The turning- and linear-maneuvering performance of birds: the cost of efficiency for coursing insectivores

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Abstract: To examine the performance compromises necessitated by adaptations for high efficiency in flight, such as high aspect ratio wings, the flight morphology and acceleration performance of a guild of coursing aerial insectivores (swifts and swallows) were compared with those of a guild of avian generalists. Though phylogenetic non-independence made inference of adaptation difficult, biologically significant differences in aspect ratio and acceleration performance probably exist between the two groups of birds. A model of aerial insectivory is presented to illustrate the performance demands of this foraging method and the impacts of the compromises between high efficiency in sustained flight and turning- and linear-maneuvering performance.

Résumé : Pour évaluer les compromis nécessités par les adaptations à une performance élevée de vol, comme la possession d'ailes très allongées, la morphologie du vol et la performance d'accélération d'une guilde d'insectivores chasseurs aériens (martinets et hirondelles) ont été comparés à ceux d'une guilde de généralistes aériens. Le fait que ces groupes ne soient pas indépendants phylogénétiquement rend difficile l'étude évolutive de ces variables, mais des différences biologiquement significatives de l'allongement des ailes et de la performance d'accélération existent probablement chez ces deux groupes d'oiseaux. Un modèle de l'insectivorisme aérien est présenté; il illustre les contraintes reliées à ce mode de quête de nourriture et tient compte de l'impact des compromis entre une efficacité élevée au cours du vol soutenu et la performance au cours des manoeuvres de vol en ligne droite et au cours des virages.
[Traduit par la Rédaction]

Introduction

While the efficiency of flight as a means of transport was undoubtedly a strong selective impetus in its early evolution, the full ecological and evolutionary potential of this mode of locomotion could not have been realized without the development of features that allow for precise maneuvering. Using a steady-state (i.e., fixed wing) aerodynamic assumption, wingloading is generally identified as determining maneuvering performance (i.e., turning radius; e.g., Pennycuick 1975; Norberg and Rayner 1987). But because most bird flight is flapping flight (thus violating the assumption of a fixed wing), the use of wingloading as the sole index of maneuvering performance is inappropriate, and severely underestimates the evolutionary history and ecological importance of this mode of flight. Recently, a distinction between intrinsic maneuverability (fixed-wing maneuvering) and facultative maneuverability (low-speed, flapping maneuvering) has been made (Warrick et al. 1998; Warrick and Dial 1998). The intrinsic maneuverability of a species is a function of wingloading: the larger the wings relative to the body mass, the smaller the radius of turn. Facultative maneuverability is a function of (*i*) the ability to generate the high mass-specific power needed to fly slowly while simultaneously (*ii*) creating force asymmetries between the two wings to effect a turn (Warrick et al. 1998; Warrick and Dial 1998).

While both intrinsic and facultative maneuvering performance are types of *turning maneuvering*, another type of maneuvering performance is *linear maneuvering.* While turning maneuvering is described by the turning radius, linear maneuvering is described by the linear acceleration. Both turning and linear maneuvering are functions of changes in velocity; in the former the direction of the velocity changes and in the latter the magnitude of the velocity changes. Though seemingly very different types of performance, they may be closely related in terms of their ecological importance (e.g., capturing prey; Appendix 1). Like facultative-maneuvering performance, linear maneuvering is a function of mass-specific power.

The morphological attributes that allow overall high efficiency in maneuvering flight may compromise mass-specific power output, which in turn would compromise facultative-maneuvering and linear-maneuvering performance (Pennycuick 1968; DeJong 1983; Marden 1987; Norberg and Rayner 1987; Ellington 1991). Selection for efficiency in maneuvering performance should lead to species with low body mass and large wings (Norberg and Rayner 1987), which allow a small turning radius with the wings held fixed, as opposed to resorting to reducing speed and flapping to facilitate the turn. In addition, a strong advantage would be conferred on individuals with high aspect ratio wings, which generate less induced drag (Mises 1959; Pennycuick 1968; Norberg and Rayner 1987), particularly during the use of the high angles of

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attack needed during maneuvering. However, such large, high aspect ratio wings may compromise mass-specific power output. The inertia of such wings (which increases with the square of their length) should be high, reducing the animal's ability to create high wing accelerations (Hill 1950; Chari et al. 1983; van den Berg and Rayner 1995), assuming that downstroke force, as provided by the pectoralis muscles, remains constant. The structural limits of the wing may preclude an increase in pectoral development that would allow birds to accelerate a long, high-inertia wing to the wingbeat frequencies of a shorter wing (Pennycuick 1989). Therefore, as lift increases with the square of incident air velocity and only linearly with area, birds with relatively long wings should suffer a reduction in lifting force and mass-specific power output, and hence in linear- and facultative-maneuvering performance, relative to birds with smaller wings and similar pectoral development. While the adverse scaling of power output with body size has been well described across a wide variety of taxa (e.g., Pennycuick 1968; Marden 1987; Ellington 1991), and many studies have correlated morphology and ecology in terms of performance advantages (e.g., Savile 1957; Waugh 1978; Norberg 1986; Møller 1991; Hedenström and Møller 1992), few studies have described the *compromises* in flight performance in a phylogenetic and ecological context. The broad purpose of this study was to determine if adaptations for highly efficient maneuvering flight impose a cost in the form of reduced mass-specific power output, and examine the ecological ramifications of the resulting compromise in linear acceleration and low-speed maneuvering performance.

In a study of intermittent flight, DeJong (1983) used acceleration performance to determine the scaling of mass-specific power output in 19 passerine species. The species in DeJong's study have been described as ground gleaners, tree gleaners, and (or) hawking aerial insectivores (Ehrlich et al. 1992), all of which I have grouped under "winged generalists." Using methods similar to DeJong (1983), I measured the flight morphology and linear-acceleration capabilities of some coursing aerial insectivores[1] (*Chordeiles minor* (Common Nighthawk), *Chlidonias niger* (Black Tern), *Cypseloides niger* (Black Swift), *Aeronautes saxatalis* (White-throated Swift), *Chaetura vauxi* (Vaux's Swift), *Tachycineta bicolor* (Tree Swallow), *Tachycineta thalassina* (Violet–green Swallow), *Hirundo rustica* (Barn Swallow), and *Petrochelidon pyrrhonota* (Cliff Swallow)). These coursing aerial insectivores were predicted to possess larger, higher aspect ratio, higher inertia wings, and hence to have poorer acceleration performance than the winged generalists studied by DeJong (1983).

Materials and methods

Morphometrics: external flight structures

Live individuals of the four swallow species and *A. saxatalis* were captured using mist nets from breeding populations in Missoula County in western Montana (elevation 1100 m) between April and August of 1994 and 1995. Birds were weighed to ±0.5 g on a 50-g Pesola spring scale. The width of the base of the tail was measured with a ruler in order to calculate the maximum continuous width of the tail (Thomas 1993). The maximum continuous width of the tail at 120° spread (Thomas 1993) was estimated geometrically using the lengths of the lateralmost and medial retrices (measured by ruler from the base of flight area of the feather to the tip, except for the lateral retrix in *H. rustica*, which was measured to the beginning of the streamer). The lift from the tail was included in calculations of total available lift and resulting turning radius (Appendix 1). The frontal area of the bird, used in calculating several flight-performance parameters (Pennycuick 1989), was estimated by measuring the maximum depth and width of the body (i.e., the pectoral region) with calipers. As the birds would also be used to measure acceleration (see the next section), handling time was minimized by using close-up video recording of spread-wing dimensions and areas. Each individual was placed in a trough (0.75 in. (≈1.9 cm) PVC pipe cut in half longitudinally) attached to a clipboard, and the bird was videotaped with its right wing outstretched (wrist angle of 170°) over 1-cm grid paper. Video images of each animal were downloaded to a computer and measured using NIH Image 1.6. Because the differences in these measurements among species were expected to be slight, only those wings found to have been stretched to 170 ± 5° at the wrist were used. Wing-root chord (c), back width (b), single-wing length (l), and single-wing area (s) were measured on the images. Total wing area (S) was calculated as $2s + cb$ and span (L) was calculated as $2l + b$ (as in DeJong 1983); aspect ratio was calculated as $L^2 \cdot S^{-1}$. I also measured the areas of the primary and secondary feather areas, the distinction between which was chosen as a line drawn from the leading edge at the wrist to the trailing edge between the last secondary and first primary feathers.

A single *Cypseloides niger* wing and tail were measured from a recently expired but emaciated specimen found in the Flathead Valley of northwestern Montana. An average body mass for the species was taken from Dunning (1993).

Wing and tail measurements for the *Chlidonias niger, C. minor,* and *C. vauxi* were taken from museum specimens with spread wing and tail (Appendix 2, Table 1). The *Chlidonias niger* specimen was a relatively small female (55 g, compared with a mean of 65.3 ± 4.65 g (n = 36) reported for the species by Dunning 1993). Body mass for individuals of these species was taken from the museum record for the individual unless these indicated that the specimen was a salvage or that it was emaciated, in which case an average body mass for the species was taken from Dunning (1993). Total wing areas include the area of the back between the wings measured from museum specimens.

Wing and body mass measurements for all species in DeJong's (1983) acceleration study were taken directly from that study. In addition, three other species were added to provide ecological and phylogenetic breadth to the analysis (Appendix 2, Table 1): *Sterna hirundo* (Common Tern, a highly migratory, plunge-feeding seabird), *Tyrannus tyrannus* (Eastern Kingbird, a hawking aerial insectivore), and *Nyctidromus albicollis* (Common Pauraque, a hawking aerial insectivore).

Morphometrics: internal flight structures

Data for skeletal elements were taken from museum specimens and from the aforementioned newly dead *Cypseloides niger* specimen. Because skeletons of several of the species from DeJong's study were unavailable, measurements of *Tyrannus verticalis* (Western Kingbird), *Sitta canadensis* (Red-breasted Nuthatch), and *Parus gambeli* (Mountain Chickadee) were added to the data set on skeletal elements (Appendix 2, Table 1). As the muscles and skeleton contribute most of the inertia of a bird's wing (65% in a pigeon; van den Berg and Rayner 1995), ulna length was used as an index of wing inertia.

The pectoral muscles of the apodid and passerine species in this

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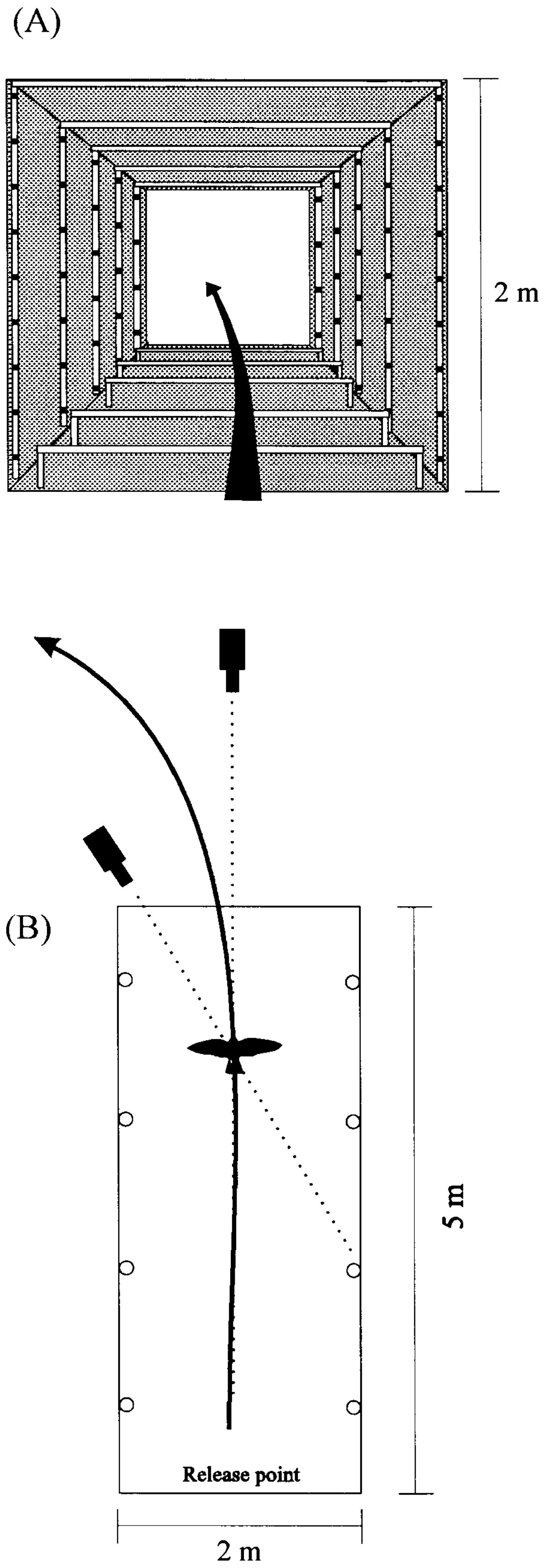
[1] I have departed from Ehrlich et al.'s (1992) "aerial forager," deeming it ambiguous, and have chosen to return to Blake's (1948) "coursing" (flying continuously in search of insect prey), as contrasted with "hawking" aerial insectivory, i.e., making short flights from a perch to capture insects in the air (Ehrlich et al. 1992).

Fig. 1. Acceleration tunnel in end-on view (A) and from overhead (B). Bars across the floor of the tunnel (A) prevented birds from descending into ground effect to facilitate acceleration.



study have been described as possessing either a mixture of red and intermediate fibers (group 5: *Apus affinis, H. rustica*; *Hirundo daurica;* George and Berger 1966) or all red fibers (group 6: most sparrows, *Hirundo concolor*, hummingbirds; George and Berger 1966; Norberg 1990). No data on fiber type were available for *C. minor* or *Chlidonias niger.* Given similar fiber types, the strength of skeletal muscle has been shown to be proportional to its cross-sectional area (Goldspink 1977). Thus, the area of pectoralis origin on the keel was used as an index of maximum downstroke force. The area of origin on the keel was estimated by taking three measurements of the perpendicular distance from the ventral margin of the keel to the linea intermuscularis (Baumel 1979) and multiplying the average of these by the distance from the anterior apex carinae to the posterior apex of the keel. The depth of the keel was measured from the apex carinae to the sulcus carinae, the latter being the site of articulation of the coracoid with the sternum (Baumel 1979).

Acceleration

Acceleration tests were conducted on the four swallow species and *A. saxatalis* after body mass and dimensional measurements were obtained. In principle, these tests used methods similar to that of DeJong (1983): release a bird, assume that it is motivated to get away as fast as possible, and measure its acceleration. To keep the escape direction of the swallows and swifts predictable and thus allow acceleration to be measured, they were released at one end of a portable 2 × 2 × 5 m tunnel constructed of black plastic over a frame of 0.75 in. (≈1.9 cm) diameter PVC pipe (Fig. 1A). Two SVHS video cameras (60 fps) positioned at the tunnel exit, one at the centerline of the flight path and another obliquely, allowed for triangulation of the bird's position as it accelerated from the release point (Fig. 1B). The PVC frame of the tunnel was marked in 10-cm increments to provide a standard for triangulation. To keep the birds from using ground effect to facilitate performance, lengths of PVC pipe were placed 30 cm above the floor of the tunnel in 1-m increments. From the view of the oblique camera, the first recorded position of the bird would be near the 4-m mark, and all acceleration data presented are to that point in the tunnel. Birds were released at a height of 75 cm; if the individual climbed more than 20 cm over this distance, its acceleration was not used. The bird's final velocity was measured as it flew through the final metre of the tunnel. All times used in calculating acceleration and wingbeat frequency were obtained from time-coded (Horita TG-50) video images.

All acceleration trials were conducted in the Missoula Valley (elevation 1100 m) at temperatures of approximately 20°C. Because the acceleration trials of DeJong (1983) were conducted at lower elevation and thus presumably in higher air density, acceleration data from the present study had to be adjusted to allow comparisons. I have assumed a difference of 10% in air density between the two study locations. Assuming equal temperature (both studies were conducted during summer months), this should be a high estimate, as it is the equivalent of the decrease in density with a 1000-m increase in elevation (the actual difference in elevation of the two study locations is approximately 800 m). Regardless of the method for calculating lift (e.g., Pennycuick 1989), the effects of air density on airfoil performance are linear. I have thus assumed that the birds tested in the present study would have demonstrated 10% higher acceleration if the trials had been performed under the atmospheric conditions in DeJong (1983). All acceleration data from the present study are thus increased by 10% (henceforth, adjusted acceleration) relative to those from DeJong (1983).

Flight behaviors

To provide an ecological context within which to view acceleration performance and morphological characteristics, a time-coded (60 fps) video image (Sony Hi-8) was used to record foraging bouts of all nine coursing insectivore species. Prey-capture maneuvers were defined as those culminating in extension of the neck to capture an insect. Wingbeat frequency during coursing and prey capture was quantified as the degree of effort expended during aerial foraging. Sample sizes are based on the number of discrete locations at which foraging data were collected (i.e., individuals at any particular location were not identified). Wingbeat frequency was calculated for each uninterrupted bout of flapping, and an average wingbeat frequency was calculated for all the bouts observed for a species at a specific time and location. Each time and location thus statistically became one individual of that species.

Though no accelerative flight wingbeat frequency data were available for winged generalists, Greenewalt (1962) reports comparable data for a few non-hirundid passerines (*Parus carolinensis* (Carolina Chickadee), *Parus bicolor* (Tufted Titmouse), *Sitta carolinensis* (White-breasted Nuthatch), *Mimus polyglottus* (Northern Mockingbird), and *Carpodacus purpureus* (Purple Finch) and a woodpecker, *Picoides pubescens* (Downy Woodpecker)). These frequencies were taken from high-speed motion pictures and are included in a data set that reports hovering hummingbird wingbeat frequencies, suggesting that the passerines filmed were probably hovering near a feeder. While hovering flight is not necessarily maximum performance for small birds (many of the listed species are capable of vertical acceleration), it better represents the maximum capabilities of a species than does wingbeat frequency during level flight.

Because of observed differences in wingbeat frequency among the foraging swifts, wingbeat amplitude and downstroke angular velocity were also quantified for periods when the birds were performing climbing flight. However, because the observed swifts were not foraging at discrete locations, and because individuals were not identified, statistical inferences were not made.

Wing kinematics may be used to infer the vortex produced during flapping flight (Rayner 1986; Spedding 1987; Tobalske and Dial 1996). Two types of vortex "gaits" have been described (Rayner 1986): (1) continuous vortex, where the wing is only slightly flexed and pronated during upstroke and lift is produced continuously throughout the wingbeat cycle; (2) vortex ring, where the wing is strongly flexed and (or) supinated during upstroke, so that lift production ceases, causing the vortex from the wing to be shed in the form of a ring (Spedding et al. 1984). Because a component of the lift produced during upstroke in the continuous-vortex gait will be negative thrust (i.e., drag), birds are predicted to use a vortex-ring gait during maximum-performance acceleration (Rayner 1988).

Statistical analyses

The differences in morphology and acceleration between the two guilds of birds (in all figures, DeJong's species are "winged generalists" and coursing aerial insectivores are "coursing insectivores") were examined using ANCOVA with body mass as covariate. To make a statistical inference regarding the intrinsic turning maneuverability and linear maneuverability of coursing aerial insectivores versus other birds, I accounted for the non-independence of the samples due to phylogeny (Felsenstein 1985) by producing null-model *F* distributions by computer simulation using software developed by Jones and Garland (1993; PDTree and PDSim) and Dickerman and Garland (1993; PDANOVA). The phylogeny (Appendix 2, Fig. 1) used was assembled from DNA–DNA hybridization data (Sibley and Ahlquist 1990; Sheldon and Winkler 1993). Because no branch lengths were available for the divergence of *A. saxatalis* from the other swifts, I used an average branch length for the swifts. For the branch lengths for *T. bicolor* and *T. thalassina*, I assumed the divergence time to be the same as that between *H. rustica* and *P. pyrrhonota*. The divergence times for *Dendroica petechia* and *Dendroica palmarum* were assumed to be the same as that for *Dendroica virens* and *Dendroica striata*; divergence of *Setophaga ruticilla* and *Geothlypis trichas* from each other and from the other warblers was estimated from the divergence of others within the Parulini. The divergence of *S. hirundo* from *Chlidonias niger* was estimated as slightly less than half that between the Larinae and Sterninae (Sibley and Ahlquist 1990).

Computer simulations (gradual Brownian motion model of evolution; random number seed = 2; 1000 simulations) used starting values of the means of each trait, and the resulting simulated data set had a mean and variance equal to those of the original data set. ANCOVAs were performed on each of these simulations (PDANOVA) and *F* ratios of the effects compiled to create null *F* distributions that accounted for the non-independence of the data due to phylogeny. The *F* ratios resulting from the ANCOVAs on the original data set (SPSS) were then compared with the simulated null *F* distribution to determine probability values (for a discussion of the simulation technique see Garland et al. 1993). Probability values using standard *F* distributions (SPSS or Microsoft Excel 5.0) are reported to provide a familiar statistical frame of reference.

Results

Morphometrics

External flight morphology

The wing areas of coursing insectivores, as a group, were not statistically different from those of winged generalists, even if the sample species had been statistically independent (Fig. 2A; also see Table A1). In contrast, there are striking differences between the aspect ratios of aerial insectivores and winged generalists ($p < 0.001$, using a standard *F* distribution; Fig. 2B): coursing insectivores would appear to have aspect ratios roughly twice those of winged generalists of a similar size. However, after phylogenetic non-independence is accounted for, the differences are not statistically significant ($p = 0.307$). The effect of the covariate (body mass) was significant for both wing area and aspect ratio (Fig. 2).

Given that the wing areas of coursing insectivores were not larger but their aspect ratios appeared higher, their wing spans would be greater. A cursory ANCOVA of wing span with body mass as the covariate confirmed the obvious ($p = 0.000$, using a standard *F* distribution). No analysis accounting for phylogenetic effects was conducted for this variable.

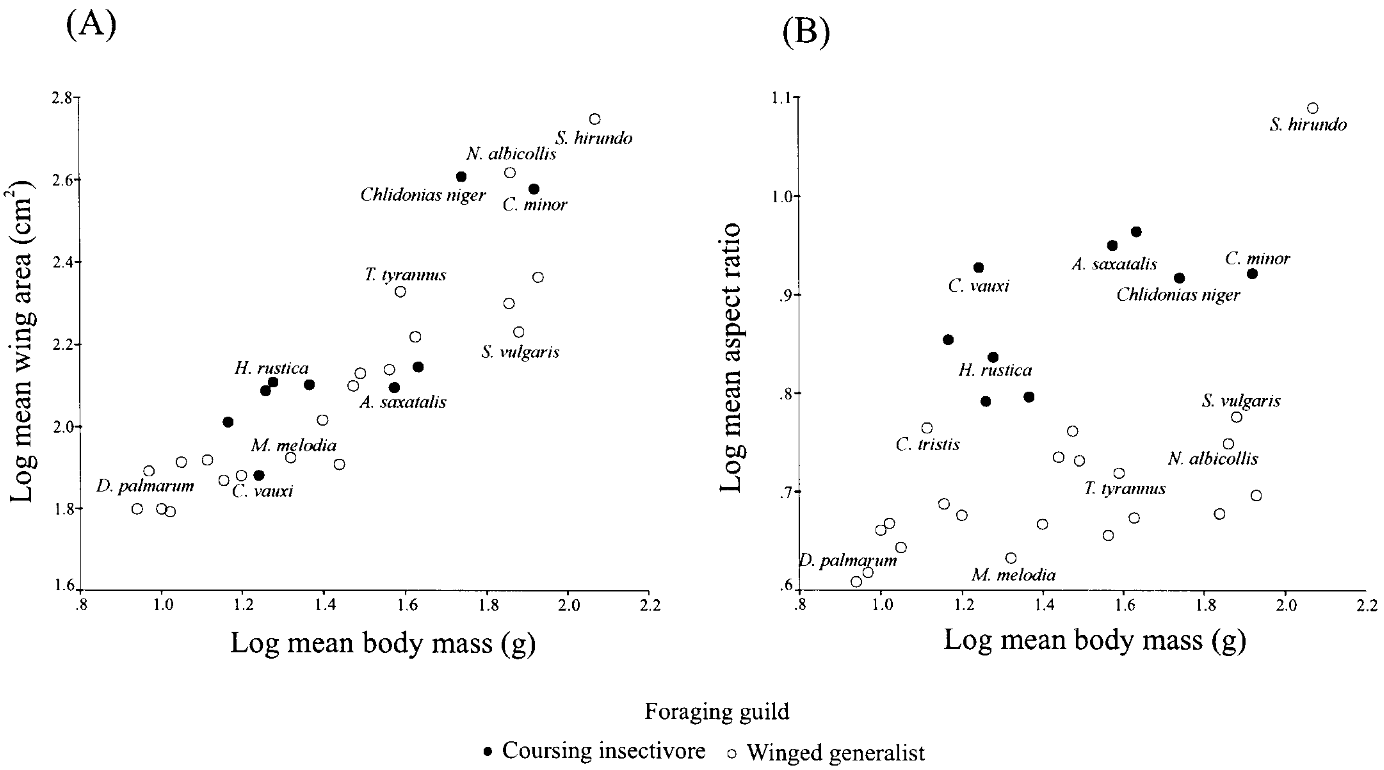
Internal flight morphology

There was no statistical evidence that coursing aerial insectivores possess longer ulnas than winged generalists (Fig. 3A; also see Table A2). While the ulna lengths of the majority of coursing insectivores lay close to a line visually fitted through the data, the ulnas of the swifts appeared to be considerably shorter than those of all other birds. When two groups (swifts, passerines) were defined, a standard ANCOVA of ulna length with body mass as covariate statistically confirmed that swifts have shorter ulnas. The inference from this test should be extended only to swifts versus passerines; no analysis accounting for phylogenetic effects was conducted.

I found no statistical difference between the groups in pectoral cross-sectional area on the keel ($p = 0.983$; Fig. 3B). Mass was a significant effect on ulna length and pectoralis cross-sectional area (Fig. 3).

Within the coursing insectivores there were some statistically significant differences in keel morphology. *Aeronautes saxatalis* had a lower pectoralis cross-sectional area per unit total body mass ($2.33\ \mathrm{mm}^2 \cdot \mathrm{g}^{-1}$) than either *Cypseloides niger* or *C. vauxi* (3.70 and $4.31\ \mathrm{mm}^2 \cdot \mathrm{g}^{-1}$, respectively; $p = 0.000$ for both comparisons, *t* test). The mass-specific keel depth in *A. saxatalis* was also less that in *C. vauxi* (0.32 vs. $0.75\ \mathrm{mm} \cdot \mathrm{g}^{-1}$; $p = 0.019$, *t* test) and possibly less than that in

Fig. 2. Plots of $\log_{10}$ mean wing length on $\log_{10}$ mean body mass (A) and $\log_{10}$ aspect ratio on $\log_{10}$ body mass (B) for the two groups tested using ANCOVA. The table below each figure gives F values (*) from standard ANCOVA (body mass as covariate), p values from the standard null F distribution, critical F values (†) ($\alpha = 0.05$) from a computer-generated F distribution from a simulated data set accounting for phylogenetic non-independence of the data, and p values (†) estimated from linear interpolation of the generated F distribution. When F distributions corrected for phylogenetic non-independence are used, there is no statistically significant difference in either wing area or aspect ratio between the two groups.



Wing area				
Source	F value*	p*	Critical F†	p†
Mass	95.15	0.000	13.35	0.000
Guild	0.78	0.386	349.52	0.999
Model	49.18	0.000	196.02	0.613

Aspect ratio				
Source	F value*	p*	Critical F†	p†
Mass	18.44	0.000	13.90	0.046
Guild	32.63	0.000	81.71	0.307
Model	28.04	0.000	49.27	0.193

Cypseloides niger (0.41 mm · g^{-1}; $p = 0.158$, t test). *Cypseloides niger* and *C. vauxi* possessed significantly greater pectoral mass-specific cross-sectional area than all other coursing insectivores (however, cross-sectional area in *T. thalassina* was 3.08 $mm^2 \cdot g^{-1}$; difference from swifts, $p = 0.059$, t test).

Acceleration performance and foraging flight behavior

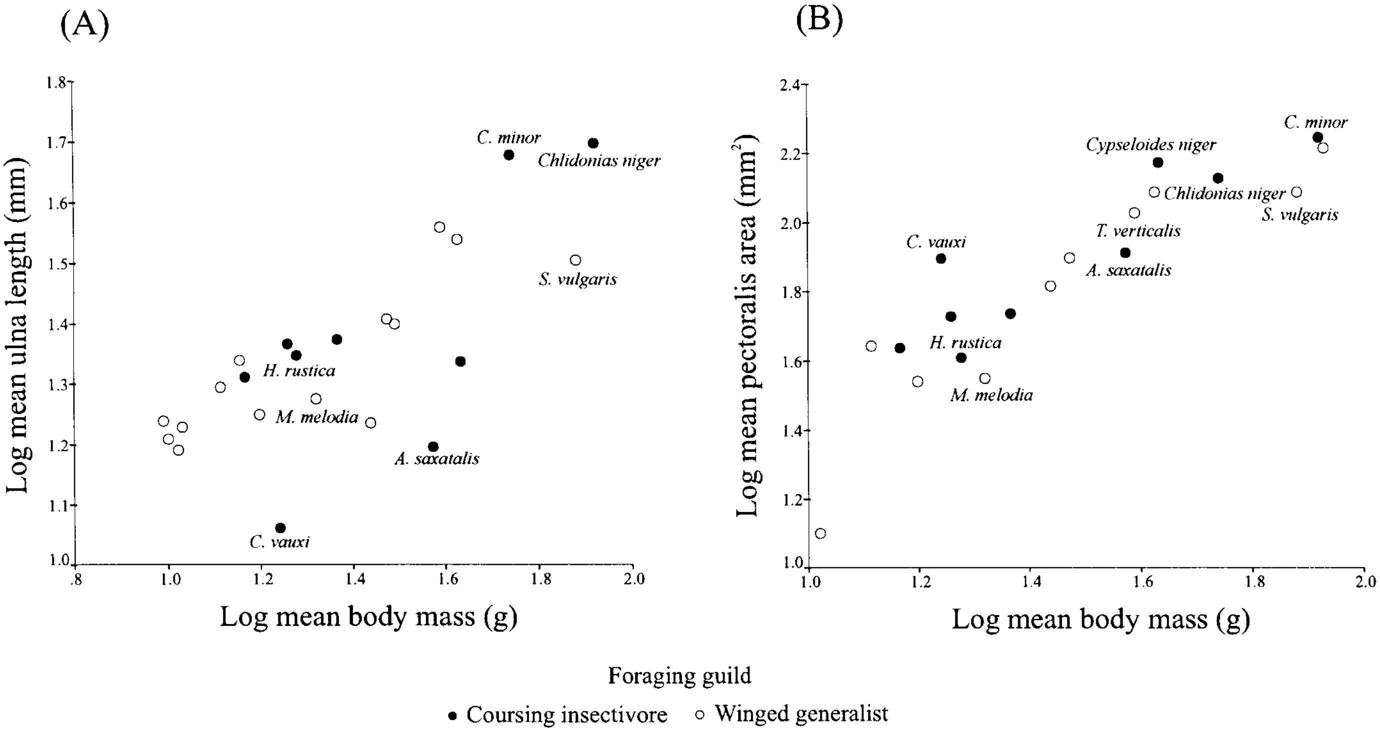
Acceleration

There seems to be some intuitive evidence that coursing insectivores differ from the winged generalists in acceleration performance (Fig. 4). However, the non-independence of the data result in an ANCOVA of relatively low power, and the differences between the groups were not statistically significant. As with the other variables, there was a statistically significant effect of body mass on acceleration ($p = 0.039$).

Among the swallows, *T. thalassina* demonstrated the highest linear acceleration (unadjusted, 8.93 $m \cdot s^{-2}$) and *H. rustica* the lowest (5.45 $m \cdot s^{-2}$; Table 1), though the differences between swallow species were not statistically significant (between highest and lowest, $p = 0.263$, t test).

The unadjusted acceleration of 2.93 $m \cdot s^{-2}$ for *A. saxatalis* is, in essence, fabricated. The two individuals of this species flown in the acceleration tunnel had an acceleration of zero; that is, they were unable to accelerate in level flight from a standing start. When positioned at the release point in the tunnel and allowed to escape, both individuals simply spread their wings, peered at the ground (75 cm below), and refused to fly. After two aborted attempts that ended in fluttering

Fig. 3. Plots of $\log_{10}$ mean ulna length on $\log_{10}$ mean body mass (A) and $\log_{10}$ mean pectoralis cross-sectional area on $\log_{10}$ mean body mass (B). For an explanation of the statistical table below each figure, see Fig. 2. No significant difference between the two groups was found for any of these variables. When standard *F* distributions were used, the ulna was significantly shorter in swifts (the three coursing insectivores below the group), though the difference was not statistically significant when phylogenetic effects were accounting for.



	Ulna length			
Source	F value*	p*	Critical F†	p†
Mass	26.00	0.000	15.70	0.040
Guild	0.34	0.568	118.65	0.997
Model	13.38	0.000	69.06	0.706

	Area of pectoralis origin (keel)			
Source	F value*	p*	Critical F†	p†
Mass	74.20	0.000	14.74	0.031
Guild	2.59	0.127	240.95	0.983
Model	38.53	0.000	143.58	0.451

landings inside the tunnel, on the third attempt the first individual dropped after release and turned to fly in the opposite direction down a gravel road. It accelerated for approximately 50 m in ground effect (10–15 cm above the ground, which it could not do inside the tunnel, owing to the presence of the PVC barriers), then climbed rapidly away. The second individual, after two failed attempts, was given a gentle toss (an acceleration of approximately $2.93 \mathrm{~m} \cdot \mathrm{s}^{-2}$) at the release point and was able to maintain altitude for the length of the tunnel, then drop into ground effect outside the tunnel and accelerate away. Both individuals were later seen flying around normally, and flying into the nest site where they had been captured. The assisted take-off acceleration value was used for the *A. saxatalis*, as it was considered statistically more conservative than a value of zero.

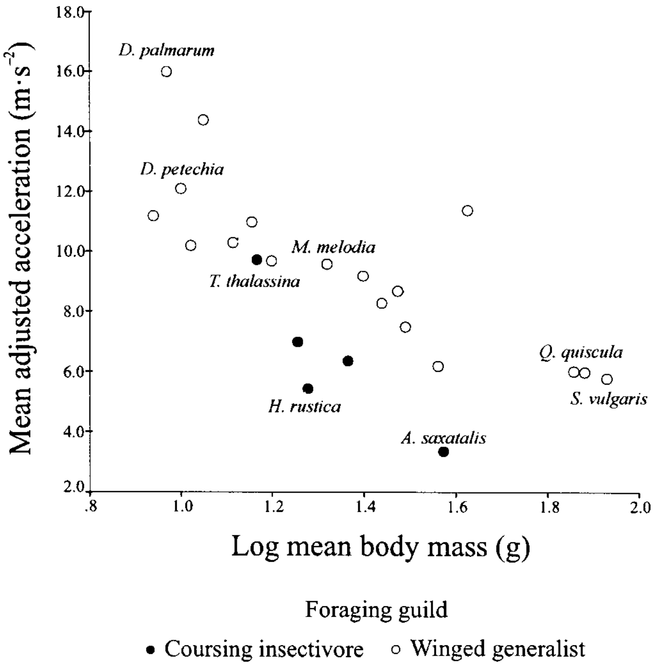
Aeronautes saxatalis had the lowest wingbeat frequency during acceleration (13.61 Hz); *T. thalassina* had the highest (15.33 Hz; Table 1).

As may be inferred from kinematics, the *A. saxatalis* individual tossed into the tunnel seemed to exhibit a continuous vortex-type wingbeat cycle when trying to accelerate (Fig. 5A). Conversely, the kinematics of swallows suggested that they utilized a vortex-ring gait when accelerating through the tunnel (Spedding et al. 1984; Rayner 1986); that is, lift production probably ceased at the end of downstroke and the wing was strongly flexed during upstroke (Fig. 5B).

Foraging flight

Wingbeat frequencies during prey capture and coursing were lower than those seen during acceleration trials for all five species (Table 1). Swallows' wingbeat frequencies during prey captures averaged 72% of the maximum observed for those species during the acceleration tests. In contrast, *A. saxatalis* wingbeat frequencies during prey capture were 98% of that demonstrated by the single individual tested in the acceleration tunnel. Similarly, while swallows' coursing wingbeat

Fig. 4. Mean adjusted acceleration plotted against $\log_{10}$ mean body mass. For an explanation of the statistical table below each figure, see Fig. 2. There was no statistically significant difference between groups. The value for *A. saxatalis* was taken from one acceleration flight where the individual was given a considerable "boost" on take-off. Neither of the two individuals of *A. saxatalis* was able to accelerate away after hand release (see the text).



	Acceleration			
Source	F value*	p*	Critical F†	p†
Mass	27.93	0.000	18.90	0.039
Guild	16.83	0.001	64.62	0.425
Model	22.39	0.000	44.60	0.314

frequencies were 62% of maximum, *A. saxatalis* wingbeat frequencies during prey capture averaged 89% of the maximum observed in the acceleration test. Coursing wingbeat frequencies for all species were, on average, 15% lower than wingbeat frequencies during prey capture.

Using a phylogenetically uncorrected ANCOVA, coursing aerial insectivores' maximum wingbeat frequencies appear to be considerably lower than those reported by Greenewalt (1962) for other, shorter winged birds of similar body size ($p < 0.001$, standard ANCOVA; Fig. 6).

During foraging, *A. saxatalis* exhibited lower wingbeat amplitude (66.92 ± 2.66° (mean ± SE)) than either *Cypseloides niger* (78.79 ± 3.17°) or *C. vauxi* (84.05 ± 4.35°). However, *A. saxatalis* exhibited a higher wingbeat frequency than *Cypseloides niger* (13.39 vs. 7.73 Hz during prey capture), which results in the two species flying with similar downstroke velocities (32.21 ± 1.31 rad·s^{-1} for *A. saxatalis*; 29.56 ± 1.20 rad·s^{-1} for *Cypseloides niger*). *Chaetura vauxi* exhibited the highest downstroke angular velocity (44.07 ± 2.28 rad·s^{-1}).

Swifts and nighthawks used continuous vortex type wing kinematics in all modes of foraging flight, including climbing flight, while swallows used a continuous vortex gait only when flapping through a hard turn, presumably to maintain constant lift production and thereby maintain a small turning radius. During climbs and fast level flight, swallows adopted a vortex-ring gait, in level flight frequently halting upstroke for ≈15 ms, with wings fully flexed at the wrist, as seen in Budgerigars (*Melopsittacus undulatus*) in high-speed flight (flap-bounding; Tobalske and Dial 1994).

Two types of foraging flight can be distinguished in *Chlidonias niger*: high-altitude coursing, where its flight behaviors closely resemble the foraging of *C. minor*, and low-altitude gleaning, where it flies at very low speed (frequently hovering in a vortex-ring gait, with pronounced manus inversion), taking insects from the surface of the water. At both altitudes, the prey taken were exclusively dragonflies and damselflies (Odonata).

Discussion

Wing morphology

The fact that coursing insectivores did not, on average, have greater wing area than winged generalists suggests that low wingloading is important not only for coursing aerial insectivory, but also more generally. In particular, the birds with wing areas (per unit body mass) as great as the swallows' were primarily hawking insectivore species (*D. palmarum*, *T. tyrannus*, *N. albicollis*). The inclusion of these species, and the relatively small wing areas of the swifts, probably diminish any statistical differences in wing area between the coursing insectivores and winged generalists.

Though the statistical inference that coursing insectivores have higher aspect ratio wings cannot be made, it may be that the statistical methods used were of insufficient power to detect biologically meaningful differences. For example, though the sample of coursing insectivores had an average aspect ratio nearly twice that of the sample of winged generalists (7.75 vs. 4.89), the difference was statistically insignificant, owing to the low degrees of freedom after phylogeny is accounted for (Fig. 2B). If the mean values accurately represent different populations, the observed difference in aspect ratios would result in large differences in flight performance between the two groups. For example, if *T. thalassina* were to have wings with the aspect ratio of those of the similar-sized *Melospiza melodia*, its best glide ratio (ratio of horizontal distance travelled to vertical distance) would be reduced from 12.1:1 to 9.6:1 (using Pennycuick 1989), meaning that it would need to flap approximately 20% more to maintain altitude when foraging. As flapping flight is probably much more expensive than gliding flight (Baudinette and Schmidt-Nielson 1974; Tatner and Bryant 1986), the observed differences in aspect ratio would translate into large differences in the metabolic costs of coursing insectivory, as empirically demonstrated by Hails (1979).

The average ulna length of coursing insectivores suggests that the extra length of the wing in coursing insectivores must be in the length of the primary flight feathers, particularly in the swifts (the three lowest points for coursing insectivores in

Table 1. Wingbeat frequencies (WBF), accelerations, and velocities for coursing insectivores.

	n*	Acceleration* ($m\cdot s^{-2}$)	Final velocity* ($m\cdot s^{-1}$)	Acceleration WBF* (Hz)	Prey capture[†]			Coursing[†]		
					n	WBF (Hz)	% max.	n	WBF (Hz)	% max.
T. bicolor	12	6.32±0.81	8.95±0.68	13.67±0.31	3 (25)	10.12±0.88	74.03	3 (49)	8.52±0.48	62.33
T. thalassina	3	8.92±2.25	9.57	15.33±0.23	3 (17)	11.10±0.92	72.41	5 (51)	10.50±0.64	68.49
H. rustica	12	5.45±0.14	8.22±1.23	13.96±0.31	4 (80)	9.87±0.37	70.70	5 (88)	8.18±0.29	58.60
P. pyrrhonota	11	5.98±0.52	7.26±0.27	14.90±0.71	4 (98)	10.93±0.41	73.36	5 (153)	9.12±0.46	61.21
A. saxatalis	1	2.93	3.71	13.61	2 (17)	13.39±1.66	98.38	2 (95)	12.15±1.56	89.27
Cypseloides niger	—	—	—	—	1 (30)	7.73	—	1 (55)	7.02	—
C. vauxi	—	—	—	—	2 (10)	14.21±0.85	—	2 (17)	12.20±0.71	—
Chlidonias niger	—	—	—	—	4 (20)	5.36±1.14	—	4 (56)	4.28±0.36	—
C. minor	—	—	—	—	4 (14)	6.41±0.30	—	4 (14)	4.27±0.11	—

Note: Data are given as the mean ± standard error; numbers in parentheses are numbers of bouts.

*From acceleration-tunnel flights; acceleration values are unadjusted for elevational effects.

[†] Data from 60 Hz video of individuals engaged in foraging flights. Sample sizes for prey capture wingbeat frequencies and coursing wingbeat frequencies represent the sample sizes used in calculating standard error, and are based on the number of discrete locations and (or) times foraging data were collected (individuals were not identified). The number of bouts was the number of uninterrupted periods of flapping flight recorded. Wingbeat frequency was calculated for each uninterrupted bout of flapping, and an average wingbeat frequency was calculated for all the bouts observed at a specific time and location. Each time and location thus represented one individual, avoiding potential pseudoreplication resulting from observing the same individual twice.

Fig. 5. The kinematics of accelerating *A. saxatalis* (A) and *H. rustica* (B) from a trace of wingtip position (60 Hz video) through one wingbeat cycle. During upstroke, swallows completely flex the wing, and lift production ceases, reducing drag. Swifts flex their wings only slightly, and lift production probably continues during upstroke. However, because of the supination of the wing, the horizontal component of the lift vector likely has a rearward (drag) direction, hindering the swift's acceleration performance.

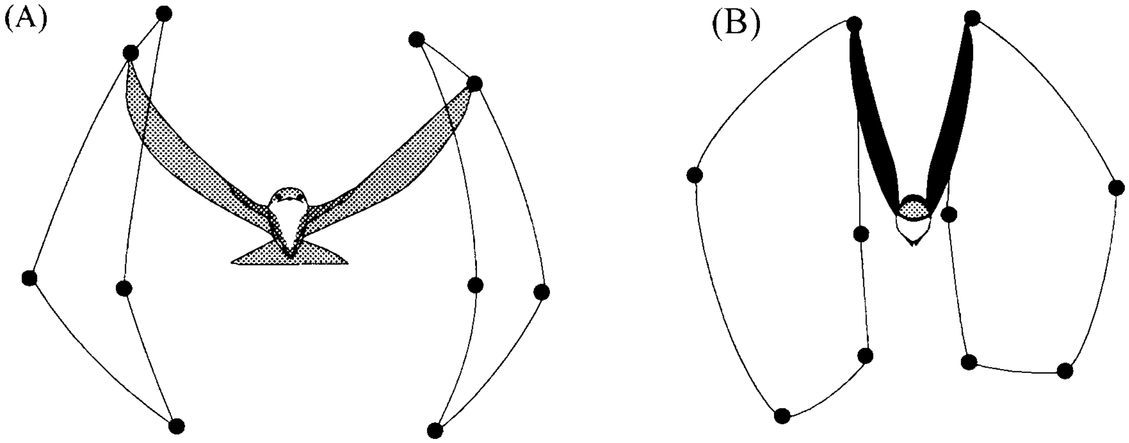
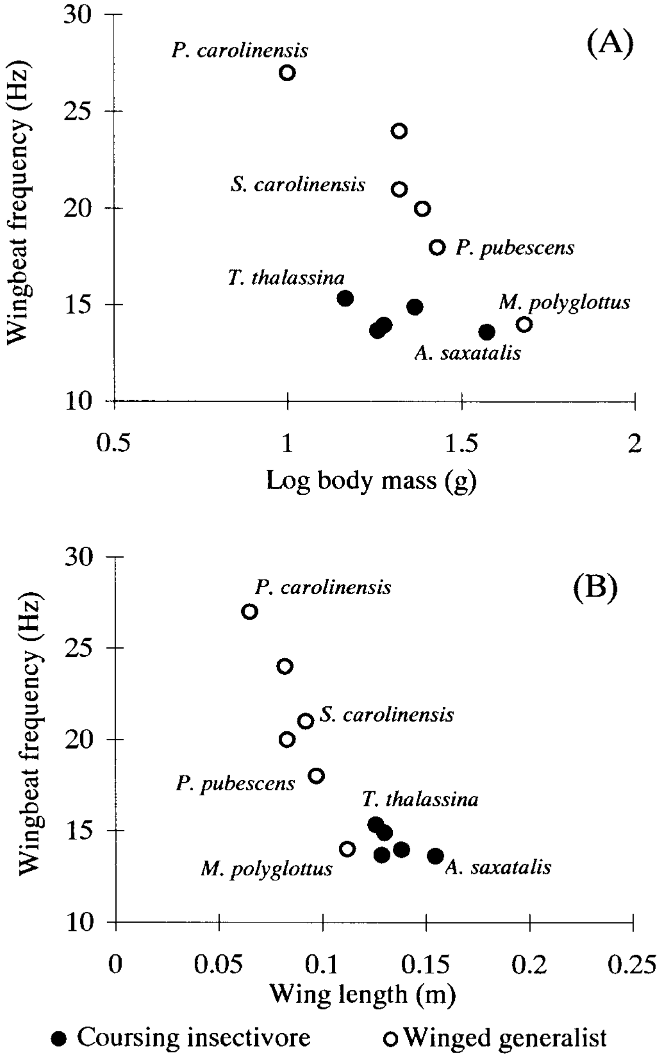


Fig. 3A). Given coursing insectivores' ulna lengths, the inertia of their wings due to the wing's mass (intrinsic inertia) should not be dramatically higher than that of other birds. However, the extrinsic inertia (inertia of the mass of air accelerated by the wing) of flapping flight may still preclude high wing acceleration. Once the wing is accelerated during downstroke, an aerodynamic force develops and the pectoral muscles must now accelerate not only the mass of the wing (overcoming intrinsic inertia) but also a mass of air. On a long wing, the integrated center of the accelerated mass of air will be farther away from the axis of rotation of the wing (the glenoid) and thus have greater inertia.

Apparently, coursing insectivores do not possess the larger pectoral muscles that would allow them to overcome this higher inertia. This may be because the structural limitations of the wing would not permit high acceleration even if the pectoral muscles could provide it. However, because they are short (Fig. 3A), the wing bones of swifts may be able to absorb higher acceleration and allow for the larger pectoral cross-sectional areas observed in these species (Fig. 3B).

The combination of their greater extrinsic wing inertia and average pectoral muscles means that coursing insectivores should exhibit lower maximum wingbeat frequencies than other shorter winged passerines of similar size. Regrettably, few comparable wingbeat frequency data are available for the winged generalist species. Though wingbeat frequencies have been reported for many of these species, the observations were generally made on birds engaged in straight and level cruising flight (e.g., Meinertzhagen 1955; Greenewalt 1962; Pennycuick 1990). While such observations have meaning with reference to the frequency of an oscillating limb as it might be used in sustained locomotion (Hill 1950; Penny-

Fig. 6. Wingbeat frequency data for coursing aerial insectivores (this study) during accelerative flight, and for other species presumed to be hovering or in slow flight (Greenewalt 1962). (A) Wingbeat frequency plotted against log$_{10}$ body mass. (B) Wingbeat frequency as a function of wing length.



cuick and Rezende 1984), they are not useful for describing maximum capabilities, as is required here. Though the few data reported by Greenewalt (1962), and the comparisons with coursing insectivores (Fig. 6), should probably be considered anecdotal, they support the suggestion that longer, higher aspect ratio wings prevent coursing insectivores from developing high wingbeat frequencies.

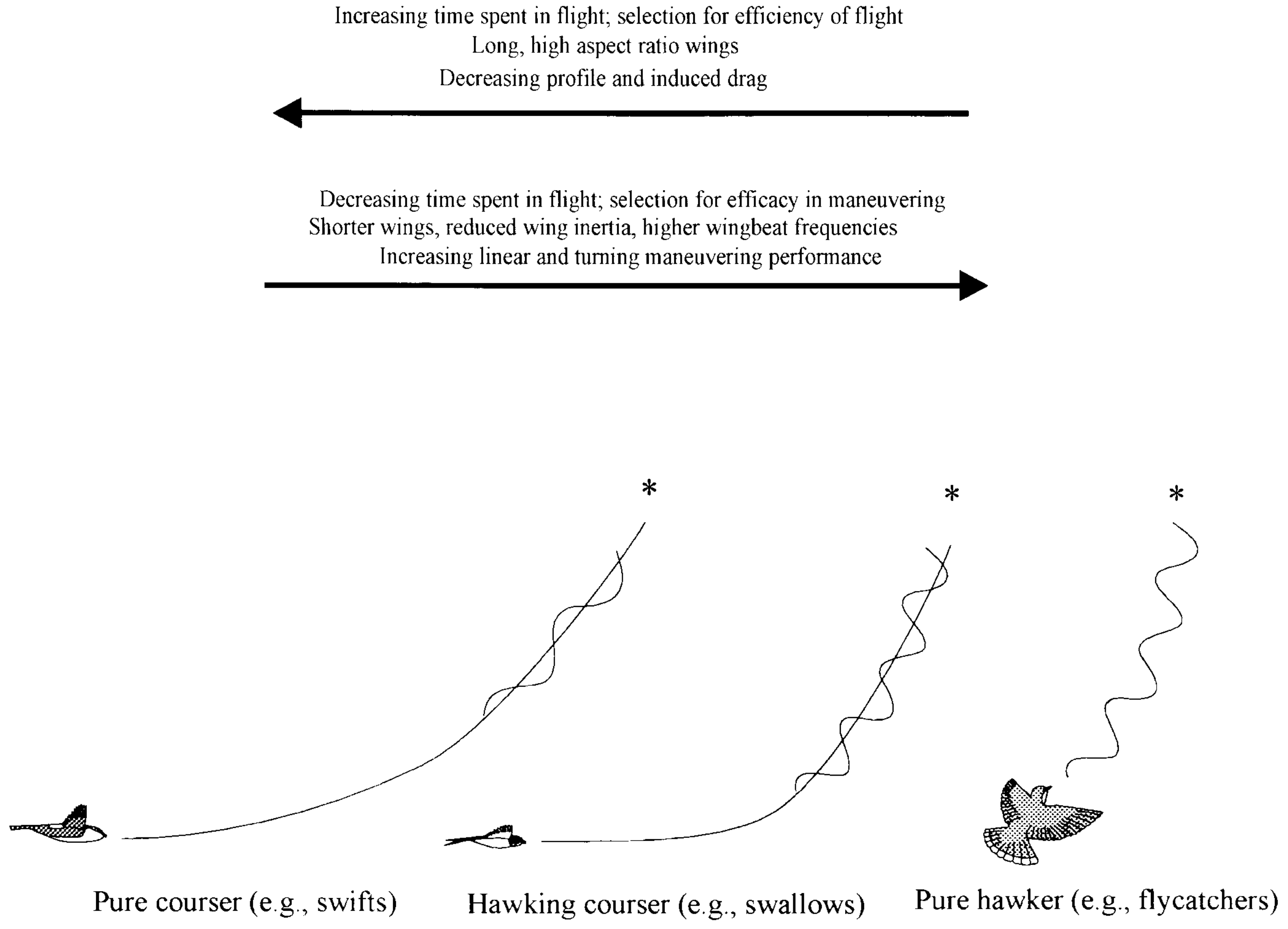
As with aspect ratio, differences in acceleration seemed to be significant in an ecological context. The difference in acceleration between *Zonotrichia albicollis* and *H. rustica* was 3.2 $\mathrm{m \cdot s^{-2}}$ (p = 0.011, t test); when all five coursing insectivores were compared with the five winged generalists of similar body mass ($\bar{x}$ = 23 g for coursing insectivores vs. $\bar{x}$ = 26 g for winged generalists), the winged generalists had an average acceleration of 2.8 $\mathrm{m \cdot s^{-2}}$ (p = 0.111, t test) greater than that of the coursing insectivores. If coursing insectivores were to engage in pure hawking, they would find themselves at a considerable disadvantage, in terms of available prey, relative to winged generalists (Appendix 1).

To determine how great the differences in acceleration performance would have needed to be for the phylogenetically correct ANCOVA to find them statistically significant, I conducted tests on three contrived data sets. Retaining the actual values for the wing generalists, the first test included hypothetical acceleration values for the four coursing insectivores not tested. The values used assumed that they would all perform better than *A. saxatalis* but less well than winged generalists of similar body mass (for example, 3.0 $\mathrm{m \cdot s^{-2}}$ was used for *C. vauxi*). Though this test used species from four independently evolved groups of coursing aerial insectivores, each with a mean acceleration performance approximately 40% lower than that of their winged generalist counterparts, the differences remained statistically insignificant (p = 0.445). Reducing the coursing insectivore's acceleration performance by another 25% resulted in a probability low enough (p = 0.076) to raise an eyebrow; if their acceleration performance was further reduced to improbably low values (80% lower than that of winged generalists), the difference in the groups would generally be considered statistically significant (p = 0.025).

To statistically infer that the evolutionary response of one morphological variable (e.g., wing aspect ratio) to another (e.g., increasing body size) is an adaptation dictated by a physical principle relating these variables in terms of the function of the animal, one must abide by the requirements of the statistical method, the most fundamental of which is independent and numerous samples.The greatest utility of methods that correct for such deficiencies due to phylogenetic effects (such as independent contrasts (Felsenstein 1985) or phylogenetic computer simulation (Garland et al. 1993)) may come when they allow us to reasonably infer adaptation without a complete understanding of the ultimate physical causalities that act as the selective pressure (e.g., some physiological processes). It should be noted, however, that statistical methods are not the only rational tools available; when the underlying selective causalities are well understood, (e.g., Newtonian physics), we may still reasonably infer adaptation even though examples of the evolutionary response are limited because of the uniqueness or rarity of the situation (i.e., small sample size), provided we remain mindful of the hazards of running away with the technique (Gould and Lewontin 1979; Felsenstein 1985; Garland and Adolph 1994).

The morphological and performance differences among the species in this study are suggestive of a continuum of compromise between efficiency in coursing and turning maneuvering and efficacy in linear maneuvering. This continuum might best be illustrated by the morphologies, performance, and foraging ecologies of aerial insectivores (Fig. 7). At one end of the continuum, swifts, with lower linear acceleration performance, depend largely on efficiently converting high airspeed (kinetic energy) into altitude (potential energy) to capture prey from below (Appendix 1). Their high aspect ratio wings are ideally suited for this strategy, as they will produce low induced drag as they increase lift to climb steeply. Further, their relatively small wing areas produce less profile drag, allowing them to recover much of this kinetic energy by descending after a prey capture, and then to maintain speed until the next climbing capture. At the other end of the continuum, pure hawking species such as *T. tyrannus*, *Empidonax traillii*, or *N. albicollis* (Ehrlich et al. 1992) launch from perches and use their high acceleration perfor-

Fig. 7. An ecological continuum of aerial insectivory based upon the compromise between general high efficiency of flight and acceleration performance. Swifts seem to have poor acceleration performance, depending instead on flying efficiently and maintaining high speed to make aerial insectivory worthwhile. At the opposite extreme, pure hawking insectivores depend on perches located near prey, and on high acceleration performance and maneuverability (both intrinsic and facultative), to capture prey. Swallows exhibit the ability to combine these two strategies because they possess high aspect ratio wings that allow them to efficiently remain in flight while retaining adequate powers of acceleration, possibly through their ability to employ more effective (relative to swifts) wing kinematics (see the text).



mance to climb and overtake prey. Swallows utilize both strategies, using high-speed flight at low altitude to “zoom climb,” to capture prey, or at higher altitudes, loiter at minimum-power airspeed (V_{mp}; Appendix 1) in an area of high insect density, and accelerate up from coursing flight using a vortex-ring gait. When foraging in this manner, swallows are essentially hawking from an aerial perch (similar to “fly and wait”; Hedenström and Alerstam 1995*a*; Fig. 7).

Comparison of the swifts

The differences in nest-site locations among the swifts provide a useful illustration of further ramifications of compromised mass-specific power. High mass-specific power is required for low-speed maneuvering flight, such as is generally required during take off and landing. *Aeronautes saxatalis* has a small keel and pectoral muscles (Fig. 8A) for its body size relative to both *Cypseloides niger* and *C. vauxi*. During foraging, *A. saxatalis* also exhibits lower wingbeat amplitude than either *Cypseloides niger* or *C. vauxi* (Fig. 8B). However, *A. saxatalis* exhibits a higher wingbeat frequency than *Cypseloides niger* (13.39 vs. 7.73 Hz during prey capture), which results in the two species flying with similar downstroke velocities (Fig. 8C). In turn, its lower wingbeat amplitude allows the high wingbeat frequencies and high downstroke velocities required for high-speed flight. Conversely, a high-amplitude wingbeat facilitates good low-speed lift production (Scholey 1983; Rayner 1988; Tobalske and Dial 1996), and coupled with high downstroke velocities, should give *C. vauxi* and *Cypseloides niger* better low-speed, flapping-flight maneuvering performance (facultative maneuvering; Warrick et al. 1998).

This seemingly complete commitment of *A. saxatalis* to high-speed flight may be the ecologically defining characteristic of the species. This species nests only in the crevices of

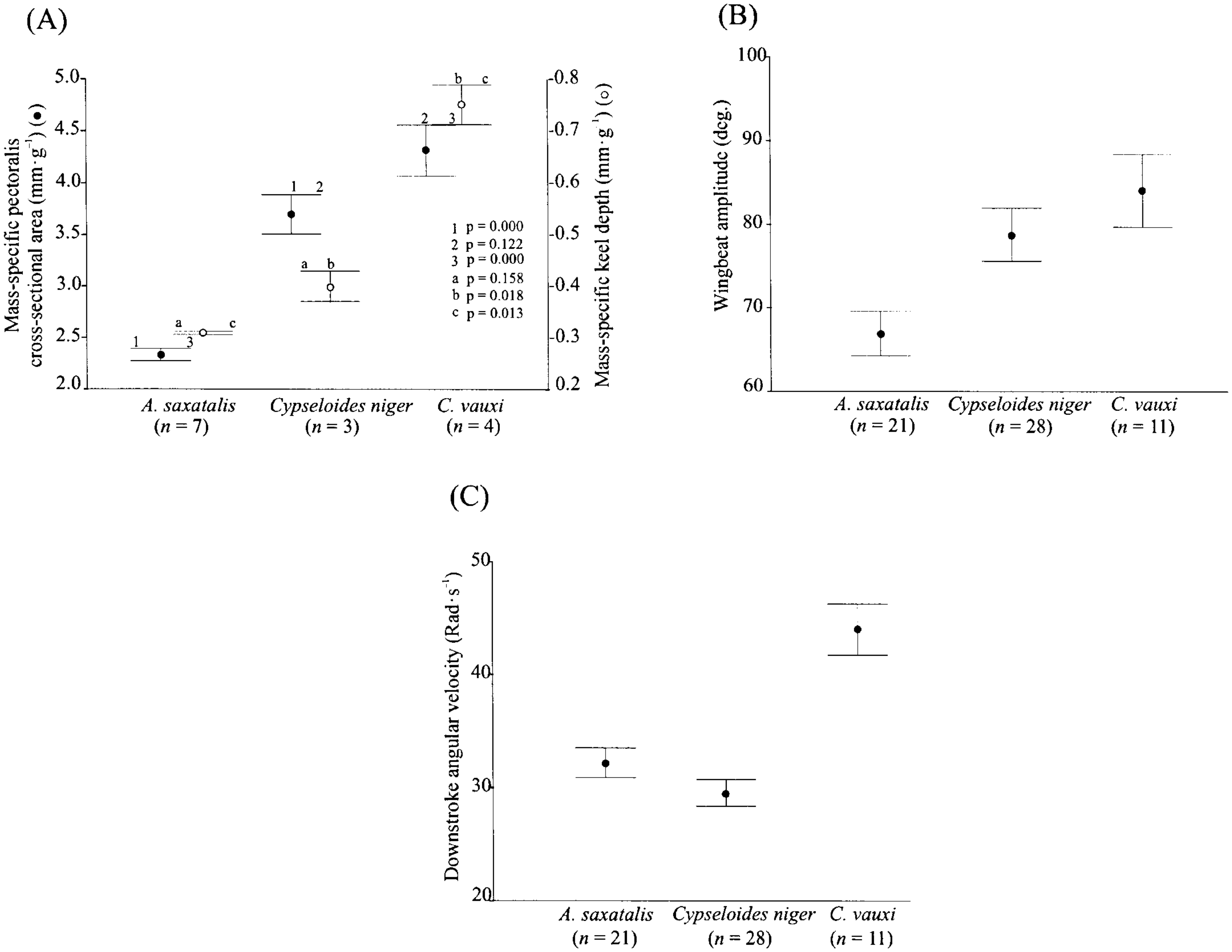


Fig. 8. Paired comparisons of morphological features that might impact swift flapping flight capability. (A) Pectoralis cross-sectional area and keel depth per unit body mass for the three species of swifts in this study. The *p* values (not Bonferroni adjusted) for paired comparisons (*t* tests) are given. (B) Wingbeat amplitudes taken from 60 Hz video as foraging individuals climbed directly away from the observer. As individuals could not be identified, and individuals of *Cypseloides niger* and *C. vauxi* were observed on only one occasion each, the samples are given a conservative size of 1; thus, no statistical inference between species can be made for wingbeat amplitude or angular velocity (C).

high, precipitous cliffs (Chantler and Driessens 1995), allowing it to use gravity to accelerate; returning, the birds approach from beneath the nest at high speed, gliding up and dissipating speed so that they arrive and enter the nesting crevice at low forward velocity, similar to the strategy of the highly wing-loaded alcids (personal observation). In contrast, *Cypseloides niger* and *C. vauxi* have relatively larger pectoral mass, and presumably better low-speed facultative maneuvering performance, allowing them to utilize more difficult-to-reach nesting sites (behind waterfalls and in chimneys, respectively; Chantler and Driessens 1995). Indeed, if mass-specific pectoral cross-sectional area is indicative of mass-specific power, the acceleration and low-speed maneuvering performance of *Cypseloides niger* and *C. vauxi* might be predicted to be good (Fig. 3B). However, the larger pectoral muscles of these swifts may be required to compensate for the stilted, continuous-vortex gait they seem to employ even during slow flight (Savile 1950, 1957; Tarburton 1986.). While all passerine coursing insectivores (as well as *Chlidonias niger*) are able to use more complex upstroke kinematics (complete wing flexion during upstroke in low-speed flight or manus inversion during hovering; personal observation) that may de-emphasize the role of the pectoral muscles (Brown 1948*a*, 1948*b*; Rayner 1988; Dial 1992), swifts may need the powerful downstroke forces to offset the negative thrust they generate during upstroke. A study of the low-speed kinematics and scaling of acceleration performance in swifts would provide insights into the performance compromises faced by the Apodidae, especially in view of their phylogenetic affinity to the masters of low-speed flight, the hummingbirds (Trochilidae).

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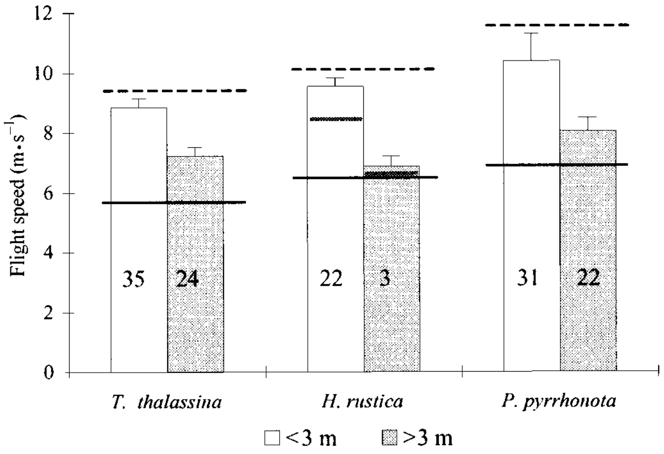
Appendix 1

Flight speeds are frequently used in models of foraging behavior (e.g., Cowie 1977; Bryant and Turner 1982; Welham and Ydenberg 1993; Hedenström and Alerstam 1995*a*, 1995*b*) that predict optimal speeds for provisioning young and maximizing caloric intake. However, these models make no predictions regarding flight speed during prey capture, an activity that probably composes the largest portion of an aerial insectivore's flight time. Here I present a conceptual model of prey-capture behavior which suggests that prey behavior and distribution could dictate the coursing speed and efficacy of the prey-capture techniques of aerial insectivores.

In a study of foraging flight speed, Blake et al. (1990) found that *H. rustica* coursed at higher speeds when flying at low altitudes and lower speeds at high altitudes. Using a radar gun (Stalker Pro in "ball mode"; 0.01 s target acquisition time, 100 m range) to measure flight speed as birds flew directly away from or toward me, I corroborated and expanded slightly upon the findings of Blake et al. (1990; Fig. A1). Why should swallows coursing at low altitude fly faster?

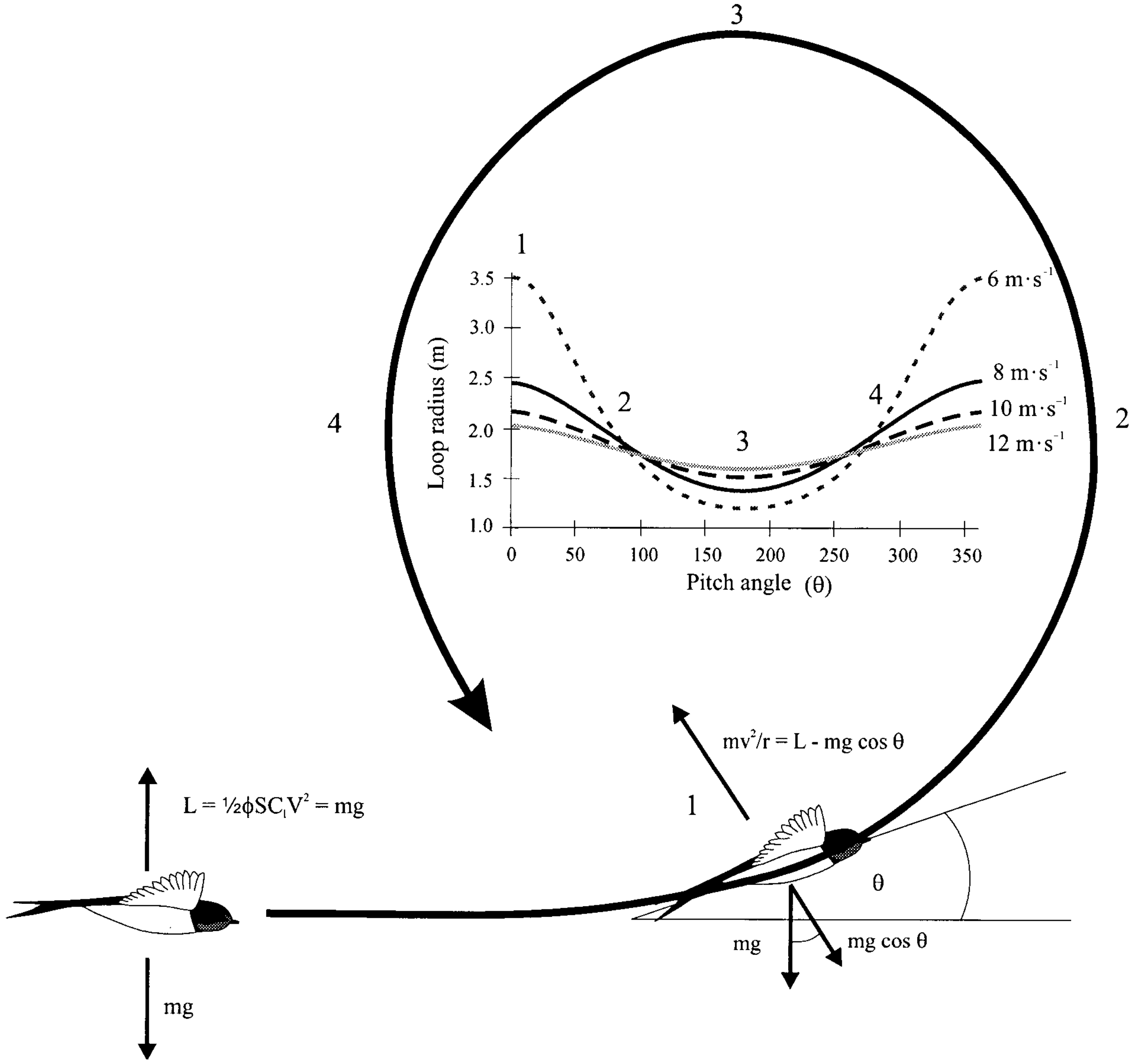
Fig. A1. Flight speeds of three species of swallow, measured using a radar gun in conditions of no wind. Data for each species were obtained at multiple locations, and samples sizes are raw numbers of speeds taken of the species, with no attempt made to identify individuals. The dotted lines and thin solid lines are the maximum range (V_{mr}) and minimum power speeds (V_{mp}) for each species, calculated from momentum jet theory (Pennycuick 1989). The thick solid lines across the bars for *H. rustica* represent the flight speeds observed by Blake et al. (1990; n = 571 and 250) using similar methods. Birds flying at low altitude were frequently extremely low (<20 cm off the ground) and probably utilizing ground effect to lower induced drag. The numbers within the bars are sample sizes.



The first reason is that their maneuvering performance is greater. In a level turn at a given bank angle, turning radius is independent of flight speed; however, whenever the turn has a vertical component, the turning radius will be dependent on flight speed (Fig. A2). That is, during a prey-capture maneuver where the bird must "pitch up" and attack prey from below (62% of prey captures by swallows and swifts; D.R. Warrick, unpublished data), the radius of the vertical turn will be smaller if the bird is travelling at a higher speed. The increase in initial maneuverability (i.e., decrease in vertical turning radius) is dramatic, with an increase in flight speed from near minimum power (≈6 $m \cdot s^{-1}$) to ≈9 $m \cdot s^{-1}$ (Fig. A2). In addition, the maximum bank angle that a bird can use and still maintain altitude (critically important at low foraging heights) increases with speed. Finally, at higher airspeeds, creating asymmetries in wing areas (by flexion) or lift coefficients (by pronation/supination of the wing) results in higher force asymmetries, which will result in higher roll rates (higher *agility*; Norberg and Rayner 1987).

Secondly, the effect of prey evasion must be considered. Figure A3 is an illustration of *H. rustica* foraging ≈25 cm over the ground, travelling at 6, 8, or 10 $m \cdot s^{-1}$. The two radii extending from the head of *H. rustica* are a conservative estimate of the field of vision of the bird as it moves forward. Inside this field, insects are randomly appearing at some rate. The critical assumption of this model is that once an insect sees the approaching predator, it will try to avoid capture, presumably by escaping downward to the refuge of the ground. Assuming for the sake of simplicity that it takes the insect 1 s to escape to the refuge of the ground at a coursing speed of 6 $m \cdot s^{-1}$, the prey horizon, that is, the point beyond which prey have time to

Fig. A2. A fixed-wing flying animal “pitching up” into a vertical turn (a “loop”) will have a smaller turning radius at higher speed during those portions of the turn where lift must provide the centripetal force to change direction as well as overcome the effects of gravity. The reduction in the radius of turn with increasing speed is greatest at the beginning and end of the loop; when the bird is flying straight up or straight down, the radius will be described strictly by the centripetal force. At the top of the loop, higher flight speed will increase the radius of the turn slightly; however, swallows rarely, if ever, pitch up beyond 90° during prey capture (personal observation), so this effect is of no consequence. More significantly, the initial turning radius (radius of turn at position 1, with a body angle 5° above horizontal) is reduced by 30% with an increase in speed from 6 to 8 $m \cdot s^{-1}$. The turning radii are calculated using the wing area and body mass of *H. rustica*.



return safely to the ground and are thus unavailable to the swallow, is 6 m away. At 8 $m \cdot s^{-1}$, the swallow’s prey horizon is now 8 m away, that is, it will be able to overtake any prey closer than 8 m. (Note that for a bird hawking from a perch and able to accelerate at 8 $m \cdot s^{-2}$, the prey horizon would be 4 m away.) The size of the area in which prey will be available will be a simple square function of the speed of the coursing swallow minus the area formed by the turning radius of the bird (darkened area in Fig. A3):

$$\text{available prey area} = \pi V^2 F/360 - \pi r^2 T/360$$

where V is the coursing speed (or the acceleration performance of a bird hawking from a perch) of the swallow and F is its field of view in degrees, r is the turning radius, and T is the portion of a complete circle the bird would move through during the turn.

Given, then, that both maneuvering performance and the prey horizon increase with velocity (or acceleration performance), it is clear why swallows foraging near the ground fly at high speed. The model also suggests that there may be a minimum turning radius and acceleration performance from a standing start which would allow low-altitude foraging to be effective. When the turning radii of the guild of coursing insectivores are superimposed on the prey horizon area (Fig. A4), it is clear that prey densities would have to be high for swifts to forage near the ground, as in the case described by Alden and Mills (1976). Qualitatively, the decreasing turning radii

Table A1. External flight morphology measurements and maneuvering performance for coursing insectivores.

	n	Mass (kg)	Wing span (m)	Wing chord (m)	Wing area (m^2)	Wing loading (Pa)	Max. continuous tail width (m)	Wing 1° (%)	Aspect ratio	Minimum level turning radius (m)*					
										10 $m·s^{-1}$	9 $m·s^{-1}$	8 $m·s^{-1}$	7 $m·s^{-1}$	6 $m·s^{-1}$	5 $m·s^{-1}$
T. bicolor	3 (15)	0.018	0.276	0.055	0.012	14.573	0.097	0.6814	6.2031	1.58	1.59	1.60	1.63	1.69	1.87
T. thalassina	3 (8)	0.015	0.271	0.046	0.010	14.080	0.089	0.6107	7.1637	1.52	1.52	1.54	1.56	1.61	1.77
H. rustica	6 (12)	0.019	0.297	0.052	0.013	14.494	0.101	0.6095	6.8751	1.56	1.57	1.58	1.61	1.67	1.84
P. pyrrhonota	6 (15)	0.023	0.282	0.054	0.013	18.016	0.093	0.5782	6.2705	1.99	2.00	2.03	2.09	2.23	2.71
A. saxatalis	2 (2)	0.038	0.334	0.052	0.012	29.498	0.116	0.7298	8.9378	3.12	3.17	3.28	3.52	4.25	—
Cypseloides niger	1 (1)	0.046	0.359	0.044	0.014	31.947	0.115	0.693	9.2247	3.48	3.57	3.73	4.11	5.48	—
C. vauxi	2 (2)	0.017	0.254	0.034	0.008	22.494	0.094	0.7827	8.4778	2.31	2.33	2.38	2.46	2.67	3.48
Chlidonias niger	1 (1)	0.055	0.580	0.078	0.041	13.262	0.154	0.5283	8.2776	1.48	1.49	1.50	1.52	1.58	1.72
C. minor	2 (2)	0.083	0.564	0.075	0.038	21.409	0.241	0.5187	8.3613	2.08	2.10	2.13	2.18	2.31	2.74

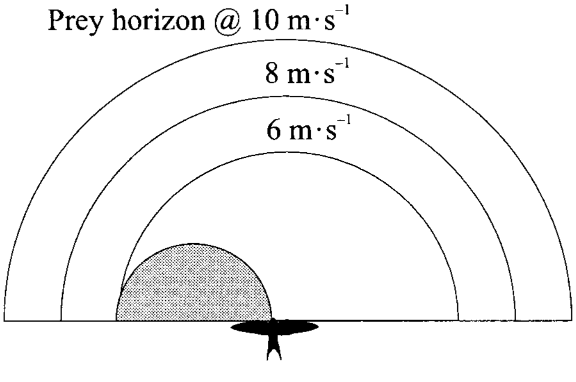
Note: *n* is the number of acceptable wing area and span measurements; numbers in parentheses show the number of samples for all other external flight morphology measurements.

*Assuming an air density of 1.11 $kg·m^{-3}$ (1000 m at standard temperature) and a lift coefficient of 1.5.

Table A2. Skeletal measurements for coursing insectivores.

	n	Mass (kg)	Pectoral cross-sectional area (cm^2)	Length (m)		
				Humerus	Ulna	Radius
T. bicolor	2	0.022	5.38×10^{-5}	0.015	0.023	0.021
T. thalassina	3	0.014	4.36×10^{-5}	0.014	0.020	0.019
H. rustica	4	0.018	4.08×10^{-5}	0.015	0.022	0.021
P. pyrrhonota	3	0.022	5.47×10^{-5}	0.015	0.024	0.021
A. saxatalis	8	0.037	8.21×10^{-5}	0.010	0.016	0.014
Cypseloides niger	2	0.039	1.50×10^{-4}	0.014	0.022	0.021
C. vauxi	4	0.019	7.91×10^{-5}	0.008	0.012	0.010
Chlidonias niger	3	0.061	1.35×10^{-4}	0.040	0.048	0.047
C. minor	2	0.083	1.76×10^{-4}	0.041	0.050	0.048

Fig. A3. Horizontal turning radius (assuming a level turn with fixed wings) of *H. rustica* superimposed on prey horizons at 6, 8, and 10 $m \cdot s^{-1}$ (see the text). The turning radius shown here represents the intrinsic maneuvering performance of *H. rustica,* based on the wing lift available from fixed wings and tail spread to 120° (Thomas 1993). This radius assumes a bank angle that would allow level flight to be maintained at a lift coefficient of 1.5 and a speed of 8 $m \cdot s^{-1}$. The turning radius would be slightly smaller at 10 $m \cdot s^{-1}$ (as a higher speed would allow a larger bank angle while maintaining level flight) and slightly larger at 6 $m \cdot s^{-1}$.



would seem to match the frequency with which those species are seen to forage at very low altitudes (Blake 1948; Wetmore 1957; Alden and Mills 1976; Hespenheide 1975, Waugh 1978, Holroyd 1983; Brown 1988).

Why then do swallows course at lower flight speeds at high altitudes? Once they find an area of high insect concentrations, swallows probably loiter there at minimum-power speed. Because insects have no refuge at high altitudes, coursing insectivores may be able to approach them in a more studied manner, then finally accelerate up to the capture. This is not to say that insect prey have no means of defense (see Srygley and Dudley 1993), and diving may be one of the more effective and frequently used evasive maneuvers available to insects (personal observation). The highly cambered airfoils of birds are poor at creating lift at negative angles of attack, and thus impose a severe limit on the pursuit of diving insects. At high altitude, the best counter to this prey behavior would be to attack from directly below the insect, thus eliminating this potential avenue of escape (note that climbing from directly below would not be an option for birds catching insects near the ground). Further, diurnal aerial insectivores probably approach from beneath prey most frequently because insects are more visible against the sky than against the ground, and the countershaded predators themselves are less visible to the prey.

Fig. A4. Level horizontal turning radii of coursing insectivores (C_L = 1.5, flight speed 8 m · s^{-1}) superimposed on a prey horizon at 8 m · s^{-1} .

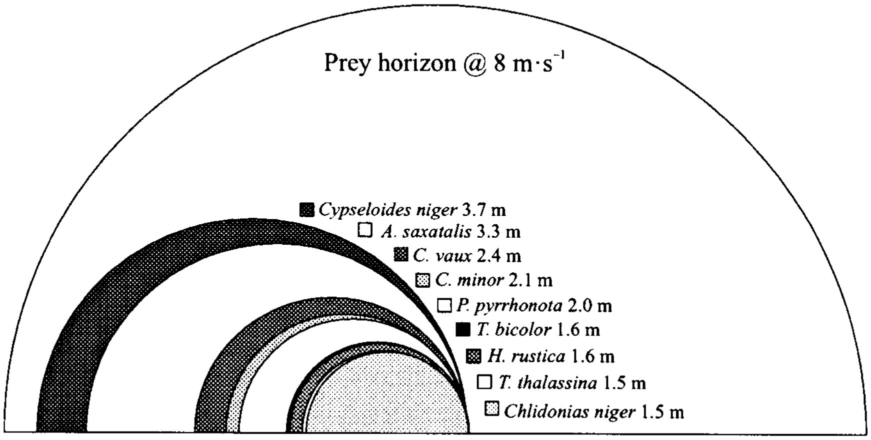
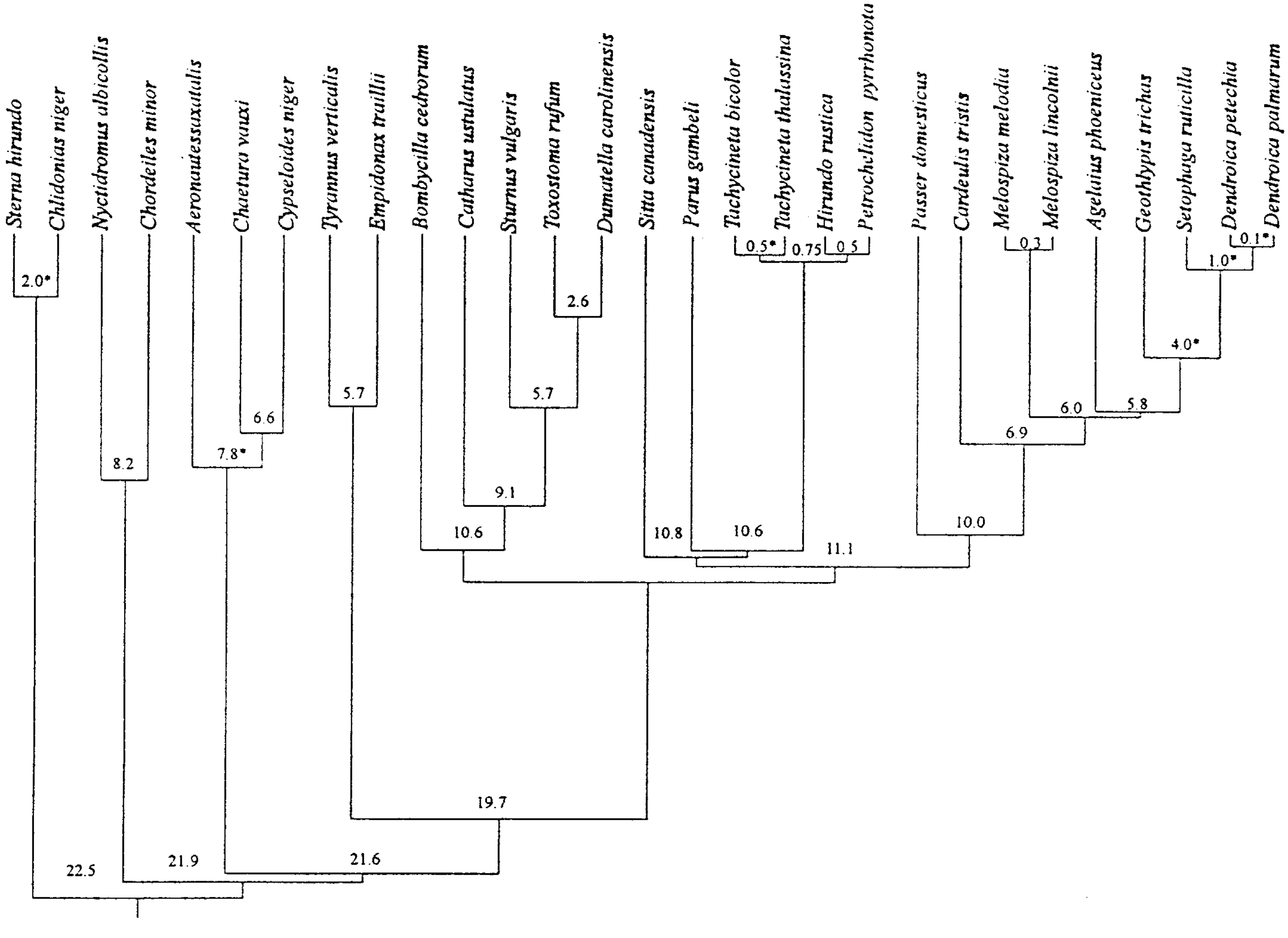


Fig. A5. Phylogeny of species used in the study, based on Sibley and Ahlquist (1990) and Sheldon and Winkler (1993). This phylogeny and divergence times were used in the computer-simulated data sets used to create null *F* distributions for ANCOVAs. An asterisk denotes an estimate of branch length based on divergence times of other species in the same family.



Appendix 2

Table A3. Sample sizes and sources of acceleration and morphological data.

				Pectoralis		
Species and common name	Acceleration	Wing area	Aspect ratio	Ulna length	cross section	References
Sterna hirundo (Common Tern)	—	?	?	—	—	Greenwalte 1962
Chlidonias niger (Black Tern)	—	1	1	3	3	Warrick 1997[a,b]
Nyctidromus albicollis (Common Pauraque)	—	1	1	—	—	Warrick 1997[c]
Chordeiles minor (Common Nighthawk)	—	2	2	2	2	Warrick 1997[a,b]
Aeronautes saxatalis (White-throated Swift)	1	2	2	2	2	Warrick 1997[a,d]
Chaetura vauxi (Vaux's Swift)	—	2	2	4	4	Warrick 1997[b,c]
Cypseloides niger (Black Swift)	—	1	1	2	2	Warrick 1997[b,d,e]
Empidonax hammondii (Hammond's Flycatcher)	—	—	—	3	—	Warrick 1997[f]
Empidonax traillii (Willow Flycatcher)	2	4	2	—	—	DeJong 1983[d]
Tyrannus tyrannus (Eastern Kingbird)	—	5	5	—	—	Holroyd 1983[d]
Tyrannus verticalis (Western Kingbird)	—	—	—	1	1	Warrick 1997[f]
Bombycilla cedrorum (Cedar Waxwing)	2	6	2	2	—	DeJong 1983[d]; Warrick 1997[f]
Catharus ustulatus (Swainson's Thrush)	2	3	2	2	—	DeJong 1983[d]; Warrick 1997[f]
Sturnus vulgaris (European Starling)	2	4	2	3	3	DeJong 1983[d]; Warrick 1997[f]
Toxostoma rufum (Brown Thrasher)	2	4	2	—	—	DeJong 1983
Dumatella carolinensis (Gray Catbird)	15	45	15	—	—	DeJong 1983
Parus gambeli (Mountain Chickadee)	—	—	—	1	—	Warrick 1997[f]
Sitta canadensis (Red-breasted Nuthatch)	—	—	—	1	—	Warrick 1997[f]
Tachycineta bicolor (Tree Swallow)	14	3	3	2	2	Warrick 1997[d,f]
Tachycineta thalassina (Violet-green Swallow)	3	3	3	3	3	Warrick 1997[d,f]
Hirundo rustica (Barn Swallow)	12	6	6	3	3	Warrick 1997[d,f]
Petrochelidon pyrrhonota (Cliff Swallow)	11	6	6	3	3	Warrick 1997[d,f]
Passer domesticus (House Sparrow)	3	5	3	1	1	DeJong 1983[d]; Warrick 1997[f]
Cardeulis tristis (American Goldfinch)	4	6	4	1	—	DeJong 1983[d]; Warrick 1997[f]
Zonotricha albicollis (White-throated Sparrow)	6	13	6	—	—	DeJong 1983[d]
Melospiza melodia (Song Sparrow)	4	12	4	1	—	DeJong 1983[d]; Warrick 1997[f]
Melospiza lincolnii (Lincoln's Sparrow)	2	3	2	1	—	DeJong 1983[d]; Warrick 1997[f]
Agelaius phoeniceus (Red-winged Blackbird)	3	4	3	3	3	DeJong 1983[d]; Warrick 1997[f]
Geothlypis trichas (Common Yellowthroat)	7	12	7	1	1	DeJong 1983[d]; Warrick 1997[f]
Setophaga ruticilla (American Redstart)	2	3	2	—	—	DeJong 1983[d]; Warrick 1997[f]
Dendroica coronata (Yellow-rumped Warbler)	2	3	2	—	—	DeJong 1983[d]; Warrick 1997[f]
Dendroica petechia (Yellow Warbler)	5	12	5	1	—	DeJong 1983[d]; Warrick 1997[f]
Dendroica palmarum (Palm Warbler)	5	12	5	—	—	DeJong 1983[d]; Warrick 1997[f]

[a] Wing data from specimens in the Burke Museum.
[b] Skeletal data from specimens in the Burke Museum.
[c] Wing data from specimens in the Carnegie Museum.
[d] Wing data from live specimens.
[e] Skeletal data from newly dead specimens.
[f] Skeletal data from specimens in the Museum of Vertebrate Zoology, University of Montana.