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WING MORPHOLOGY AND FLIGHT BEHAVIOR OF SOME NORTH AMERICAN HUMMINGBIRD SPECIES

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Abstract.—We explored the relationship between wing morphology and flight behavior with respect to sex and age in five species of North American hummingbirds. We first measured the length, chord or "width," and area of entire hummingbird wing planforms. We then calculated additional parameters of wing shape and size, including aspect and shape ratios, degree of taper or "pointedness," wing loading, and wing disc loading (WDL). Wings of adult males are not only shorter but also more narrow and tapered than those of adult or immature females; immature males have larger wings and lower WDL, more like those of females. A proposed relationship between WDL and territorial behavior and dominance is not supported, given that adult and immature males show similar feeding territoriality outside the breeding season but females rarely do. The more extreme and divergent wings of adult males probably reflect sexual selection in connection with aerial displays that include species-specific sound effects given during the breeding season. North American species are unusual among hummingbirds in showing reversed sexual size-dimorphism (males smaller, with relatively shorter wings), a feature shared with some other small hummingbirds, notably the "*Pygmornis*" hermits. Attempts to explain hummingbird foraging and territorial behavior on the basis of differences in WDL have failed because many aspects of wing morphology, physiology, and flight behavior were not taken into account. Several wing parameters appear more related to other modes of flight than to strategies of nectar exploitation, and the morphology of any given wing represents a compromise between the often conflicting aerodynamic demands of different flight modes. Understanding hummingbird flight will require broad comparative studies of wing morphology and wingbeat kinematics in relation to flight behavior, and new theoretical models and experimental data will be needed to elucidate physiological and aerodynamic mechanisms underlying forward flight and maneuvering. *Received 9 February 2004, accepted 12 January 2005.*

Key words: aerodynamics, flight behavior, hummingbirds, sexual selection, wing morphology.

Morfología Alar y Comportamiento de Vuelo de Unas Especies de Colibríes de Norteamérica

Resumen.—Exploramos la relación entre la morfología del ala y el comportamiento de vuelo con respecto al sexo y la edad en cinco especies de colibríes norteamericanos. Primero medimos el largo, la cuerda o "ancho" y el área de una planforma de cada ala, luego calculamos varios parámetros del tamaño y la forma de cada ala

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incluyendo las razones de forma y aspecto, el grado de "puntiagudeza", la carga alar y la carga del disco alar (wing disc loading o WDL). Las alas de los machos adultos son más cortas, angostas y puntiagudas que las de las hembras adultas y inmaturas; machos inmaturos tienen alas más grandes con WDL más bajas, más similares a las de las hembras. Estos datos no corroboran una supuesta relación entre WDL, comportamiento territorial y dominancia, puesto que machos adultos e inmaturos muestran comportamiento territorial similar fuera de la época reproductiva mientras las hembras rara vez defienden flores. Las alas más extremas y divergentes de los machos adultos probablemente reflejan la selección sexual sobre despliegues aéreos que incluyen sonidos propios de cada especie, producidos por las alas. Los colibríes norteamericanos son excepcionales entre la familia Trochilidae en su dimorfismo sexual invertido (machos más pequeños, hembras más grandes excepto en *Calypte anna*), una característica compartida con algunos otros colibríes pequeños, especialmente los ermitaños "*Pygmornis*"). Los intentos de explicar diferencias en comportamiento de forrajeo y territorialismo con base en WDL fracasaron porque no se tomaron en cuenta muchos otros aspectos de la morfología alar, fisiología y comportamiento de vuelo. Varios parámetros alares parecen ser más relacionados con otros tipos de vuelo que con estrategias de explotación de néctar floral. La morfología de cualquier ala representa un compromiso entre las demandas a veces contrapuestas de diferentes modos de vuelo. Para entender el vuelo de los colibríes sería preciso llevar a cabo estudios comparativos amplios sobre la morfología alar y la cinemática de los aleteos en relación con el comportamiento de vuelo. Se requieren tanto nuevos modelos teóricos como datos experimentales para entender los mecanismos subyacentes del vuelo hacia adelante y las capacidades de maniobra de los colibríes.

Hummingbirds (Trochilidae) are the second-largest strictly New World bird family and the most specialized avian nectarivores (Stiles 1981). The only birds capable of sustained hovering and backward as well as forward flight, they alone can probe flowers without perching. However, within that high degree of locomotor specialization, hummingbirds exhibit considerable diversity in wing sizes and shapes, both within and between species (Ridgway 1892, Stiles 1995). That diversity is only beginning to be understood in aerodynamic, ecological, and behavioral terms.

Previous attempts to link hummingbird ecology and wing morphology have mostly focused on a morphology-based estimate of the power requirements for hovering. Borrowing from the aeronautical literature, Weis-Fogh (1972, 1973) adapted the momentum theory of helicopter rotors to the study of animal flight. In his model, a hovering animal exerts on the surrounding air a mean downward pressure impulse equal to its own weight. The pressure is applied horizontally over the circular area swept out by the wings (the actuator disc), usually assuming a wing stroke amplitude of 180°. Dividing body mass by actuator disc area yields a ratio termed "wing disc loading" (WDL), which corresponds to the pressure impulse required for hovering. This relationship was supported by Epting (1980), who found that mass-specific metabolic input (oxygen consumption) during hovering scaled as $WDL^{0.5}$ but was independent of body mass among seven hummingbird species. Assuming that the downward airflow induced by the wing is constant across the actuator disc (Ellington 1984b), the associated induced power input will be inversely proportional to disc area, in turn a function of wing length (and not of wing span; see Altshuler et al. 2004b). Hence, relatively longer-winged hummingbirds should have lower WDL and thus lower induced power requirements (Epting and Casey 1973). Total power to hover will, however, also involve additional expenditures to overcome profile drag forces on the wings.

The relationship between WDL and induced power was used by Feinsinger and Chaplin (1975) and Feinsinger and Colwell (1978) to interpret hummingbird foraging strategies, competitive ability, and dominance. They posited that selection for efficient hovering should be strongest in nonterritorial hummingbirds like trapliners, and relaxed in those

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able to defend flowers and harvest nectar more predictably. The latter birds should instead be under stronger selection for speed and maneuverability in chases, assumed to increase with decreasing wing length. Thus, low WDL should characterize subordinate trapliners; and high WDL, dominant territorialists. Feinsinger and Colwell (1978) incorporated WDL into a functional-morphological package considered to largely determine a hummingbird's "ecological role." Their "helicopter dynamics" model has been used to explain differences in foraging strategies and dominance among species and age–sex groups of North American hummingbirds by Kodric-Brown and Brown (1978), Brown and Bowers (1985), Ewald (1985), and Carpenter et al. (1993a, b), among others.

Recent studies, however, have called this model into question. Among a diverse assemblage of Costa Rican hummingbirds, predicted within- and between-species relationships between WDL and nectar-foraging did not hold, whereas wing-shape parameters not included in the model showed tight correlations with other behaviors, notably foraging for arthropods (Stiles 1995). Moreover, WDL was found to be a poor predictor of competitive ability, dominance, and nectar-foraging strategy among hummingbird assemblages of Peru, Mexico, and Costa Rica (Altshuler et al. 2004a). The model's failure ultimately reflects its simplicity: only body mass and wing length enter into its calculation, and it applies directly only to hovering. Recent studies with wing models suggest that the aerodynamic forces and associated power expenditure of hummingbird wings also may be influenced by the distribution of the wing's area along its length, its camber, and the sharpness of its leading edge (Usherwood and Ellington 2002, Altshuler et al. 2004a).

Theoretical relationships between wing morphology and efficiency for different modes of flight have been reviewed by Norberg (1990). Aerodynamics theory partitions the mechanical power requirements of flying into aerodynamic power, required to move the flier through the air, and inertial power, required to accelerate and decelerate the wings during each halfstroke (Casey 1981). Inertial power requirements are potentially significant for animals with high wingbeat frequencies, such as hummingbirds, but are difficult to estimate if wing inertial energy is stored elastically between halfstrokes. If inertial requirements are high, smaller wings (of either reduced length or mass) are advantageous in inverse proportion to the degree of elastic storage.

Aerodynamic power is divided into three components: (1) induced power, required to offset the force of gravity; (2) profile power, expended to offset drag on the wings; and (3) parasite power, expended to offset drag on the body. Parasite power is, by definition, independent of wing shape. During hovering and slow forward flight, induced power requirements are assumed to dominate, and larger wings (in length, area, or both) are advantageous. During fast forward flight, profile power becomes dominant over induced power, favoring smaller, narrower wings with a higher aspect ratio (the ratio of a wing's length to its mean chord or "width"). Thus, wing morphology must be interpreted in terms of conflicting mechanical power requirements of different flight modes (Norberg 1990).

A first step toward understanding the variation in hummingbird wing morphology, therefore, will be to characterize in greater detail the wing sizes and shapes in a group of species whose ecology and behavior are relatively well known. Variation in wing morphology can then be related to reported differences in flight behavior; this, in turn, may permit more detailed behavioral predictions from wing measurements for the many species whose ecology is poorly known. The ecology and behavior of North American hummingbirds have been studied in considerable detail, but their wing morphology has been described only superficially. Our objectives here, therefore, are (1) to provide a more comprehensive, quantitative characterization of the wings of different sex–age groups in five species of North American hummingbirds and (2) to interpret differences in wing morphology in terms of reported differences in ecology and behavior.

METHODS

Wing and body-mass data were taken from intact hummingbird carcasses sent frozen to F.G.S. from several U.S. museums or, in a few cases, from birds caught at a feeder. At the Academy of Natural Sciences of Philadelphia (ANSP) or the American Museum of Natural History (AMNH), New York, carcasses were thawed, measured, dissected for sex and age

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determination, prepared as study skins, and either returned to the museum of origin or deposited in the collections of ANSP or AMNH. Body mass was measured to the nearest tenth of a gram with a Pesola spring balance if fresh mass had not been taken. To standardize, we included only birds whose masses were within two standard deviations of the corresponding means specified in the *Birds of North America* (BNA) series (Calder 1993, Robinson et al. 1996, Russell 1996, Baltosser and Russell 2000, Mitchell 2000), thus excluding gravid females and carcasses excessively desiccated in the freezer. A number of carcasses had significant deposits of migratory fat, which was carefully removed manually during preparation and weighed, its mass then being subtracted from that of the intact carcass; in nearly all cases, the resulting masses were much closer to the respective BNA means.

We measured the chord of the closed or folded wing f (the standard ornithological measure of wing "length," though it involves only the distal portion; see Stiles and Altshuler 2004) to the nearest tenth of a millimeter with dial calipers. A tracing was made of the fully extended wing in a standard position, with the long axis of the wing 15–20° anterior to a perpendicular line from the body axis. The remiges were aligned so that their tips formed a straight line over the basal half or more of the trailing edge of the wing, which then curved gradually toward the tip, with the outer primaries fully extended but maintaining their natural conformation (see Fig. 1). This position was chosen to conform as closely as possible to the maximum wing extension revealed by high-speed photographs of hovering hummingbirds (e.g. Greenewalt 1960).

From the tracings, wing length R was measured from the tip of the fifth secondary (the sixth or innermost being reduced in size) to the tip of the longest primary. Because the inner secondaries extend slightly proximally, that measure should closely approximate the distance from the shoulder joint to the wingtip. The ratio f/R is then an indication of the proportion of the whole wing's length that is contributed by the distal (wrist-to-tip) portion. The wing's width was measured between the leading and trailing edges at about the level of the second or third primary; in the standard position, that width is nearly constant over the proximal half or more of most wings and is, in effect, the maximum wing chord (in aerodynamics, the wing chord is defined as any straight-line distance between the leading and trailing edges, measured perpendicularly to the wing's long axis; see Stiles and Altshuler 2004). The ratio of length to width provides one measure of wing shape, termed "aspect ratio" by Stiles (1995); here we call it the shape ratio R_S. Wing area S was measured by the SIGMASCAN program and an area digitizer at a scale of 100 pixels = one inch. The standard aerodynamic aspect ratio is the quotient of twice the square of the wing's length divided by its area; this is equivalent to using the mean wing chord, averaged over the length of the wing. The ratio $R_A/2R_S$ is, in effect, the ratio of mean to maximum wing chord and provides a measure of how abruptly or gradually the wing tapers to a pointed tip, in relation to a rectangular wing (with chord constant at the maximum value throughout). We subtracted 1 from that ratio to set the value for the rectangular wing (zero taper) at zero; we call the resulting parameter "wing taper" or T_W. In practice, T_W varies between ~0.1 for very blunt-tipped, nearly rectangular wings, to 0.4 for the most triangular, pointed wings. Wing loading P_W was calculated as the ratio of body mass m to the area of both wings S in square centimeters. We calculated WDL using wing length R and not wing span, because Altshuler et al. (2004b) found that this procedure gave values of WDL significantly better at predicting induced power requirements. Relative lengths of closed and extended wings (f_{rel}, R_{rel}) were calculated by dividing the respective lengths by the cube root of the body mass for each bird.

We define "adult" as any bird that has completed its first annual (prebasic) wing molt and has therefore acquired definitive remiges (some first-year males may still be molting on the gorget and crown). "Immatures" are birds in their first fall or winter that are full-grown (i.e. no growing flight feathers, bill at adult length) but retain juvenile-type remiges. In most North American species, the annual molt occurs on the wintering grounds, though in the winter-breeding, more sedentary Anna's Hummingbird (*Calypte anna*), it occurs in summer and fall (Stiles 1973, Russell 1996).

We obtained data on wing morphology from individual hummingbirds with representative body masses (see above) of both sexes for five species: Black-chinned (*Archilochus alexandri*),

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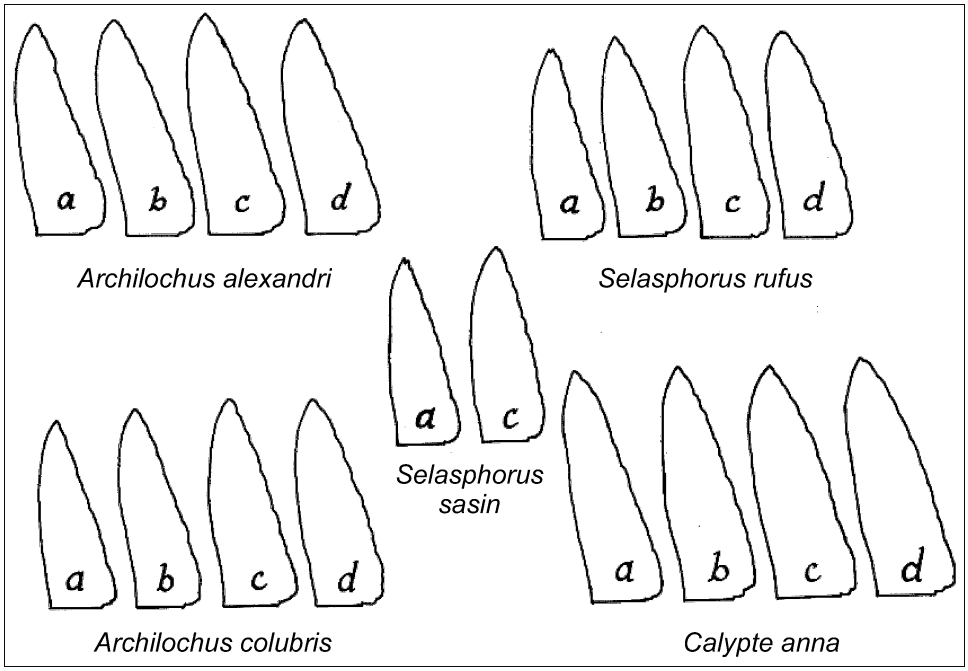


FIG. 1. Representative wing tracings from sex–age categories of five species of North American hummingbirds (a = adult male; b = immature male; c = adult female; d = immature female). Note the smaller, narrower wings of adult males as compared with those of females and immature males, and the more pointed wings of *Selasphorus* spp. and *Archilochus colubris.*

Ruby-throated (*A. colubris*), Rufous (*Selasphorus rufus*), Allen's (*S. sasin*), and Anna's hummingbirds. Sample sizes for *S. sasin* were too small to permit statistical testing (no immatures were measured), and only for *A. alexandri* and *colubris* were enough immatures of both sexes measured to permit statistical comparisons among all sex–age categories. To compare various wing parameters among sex–age groups, we used one-way ANOVA (for sex–age classes in *Archilochus* spp. and interspecies comparisons within sexes of adults). Where significant variation among groups existed, group means were compared using the sequential Bonferroni adjustment to insure a constant error rate of 0.05 for multiple comparisons. Comparisons between adult males and females of *S. rufus* and *C. anna* were made with Student's *t*-tests.

RESULTS

Wing tracings (Fig. 1) clearly show variation in wing size and shape among species, and also among sex–age groups within species in these hummingbirds. The wings of *S. rufus, S. sasin*, and *A. colubris* are noticeably more pointed, especially in adult males. In *A. alexandri,* wings of all sex–age groups are notably blunt-tipped; in adult males, the trailing edge often appears convex because the inner six primaries are relatively shorter, with angular tips. This is also true of immature male *A. colubris*; but in adult males, the outer primaries appear shortened, such that the effect on the wing's planform is much less noticeable. In all species, females appear to have longer and broader wings than adult males, an effect especially notable in *C. anna*; wings of immature males appear to be more similar to those of females. The variations in wing length, combined with differences in body mass, produce differences in WDL (Table 1). Relative lengths of closed and extended wings indicate differences in wing proportions; differences in wing areas combined with variations in body mass yield differences in wing loading (Table 2). Shape and aspect ratios and wing taper also show considerable variation within and between species in North American hummingbirds (Table 3).

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TABLE 1. Means (± SD) for four parameters—body mass (*m*) in grams, length of folded wing (*f*) and wing length (*R*) in centimeters, and wing disc loading (WDL_R) in grams per square centimeter—in sex–age groups of five North American hummingbird species. Note that WDL_R is highest in adult males, except in *S. sasin*. Immatures have lower WDL than adults of the same sex, and that difference is greater in males.

Species	Sex–age group [a]	*n*	*m*	*f*	*R*	WDL_R
Archilochus alexandri	M	9	2.97 ± 0.14	4.322 ± 0.076	4.786 ± 0.178	0.0413 ± 0.0031
	F	9	3.42 ± 0.17	4.702 ± 0.087	5.168 ± 0.135	0.0408 ± 0.0021
	m	5	3.01 ± 0.17	4.520 ± 0.049	5.038 ± 0.120	0.0378 ± 0.0033
	f	6	3.43 ± 0.10	4.687 ± 0.107	5.193 ± 0.103	0.0404 ± 0.0023
A. colubris	M	15	2.84 ± 0.18	3.924 ± 0.081	4.460 ± 0.115	0.0456 ± 0.0027
	F	12	3.15 ± 0.15	4.457 ± 0.117	4.975 ± 0.126	0.0407 ± 0.0030
	m	12	2.80 ± 0.15	4.158 ± 0.069	4.639 ± 0.108	0.0413 ± 0.0027
	f	6	3.11 ± 0.21	4.505 ± 0.134	5.017 ± 0.118	0.0389 ± 0.0021
Selasphorus rufus	M	8	3.01 ± 0.17	4.093 ± 0.074	4.494 ± 0.139	0.0477 ± 0.0025
	F	5	3.40 ± 0.17	4.472 ± 0.064	4.912 ± 0.136	0.0449 ± 0.0018
	m	3	3.00 ± 0.10	4.237 ± 0.038	4.620 ± 0.040	0.0448 ± 0.0020
	f	2	3.35 ± 0.07	4.525 ± 0.021	4.910 ± 0.085	0.0442 ± 0.0006
S. sasin	M	2	2.82 ± 0.04	3.875 ± 0.035	4.385 ± 0.071	0.0468 ± 0.0007
	F	1	3.20	4.170	4.590	0.0483
Calypte anna	M	14	4.31 ± 0.21	4.952 ± 0.078	5.491 ± 0.116	0.0455 ± 0.0022
	F	10	3.94 ± 0.23	5.030 ± 0.077	5.498 ± 0.115	0.0415 ± 0.0023
	m	3	4.15 ± 0.31	5.091 ± 0.020	5.533 ± 0.038	0.0432 ± 0.0036
	f	2	3.90 ± 0.14	5.065 ± 0.064	5.505 ± 0.064	0.0410 ± 0.0005

[a] M = adult males, F = adult females, m = immature males, f = immature females.

Variation in wing parameters among sex and age groups was more pronounced in *A. colubris* than in *A. alexandri* (Table 4). In both, body mass was significantly smaller in males than in females; no age-related differences were apparent within either sex. Adult and immature females had significantly longer wings, in relation to body mass, than adult males in *A. colubris*, with immature males intermediate; the same tendencies were suggested in *A. alexandri* but were not significant. The ratio of closed to extended wings (*f*/*R*) was lowest in adult males in both species, but no sex–age group differed significantly. Adult males of both species showed significantly less wing area than other groups; in both, wing areas of young males were intermediate between those of adult males and females. Wing loading and WDL were highest in adult males of both species, though significantly so only in *A. colubris*; young males were intermediate between adult males and females in both parameters (Table 4; compare Tables 1 and 2). Wings of adult males were narrower (higher R_S and R_A) and more pointed (higher T_W) than those of females in both species; again, values for immature males fell between those for adult males and females, with differences being significant only in *A. alexandri*. In all parameters, values for adult and immature females were similar (Tables 3 and 4).

Comparisons between adult males and females of *S. rufus* and *C. anna* yielded many of the same relationships, though in the latter, males were significantly heavier than females (Table 5). In both, females had significantly longer wings in relation to body mass and greater wing areas, producing significantly lower wing loading and WDL. Adult males showed lower ratios of closed to total wing lengths (f_{rel}/R_{rel}), though the difference was significant only in *C. anna*. In *S. rufus*, males had slightly lower R_S, whereas male *C. anna* had significantly higher R_S; in both, adult males had significantly higher aspect ratios (R_A) and significantly more-tapered wings (higher T_W) than adult females. In nearly all comparisons of wing size and shape, wings of immature males were intermediate between those of adult males and females or closer to the

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Table 2. Measurements of wing size (means ± SD; see text and Table 1) in five species of North American hummingbirds. Note that adult males of all species have smaller wings than other sex–age classes, with resultant higher wing loadings; wings of immature males are more similar to those of females. Differences between species are greater among adult males than females or immatures.

Species	Sex–age group [a]	n	f_{rel} (cm)	R_{rel} (cm)	f_{rel}/R_{rel}	S_1 (cm^2)	P_W (g/cm^2)
Archilochus alexandri	M	9	3.017 ± 0.047	3.340 ± 0.119	0.903 ± 0.026	5.975 ± 0.484	0.248 ± 0.020
	F	9	3.122 ± 0.077	3.430 ± 0.080	0.912 ± 0.032	7.196 ± 0.311	0.238 ± 0.010
	m	5	3.136 ± 0.088	3.496 ± 0.126	0.894 ± 0.033	6.679 ± 0.499	0.227 ± 0.024
	f	6	3.107 ± 0.064	3.443 ± 0.086	0.903 ± 0.025	7.305 ± 0.287	0.236 ± 0.013
A. colubris	M	15	2.774 ± 0.058	3.152 ± 0.073	0.880 ± 0.015	4.991 ± 0.283	0.285 ± 0.015
	F	12	3.041 ± 0.107	3.394 ± 0.106	0.897 ± 0.019	6.488 ± 0.245	0.244 ± 0.017
	M	12	2.948 ± 0.062	3.289 ± 0.101	0.897 ± 0.012	5.527 ± 0.301	0.254 ± 0.018
	f	6	3.110 ± 0.100	3.463 ± 0.057	0.898 ± 0.020	6.598 ± 0.192	0.234 ± 0.014
Selasphorus rufus	M	8	2.817 ± 0.028	3.105 ± 0.070	0.907 ± 0.016	5.072 ± 0.388	0.300 ± 0.020
	F	5	2.988 ± 0.034	3.267 ± 0.051	0.915 ± 0.017	6.337 ± 0.373	0.268 ± 0.013
	m	3	2.938 ± 0.039	3.227 ± 0.016	0.910 ± 0.008	5.485 ± 0.135	0.274 ± 0.015
	f	2	3.024 ± 0.007	3.281 ± 0.034	0.922 ± 0.012	6.511 ± 0.270	0.257 ± 0.005
S. sasin	M	2	2.741 ± 0.036	3.102 ± 0.018	0.884 ± 0.007	4.705 ± 0.247	0.310 ± 0.021
	F	1	2.830	3.114	0.909	5.375	0.298
Calypte anna	M	14	3.044 ± 0.063	3.375 ± 0.068	0.902 ± 0.013	7.335 ± 0.288	0.294 ± 0.015
	F	10	3.182 ± 0.073	3.477 ± 0.073	0.915 ± 0.018	7.992 ± 0.375	0.247 ± 0.012
	m	3	3.170 ± 0.084	3.446 ± 0.104	0.918 ± 0.004	7.825 ± 0.207	0.265 ± 0.022
	f	2	3.205 ± 0.017	3.483 ± 0.023	0.920 ± 0.022	8.072 ± 0.046	0.242 ± 0.005

[a] M = adult males, F = adult females, m = immature males, f = immature females.

TABLE 3. Parameters (means ± SD; see text and Table 1) of wing shape in five species of North American hummingbirds. Note that adult males have narrower (highest shape and aspect ratios) and more strongly tapered wings than adult females; adult males have more strongly tapered wings than immature males, except in *S. rufus*, but no consistent trend occurs in females.

Species	Sex–age group [a]	*n*	Shape ratio (R_S)	Aspect ratio (R_A)	Wing taper (T_W)
Archilochus alexandri	M	9	3.207 ± 0.075	7.682 ± 0.210	0.198 ± 0.015
	F	9	3.169 ± 0.069	7.461 ± 0.207	0.177 ± 0.026
	m	5	3.201 ± 0.097	7.618 ± 0.292	0.190 ± 0.026
	f	6	3.118 ± 0.092	7.389 ± 0.183	0.185 ± 0.015
A. colubris	M	15	3.161 ± 0.062	7.980 ± 0.141	0.263 ± 0.027
	F	12	3.103 ± 0.040	7.634 ± 0.237	0.230 ± 0.033
	m	12	3.138 ± 0.033	7.797 ± 0.176	0.242 ± 0.025
	f	6	3.110 ± 0.044	7.630 ± 0.228	0.227 ± 0.024
Selasphorus rufus	M	8	3.128 ± 0.109	7.981 ± 0.267	0.238 ± 0.023
	F	5	3.206 ± 0.050	7.622 ± 0.200	0.189 ± 0.022
	m	3	3.130 ± 0.026	7.901 ± 0.289	0.262 ± 0.036
	f	2	3.157 ± 0.011	7.408 ± 0.051	0.173 ± 0.012
S. sasin	M	2	3.178 ± 0.060	8.184 ± 0.404	0.287 ± 0.039
	F	1	3.060	7.839	0.281
Calypte anna	M	14	3.334 ± 0.086	8.228 ± 0.223	0.234 ± 0.023
	F	10	3.113 ± 0.070	7.571 ± 0.149	0.216 ± 0.013
	m	3	3.205 ± 0.026	7.828 ± 0.132	0.221 ± 0.013
	f	2	3.128 ± 0.039	7.516 ± 0.252	0.201 ± 0.025

[a] M = adult males, F = adult females, m = immature males, f = immature females.

TABLE 4. Results of statistical analyses comparing various wing parameters (see text and Table 1) among sex–age groups in *Archilochus alexandri* and *A. colubris* using one-way ANOVA. Where value of *F* is significant ($P < 0.05$), significantly different groups are indicated (as determined by sequential Bonferroni adjustment). Where groups do not overlap, differences are indicated by >; where one or more groups overlap, differences are indicated by /. Probability values for *F* are indicated as follows: ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

	A. alexandri		*A. colubris*	
Parameter	*F*	Significantly different groups [a]	*F*	Significantly different groups [a]
m	23.83***	Ff > Mm	13.16***	Ff > mM
R_{rel}	2.85ns	–	24.75***	fF > m > M
f_{rel}/R_{rel}	0.44ns	–	3.85*	–
S	17.85***	fFm > M	92.90***	fF > m > M
P_W	1.77ns	–	21.05***	M > mFf
WDL_R	1.93ns	–	9.72***	M > mFf
R_S	1.65ns	–	3.83*	Mmf/mfF
R_A	3.35ns	–	8.97***	Mm/mFf
T_W	2.68ns	–	4.06*	M > f

[a] M = adult males, F = adult females, m = immature males, f = immature females.

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TABLE 5. Results of comparisons between mean values of various wing parameters (see text and Table 1) of adult males and adult females in *Selasphorus rufus* and *Calypte anna* using Student's *t*-tests (sample sizes of immatures too small to permit statistical analysis). Probabilities are indicated as in Table 4. "Comments" show the value of the given parameter in males versus females where significant differences exist and how the value for immature males compares to those (in virtually all cases, the values for immature and adult females are similar).

	S. rufus		*C. anna*	
Parameter	*t*	Comments [a]	*t*	Comments [a]
m	4.21**	F > M; m ≈ M	4.05**	M > F; m ≈ M
R_{rel}	2.25*	F > M; m closer to F	3.50**	F > M; m closer to F
f_{rel}/R_{rel}	0.82ns	–	2.33*	F > M; m ≈ F
S	5.80***	F > M; m closer to M	4.80***	F > M; m closer to F
P_W	2.38*	M > F; m closer to F	8.34***	M > F; m intermediate
WDL_R	2.43*	M > F; m ≈ F	4.36***	M > F; m intermediate
R_S	0.41ns	–	6.70***	M >F; m intermediate
R_A	2.57*	M > F; m intermediate	8.10***	M > F; m closer to F
T_W	3.78**	M > F; m > M	2.23**	M > F; m closer to F

[a] M = adult males, F = adult females, m = immature males, f = immature females.

latter (Table 5; compare Tables 2 and 3); indeed, in *C. anna*, their wings exceeded in length those of adult females, as might be expected given their greater mass (Table 1).

Highly significant differences among adult males of these four species were found in most wing parameters (Table 6). Males of *C. anna* and *A. alexandri* had significantly longer wings and greater wing areas, whereas those of *A. colubris* and *S. rufus* had shorter wings with less wing area. However, *C. anna* males were also significantly heavier than those of other species, such that their wing loadings and wing disc loadings were similar to those of male *A. colubris* and *S. rufus*; values for P_W and WDL_R of male *A. a.exandri* were significantly lower. The impression of narrow wings in male *C. anna* (Fig. 1) was confirmed by their significantly higher shape ratio (R_S). The most strongly divergent aspect ratio was that of *A. alexandri*

TABLE 6. Results of statistical comparisons among adult males and adult females of four hummingbird species: *Archilochus alexandri* (aa), *A. colubris* (ac), *Selasphorus rufus* (sr), and *Calypte anna* (ca) using one-way ANOVA. Where significant differences were found, significantly different groups of species were determined using the sequential Bonferroni adjustment for multiple comparisons. Parameters are explained in the text and Table 1; probabilities are indicated as in Table 4.

	Adult males		Adult females	
Parameter	*F*	Significantly different groups	*F*	Significantly different groups
m	201.69***	ca > aa.sr/sr.ac	13.16***	ca > aa.sr.ac
R_{rel}	29.87***	ca.aa > ac.sr	7.05**	ca.aa.ac/ac.sr
f_{rel}/R_{rel}	6.96**	sr.aa.ca > ac	1.54ns	–
S	127.80***	ca > aa > ac.sr	50.40***	ca > aa > ac.sr
P_W	17.87***	sr.ca.ac > aa	5.83**	sr > ca.ac.aa
WDL_R	9.06***	sr.ca.ac > aa	7.20**	sr > ca.aa.ac
R_S	11.52***	ca > sr.aa.ac	5.17**	sr.aa/aa.ca.ac
R_A	12.98***	ca.sr/sr.ac > aa	2.38ns	–
T_W	14.82***	ac.sr/sr.ca > aa	11.36***	ac.ca/ca.sr/sr.aa

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(lower), reflecting the blunt-tipped wings and consequently greater mean wing chord of these males, who also showed significantly less-tapered wings than the other species. The highest values of T_W were those of male *A. colubris* and *S. rufus*, confirming the visual impression (Fig. 1) of pointed wings (though the wings of the latter were not significantly more tapered than those of male *C. anna*).

Similar interspecific differences occurred among adult females, but were less pronounced and not significant in several cases; the rank order of species with respect to a given parameter sometimes differed (Table 6; compare Tables 1, 2, and 3). The rather sharp distinction between relatively long- and short-winged species changes, given that only females of *S. rufus* (short) differ significantly from the rest. *Archilochus colubris* has the shortest wingtips (lowest *f*/*R* ratios) in males, but the difference all but disappears in females. Interspecies differences in wing area among males are also found in females, but the order of species with respect to the shape ratio R_S is quite different, with the narrowest wings being those of *S. rufus* and *A. alexandri*, and the broadest those of *C. anna* and *A. colubris*. No significant differences among females were found in aspect ratio (R_A). Only female *S. rufus* differed (significantly) from the rest in their (higher) wing loading (P_W) and WDL (compare Tables 1 and 2). The data indicate that the wings of adult males have diverged much more strongly than those of females in these species.

In nearly all these parameters, sexual differences in *S. sasin* paralleled those in the other species (Tables 1, 2, and 3). Adult males showed lower body mass; absolutely and relatively shorter wings; less wing area; and higher wing loading, shape and aspect ratios, and wing taper. The only notable difference was that the one female had a higher WDL than either of the males; given the tiny sample size, that result should be considered tentative. In many respects, *S. sasin* shows the most extreme wing morphology among the species examined: in both sexes, it has the shortest (absolutely and relatively) and most strongly tapered wings, with the smallest areas and the highest WDLs and wing loadings. This suggests that the species, because of its extreme wing reduction, is operating closer to the physiological and aerodynamic limits for flight than any other. Although that conclusion is certainly tentative, pending examination of adequate samples of all sex–age groups, *S. sasin* might well be especially interesting for further studies of aerodynamic and aerobic limits to flight performance (e.g. Chai et al. 1997, Chai and Dudley 1999, Altshuler et al. 2001, Altshuler and Dudley 2002).

Taking all comparisons together, adult males differed most from other sex–age classes in having smaller wings with respect to all parameters investigated. On average, they also had the lowest ratios of lengths of folded to extended wings (f_{rel}/R_{rel}), which indicates that reductions in wing size have occurred disproportionately in the distal part of the wing. In all wing dimensions, immature males tended to be intermediate or to more closely resemble adult and immature females (which scarcely differed). Differences among adult males of these species were much greater than those among adult females in nearly all parameters. Finally, *A. alexandri* showed much smaller differences in wing morphology among sex–age classes than any other species studied.

Discussion

Differences in flight behavior among sex–age groups.—Among North American hummingbirds, males are much more likely to defend rich nectar sources (or feeders) against all other hummingbirds, regardless of species or sex, whereas females either move more widely between poorer sources or poach nectar furtively from male territories (Pitelka 1942, Bené 1946, Stiles 1973, DesGranges 1978, Kodric-Brown and Brown 1978, Carpenter et al. 1993a; see also the BNA citations above). During the breeding season, males defend mating territories that may or may not contain flowers; such breeding territoriality often involves intense male–male competition, including chases and aerial displays (e.g. Stiles 1982, Baltosser and Russell 2000, Mitchell 2000). Dive displays, in which males attain much higher velocities than in fast forward flight (Pearson 1960, Stiles 1982), are performed on hundreds of occasions in the course of a breeding season. The final phase of courtship consists of violently oscillating "shuttle" displays close to the female. Both types of display involve specific sound effects, some of which are produced by the wings (see Miller and Inouye 1983).

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Feeding territoriality in fall and winter is similar in adult and immature males of North American hummingbirds, allowing for the fact that adults usually dominate immatures (Stiles 1973, Carpenter et al. 1993a), probably because of higher testosterone levels and greater experience. Females of most species rather rarely defend flowers, being usually subordinate to males; defense is most likely when males are scarce or absent (compare Carpenter et al. 1993a). Breeding females typically defend their nest sites from other hummingbirds (and sometimes from other birds as well), but this generally incurs a much smaller expenditure of time and energy than male territoriality (see Hainsworth 1977, Stiles 1995). Gender differences in flight also may occur in foraging for arthropods, a daily necessity for all hummingbirds to obtain nutrients absent in flower nectar. During the breeding season, females dedicate more time and energy to that activity, to obtain nutrients for egg production and feeding of young. Wing morphology may thus show a closer correspondence with the aerodynamic requirements of arthropod foraging in females than in males (Stiles 1995).

Differences in wing morphology in relation to flight behavior.—Adult males of most North American species studied here showed higher WDL than females, which apparently supports the predicted association between high WDL and territoriality. However, the similar or lower WDL of immature males as compared with that of adult females is incompatible with this hypothesis, because they are usually more territorial than and dominant to conspecific females (Stiles 1973, Carpenter et al. 1993b). Carpenter et al. (1993b) reported higher WDL in young males at a migratory stopover site, but that surely reflected greater migratory fat deposits, consistent with their observations that males usually departed their study area earlier than females and that departure time was largely determined by accumulation of adequate fat reserves (Carpenter et al. 1983). Elsewhere (Altshuler et al. 2004b), we have shown that the slope of the regression of induced power on WDL is significantly higher for adult male *S. rufus* than for females among birds captured during migration, as is to be expected, given that hovering costs should increase more rapidly with increasing body mass (fat loads) in adult males because of their smaller wings.

Therefore, it seems unlikely that defense of flowers following the breeding season or migratory behavior would select for short wings (and high WDL), given that wings of immature males are not short. In fact, given their overall similarity in flight behavior, the degree of divergence in wing morphology among adult male North American hummingbirds is difficult to account for in strictly aerodynamic terms. This strongly suggests sexual selection, especially in a promiscuous mating system like that of hummingbirds; specifically, these wing modifications may partially function in generating sound effects associated with dive and shuttle displays. Among the species considered here, the six inner primaries in *Archilochus* spp. are shortened, with angular tips, and may serve to produce a strikingly loud buzz in shuttle displays, very different from the normal humming sound of hovering females and immatures. In *A. colubris*, but not *A. alexandri*, the outer primaries are reduced in length and very acuminate (Fig. 1). At the bottom of the dive display, the former produces a sharp crackle or rattle, whereas the latter produces a softer, "whiffing" trill. The latter sound has been considered vocal, because of a general acoustic resemblance to the species' *chip* note (Pytte and Ficken 1994). However, it is more likely that the wings produce these sounds as they beat by directing airflow through the highly modified rectrices, much as occurs in the "winnowing" of snipe (a mechanism likely to characterize males of all related species with specialized rectrices). In *S. rufus* and *S. sasin*, reduction and emargination of the outer primaries are even more extreme, and males produce a shrill trilling sound in normal flight that is intensified in the shuttle. In the dive, a deeper whine or whiff, either broken or continuous, is produced (Calder 1993, Mitchell 2000). Only the male *C. anna* lacks such modifications of the primaries, and the sound effects during its displays are much more vocal (Stiles 1982); however, the bottom sound of the dive, also considered a vocalization by Baptista and Matsui (1979), is probably produced by the remiges and rectrices, as in related species. Acoustic similarities to vocal notes more likely reflect selection on the dive sounds to conform to frequencies already important in the vocal communication of the respective species. Although young males of several species with unmodified rectrices begin to practice dive

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displays during their first fall, the correct sound effects are absent until they acquire adult-type remiges and rectrices during their first prebasic molt (Stiles 1973); from that point on, their performance will doubtless affect their fitness, and the sound effects become important. Hence, the modified primaries of adult males are best regarded as products of sexual selection. Indeed, the small wings and consequently higher cost of hovering, with less power reserves for maximal demands of adult males (Chai et al. 1997, Chai and Dudley 1999), might be regarded as an example of the handicap principle (Zahavi 1975; see Mulvihill et al. 1992).

Leaving aside the divergent wing modifications for displays among adult male North American hummingbirds, as a group their wings differ from those of the females (and immature males) in several consistent ways. In addition to being shorter, they are also narrower (higher shape and aspect ratios) and more pointed (higher taper, implying reduction of wing area toward the wingtip). Compared with the wings of females and immatures, those of adult males should be associated with higher induced power requirements but should incur lower profile drag, especially during fast forward flight. Profile power requirements are proportional to the third moment of wing area (skewness of wing area distribution); thus, the more tapered wings of males should require less profile power to flap. Inertial power (required to accelerate and decelerate the wing) is more related to the distribution of wing mass, which is not strongly correlated with distribution of wing area in hummingbirds because the bones and muscles are concentrated toward the proximal part of the wing (Altshuler 2001).

The implications of these differences in wing shape for maneuvering may well be complex. It was previously believed that because hummingbirds with shorter wings generally have higher wingbeat frequency, they will be more maneuverable in competitive interactions (Feinsinger and Chaplin 1975, Feinsinger and Colwell 1978). However, assessment of a flying organism's maneuverability can involve up to three axial and three torsional components of speed and acceleration (Dudley 2002), and how each of those might relate to competitive ability has yet to be assessed. A given wing shape may enhance performance along one of those maneuverability axes, yet hinder performance along another. For example, longer wings have higher moments of inertia, which will reduce the rapidity of body rotations for any applied torque but will also facilitate overall torque generation by virtue of a longer moment arm (see Calder et al. 1990). Similarly, more tapered wings will reduce torque generation but also will reduce inertial and profile drag associated with rapid changes in wingbeat orientation. Wingbeat frequency itself should relate not only to wing length but also to wing shape, specifically the distribution of wing mass and area, because those will affect inertial and profile power requirements. Inertial power requirements increase with increasing wingbeat frequency, though that would likely be offset, to some degree, by elastic storage of kinetic energy in the wing muscle fibers and tendons (Alexander 1988). The unique arrangement of muscle fibers and motor end plates in hummingbird pectoral muscle (Gaunt and Gans 1993) may be related to such energy storage. Transitory increases in wingbeat frequency accompanied by decreases in amplitude may also be implicated in producing sound effects during the shuttle display in *Archilochus* species and perhaps other taxa (F. G. Stiles pers. obs.), and that may be feasible only with small, tapered wings. In sum, the relationships between wing morphology, kinematics, maneuverability, and other aspects of performance are surely far more complex than is implied by the actuator disc model. There is a critical need for more comparative experimental data on wing kinematics and force generation during maneuvering in different, ecologically and behaviorally meaningful contexts.

Are North American hummingbirds representative?—The North American species studied here are all close relatives within a single clade, the "bees" of Bleiweiss et al. (1997), and thus may not be representative of the morphological and ecological diversity of the Trochilidae as a whole. Certainly, the reversed sexual size-dimorphism (with larger females) of all except the largest, *C. anna*, is unusual in the family, being frequent only among the smallest species (Colwell 2000). Even among these, reversed sexual size-dimorphism is not universal, occurring in small "*Pygmornis*" hermits (Stiles 1995 and F. G. Stiles unpubl. data) but not in some other groups (e.g. *Chlorostilbon*; see Stiles 1996). The "*Pygmornis*" hermits also show reduced wing size in males, which, as in the North American species, may

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be associated with producing a sharp buzz in close-range flight displays (Stiles 1995; see also Skutch 1965, Snow 1968). An interesting analogy may occur in some manakins (e.g. *Pipra*, *Corapipo*) in which males are smaller than females; in those species, the dimorphism is apparently related to agility in aerial displays (Snow 1962, Rosselli et al. 2002). However, the extent to which such features as higher shape and aspect ratios and wing taper are characteristic of male hummingbirds in general, and the implications of such differences for flight performance, remain uncertain, pending a broad comparative study of wing morphology in a wide variety of species, representing all major clades, currently in progress (F. G. Stiles and D. L. Altshuler unpubl. data).

It seems clear, from the data presented here and by Altshuler et al. (2004b), that the associations between high WDL and dominance, competitive ability, and territoriality (Feinsinger and Chaplin 1975, Feinsinger and Colwell 1978) cannot be sustained. The apparent support for that hypothesis provided by the North American hummingbirds breaks down when a wider variety of species and all sex–age groups are considered in detail. Wing length and WDL are but two of many parameters of wing shape and size, and flower visitation but one of the behaviors that must be taken into account. Comparative experimental studies of wingbeat kinematics and the related fluid mechanics are needed to refine and extend recent theoretical models (Rayner 1979, Ellington 1984a, Dudley 2000), which in turn must incorporate, in more detail, parameters of real hummingbird wings, given that optimum wing design may well differ for different flight modes. Moreover, certain features of hummingbird wings heretofore not adequately replicated by models may be important in explaining hummingbird flight performance (Altshuler et al. 2004a). Clearly, many challenges remain in the quest to understand hummingbird flight, and perhaps for no other bird family does flight occupy such a pivotal role in behavior and ecology.

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