

Of Hummingbirds and Helicopters: Hovering Costs, Competitive Ability, and Foraging Strategies

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ABSTRACT: Wing morphology and flight kinematics profoundly influence foraging costs and the overall behavioral ecology of hummingbirds. By analogy with helicopters, previous energetic studies have applied the momentum theory of aircraft propellers to estimate hovering costs from wing disc loading (WDL), a parameter incorporating wingspan (or length) and body mass. Variation in WDL has been used to elucidate differences either among hummingbird species in nectar-foraging strategies (e.g., territoriality, traplining) and dominance relations or among gender-age categories within species. We first demonstrate that WDL, as typically calculated, is an unreliable predictor of hovering (induced power) costs; predictive power is increased when calculations use wing length instead of wingspan and when actual wing stroke amplitudes are incorporated. We next evaluate the hypotheses that foraging strategy and competitive ability are functions of WDL, using our data in combination with those of published sources. Variation in hummingbird behavior cannot be easily classified using WDL and instead is correlated with a diversity of morphological and physiological traits. Evaluating selection pressures on hummingbird wings will require moving beyond wing and body mass measurements to include the assessment of the aerodynamic forces, power requirements, and power reserves of hovering, forward flight, and maneuvering. However, the WDL—

helicopter dynamics model has been instrumental in calling attention to the importance of comparative wing morphology and related aerodynamics for understanding the behavioral ecology of hummingbirds.

Keywords: behavioral ecology, energetics, flight, hovering, hummingbird, wing morphology.

The study of animal flight has rapidly advanced through recent experiments using dynamically scaled robotic models of flying animals (Dickinson and Götz 1993; Ellington et al. 1996; Dickinson et al. 1999) and flow visualization of the fluid movements produced by real animal wings (Willmott et al. 1997; Srygley and Thomas 2002; Spedding et al. 2003). It is now clear that animals employ a diverse suite of aerodynamic mechanisms to generate the forces necessary to stay aloft, and new research is focusing on how flying animals can manipulate the fluid medium and generate forces to perform complex maneuvers (Dudley 2002; Fry et al. 2003). Historically, as the science of animal flight has progressed, theories linking flight performance and animal behavior have followed thereafter. A model taxon for the marriage of aerial animal behavior and aerodynamics has been the hummingbirds, which have easily observable behaviors and the most energetically demanding flight modes of any volant vertebrate. Because present-day aerodynamic theories of animal flight are more realistic than the simpler models previously used to analyze hummingbird behavioral ecology, it is timely to reevaluate hypotheses relating hummingbird flight mechanics to their behavior.

Prior aerodynamic analyses of hummingbird hovering flight relied on principles from aeronautics using force measurements from stationary or revolving wings. Weis-Fogh (1972, 1973) adapted the Rankine-Froude momentum theory of propellers as applied to helicopter rotors to estimate the power requirements of hovering animals including hummingbirds. In essence a quasi-steady approach, this helicopter dynamics model states that the average pressure exerted on the surrounding air by a

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hoverer is proportional to its weight and is inversely proportional to the area over which downward momentum is generated by a geometric actuator disc. In animals, the area of the actuator disc is best defined as the horizontal projection of the area swept out by the wings during the wingbeat; in the theory's simplest form, downward air flow induced by the actuator disc is assumed to be of constant magnitude in time and across the disc area (Ellington 1984a). For animals the size of hummingbirds, much of the aerodynamic cost of hovering is assumed to be associated with this downward momentum flux (the so-called induced power requirement). The helicopter dynamics model has been used to compare induced power requirements in hummingbirds for which body weight and certain features of wing morphology and kinematics are either known or assumed (Feinsinger and Chaplin 1975; Feinsinger and Colwell 1978; Feinsinger et al. 1979).

Because hovering hummingbirds beat their wings nearly horizontally (Stolpe and Zimmer 1939), the area swept out by the wings can be taken to be the actuator disc in question. The ratio of body weight to this area has been termed wing disc loading, hereafter WDL (Weis-Fogh 1972, 1973). Epting and Casey (1973) introduced WDL to the hummingbird literature and defined the actuator disc area as $\pi(b/2)^2$, where b is the wingspan. This definition explicitly assumes that the wings rotate about a point in the center of the body and that each wing flaps through a stroke amplitude of 180° . A definition of WDL conforming to the above criteria has been repeatedly used as a surrogate measure for induced power requirements in hovering (Epting and Casey 1973; Feinsinger and Chaplin 1975; Feinsinger and Colwell 1978; Feinsinger et al. 1979; Epting 1980; Carpenter et al. 1993b). However, this model contains several uncorroborated assumptions. One potential problem is that wingspan is usually estimated from the regression of Greenewalt (1975) relating this parameter to the chord of the closed (folded) wing f (a standard ornithological measure sometimes called "wing length," available for many species from the literature), rather than actually measuring wingspan directly. This approach eliminates species-, sex-, and age-specific variation due to differences in wing proportions (Stiles 1995). Because the wings rotate about the shoulder joints rather than about a single body midpoint, a true measure of wing length would be a more accurate estimate of disc radius than using wingspan for disc diameter. With respect to wingbeat kinematics, the stroke amplitude is often much less than 180° (Chai and Dudley 1995; Chai and Millard 1997). Thus the usual calculation of WDL will tend to overestimate the area of the actuator disc and underestimate the true WDL and induced power requirements.

Here we first illustrate how the predictive power of the helicopter model for induced power requirements of hummingbirds is increased as more detailed morphological and kinematic data are incorporated. Values for different methods of calculating WDL are compared to estimates of induced power according to the vortex model of Ellington (1984a, 1984b). The morphological quantities required for Ellington's model include body mass, wing length, wing area, distribution of wing area along wing length, and aspect ratio of the wings. Kinematic parameters include stroke amplitude, wingbeat frequency, stroke plane angle, and angular velocity and acceleration of the wing assuming simple harmonic motion. Air density, which varies systematically with elevation, is also an integral physical parameter of the model.

Features of hummingbird behavior that have been investigated using the helicopter model of hovering costs include competitive ability and foraging strategy. With respect to the former, the major hypothesis is that dominant individuals will have higher WDL than subordinates (Feinsinger and Chaplin 1975; Feinsinger and Colwell 1978; Feinsinger et al. 1979). Dominance was proposed to correlate positively with WDL and/or inversely to wing length, under the assumption that maneuverability in general and turning speed and angular acceleration specifically should increase as wing size decreases. To evaluate potential links between WDL and competitive ability, we present the results of field observations on competitive interactions among species of hummingbirds along with analysis of previously published data on hummingbird competitive abilities from other authors.

In addition to defending flower clusters or artificial feeders, hummingbirds also engage in another foraging strategy in which the birds "trapline" along a route of smaller patches of undefended flowers (Colwell 1973; Feinsinger and Chaplin 1975; Feinsinger 1976; Feinsinger and Colwell 1978; Stiles and Wolf 1979; Tiebout 1991; Sazima et al. 1995; Garrison and Gass 1999). Feinsinger and Chaplin (1975) proposed that trapliners would maximize foraging efficiency by having low WDL and concomitantly reduced power requirements (Epting 1980), thus yielding more efficient nectar extraction from flowers while hovering. More territorial species and gender or age subclasses, in contrast, could increase foraging efficiency by defending clumped flowers for their exclusive use, thus avoiding nectar loss to competitors (*sensu* Gill 1978). Selection for efficient hovering would therefore be relaxed, and these territorial birds might instead be under selective pressure to increase the speed and maneuverability of flight, the better to chase intruders. Hence, higher WDL should characterize territorial hummingbirds relative to trapliners. Here, we reexamine this

Table 1: Regression coefficients and probability values for regressions between loading values and body mass-specific induced power requirements of three species of hummingbirds

Variable and Sex	<i>Selasphorus rufus</i>		<i>Thalurania furcata</i>		<i>Phaethornis koepckeae</i>	
	R^2	P	R^2	P	R^2	P
P_w :						
Females	.361	.0232	.639	.0097*	.387	.3915
Males	.480	.0263	.148	.2435	.007	.8176
WDL_b :						
Females	.242	.0742	.855	.0004*	.058	.6022
Males	.506	.0211	.034	.5875	.037	.5948
WDL_f :						
Females	.353	.0250	.819	.0004*	.039	.6730
Males	.554	.0136	.014	.7328	.011	.7725
WDL_R :						
Females	.682	.0003*	.940	<.0001*	.226	.2810
Males	.632	.0060*	.263	.1068	.004	.8648
WDL_A :						
Females	.701	.0002*	.994	<.0001*	.268	.2343
Males	.762	.0010*	.935	<.0001*	.452	.0331

Note: Significant α levels were determined with sequential Bonferroni correction (Rice 1989). WDL = wing disc loading.

* Significant after Bonferroni correction.

hypothesis using additional published data on foraging behavior of hummingbirds.

Morphology and the Costs of Hovering

Induced Power Estimation

We examined the connection between WDL and the power costs of hovering using 10 male and 14 female rufous hummingbirds (*Selasphorus rufus*), nine female and 11 male fork-tailed woodnymphs (*Thalurania furcata*), and seven female and 10 male Koepcke's hermits (*Phaethornis koepckeae*). These birds were captured using mist nets or feeder traps in Colorado and southeast Peru and were subsequently tested for flight performance. Immediately upon capture, body masses were measured using a digital balance (Acculab PP2060D), and for each bird the folded wing chord and the wingspan were measured to the nearest 0.5 mm. An image of the wing was recorded by holding the left wing of each bird against graph paper and then filming the stationary wing with a handheld video camera (Sony Video 8XR CCD-TRV16). Still images were digitized from video film using Adobe Premiere (version 5.0.1) and were imported into NIH Image (version 1.6.2) for subsequent analysis. Scale within images was set using known linear distances on the filmed graph. Wing length (R) was first measured from the wing outline, and spanwise wing chords were then determined at 1-pixel intervals using the plot profile function of NIH Image. Total wing area (S ;

for both wings) was then calculated as the sum of the areas of each wing strip, defined as the wing chord (in millimeters) multiplied by the width (in millimeters) of each pixel.

Flight trials were carried out in a chamber (0.45 m \times 0.45 m \times 0.9 m) large enough to avoid boundary effects. The wingbeat kinematics of hovering birds were filmed using a Sony Video 8 CCD-TR44 focused on a mirror oriented at 45° above the flight chamber to obtain horizontal projections of wing motions. The camera recorded flight sequences at 60 Hz with a 1/4,000 shutter speed. Frame-by-frame analysis of video films allowed measurement of the stroke amplitude of the wings and the wingbeat frequency. Wingbeat frequency was calculated using the interaction frequency between the wing stroke cycle and the camera filming rate (Chai and Dudley 1996). Wing stroke amplitude was measured from extreme wing positions within the wingbeat using a protractor held against a flat video screen. Wingbeat kinematics, physical properties of local air, and morphological characteristics of each bird were then used to calculate body mass-specific induced power output (Ellington 1984b; Wells 1993). Further details of these methods for hummingbirds are given by Chai and Dudley (1996).

Load estimates for flying animals consist of ratios of the body weight (body mass \times gravity) to the relevant projection of the wings in the horizontal plane. The simplest estimate, wing loading P_w , uses the area of both wings S as the denominator and thus assumes nothing about wing movement. We compared values of P_w to four estimates of WDL that vary in how the actuator disc is calculated: WDL_D , using wingspan b from the Greenewalt (1975) regression of this variable on the measured chord of the folded wing f ; WDL_b , using the measured wingspan b ; and WDL_R , using the measured wing length R . In each of these calculations, we assumed stroke amplitude of 180°. Our final estimate, WDL_A , employs a kinematically based version of the actuator disc, defined as the measured stroke amplitude of the wings multiplied by the measured wing length squared (Ellington 1984a). This final derivation represents the actual area swept out by the wings and is thus the most accurate measure of the actuator disc area (Ellington 1984a). The explanatory power of P_w and the different definitions for WDL was assessed using regressions of the induced power costs against the five values of loading.

Predicting Induced Power Requirements from WDL

For both genders of all three species, the coefficients of determination were maximal with the inclusion of both wing length and wing stroke amplitude in the WDL_A model (table 1). Relative to WDL_R , the increase in predictive

power obtained by incorporating stroke amplitude was considerable for males but relatively modest for females. Induced power requirements were significantly correlated with all of the loading models for females of *T. furcata* and were not significant for any of the models for both genders of *P. koepckeae*. WDL_f and WDL_b performed poorly relative to WDL_R in most cases and to WDL_A in all cases, indicating that wingspan, however calculated, is inferior to wing length for calculating the actuator disc area and for predicting induced power. Appreciable error is incurred by assuming that the wings rotate about the geometric center of the body rather than about the shoulder joints and by assuming a wing stroke amplitude of 180° . The simplest metric for comparison is the wing loading P_w , which makes no assumption concerning the axis of rotation or the stroke amplitude of the wings; its ability to explain variation in induced power costs is comparable to that of WDL_b and WDL_f .

Competitive Ability

Assessing Dominance

Because many hummingbird species hold and defend territories, it is relatively easy to observe competitive encounters between pairs of con- or heterospecifics as birds compete for flower or feeder access. In a typical scenario, one hummingbird will perch while observing a cluster of flowers or a feeder. As invaders attempt to feed from this territory, the holder will chase the intruder away. In a variation on this theme, a vagrant hummingbird may notice another hummingbird feeding from a patch and attempt to chase off the second bird to free up the patch. By observing these and other behaviors, dominant and subordinate individuals can be identified as the chaser and the chased, respectively. Such observations have been used to study interspecific competition and community structure in many hummingbird communities (Feinsinger 1976; DesGranges 1978; Kodric-Brown and Brown 1978; Kuban and Neill 1980; Feinsinger et al. 1985).

Of the species-rich hummingbird communities in the tropics, three have been studied intensively with respect to interspecific competition: the cloudforest of Monteverde in Costa Rica (Feinsinger 1976), the Volcan de Colima in Mexico (DesGranges 1978), and the islands of Trinidad and Tobago (Feinsinger et al. 1985). From observations of numerous chases and other competitive interactions over the course of many months, large records of aggressive interactions with clear winners and losers were assembled and are presented in the form of dominance matrices from which the intensity of reciprocal competitive interactions can be gauged.

We have studied tropical hummingbird communities

along an elevational gradient in southeast Peru in the Departments of Cusco and Madre de Dios between December 1998 and October 1999. Nine sites were visited, spanning an elevational range from 400 to 4,300 m. Over the course of the study, we spent 510 h in formal observations of focal flower patches, with each observation period lasting 1 h. In addition, we recorded the outcomes of aggressive encounters that were casually observed as we were engaged in other field activities. In total, we recorded 469 chases within and among 29 species at seven of the study sites, but most of the chases (401) were between conspecifics (appendix table A1, available in the online edition of the *American Naturalist*). Of the intraspecific chases, most of these were between individuals of *Heliodoxa leadbeateri*, and in many cases it was also possible to distinguish males and females of this highly aggressive species.

Does Dominance Correlate with WDL?

To test the hypothesis that birds with high WDL are competitively dominant to birds with lower WDL, we compared the WDL values of species that consistently either won or lost in pairwise interactions from the studies in Costa Rica, Mexico, and Trinidad and Tobago, as well as from our own study in Peru. We define dominance as success in more than 70% of pairwise interactions, regardless of the number of interactions for any given pair. Although this criterion treats all pairwise interactions equally, including those in which only one chase was observed, this method does not bias the results with respect to the hypothesis being tested.

Values for WDL_f for the species from Costa Rica, Mexico, and Trinidad and Tobago were available from the original articles (Feinsinger 1976; DesGranges 1978; Feinsinger et al. 1985). We also collected morphological and kinematic data for the species in our Peruvian study. Hummingbirds were captured in mist nets, measured immediately, filmed in the flight chamber, banded, and then released. The protocols for measuring morphology, filming free flight, and acquiring kinematic data were the same as for hummingbirds in Colorado. Values for WDL_A as well as the elevational sites at which the species were encountered are given in table 2, available in the online edition of the *American Naturalist*. These values are species averages including morphological and kinematic data for what in some species is a broad elevational range. Elevation-specific values for WDL_A are available upon request.

The WDL values for interspecific species pairs in which one of the species consistently won are plotted in figure 1. If the hypothesis that competitively dominant birds had higher WDL than subordinate birds were supported, then the points in the graphs would tend to fall in the shaded triangle. No such pattern was detected for any of the com-

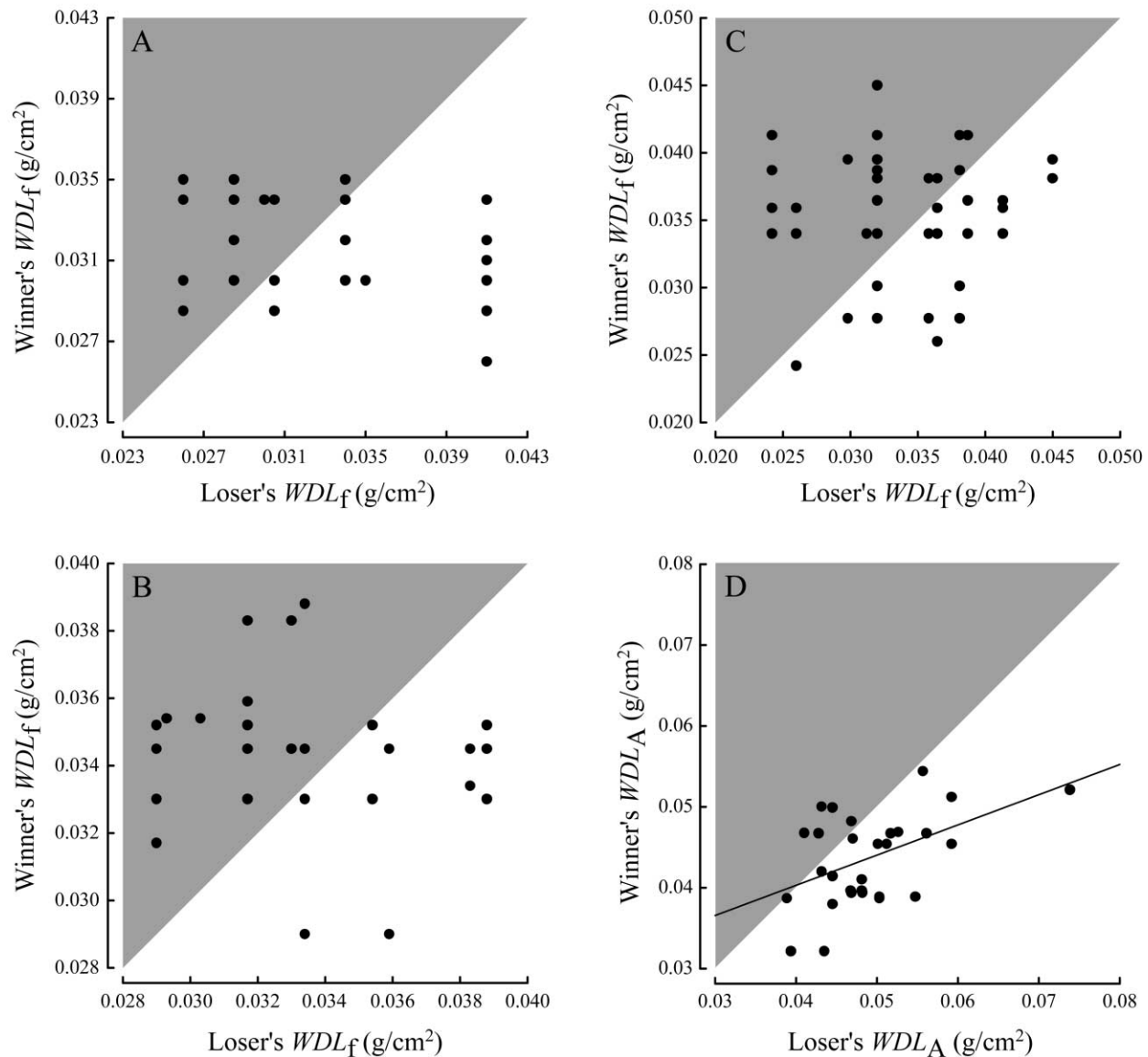


Figure 1: Wing disc loading (WDL) values for species pairwise interactions in which one species (winner) consistently dominated another species (loser). The hypothesis that dominant species have higher WDL than subordinate species would be supported if all or most of the data fell in the shaded region. This hypothesis was not supported with the data from Costa Rica (A), Trinidad and Tabago (B), or Mexico (C), in which WDL was calculated from the folded wing chord. The hypothesis was also unsupported when WDL was calculated using measured kinematics and wing length for Peruvian hummingbirds (D).

munities studied thus far. The communities in Monteverde, Costa Rica ($y = -0.138x + 0.037$, $R^2 = 0.097$, $P > .1$), and Trinidad and Tobago ($y = -0.086x + 0.037$, $R^2 = 0.016$, $P > .5$) actually had a slight tendency for birds with lower WDL_f to be dominant, but the regression model explained little of the variation observed in competitive dominance. The community in Volcan de Colima, Mexico, exhibited no relationship between WDL_f of the dominant

and subordinate species ($y = 0.0260x + 0.035$, $R^2 = 0.001$, $P > .8$).

Data for competitive interactions across the elevational gradient in Peru are plotted in figure 1D. Values for WDL_A represent site-specific means for the dominant or subordinate species, and no species pairs were observed to compete at more than one site. Unlike the hummingbird communities studied thus far, these data ex-

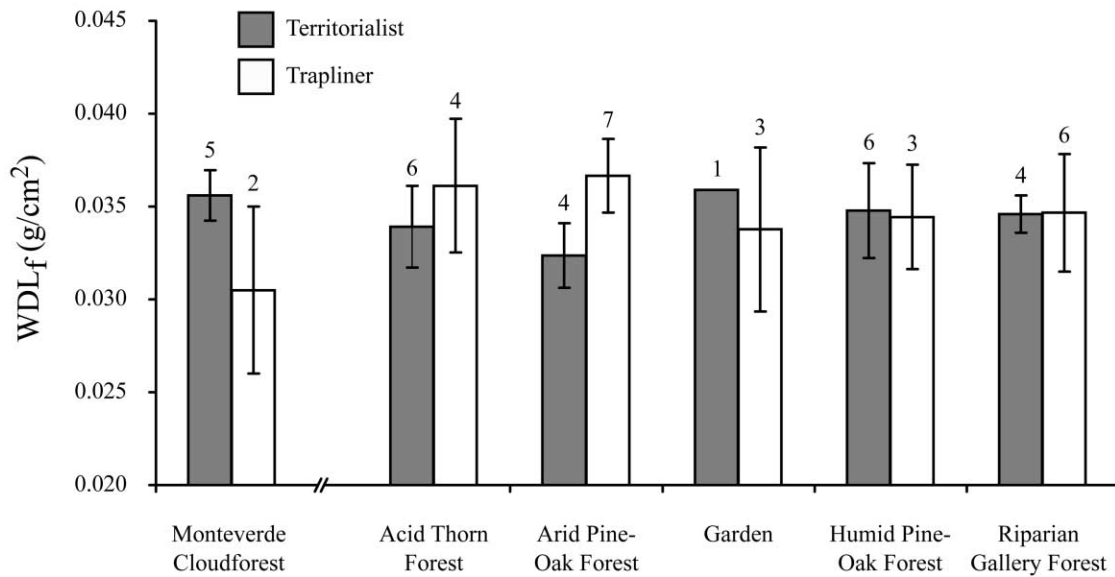


Figure 2: The mean wing disc loading (WDL_f) values for territorial and traplining hummingbirds. Bars are standard errors about the mean, and sample sizes are given above.

hibit a significant pattern between WDL and competitive ability ($y = -0.374x + 0.025$, $R^2 = 0.227$, $P < .01$). However, this is the opposite pattern than predicted because the slope is <1 and the majority of the points fall outside the shaded triangle. These results indicate that losers have a consistently higher WDL_A than the winners. This result is robust and remains significant using each of the formulas for calculating either WDL or wing loading (all $P < .05$).

Foraging Strategies

Besides holding and defending territories, hummingbirds also frequently feed from undefended flowers and “trap-line” among dispersed individual flowers or small clusters of them. The major hypothesis is that territorial species have high WDL and traplining species have low WDL , corresponding to high and low power requirements for flight, respectively (Feinsinger and Chaplin 1975). Observations of foraging behavior and classification of hummingbird species into territorial and traplining guilds have been made at the communities of Monteverde in Costa Rica (Feinsinger 1976) and the Volcan de Colima in Mexico (DesGranges 1978).

The foraging behavior of Monteverde hummingbirds has been evaluated in two articles, with slight differences in behavioral classification (Feinsinger 1976; Feinsinger and Colwell 1978). Here we restrict our analysis to the resident Monteverde community for species that are un-

equivocally classified as either territorial or traplining in these prior studies. Under such criteria, territorial hummingbirds in the community are made up of males and females of *Amazilia saucerrottei*, *Amazilia tzacatl*, *Hylocharis eliciae*, and *Philodice bryantae* and males of *Lampornis calolaema*. Traplining hummingbirds include males of *Chlorostilbon canivetii* and females of *Heliomaster constantii*. Values for WDL_f of these hummingbirds at Monteverde are given in Feinsinger and Chaplin (1975). Hummingbirds of the Volcan de Colima community in Mexico were observed over eight months in five habitats (DesGranges 1978). Some taxa that occurred in multiple habitats switched foraging strategies as the species assemblage also varied among habitats. Values for WDL_f of hummingbirds at the site were also presented by DesGranges (1978).

Mean values of WDL_f for territorial and traplining hummingbirds at Monteverde and at the five habitats of Volcan de Colima are presented in figure 2. Overall, the WDL_f values for territorial and traplining hummingbirds are very similar. These data were analyzed with a two-way ANOVA. The two independent variables were foraging behavior (territorial vs. traplining) and site, whereas WDL_f was the dependent variable. None of the model terms were significant (all $P > .7$). Furthermore, the null hypothesis of no difference between values of WDL_f for hummingbirds employing different foraging strategies was not rejected when the data sets from Costa Rica and Mexico were tested separately (all $P > .15$) and when each species was included only once in the analysis ($P > .5$).

Discussion

We have shown that wing disc loading (WDL) is an unreliable predictor of induced power costs but functions best when measured wing lengths and actual stroke amplitudes are used to calculate the area of the actuator disc. Use of wingspan or folded wing chord significantly reduces the predictive power of WDL calculations and weakens conclusions regarding hovering costs. The comparative value of wing disc loading so calculated (WDL_f) is further compromised because the relationship between folded wing chord and wing length is not constant across sex-age categories either within or among species; wings vary in relative proportions as well as in length (F. G. Stiles, unpublished data). Two major hypotheses relating WDL to hummingbird behavior were tested, and the available data were found to support neither one. No evidence was found to suggest either that high WDL confers a competitive advantage or that territorial hummingbirds have higher WDL than do traplining hummingbirds.

A central tenet of the WDL-helicopter hypothesis is that high WDL increases maneuverability and competitive advantage (Feinsinger and Chaplin 1975; Feinsinger and Colwell 1978; Feinsinger et al. 1979). However, maneuverability refers to diverse aspects of torsional and axial agility. It can be generally defined as the ability to change the speed and direction of movement (Dudley 2002) and sometimes is specifically defined as the minimum turning radius without loss of momentum (Norberg 1994). However, under this more specific definition, maneuverability actually decreases with high wing loading because larger wings are required to generate aerodynamic forces during the slow flight of turns if stalling is to be prevented (Norberg 1994). Similarly, some components of axial agility in vertical load lifting and horizontal forward flight for hummingbirds also increase with decreasing WDL (Chai et al. 1997, 1999), although axial acceleration performance has not been evaluated. Experimental data for torsional agility in hummingbirds is also lacking, but the dependence on WDL is likely to be context specific. For example, acceleration for roll in bats is negatively correlated with wing loading during slow flight speeds but is positively correlated with this parameter during high flight speeds (Norberg 1994). Thus much available data suggest that hummingbird maneuverability is enhanced at lower WDL, but the links between competitive ability and specific aspects of acceleration and torsional agility in particular have not been established.

The best-known and most universal behavioral difference between the genders in hummingbirds is the much stronger territorial behavior of males. Males are more likely to defend rich nectar sources (or feeders) against all other hummingbirds regardless of species or body size, whereas

females are more likely to move more widely between poorer sources or to poach nectar furtively from the territories of males (Pitelka 1942; Bené 1946; Stiles 1973; DesGranges 1978; Kodric-Brown and Brown 1978; Carpenter et al. 1993a). Hummingbird competitive behavior has been most intensively studied in the species with breeding ranges north of the border regions between the United States and Mexico. These hummingbirds are from the bee clade (*sensu* Bleiweiss et al. 1997), which are also among the smallest hummingbirds in the family Trochilidae (Schuchmann 1999). Small hummingbirds are atypical because these birds exhibit reversed sexual dimorphism relative to medium- and larger-sized species. In small hummingbirds, the females are larger than males, whereas males of larger hummingbird species are also typically larger than conspecific females, a pattern known as Rensch's rule (Colwell 2000). For all hummingbird taxa distributed north of the border regions between the United States and Mexico, males are smaller and have higher WDL than females (F. G. Stiles, unpublished data). In addition to lower body mass, higher WDL in males is also unusual in tropical hummingbirds, as suggested by the data of Stiles (1995). Thus, the perception that high WDL confers competitive advantage in hummingbirds may have arisen in part because many published observations refer to species in which males have higher WDL due to phylogenetic associations.

Observations of chases illustrate discrete competitive outcome but alone cannot fully classify dominance status among hummingbirds. Because dominant hummingbirds are attempting to defend either feeding or breeding territories, measurements of success in associated pursuits should also be incorporated. With regard to feeding territories, Pimm et al. (1985) introduced an index of hummingbird competition that measures the ability to dominate a preferred habitat, namely a site with an artificial feeder containing high molarity sucrose. Time spent feeding at the high sucrose feeder is then compared to time spent at a low molarity feeding site, enabling species-specific values of dominance to be determined. When studying natural flower visitation, flowering patches of different nectar quantity and quality could be substituted for artificial feeders. Dominance at preferred feeders has been used to detect subtle changes in competitive ability according to variable competitor density and information about habitat types (Mitchell 1989; Sandlin 2000a, 2000b). Use of this or other techniques to discreetly quantify and classify dominance will benefit further study of the link between flight performance and competitive ability.

Similarly for competitive behavior, our analysis of foraging behavior did not reveal a relationship with WDL. However, the distinction between territorial and traplining behavior in hummingbirds is almost certainly an oversim-

plification of actual foraging options. Feinsinger and Colwell (1978) proposed six community roles based on qualitative observations of nectar foraging behavior from multiple sites, which were found to correlate with differences in body size and WDL_f as well as with bill length and foot size. In addition, insect foraging behavior has been observed to fall into discrete categories that also correlate with morphology (Stiles 1995). The emerging view is that hummingbirds have a menu of foraging options, and the current challenge is to understand what drives particular choices and how hummingbirds are limited to a subset of these options. The quantitative approach to studying hummingbird competitive ability has proven powerful and is likely to also clarify the influence of flight performance on foraging behavior.

Finally, we wish to emphasize that future attempts to link hummingbird behavior with flight performance would benefit from examining these traits in the context of phylogeny. It is now recognized that species cannot be treated as independent and that trait values must be weighted relative to phylogenetic relationship (Felsenstein 1985). A robust molecular phylogeny of the major lineages of hummingbirds is now available (*sensu* Bleiweiss et al. 1997) along with lower-level coverage within some of the major clades (Gerwin and Zink 1989; Gill and Gerwin 1989; Roy et al. 1997; García-Moreno et al. 1999), and larger analyses should appear shortly.

Conclusions

Despite the obviously close relationship between power requirements and the body weight and wing area of hummingbirds, estimations of WDL do not clearly predict hummingbird hovering costs. Flapping hummingbird wings are more complex and variable than helicopter rotors, and the sole wing metric entering into calculation of WDL (wing length or span) is but one of many parameters that will have to be considered before deeper understanding of hummingbird flight is possible (Altshuler and Dudley 2002). Flapping wings in general cannot be modeled as actuator discs imparting a constant downward pressure impulse but rather are oscillating structures that generate complex vortices and time-dependent fluid flows (van den Berg and Ellington 1997a, 1997b; Dickinson et al. 1999; Sane and Dickinson 2001, 2002; Spedding et al. 2003). In retrospect, the main contribution of the helicopter-WDL model has been to call attention to the importance of wing morphology and kinematics in understanding hummingbird flight and behavior. Further progress will come from in-depth study of the power requirements and aerodynamic mechanisms used by hummingbird for hovering, forward flight, and maneuvering, in combination with

quantitative measures of foraging and competitive behavior.

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