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Review

The ecological and evolutionary interface of hummingbird flight physiology

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Summary

The hovering ability, rapidity of maneuvers and upregulated aerobic capacity of hummingbirds have long attracted the interest of flight biologists. The range of intra- and interspecific variation in flight performance among hummingbirds, however, is equally impressive. A dominant theme in hummingbird evolution is progressive invasion of higher-elevation habitats. Hypobaric challenge is met behaviorally through compensatory changes in wingbeat kinematics, particularly in stroke amplitude. Over evolutionary time scales, montane colonization is associated with increases in body mass and relative wing area. Hovering ability has been well-studied in several North American hummingbird taxa, yet the broad range of interspecific variation in hummingbird axial and appendicular anatomy remains to be assessed mechanistically. Such varied features as tail length, molt condition and substantial weight change due to lipid-loading can dramatically alter various features of the flight envelope. Compared with our present knowledge of hovering performance in hummingbirds, the mechanics of forward flight and maneuvers is not well understood.

Relationships among flight-related morphology, competitive ability and foraging behavior have been the focus of numerous studies on tropical and temperate hummingbirds. Ecologists have hypothesized that the primary selective agents on hummingbird flight-related morphology are the behaviors involved in floral nectar consumption. However, flight behaviors involved in foraging for insects may also influence the evolution of wing size and shape. Several comparisons of hummingbird communities across elevational gradients suggest that foraging strategies and competitive interactions within and among species vary systematically across elevations as the costs of flight change with body size and wing shape.

Key words: aerodynamics, biomechanics, evolutionary physiology, flight, hovering, hummingbird.

Introduction

Hummingbirds (family Trochilidae) represent extremes of locomotor and metabolic capacity among the vertebrates. Yet even many students of animal flight are unaware that the more than 325 described hummingbird species make up one of the largest avian families and encompass a remarkable diversity of flight-related morphology, behavior and ecology (Greenewalt, 1960; Suarez, 1992, 1998; Johnsgard, 1997; Schuchmann, 1999). Most reviews of trochilid physiology typologically emphasize only one or several species, with little or no consideration being paid to either ecological associations or evolutionary diversification within the family. Here, we place hummingbird flight within a broader biological context, emphasizing intraspecific variation in locomotor mechanics, interspecific diversity in morphology and flight behavior, and evolutionary trends in flight aerodynamics and physiology.

The earliest fossil trochilids date from the Pleistocene, and estimates for the origination of hummingbirds are strongly dependent on assumptions for the molecular clock (Bleiweiss et al., 1994; Bleiweiss, 1998; Gerwin and Zink, 1998). It is nonetheless clear that hummingbirds split from the swifts, their sister taxon, some time in the early Tertiary and probably in the Paleocene. Today's major lineages of hummingbirds all date to the Miocene and reflect a vigorous expansion of lowland taxa into mid and high elevations (see Bleiweiss, 1998; Dudley, 2001). Adaptation to hypobaric hypoxia has thus been an essential underpinning to hummingbird diversification and represents a physiological feat all the more impressive given the aerobically demanding flight behaviors, including hovering and vertical ascent, characteristic of this taxon. Hummingbirds are found only in the New World and, with the exception of transient hovering in sunbirds and other flower-visiting birds (see Westerkamp, 1990), have no behavioral counterpart in the Old World avifauna.

For hummingbirds, the evolution of hovering required

integration of morphological (e.g. the fusion of radial wing bones) and physiological (e.g. elevated wingbeat frequencies, increased aerobic capacity) traits within the ecological context of dedicated nectarivory. Nonetheless, evolutionary pathways for the acquisition of this unique avian flight behavior remain unclear. The eponymous swifts, for example, virtually never hover, and no transitional forms are evident within the most basal yet adeptly hovering hummingbird lineage, the hermits (subfamily Phaethornithinae). Miniaturization relative to apodiform ancestors has been a predominant morphological theme of hummingbird evolution, and upregulation of metabolic capacity necessarily occurred in concert with a reduction in body size (Cotton, 1996). The allometry of flight performance among trochilid taxa is, accordingly, of substantial physiological interest, particularly given the extremes of endothermic design represented by the smallest hummingbirds.

Hovering, and, more generally, the ability to generate vertical forces, represents only one component of flight performance. Other axial forces (e.g. thrust generation during forward flight) and the torques underlying changes in body orientation are much less studied in hummingbirds, but are equally important components of flight performance in this extraordinary avian lineage. Extended maneuvers and chases, for example, involve the production of either linked or temporally decoupled rotations about orthogonal body axes, together with the modulation of vertical forces, thrust and sideslip (see Dudley, 2000, 2002). On much longer time scales, many hummingbirds engage in migratory flight across both elevational and latititudinal gradients. Here, we emphasize current understanding of hovering aerodynamics and energetics, but emphasize that many other aspects of the hummingbird flight envelope probably derive from as yet unrecognized physiological novelties.

Mechanistic underpinnings to hummingbird flight performance

The ability to hover is the most salient behavioral feature of hummingbirds, but flight in this taxon, more generally, involves remarkable abilities to alter flight speed, trajectory and body orientation. Our perceptions, however, of such performance derive, in part, from the fact that hummingbirds are also among the smallest birds. Allometric considerations suggest that, under isometric size change, translational accelerations should scale as $\text{mass}^{-1/3}$, whereas the magnitude of rotational accelerations changes in proportion to $\text{mass}^{-2/3}$ (see Andersson and Norberg, 1981; Dudley, 2000, 2002). Relative to other birds, hummingbirds do indeed appear to be exceptionally maneuverable, but such aerial agility may to a large extent be simply mediated allometrically. The rapidity of body rotations, usually observed at feeders, is particularly likely to increase with smaller size.

Miniaturization, in fact, underlies many of the physiological and biomechanical extremes for which hummingbirds are so notorious. Increased heart rates, high wingbeat frequencies and extraordinary mass-specific rates of oxygen consumption are often attributed to the demands of hovering flight. Very fast forward flight in hummingbirds, however, requires oxygen uptake at rates substantially higher than those during hovering or at intermediate flight speeds (Berger, 1985). Rapid accelerations and vertical ascent also require the expenditure of aerodynamic and metabolic power well in excess of that for normal hovering (see Dudley, 2000). The morphological and biochemical specializations of hummingbird flight muscle are well known (e.g. Suarez et al., 1991; Mathieu-Costello et al., 1992; Suarez, 1992), but those features of the circulatory and respiratory systems required to sustain aerobic performance are similarly impressive. In common with other birds, trochilids exhibit an enhanced pulmonary diffusion capacity relative to that of bats (Dubach, 1981; Duncker and Güntert, 1985; Maina, 2000). Cardiovascular performance may, however, ultimately limit hummingbird flight energetics. Maximum cardiac output is a strong predictor of aerobic capacity in many birds and mammals (Bishop, 1999), whereas the relative heart mass of hummingbirds is substantially higher than that predicted by allometric regressions of heart mass for all other birds (see Hartman, 1961; Bishop, 1997). Heart mass increases isometrically in hummingbirds when phylogenetic relatedness among species is accounted for (Table 1; Fig. 1), but the relevant cardiac and respiratory variables are not known for hummingbirds under conditions of either maximal hovering or fast forward flight. Given that the muscle-mass-specific metabolic rates of flying hummingbirds represent the highest known values for vertebrate striated muscle (Lasiewski, 1963; 1964a; Epting, 1980; Suarez et al., 1991), any hypothesis that cardiovascular supply of oxygen limits overall aerobic performance must be shown to pertain specifically to hummingbirds for general validation.

During hovering flight, hummingbirds exhibit approximate kinematic and aerodynamic symmetry between the down- and upstrokes (Weis-Fogh, 1972), although precise data are lacking. Kinematic features such as the frequency and amplitude of wing motions are well described for hovering, but we know little about more detailed kinematic features that influence aerodynamic force production. A partial list of variables includes angle of attack, pronational and supinational velocities, the deviation of wing motions from simple harmonic motion and the elevation of the wing relative to the stroke plane broadly defined by wingtip motions. These static variables and the dynamic time courses are known to influence the magnitude and direction of steady and unsteady forces generated on flapping wings at comparable Reynolds numbers (see Ellington et al., 1996; Van den Berg and Ellington, 1997a,b; Dickinson et al., 1999; Sane and Dickinson, 2001, 2002). Relative to hovering insects, hummingbirds exhibit a much stronger negative allometry of wingbeat frequency and a correspondingly greater positive allometry of wing area relative to body mass (Dudley, 2000). The aerodynamic implications of these allometries are unclear, although a reduction in wingbeat frequency may mitigate inertial power requirements that increase in proportion to the cube of oscillation frequency. The relative wing mass of

hummingbirds substantially exceeds that of most insects, and the overall inertial costs of wing oscillation may therefore be substantial. Elastic energy storage of wing inertial energy may reduce or even eliminate such costs (see Weis-Fogh, 1972, 1973; Wells, 1993), but this possibility has yet to be demonstrated experimentally.

In addition to their obligate hovering at flowers, hummingbirds are exposed to forces of natural and sexual selection that require forward flight, linear accelerations, quick directional changes and evasive responses. The modulation of aerodynamic output is best termed agility, a term that specifically refers to changes in the speed and direction of flight (Dudley, 2002). Axial agility involves the capacity to accelerate in the forward, lateral and vertical dimensions, whereas torsional agility indicates rotational accelerations about each of the three mutually orthogonal body axes (i.e. speed of initiation of roll, pitch and yaw). In hummingbirds, axial agility has been studied predominantly in the context of

Table 1. *Body, heart and flight muscle mass for 33 species of hummingbird*

Species	*n*	Body mass (g)	Heart mass (g)	Pectoralis muscle mass (g)
Amazilia amabilis[1]		4.30	0.10	
Amazilia edward[1]		4.64	0.11	1.33
Amazilia tzacatl[1]		5.06	0.11	1.35
Anthracothorax nigricollis[1]		7.10	0.16	
Archilochus alexandri[2]	1	2.93		0.85
Archilochus colubris[1]		3.28	0.07	
Archilochus colubris[2]	6	3.78		0.95
Campylopterus hemileucurus[1]		11.92	0.23	4.02
Campylopterus largipennis[3]	3	8.76	0.19	2.75
Chlorostilbon canivelii[1]		3.08	0.06	0.81
Colibri thallassinus[1]		5.07	0.10	
Damophila julie[1]		3.19	0.06	
Doryfera ludovicae[3]	1	5.20	0.12	1.50
Elvira chionura[1]		2.88	0.06	
Eugenes fulgens[1]		5.70	0.12	
Eugenes fulgens[2]	1	7.62		2.06
Eupherusa eximia[1]		4.35	0.10	
Florisuga mellivora[1]		6.96	0.13	
Glaucis hirsuta[1]		6.54	0.15	1.81
Heliangelus amethysticollis[3]	1	6.05	0.12	1.64
Heliodoxa jacula[1]		7.39	0.15	2.06
Lampornis castaneoventris[1]		5.26	0.11	1.18
Lampornis clemenciae[2]	1	9.09		2.64
Phaeochroa cuvierii[1]		8.60	0.15	
Phaethornis guy[1]		5.78	0.14	1.65
Phaethornis hispidus[3]	1	5.89	0.13	1.57
Phaethornis longuemareus[1]		2.64	0.06	
Phaethornis malaris[3]	1	5.90	0.12	1.10
Phaethornis superciliosus[1]		6.15	0.13	
Schistes geoffroyi[3]	1	3.99	0.10	1.10
Selasphorus platycercus[4]	8	3.97		0.97
Selasphorus rufus[4]	4	4.28		1.00
Selasphorus scintilla[1]		2.28	0.05	0.56
Thalurania furcata[3]	2	4.31	0.10	1.09
Threnetes leucurus[3]	1	5.06	0.09	1.01

[1]Data from F. A. Hartman (1961); [2]data from P. Chai, D. Millard, R. Dudley and D. L. Altshuler (unpublished results); [3]data from D. L. Altshuler and R. Dudley (unpublished results); [4]data from D. J. Wells (1990).

Pectoralis muscle mass is the combined mass of the pectoralis major and the supracoracoideus. Data on heart, muscle and body mass were collected within 30 min from birds that had been killed or that had died inadvertently during mist net collection.

Masses were measured to within 0.001 g using an Acculab digital scale (model no. PP-2060D).

Sample sizes from Hartman (1961) were different for each of the morphological variables.

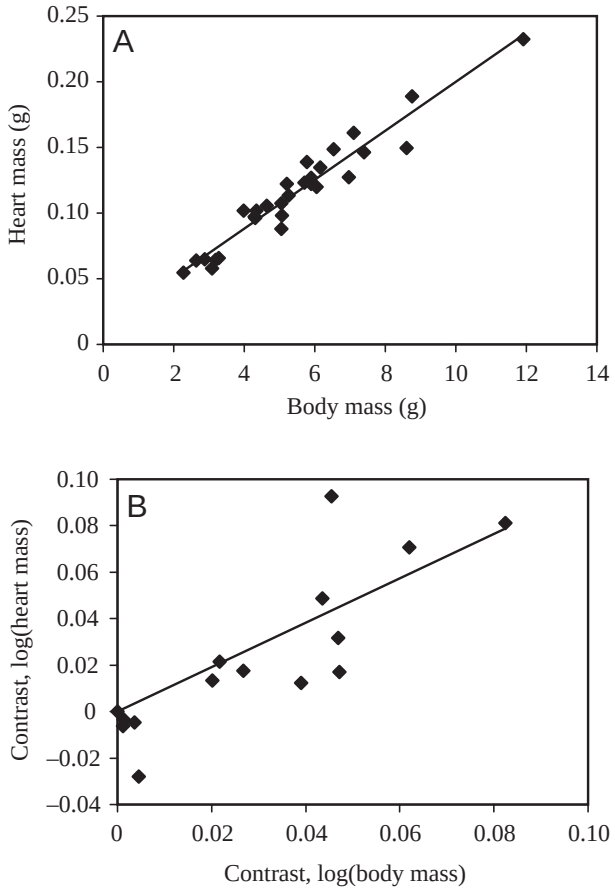

Fig. 1. The relationship between heart mass (g) and body mass (g) for hummingbirds: (A) raw species data (y=0.02x+0.01, r^2=0.93, P<0.0001); (B) independent contrasts (y=0.957x, r^2=0.79, P<0.0001). The regression using independent contrasts is forced through the origin (Garland et al., 1992). The phylogenetic hypothesis used to calculate independent contrasts contains 73 hummingbird taxa and was generated using Bayesian phylogenetic analysis (Larget and Simon, 1999; Huelsenbeck and Ronquist, 2001). Two nuclear genes (AK1, ND2) and one mitochondrial gene (Beta-fibrinogen) were sequenced and analysed using a general time-reversible (GTR) plus site-specific gamma model of evolution (J. A. McGuire and D. L. Altshuler, unpublished data).

vertical force production. Wing motions are bilaterally symmetrical in this case, and an increase in stroke amplitude is the predominant means of increasing total aerodynamic force output. Anatomical limits to stroke amplitude ultimately limit force production for flight both in hypodense gas mixtures and during maximal vertical load-lifting (Chai and Dudley, 1995; Chai et al., 1997; Chai and Millard, 1997). Excess capacity in lift and power exhibited under such conditions is presumably used in nature for the purposes of vertical ascent, climbing flight, translational accelerations and fast forward flight. Maximal flight performance can also be strongly context-dependent. For example, ruby-throated hummingbirds (*Archilochus colubris*) engaged in vertical load-lifting exhibit short-duration, but high-intensity, power outputs that exceed maxima exhibited in hypodense air (Chai et al., 1997). Interspecific comparisons of hummingbirds also suggest a trade-off between maximum power and flight duration (Chai and Millard, 1997; see below), although phylogenetically controlled studies are lacking.

Intraspecific morphological variability among hummingbirds can also be correlated with variation in axial agility. Transient weight reduction imposed on individual ruby-throated hummingbirds decreases wing loading (given an invariant wing area) and increases hovering performance in hypodense gas media (Chai and Dudley, 1999). Sexual dimorphism in the same species is pronounced, with the heavier females being less capable of sustaining hovering flight (Chai et al., 1996; Chai and Dudley, 1999). In common with other birds, molting in ruby-throated hummingbirds results in a substantial increase in the metabolic costs of flight and a reduction in maneuverability (see Chai, 1997; Rayner and Swaddle, 2000). Similar effects are presumably associated with the extensive lipid loading exhibited by premigratory hummingbirds. The extraordinary energetic consequences of non-stop flight in those neotropical trochilid taxa that migrate to and from the North American continent were modeled by Lasiewski (1964b), but we know little empirically about fuel use, water balance and nectaring strategies during sustained flights. The only available estimate of mechanical power requirements for hummingbird in forward flight (Pennycuick, 1968) suggests a power curve that the parallels aforementioned metabolic requirements, namely relatively constant power expenditure up to airspeeds of approximately $10\,m\,s^{-1}$, followed by a steep increase. Airspeeds during migration might be expected to occur near this rise in the curve if energetic expenditure per unit distance traveled is to be minimized.

Most present-day hummingbirds are mid-montane specialists, whereas phylogenetic relationships among major trochilid lineages suggest progressive colonization of higher elevations (see Bleiweiss, 1998; Dudley, 2001; Schuchmann, 1999). An increase in altitude involves parallel reductions in air density, oxygen partial pressure and air temperature. Each of these physical features potentially influences hummingbird flight performance. Also, mechanical power expenditure during hovering increases with greater body mass and with decreased air density (Ellington, 1984b), but heavier

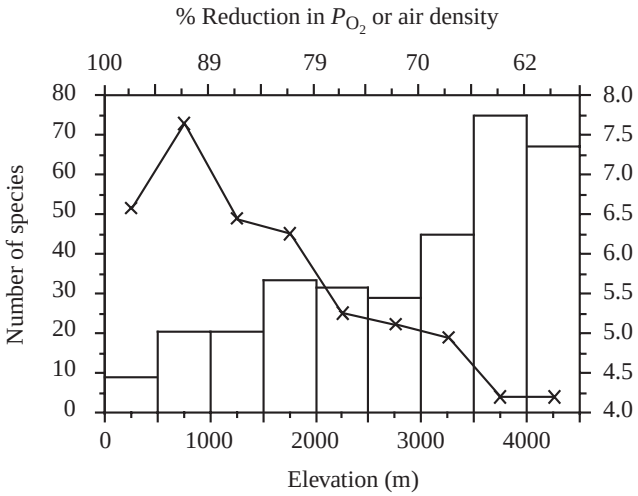

Fig. 2. Body mass (columns) and number of species (crosses) for averaged minimum and maximum elevations among hummingbird species. Data were derived from Schuchmann (1999). Percentage reduction in oxygen partial pressure (P_{O_2})/air density is also indicated.

hummingbird species tend, somewhat paradoxically, to occur at higher elevations (Fig. 2). Compared with hovering under normobaric conditions, substantial excess lift and power capacity are exhibited by hummingbirds hovering in hypobaria (Berger, 1974a,b). Concomitant increases in stroke amplitude but relative constancy in wingbeat frequency parallel those kinematic changes seen under conditions of hypodense challenge (Chai and Dudley, 1995). Even when aerodynamic and energetic demands remain constant under normodense conditions, hummingbirds display considerable resistance to hypoxia (Chai and Dudley, 1996). Hypobaric conditions are thus well met by hummingbirds through a combination of substantial lift power reserves and relative insensitivity to hypoxia, the latter extending in hovering ruby-throats to conditions of oxygen availability equal to those found at 4000 m (Chai and Dudley, 1996).

Natural hypobaria is also associated with reductions in mean air temperature. The flight metabolic rate of hovering hummingbirds varies only slightly with ambient temperature (Chai et al., 1998; Berger and Hart, 1972), but the physiological effects of convective heat loss during forward flight, as yet unstudied, may be substantial. Variation in air temperature may also influence maximal lift and power production. For example, the wingbeat frequency and stroke amplitude of ruby-throated hummingbirds engaged in maximal load-lifting vary inversely as air temperature increases, possibly in response to thermoregulatory demand (Chai et al., 1997). One pronounced physiological feature of hummingbirds that probably evolved in parallel with the occupation of higher elevations is torpor. Daily torpor is pronounced in montane hummingbirds and also well suits those taxa that migrate into temperate-zone regions for survival in colder climates (see Carpenter, 1974; Hiebert, 1993; Calder, 1994; Bicudo, 1996). Phylogenetic variation in hummingbird hypometabolism has not been systematically studied, and the phylogenetically basal

and generally lowland phaethornithines would be particularly interesting in this regard. We finally note that hyperoxia fails to enhance maximal hovering ability (Chai et al., 1996; Altshuler et al., 2001), a finding consistent with the convective (and particularly cardiovascular) limits on metabolic capacity mentioned above.

Forward flight requires the generation of thrust to overcome body drag in addition to the body weight support that characterizes hovering. Particularly at higher airspeeds, some mitigation of vertical force production may be attained *via* lift generation on the body. Modulation of forward thrust derives primarily from the reorientation of an otherwise vertically directed aerodynamic force vector. In hummingbirds, as in other flying animals, variable partitioning of this output vector between vertical and horizontal components is correlated with changes in body pitching moments, which may derive from torques generated actively by the wing and passively by the body (see Greenewalt, 1960; Dudley, 2000). During forward flight, wing flapping velocities are augmented by the translational airspeed, an effect that substantially mitigates aerodynamic demand. For example, ruby-throated hummingbirds in fast forward flight exhibit stroke amplitudes well below limiting values characteristic of hovering flight (Greenewalt, 1960). In wind tunnels, the maximum airspeeds of hummingbirds range from 13 to 15 m s^{-1} (Greenewalt, 1960; Berger, 1985; Chai and Dudley, 1999; Chai et al., 1999). Maximum forward flight speeds do not differ substantially either between the genders of ruby-throated hummingbirds or between molting and non-molting individuals (Chai et al., 1999; Chai and Dudley, 1999). For obvious logistical reasons, little is know about the forward flight of hummingbirds in nature. Groundspeed measurements of hummingbirds commuting between flowers or escaping from experimenters suggest flight speeds of between 5 and 11 m s^{-1} (Pearson, 1961; Gill, 1985), whereas short-distance flights between flowers occur at speeds no greater than 1.2 m s^{-1} (Wolf et al., 1976). By contrast, display dives using gravitational acceleration may exceed 20 m s^{-1} (see Stiles, 1982; Tamm et al., 1989).

Changes in the body roll, pitch and yaw of flying hummingbirds derive from aerodynamic and inertial torques applied about the body axis in question; the rapidity of body rotation is termed torsional agility. Alteration of body pitch can derive from bilaterally symmetrical changes in a variety of wingbeat kinematic features or from dorsoventral tail motions (Dudley, 2002). Bilaterally asymmetric motions of the wings, the tail or the body itself yield the rotational moments underlying body roll and yaw. Although famously maneuverable, hummingbirds have never been the subject of relevant three-dimensional studies. Both the magnitude of applied aerodynamic torque and the moment of inertia about the rotational axis in question influence instantaneous rotational acceleration. The wings of volant vertebrates represent substantial contributions to body rotational inertia (Thollesson and Norberg, 1991; Van den Berg and Rayner, 1995; Dudley, 2002), and instantaneous wing position may therefore affect the inertial responsiveness of the wing/body system. The often greatly exaggerated tails of many hummingbirds may impose a similar inertial constraint on rotational accelerations. Although remarkably diverse in morphology and size, the potential aerodynamic roles of hummingbird tails have never been investigated, but contributions to roll, pitch and yaw are all likely possibilities. Unsteady forces on the tail, as well as aeroelastic twisting of individual tail feathers, may also enhance force and moment production during maneuvers (see Norberg, 1994).

Ecological implications

Flight performance is integral to diverse features of avian behavior and ecology, and hummingbirds have historically served as model organisms in studies of competition and pollination (Darwin, 1871; Wolf and Hainsworth, 1978). Following the development of aerodynamic models for avian flight (Pennycuick, 1968, 1969), the foraging behavior and ecology of hummingbirds were evaluated in terms of the energetic costs of locomotion. Biologists initially sought to identify those morphological variables that might be strongly correlated with actual energetic costs. Most interest focused on hovering flight and, in particular, on ways to estimate induced power requirements (the power required to offset gravitational forces), thought to be the major avenue of energetic expenditure for this behavior.

Accurate calculation of induced power requirements requires knowledge of the region in space through which the wings beat and apply a downward pressure impulse (Ellington, 1984a). The average pressure thus applied to the surrounding air is indicated by the aerodynamic parameter of disc loading, the ratio of the body weight ($m\boldsymbol{g}$, where m is mass and $\boldsymbol{g}$ is gravitational acceleration) to the disc area swept by the wings A and across which body weight is supported. Disc loading varies in inverse proportion to the wing length R, but must also incorporate effects of variation in the stroke plane angle β and the stroke amplitude Φ. During hovering flight, disc loading is given by $m\boldsymbol{g}/\Phi R^2\cos\beta$, where Φ is given in radians (see Ellington, 1984a). Induced power costs are directly proportional to the square root of disc loading, but also vary in inverse proportion to the square root of air density (Ellington, 1984b; Norberg, 1990).

Specifically with reference to hovering hummingbirds, Epting and Casey (1973) defined wing disc loading as the ratio of $m\boldsymbol{g}$ to A, but estimated A as $\pi(b/2)^2$, where b is the wing span (i.e. the distance between the outstretched wing tips; Norberg, 1990). Subsequent estimates of wing disc loading for hummingbirds estimated b using the more easily measured chord distance from the wrist joint to the wingtip (Carpenter et al., 1993; Feinsinger and Chaplin, 1975; Feinsinger and Colwell, 1978; Feinsinger et al., 1979; Kodric-Brown and Brown, 1978). Note that, in these and other ornithological studies, this distance is termed the ‘wing chord’, whereas aerodynamic usage designates the wing chord as orthogonal to such radial measures. In any case, the estimated relationship between wrist joint to wingtip distance and wing span (see

Greenewalt, 1960, 1975) contains considerable scatter in part because wing proportions vary among species.

Relative to contemporary understanding of hovering mechanics, estimates of hummingbird disc loading contain many assumptions potentially subject to error. Particularly noteworthy are (i) that wing length equals half the wing span, and (ii) that stroke amplitude equals 180°. Both these assumptions will tend to overestimate disc loading and thus systematically to underestimate induced power expenditure. Nonetheless, mass-specific metabolic power input during hovering is correlated with this estimate of disc loading in a comparison of seven hummingbird species (Epting, 1980).

A variety of studies have sought to associate Epting and Casey's (1973) estimate of hummingbird disc loading with competitive ability (Feinsinger and Chaplin, 1975; Feinsinger and Colwell, 1978; Kodric-Brown and Brown, 1978; Kuban and Neill, 1980). In the sexually dimorphic species examined so far, male dominance is correlated with greater disc loading in males (Carpenter et al., 1993). It is worth noting, however, that the North American species (mostly rufous hummingbirds, *Selasphorus rufus*) tend to be smaller and show reversed sexual dimorphism compared with the majority of larger hummingbirds (see Colwell, 2000). In addition, the wingtips of males in the genus *Selasphorus* are modified for sound production, which tends to reduce wing length and to yield higher wing disc loading. One notable exception to this trend is in broad-tailed hummingbirds (*S. platycercus*), in which the outer primary is slightly lengthened and attenuated. The effects of sexual dimorphism in body mass and wing area on competitive behavior have not been examined across the full range of body sizes in hummingbirds. Gender-specific evaluation of the aerodynamic and metabolic costs of flight is clearly required if biomechanical underpinnings to behavior are to be inferred.

Estimates of disc loading have also been broadly correlated with hummingbird foraging strategies, species being categorized either as territorial and defending floral aggregations or as trapliners that forage among dispersed flowers and that do not engage in resource defense. Territorial hummingbirds were predicted to have high values of wing disc loading because effective aerial defense was presumed to require shorter wings and greater aerial maneuverability. In contrast, the wing disc loading of trapliners was predicted to be lower than that of territorial hummingbirds (Feinsinger and Chaplin, 1975). Using data from the cloudforests of Monteverde, Costa Rica, and the eastern Rockies of Colorado, Feinsinger and Chaplin (1975) found support for the prediction that territorialists had higher wing loading than trapliners, although their data did not control for the effects of phylogeny or elevation.

Further associations between disc loading and hummingbird ecology were proposed by Feinsinger and Colwell (1978), who observed trochilid species from the Caribbean and Central and South America. From these observations, they proposed six foraging guilds, each defined by body size, bill length, foot size and wing disc loading. The aforementioned hummingbirds from Monteverde were recategorized into these six foraging guilds, and data for competitive interactions between two species from the Lesser Antilles were presented in support of this hypothesis. However, evidence from other authors indicates that the division among guilds may be less clear, with one notable example being the competitive interactions between a 'high-reward' trapliner, the long-tailed hermit (*Phaethornis superciliosus*), and hummingbirds from other 'guilds' (Stiles and Wolf, 1979).

How tightly do qualitative categorizations of foraging strategy correspond to quantitative features of flight physiology? Thus far, the relationship between competitive ability and flight-related morphology has been addressed through analyses of relatively small species assemblages in North America and on Caribbean islands (Kodric-Brown and Brown, 1978; Kodric-Brown et al., 1984). Competitively dominant hummingbird species exhibit higher wing disc loadings (*sensu* Epting and Casey, 1973), but are also heavier, thereby precluding causal association of competitive ability and the relative magnitude of induced power expenditure. Existing interspecific comparisons of hummingbird competitive ability are also confounded by potentially non-random phylogenetic relatedness among the species in question. More generally, flight performance during competitive interactions probably derives from a variety of behaviors supplemental to hovering. Differing components of both axial and torsional agility can potentially influence the outcome of aerial interactions (Dudley, 2000, 2002), and a comparison of wing disc loading alone captures but a limited subset of the relevant flight mechanics. Context-specificity may also be critical to the interpretation of behavioral dominance. Other factors that potentially influence the foraging strategies of most species included (i) age, (ii) gender, (iii) the abundance and distribution of resources, (iv) the presence and relative dominance of competitors, and even (v) the time of day (Wolf et al., 1976; Feinsinger and Colwell, 1978; Feinsinger et al., 1979; Pimm et al., 1985; Sandlin, 2000). In addition, foraging strategies may vary latitudinally. *Selasphorus rufus*, for example, is a dominant territorialist during breeding in North America, but is mostly a subordinate, non-territorial species on its wintering grounds.

Experimental tests of the influence of hummingbird flight morphology on competitive outcomes have relied upon manipulations of feeder density. In staged encounters between heterospecific hummingbird pairs, a larger species maintained positive energy balance whereas a smaller competitor species always lost mass (Tiebout, 1993). However, the smaller species was able to the feed more often when the feeders were more dispersed (Tiebout, 1992).

Most ecomorphological studies of hummingbirds have examined links between characters thought to influence flight performance and foraging for flower nectar or feeder solutions. The consumption of arthropods by hummingbirds has largely been ignored in these considerations despite the prevalence of arthropods in the diet of many hummingbirds (Remsen et al., 1986). One exception is an analysis of arthropod feeding flight

behavior of the hummingbirds of La Selva, Costa Rica (Stiles, 1995). Four types of insect feeding flight behavior were described, and the tactics used for arthropod foraging were constant across habitats and seasons, whereas the tactics of nectar-foraging varied systematically. In addition, several wing variables (including wing disc loading and aspect ratio) correlated much more closely with arthropod-foraging than with nectar-foraging tactics. From these results, Stiles (1995) proposed an alternative hypothesis, namely that the primary direct selective force on wing morphology has been arthropod-foraging, whereas selection *via* nectar-foraging may have been indirectly imposed *via* constraints on arthropod-foraging imposed by bill morphology. In any case, it appears likely that arthropod-foraging, as well as other behaviors such as predator avoidance and mating displays, must have influenced the evolution of hummingbird flight performance and related morphology.

Several lines of evidence suggest that hummingbirds actively regulate body mass and that such variation influences flight behavior. During the breeding season, male ruby-throated hummingbirds maintain a low body mass, but they gain weight following the cessation of reproductive activity (Mulvihill et al., 1992). Daily measurements of the mass of breeding broad-tailed hummingbirds indicate that males actively regulate low body mass during the day and then engorge themselves immediately before sunset (Calder et al., 1990).

The influence of wing morphology and body mass on flight performance has also been investigated within sexually dimorphic species. As part of their larger studies of montane hummingbirds, Feinsinger and colleagues (Feinsinger and Chaplin, 1975; Feinsinger and Colwell, 1978) made guild classifications for seven species in which the sexes differed in body mass and/or wing disc loading. The males and females of two of these species, purple-throated mountain-gems (*Lampornis calolaema*) and broad-tailed hummingbirds, were classified in different guilds. In both cases, males were heavier, had higher wing loadings and were placed in a more competitive guild (i.e. territorialist or facultative trapliner, respectively) compared with females (classified as generalists and trapliners, respectively). Male violet sabrewings (*Campylopterus hemileucurus*) were also substantially heavier and had higher wing disc loadings than females, but both were classified as generalists. Two of the remaining species had heavier males but equivalent values for wing disc loading, and both sexes were classified in the same guild. The final two species exhibited slight differences between the sexes, but the sexes were again classified into the same guild. Addressing this question further will require a more refined measurement of competitive ability (*sensu* Pimm et al., 1985; Sandlin, 2000) and a much broader sample of species than is presently available.

Mechanistically, the implications of variable body mass for flight performance and indirectly for competitive ability are unclear. Calder et al. (1990) predicted that reduced body mass would facilitate acceleration for courtship displays and aerial encounters with competitors (see also Dudley, 2002). In ruby-throated hummingbirds, maximum flight speeds, both among individuals and for the same individual in differing molt condition, are unchanged in spite of changes in body mass of up to 27 % (Chai et al., 1999; Chai and Dudley, 1999). Neither translational nor rotational accelerations have been determined, however, for any hummingbird species. Moreover, rufous hummingbirds vigorously maintain territories while concurrently increasing body mass by up to 33 % (Carpenter et al., 1983). The potential influences of body mass on competitive ability and foraging behavior are multifarious in nature and, to date, have not been causally associated with effects on flight performance *per se*.

Hummingbird body mass appears to undergo substantial variation during migration. Carpenter et al. (1983) created perches on scales to measure instantaneous mass in rufous hummingbirds during their migratory stopover. These highly territorial birds adjusted territory size to gain mass as quickly as possible during stopovers and departed after reaching a body mass threshold (Carpenter et al., 1983). Resident Costa's hummingbirds (*Calypte costae*) at the same site maintain a relatively steady moderate body mass and adopt a strategy that minimizes foraging time (Hixon and Carpenter, 1988). Some populations of ruby-throated hummingbirds cross the Gulf of Mexico for the spring migration. Before departing, these birds often double their mass (Robinson et al., 1996) and thus fly with extra weight relative to non-migratory periods. In these examples, the fattened hummingbirds engage primarily in forward flight during migration, and maximum forward velocity is probably unaffected by changes in body mass (see Chai et al., 1999). Actual flight speeds during migration are unknown for any hummingbird.

In summary, our understanding of the ecological implications of intra- and interspecific variation in hummingbird morphology and flight performance is at a rudimentary stage. Most measures of hummingbird competitive ability and foraging behavior have relied upon qualitative assessments. A quantitative method for assessing competitive ability has been introduced by Pimm et al. (1985), in which species dominance is assessed through observations of feeding activity at microhabitats that differ in quality. A high-quality site with a feeder of high-concentration sucrose solution is defended by the most aggressive birds, whereas feeders with low-concentration sucrose solutions are used by subordinate individuals. A comparison of the time spent feeding at the preferred habitat with overall time spent at the feeder thus provides a numerical index of competitive ability that can be compared with other variables such as population densities. These methods have also been used to assess the influence of learning on behavior (Mitchell, 1989; Sandlin, 2000). Applying the methods of Pimm et al. (1985) to several species complexes and combining behavioral data with morphological and biomechanical variables may greatly enhance our ecological understanding of hummingbird flight performance. An important caveat is that behavioral studies in artificial settings (i.e. feeders in the field or in laboratory

contexts) may not adequately capture natural foraging performance.

Elevational variation in flight performance

To date, montane regions have provided the best understood context for ecomorphological interpretations of flight in hummingbirds. Flight at high elevations presents a double challenge: reduced air density demands higher lift and power output, whereas reduced oxygen availability can constrain metabolic power input (Wolf and Gill, 1986; Dudley and Chai, 1996). Yet the highest diversity of hummingbirds is found along mid-montane Andean slopes, and some species range to elevations as high as 5000 m (Carpenter, 1976; Schuchmann, 1999). How are the highly aerobic activities of flight maintained under such conditions? Hypoxia is known to place limits on the hovering performance of ruby-throated hummingbirds, but only under conditions of oxygen availability well below those experienced naturally by this lowland species (Chai and Dudley, 1996). Nonetheless, the use of oxygen by hummingbirds is probably limited by hypoxia, as demonstrated by the increased hovering durations of hummingbirds hovering in hyperoxic air at intermediate densities equivalent to the higher elevations of hummingbird altitudinal distributions (Altshuler et al., 2001). Other adaptations to high-elevation habitats probably include increased wing area, increased stroke amplitude during flapping, increased use of perch feeding and decreased use of hovering flight.

Comparisons in a phylogenetic context will also be necessary to determine why hummingbird species might have diversified under environmental conditions that exacerbate the costs of flight in general and, specifically, of hovering. A historical perspective may also aid in our understanding of how hummingbirds expanded into high-elevation niches and whether such an invasion was a unique event or one of several radiations (Bleiweiss, 1998). The largest phylogeny currently available for trochilids contains 73 taxa, including many high-elevation species (J. A. McGuire and D. L. Altshuler, unpublished data). Consideration of the elevational ranges of the taxa included in this analysis suggests that hummingbirds may have evolved at mid elevations and subsequently invaded both low and high elevations in several lineages (Fig. 3). An alternative explanation is that hummingbirds originated in moist, lowland forests and subsequently invaded mid- and high-elevation habitats (see Bleiweiss, 1998; Dudley, 2001).

Allometric considerations potentially confound the interpretation of elevational effects on hovering performance and body size evolution of hummingbirds. Larger body size presents a double mechanical/metabolic challenge to hovering flight in that the mass-specific induced power requirements increase with (body mass)$^{1.17}$ (Norberg, 1995), whereas the maximum aerobic capacity of volant animals tends to scale negatively with body mass (Bishop, 1997; Norberg, 1990). Flight is thus relatively more costly and metabolically challenging for heavier animals. Somewhat surprisingly, then,

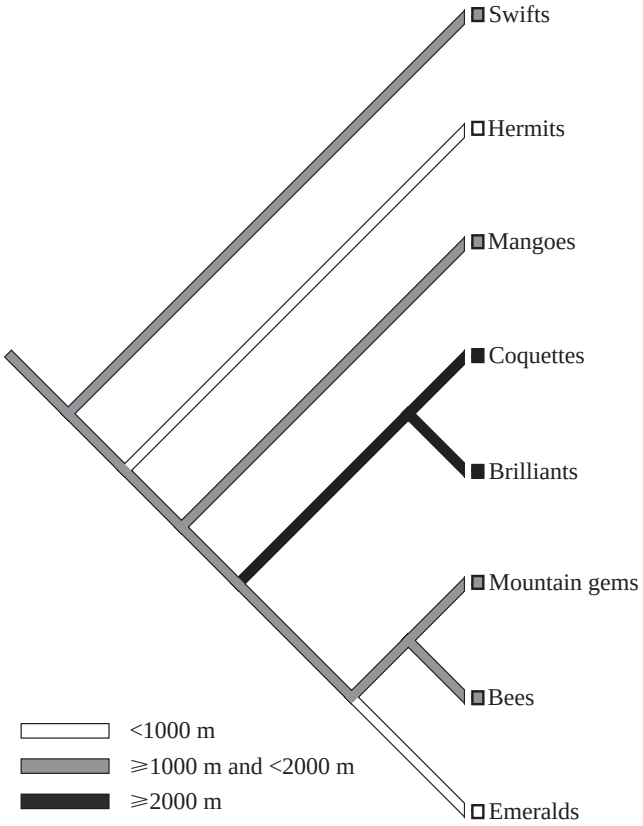

Fig. 3. The major lineages of hummingbirds as determined using DNA–DNA hybridization (Bleiweiss et al., 1994, 1997) and corroborated using sequences from one mitochondrial and two nuclear genes (J. A. McGuire and D. L. Altshuler, unpublished data). Mapped onto the phylogeny are the means of the midpoints of elevation ranges (from Schuchmann, 1999) for all taxa whose genera have been included in either phylogenetic analysis.

mean body mass among over 325 described hummingbird species increases significantly at higher elevations, whereas species diversity decreases (Fig. 2). One possible evolutionary response to the increased relative cost of flight with body mass is a positive allometry in the flight muscle mass of hummingbirds (Table 1; Fig. 4). Also, greater body mass at higher elevations probably enhances thermoregulatory ability, storage capacity and feeding rate, the last variable being an important determinant of the outcome of competitive interactions (Wolf and Gill, 1986). Our analysis of Peruvian hummingbirds from the eastern slopes of the Andes indicates that hummingbirds above 3000 m have a greater mean body mass [8.3 g; N=7 species; mean of 6.0 g excluding the giant hummingbird (*Patagona gigas*)] relative to species below this elevation (5.4 g; N=32 species; D. L. Altshuler and R. Dudley, unpublished data). Most revealingly, the giant hummingbird weighs over 20 g but occurs not in the lowlands but rather at mid and high elevations (see also Schuchmann, 1999). What biomechanical and physiological adaptations are characteristic of high-elevation hummingbirds?

Feinsinger et al. (1979) predicted that wing disc loading of

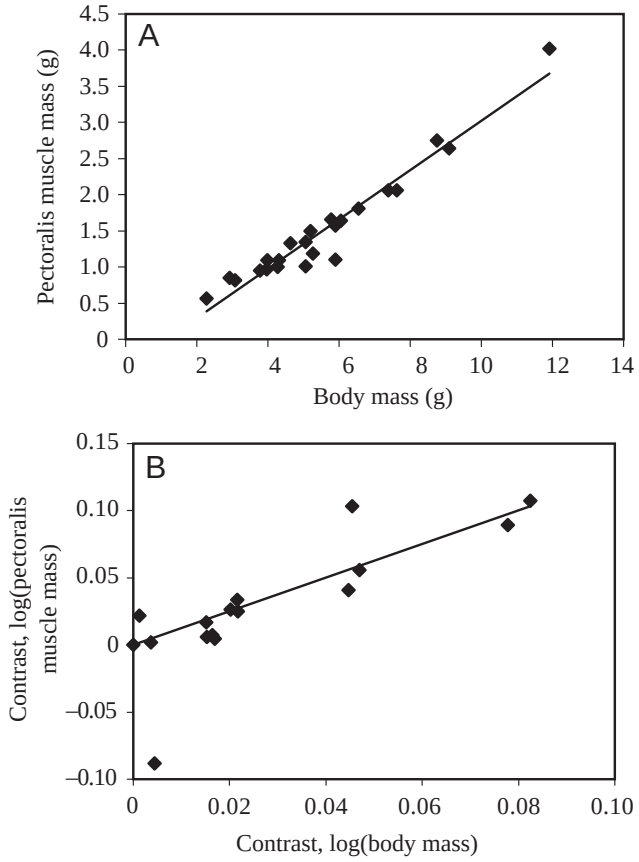

Fig. 4. The relationship between flight muscle mass (g) and body mass (g) for hummingbirds: (A) raw species data (y=0.34x+0.39, r^2=0.94, P<0.0001); (B) independent contrasts (y=1.25x, r^2=0.73, P<0.0001). The regression using independent contrasts is forced through the origin (Garland et al., 1992). The phylogenetic hypothesis used for this analysis is the same as for Fig. 1.

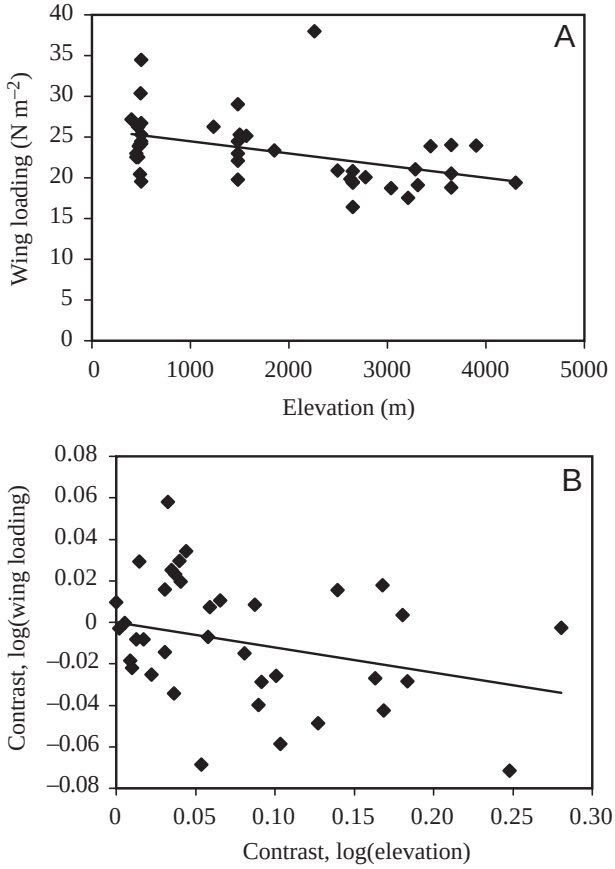

Fig. 5. The relationship between wing loading (kg m^{-2}) and elevation (m) for hummingbirds: (A) means of raw species data (y=–0.002x+26, r^2=0.196, P=0.003); (B) independent contrasts (y=–0.11x; r^2=0.18, P=0.04). The regression using independent contrasts in forced through the origin (Garland et al., 1992). The phylogenetic hypothesis used for this analysis is the same as for Fig. 1.

hummingbirds (*sensu* Epting and Casey, 1973) would decrease with increasing elevation if hovering costs and competitive ability were positively linked and if other selective forces on body size and wing length were relatively unimportant. For 38 hummingbird species in southeast Peru, Feinsinger et al. (1979) determined an inverse relationship between wing disc loading and the midpoint of elevational range. Feinsinger et al. (1979) also calculated that induced power expenditure during hovering was independent of elevation, a surprising result given the dependence of this variable on the square root of air density.

We have expanded upon the work of Feinsinger and Colwell and their collaborators by investigating the load-lifting performance of hummingbirds along the eastern slopes of the Peruvian Andes. Hummingbirds were filmed during free hovering flight and also when hovering with maximum weight imposed *via* an asymptotically increasing load-lifting assay (see Chai et al., 1997; Chai and Millard, 1997). We currently have data from 43 species spanning an elevation gradient from 400 to 4300 m, and we are using the aforementioned phylogeny to aid in the interpretation of the results. A comparison of wing loading and mean elevation for a species' range using phylogenetically independent contrasts has revealed a significantly negative relationship between these variables (Fig. 5), in agreement with the results of Feinsinger et al. (1979). Estimated power output was also found to be unrelated to changes in elevation for both normal hovering and hovering during maximal load-lifting, further supporting earlier findings. However, a comparison of power requirements during free flight with the maximum power produced during load-lifting revealed that the power margin (the ratio of maximum power produced during load-lifting to the power required during free hovering) decreased significantly with increasing elevation. Thus, high-elevation hummingbirds are operating with a narrow capacity for flight during competitive or other behaviors that require burst activity.

In addition to the flight costs imposed by low air pressure, flight metabolic rate is affected by the decreased ambient temperature at high elevations. As air temperature decreases, resting hummingbirds increase their metabolic rate, heart rate and breathing rate (Lasiewski, 1963, 1964a; Lasiewski et al.,

1967). Hummingbirds can compensate for these increased physiological costs by falling into torpor and drastically reducing metabolic functions (Carpenter, 1974; Hainsworth and Wolf, 1970; Lasiewski, 1963; Wolf and Hainsworth, 1972). Changes in wingbeat kinematics during hovering at low ambient temperatures are apparently associated with decreased muscle efficiency and thus increased heat production (see Berger and Hart, 1972; Chai et al., 1998).

Little is known about the flight performance of hummingbirds at high elevations. Although wingbeat kinematics and mechanical power output have been the subject of numerous laboratory manipulations in low-density and low-temperature air (Chai et al., 1996, 1998, 1999; Chai and Dudley, 1995, 1996; Dudley and Chai, 1996; Altshuler et al., 2001), no study has yet to incorporate the full variety of environmental features characteristic of high elevation to assess whole-animal flight capacity. Interesting areas of research will include measurements of wingbeat kinematics and power margins at high elevations to determine how hummingbirds compensate for the increased costs of flight. In addition, it has been suggested that hummingbirds at high elevations often perch or land on the ground to feed. It would be worthwhile to obtain time budgets for flight behaviors across elevations to determine whether hummingbirds adjust their flight modalities accordingly. Casual observations of large species in the high Andes also suggest that these taxa may use bounding and undulating flight, in contrast to low-elevation taxa, which engage in continuous flapping flight.

Directions for future research

Even for the best-studied of hummingbird species, characterization of the flight envelope is restricted to but a small subset of possible features of axial and torsional agility. Courtship displays, territorial defense and rapid accelerations and turning during chases all represent unexplored features of aerial performance that may be critical to survival and reproduction. The spatial scales over which many such behaviors occur pose logistical challenges to investigators; display dives of male hummingbirds, for example, often occur at heights of tens of meters. In experimental contexts, however, three-dimensional tracking of wing and body positions is readily tractable using infrared-reflective markers and automated image reconstruction from multiple camera views. A variety of interesting biomechanical and evolutionary hypotheses can be validated once various features of maneuverability can be quantitatively assessed. For example, are small hummingbirds more agile in body rotation than larger ones? Are those features of hummingbird mating systems that involve such maneuvers more likely to evolve in smaller taxa? Does the widespread sexual dimorphism seen among hummingbirds have functional implications for flight performance above and beyond gender differences in body mass and wing area? Modulation of stroke amplitude is clearly one important means used by hummingbirds to regulate total force output, yet the time courses of variable force production and associated accelerations have not been described for any maneuver. It will be equally informative to determine, under field conditions, the extent to which such capacities are actually elicited by various agents of natural and sexual selection.

Adaptation to montane conditions has been a major feature of hummingbird evolution, yet most information about hummingbird flight derives, for anthropogenic reasons, from studies within laboratories at or near sea level. Parallel reductions in air density, oxygen partial pressure and air temperature represent important abiotic challenges that can be decoupled in laboratory contexts, but that also may be correlated with biotic features of the environment and that influence flight behavior. For example, are there systematic changes with elevation in the quantity and composition of floral rewards obtained by hummingbirds? Are hovering duration and territoriality adjusted accordingly? Can variable floral geometry influence wingbeat kinematics and associated power expenditure? Does specificity of co-evolutionary mutualism between hummingbirds and flowers vary across elevational gradients? Does latitudinal migration in a minority of trochilid taxa derive evolutionarily from the capacity to engage in altitudinal migration? Seasonal movements up and down mountains are well-known in many South American hummingbird taxa and present an excellent opportunity to assess behavioral and biomechanical responses to natural hypobaria.

Finally, we wish to draw attention to the other, lesser known lineage of hovering vertebrates. Glossophagine phyllostomids, also known as flower bats, are important neotropical pollinators that regularly engage in hovering, albeit for relatively short periods (Winter and von Helversen, 2001). The 32 described glossophagine species range in mass from 7 to 32 g and thus easily exceed in body size the largest hummingbirds (see von Helverson, 1993). In bats generally, the anatomical connection of the wings to the hindlegs yields a relative increase in wing surface area, but also limits rotational capacity about the longitudinal wing axis. The kinematic symmetry between down- and upstrokes characteristic of hovering hummingbirds is thereby precluded, yet glossophagines nectaring at flowers are remarkably stationary. Instead of half-stroke symmetry, glossophagines rotate only the distal regions of the wing during the upstroke (von Helversen, 1986), but apparently use faster tip velocities to generate the requisite weight support. Also, the much lower wing loadings of glossophagines relative to hummingbirds yield substantially lower mass-specific costs of hovering mediated *via* a reduction in induced power requirements (see Winter, 1998; Voigt and Winter, 1999).

Hovering is extremely rare among volant vertebrates, yet size limits to hovering performance, be they aerodynamic or energetic in character, remain poorly understood. Why is sustained hovering of such restricted taxonomic occurrence, and why did it evolve only in the New World? How exactly did hummingbirds evolve from a fast-flying, swift-like ancestor? Armed with a well-resolved phylogeny and the

apparatus of modern flight biomechanics, students of hummingbird biology are now well equipped to answer these interesting questions.

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