. Waser. 1981. The production of dilute nectars by hummingbird and honeyeater flowers. *Biotropica* **13**:260–270.

Rahbek, C. and G. R. Graves. 2000. Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale. *Proc. R. Soc. Lond* B-*Biol. Sci.* **267**:2259–2265.

Rayner, J. M. V. 1990. The mechanics of bird migration performance. In E. Gwinner (ed.), *Bird migration: Physiology and ecophysiology*, pp. 283–327. Springer-Verlag, Berlin.

Reid, R. C., J. M. Prausnitz, and B. E. Poling. 1987. *The properties of gases and Liquids (4th ed.).* McGraw-Hill, New York.

Saunders, D. K. and M. R. Fedde. 1991. Physical conditioning: Effect on the myoglobin concentration in skeletal and cardiac muscle of bar-headed geese. *Comp. Biochem. Physiol.* A-*Physiol.* **100**:349–352.

Schaub, M., F. Liechti, and L. Jenni. 2004. Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. *Anim. Behav.* **67**:229–237.

Schuchmann, K. L. 1999. Family Trochilidae (Hummingbirds). In J. del Hoyo, A. Elliott, and J. Sargatal (eds), *Handbook to the Birds of the World*, pp. 468–680. Lynx Edicions, Barcelona.

Shams, H. and P. Scheid. 1989. Efficiency of parabronchial gas exchange in deep hypoxia: Measurements in the resting duck. *Respir. Physiol.* **77**:135–146.

Shams, H. and P. Scheid. 1993. Effects of hypobaria on parabronchial gas exchange in normoxic and hypoxic ducks. *Respir. Physiol.* **91**:155–163.

Stewart, A. G. 1978. Swans flying at 8000 meters. *Brit. Birds* **71**:459–460.

Stull, R. B. 2000. *Meteorology for scientists and engineers.* Brooks/Cole, Pacific Grove, CA.

Suarez, R. K. 1992. Hummingbird flight: Sustaining the highest mass-specific metabolic rates among vertebrates. *Experientia* **48**:565–570.

Torre-Bueno, J. R. 1976. Temperature regulation and heat dissipation during flight in birds. *J. Exp. Biol.* **65**:471–482.

Torre-Bueno, J. R. 1978. Evaporative cooling and water-balance during flight in birds. *J. Exp. Biol.* **75**:231–236.

Traylor, M. A. 1950. Altitudinal variation in Bolivain birds. *Condor* **52**:123–126.

Tucker, V. A. 1968a. Respiratory exchange and evaporative water loss in flying budgerigar. *J. Exp. Biol.* **48**:67–87.

Tucker, V. A. 1968b. Respiratory physiology of house sparrows in relation to high-altitude flight. *J. Exp. Biol.* **48**:55–66.

Usherwood, J. R. and C. P. Ellington. 2002. The aerodynamics of revolving wings II. Propeller force coefficients from mayfly to quail. *J. Exp. Biol.* **205**:1565–1576.

Vogel, S. 1988. *Life's Devices: The physical world of animals and plants.* Princeton University Press, Princeton.

Weimerskirch, H., O. Chastel, C. Barbraud, and O. Tostain. 2003. Frigatebirds ride high on thermals. *Nature* **421**:333–334.