

## FLIGHT MORPHOLOGY, ENERGETIC CONDITION, AND THE STOPOVER BIOLOGY OF MIGRATING THRUSHES

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**ABSTRACT.**—Flight morphology affects aerodynamic performance and the energetic demand for migration. We investigated the relationship between flight morphology and energetic condition of Wood Thrush (*Hylocichla mustelina*), Veery (*Catharus fuscescens*), Swainson's Thrush (*C. ustulatus*), and Gray-cheeked Thrush (*C. minimus*) during migration and the consequences for stopover behavior following spring trans-Gulf passage. Differences in morphological variables were found among *Catharus* thrushes, and between Wood Thrush and *Catharus* thrushes. Species with longer migratory distances have longer, more pointed wings and higher aspect ratios. The relatively larger wing area and lower body mass of Gray-cheeked Thrush and Veery result in lower wing loadings. Whereas wing size increased with increasing lean body mass in all species, the interrelations of wing span and wing area with lean body mass were allometrical (i.e. deviated from expected isometric relationship). Larger individuals in each species have disproportionately large wings. Wing size was negatively related to amount of stored fat, which indicated that larger individuals within each species have smaller fat stores remaining after trans-Gulf migration. Species or individuals with relatively long, pointed wings are more efficient migrants, and their energetic demand per unit distance travelled is lower. The consequences vis-a-vis stopover biology are considered. Received 2 April 1993, accepted 12 February 1994.

**MORPHOLOGY AFFECTS** the aerodynamics of migratory flight. If long-distance migration selects for reduced cost of transport, migratory birds should have wings with a high aspect ratio and low loading, thereby reducing drag and the energetic cost of powered flight (Pennycuik 1975, Rayner 1988, 1990). These morphological features and others are interpreted as adaptations for migration (Averill 1922, Dillger 1956b, Greenwalt 1962, Cox 1968, Gaston 1974, Leisler and Winkler 1985, Winkler and Leisler 1985, 1992, Leisler 1990).

Since flight morphology affects aerodynamic performance (Tucker 1974, Pennycuik 1975, Rayner 1988, 1990), it may also influence a migrant's energetic condition (fat stores) for migration and behavior during stopover. When landbird migrants arrive along the northern coast of the Gulf of Mexico, energetic condition varies. Some individuals have mobilized their lipid stores during passage and arrive essentially fat free, whereas other birds retain sufficient fat to continue migrating the day of their arrival (e.g. Rappole and Warner 1976, Moore and Kerlinger 1987, Kuenzi et al. 1991). Ener-

getic condition affects the migrant's likelihood of stopover, length of stay, and foraging behavior during stopover (e.g. Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Safriel and Lavee 1988, Loria and Moore 1990). If energy consumption varies in relation to flight morphology, the amount of fat required for migration would not be equivalent across individuals within a species or among species, and some individuals or species might experience reduced energy demand during migration and increased rate of passage.

Our objective was to examine the relation between flight morphology and energetic condition (i.e. how might the relationship affect behavior of thrushes during stopover). We hypothesize that variation in flight morphology, both within and among species, affects energetic requirements for migration. Species or individuals with more efficient flight morphology should carry less fat stores during migration. We also predicted that, if variation in flight morphology affects energy demand, behavioral decisions regarding migration timing and length of stopover should be influenced. Morphological variations among and within species are a function of differences not only in migratory behavior, but also foraging behavior and habitat use; in addition, there undoubtedly

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are phylogenetic constraints. Our study was not designed to determine the cause(s) of morphological variation, but rather to investigate the energetic and behavioral consequences during migration of morphological differences.

#### METHODS

*Species.*—We studied the morphology of Wood Thrush (*Hylocichla mustelina*), Veery (*Catharus fuscescens*), Swainson's Thrush (*C. ustulatus*), and Gray-cheeked Thrush (*C. minimus*) between 25 March and 13 May 1988 following passage across the Gulf of Mexico. The species are closely related (Bent 1949, Dilger 1956a, b, c, Winker and Rappole 1988, Sibley and Monroe 1990) intercontinental landbird migrants (Stevenson 1957, Rappole et al. 1979). Based on average breeding and wintering latitudes (Bent 1949, Graber et al. 1971, AOU 1983, Rappole et al. 1983), migratory distance averages approximately 2,200 km for Wood Thrushes, 5,200 km for Veerys, 5,500 km for Swainson's Thrushes, and 6,200 km for Gray-cheeked Thrushes.

*Study site.*—Our study site was a 3-ha coastal woodland located in southwestern Louisiana (29°45'N, 93°37'W). This woodland and others like it along the northern coast of the Gulf of Mexico are important stopover sites for Nearctic-Neotropical landbird migrants (e.g. Rappole and Warner 1976, Moore and Kerlinger 1987). They provide the last place to stop before fall migrants cross this ecological barrier and the first landfall for birds returning north from wintering sites in spring.

*Measurement of variables.*—Thrushes were captured using mist nets (12 m × 2.6 m; 30-mm mesh), weighed to the nearest 0.1 g using a digital electronic balance, and banded with U.S. Fish and Wildlife Service leg bands. Measurements of several morphological characters were taken on a subsample of each species (Gray-cheeked Thrush,  $n = 30$ ; Swainson's Thrush,  $n = 31$ ; Veery,  $n = 30$ ; and Wood Thrush,  $n = 20$ ). Characters were grouped into three functional units: feeding (bill), flying (wing and tail) and pedal locomotion (hind limb).

Wing span and breadth were recorded from outstretched wings. We measured length between wing tip to tenth primary, length between wing tip to first secondary, ninth-primary length, notch on inner web of ninth primary, and wing chord (length from leading edge of folded wrist to tip of ninth primary). Although wing chord has limited use in aerodynamic research (cf. Kerlinger 1989, Pennycuick 1989), it is a widely used correlate of wing size. These characters describe wing size and wing shape, especially the shape near the tip, which affects flight ability and aerodynamic performance. All linear measurements are accurate to 0.1 mm (except wing chord to 0.5 mm).

The outstretched left wing of each bird was traced

while the upper edge of the wing was straight and feathers spread evenly. The right wing was used when flight feathers on the left wing were missing or broken. The resultant outline was used to determine wing area using a computerized video image analyzer, which provided a rapid integration of the area within the trace. The resultant was doubled to estimate the area of both wings. The portion of the body between the two wings was not included in wing area. We used total wing area to calculate wing loading (mass/wing area; expressed in Newtons per meter<sup>2</sup>); and aspect ratio ([wing span]<sup>2</sup>/wing area). The tail length was measured from the base of central pair of rectrices to tip of longest rectrix when the tail was naturally folded. The tail graduation was measured from tip of longest to tip of shortest rectrices when the tail was closed. To adjust for body-size differences, original linear measurements were divided by the cube root of body mass (Leisler and Winkler 1985, Bairlein 1992). The estimated amount of available fat was calculated as total body mass minus fat-free mass. Fat-free mass was estimated according to species-specific iterative regression models (Yong 1993).

*Statistic analysis.*—A one-way ANOVA was used to test for difference among species on all variables. Student's *t*-tests were used to contrast *Catharus* thrushes and Wood Thrush ( $\alpha = 0.05$  unless otherwise stated). Multiple-discriminant analysis (MDA) identified morphological variables responsible for differences among species. MDA derived a linear combination of morphological variables that best discriminated among species (Hair et al. 1987).

We first identified a set of character dimensions using principal-components analysis (PCA) based on correlation matrix to investigate how morphological and aerodynamic variables related to energetic condition during stopover. PCA projections were calculated on original data with all linear measurements standardized by cubic body mass (see Winkler and Leisler 1985). Oblique rotation, rather than orthogonal rotation, was used to facilitate interpretation because the former approach does not assume that underlying dimensions are uncorrelated (see Hair et al. 1987). Pearson's correlation coefficients of PC scores with estimated fat-free body mass were calculated within and among species.

All variables were normally distributed and variances among species for all variables were not statistically different (Cochran's test,  $C$  between 0.59 and 0.27,  $P > 0.05$ ). The Kaiser-Meyer-Olkin value for sampling adequacy (0.73) and Bartlett test of sphericity (2,535.6,  $P < 0.001$ ), as well as similar sample sizes for each species, indicated the appropriateness of the multivariate analysis (SPSSX users guide 1986).

#### RESULTS

*Morphological differences among species.*—Significant differences were found on all flight

TABLE 1. Flight morphology of migratory thrushes ( $\bar{x} \pm SE$ ). Statistic differences are detected both among *Catharus* thrushes and between *Catharus* thrushes and the Wood Thrush for all variables except notch and tail graduation.

Characters	Gray-cheeked Thrush	Swainson's Thrush	Veery	Wood Thrush
<i>n</i>	31	30	29	20
Mass (g)	5.10 $\pm$ 0.52	27.65 $\pm$ 0.60	25.29 $\pm$ 0.58	40.18 $\pm$ 0.87
Wing length (mm)	101.94 $\pm$ 0.64	98.63 $\pm$ 0.55	98.78 $\pm$ 0.70	106.35 $\pm$ 0.85
Wing width (mm)	65.86 $\pm$ 0.43	63.92 $\pm$ 0.54	66.72 $\pm$ 0.57	73.85 $\pm$ 0.60
Wing area (cm <sup>2</sup> )	50.26 $\pm$ 1.66	141.77 $\pm$ 1.43	149.08 $\pm$ 1.69	179.56 $\pm$ 2.57
Wing span (mm)	305.36 $\pm$ 1.47	297.13 $\pm$ 1.27	299.41 $\pm$ 1.55	327.35 $\pm$ 2.11
Wing tip to first secondary (mm)	33.95 $\pm$ 0.40	32.55 $\pm$ 0.38	30.48 $\pm$ 0.31	30.85 $\pm$ 0.55
Wing tip to tenth primary (mm)	64.05 $\pm$ 0.53	62.88 $\pm$ 0.55	61.93 $\pm$ 0.64	65.88 $\pm$ 0.63
Notch (mm)	21.39 $\pm$ 0.28	21.12 $\pm$ 0.28	20.83 $\pm$ 0.30	24.53 $\pm$ 0.42
Ninth primary length (mm)	79.82 $\pm$ 0.56	77.15 $\pm$ 0.49	77.66 $\pm$ 0.92	83.33 $\pm$ 0.70
Tail length (mm)	68.79 $\pm$ 0.64	67.17 $\pm$ 0.57	70.45 $\pm$ 0.57	69.48 $\pm$ 0.58
Tail graduation (mm)	1.74 $\pm$ 0.41	1.58 $\pm$ 0.38	1.76 $\pm$ 0.51	2.22 $\pm$ 0.32
Wing load (N/m <sup>2</sup> )	16.40 $\pm$ 0.30	19.16 $\pm$ 0.41	16.66 $\pm$ 0.36	22.01 $\pm$ 0.51
Aspect ratio	6.22 $\pm$ 0.04	6.24 $\pm$ 0.02	6.02 $\pm$ 0.03	5.98 $\pm$ 0.05
Wing-span ratio	0.22 $\pm$ 0.001	0.22 $\pm$ 0.002	0.23 $\pm$ 0.001	0.236 $\pm$ 0.001

morphological characters among the four species (Table 1); exceptions were notch and tail graduation, both of which varied widely within species. The differences were also significant when *Catharus* thrushes as a group were compared to Wood Thrush. The Wood Thrush has greater body mass, longer wing length, wing width, wing span and, consequently, larger wing area. Morphological characters are still significantly different after accounting for body size differences among species. However, the direction of difference is reversed as Wood Thrush has smaller values for most measurements. The lower aspect ratio and higher width/span ratio suggested that Wood Thrush have shorter and broader wings relative to body size compared to *Catharus* thrushes. The relatively small wings resulted in greater wing loading, which is 26% higher than *Catharus* thrushes (22.00 N/m<sup>2</sup> vs. 17.40 N/m<sup>2</sup>).

Among *Catharus* thrushes, Gray-cheeked Thrush have longer, more pointed wings and greater wing area than the other species. Longer wings and large wing area resulted in reduced wing loading for Gray-cheeked Thrush (15% lower than Swainson's Thrush and 18% lower than Wood Thrush). Swainson's Thrushes are characterized by relatively short wings, short tails, narrow wing widths, and small wing areas, which resulted in greater wing loadings. The Veery, which has the lowest aspect ratio among *Catharus* thrushes, was intermediate between Gray-cheeked Thrush and Swainson's Thrush; wing length, wing span, length from

wing tip to tenth primary, ninth primary length, and wing loading were similar to those of the Swainson's Thrush, whereas wing width, wing area, and tail length were similar to Gray-cheeked Thrush.

Discriminant analysis produced three significant axes along which the four species are distinguished (Table 2). The first axis, which accounted for 78.6% of the among-species variance, was associated with large wing area and small tail graduation. The second axis (13.5% of among-species variance) was associated with decreasing wing loading, and increasing wing size and tail length. The third axis (7.9% of variance) was associated with increasing wing width and decreasing length from wing tip to first secondary and aspect ratio. The first axis separated the Gray-cheeked Thrush and Wood Thrush (which have absolutely large wing area) from Swainson's Thrush and Veery. The second axis separated Gray-cheeked Thrush and Veery, which have relatively longer wings and tail, from Wood Thrush and Swainson's Thrush. The third axis separated Wood Thrush and Veery, which have larger wing width and lower aspect ratio wings, from Swainson's Thrush and Gray-cheeked Thrush.

The principal-component analysis generated three factors that explained 81.1% of the overall variance (Table 2). Principal component I (wing size factor), which is similar to discriminant function 2, was associated with overall large wing size and reduced wing loading. Principal component II (broadness factor), which is sim-

TABLE 2. Factor loadings varimax rotated discriminant analysis and principal-components analysis of flight morphology differences among four species of thrushes.

Variable	Discriminant function <sup>a</sup>			Principal component <sup>b</sup>		
	1	2	3	I	II	III
Wing area	0.627*	0.166	0.304		0.722	
Tail graduation	-0.280*	0.050	0.052			-0.837
Wing span	0.074	0.874*	0.065	0.976		
Wing load	0.108	-0.860*	-0.188	-0.569		0.410
Wing length	0.058	0.836*	-0.048	0.983		
Tail length	-0.241	0.753*	0.359	0.930		
Feather length	0.010	0.675*	0.004	0.971		
Wing width	0.077	0.668*	0.379	0.969		
Wing tip to first secondary	0.009	0.667*	-0.525	0.945		
Wing tip to tenth primary	-0.052	0.663*	-0.161	0.820		
Notch	0.146	0.268*	-0.021	0.761		0.454
W. width/span	0.045	-0.001	0.491*		0.828	
Aspect ratio	0.009	-0.038	-0.399*		-0.867	

<sup>a</sup> Variables with asterisk (\*) used for function explanation. Canonical correlations (all  $P < 0.001$ ), chi-square, and degrees of freedom for functions were: (1) 0.922 ( $X^2 = 303.52$ ,  $df = 22$ ); (2) 0.701 ( $X^2 = 113.25$ ,  $df = 16$ ); (3) 0.602 ( $X^2 = 45.28$ ,  $df = 7$ ).

<sup>b</sup> Eigenvalues and percent variance explained for rotated principal components were: (I) 7.266 (55.9%); (II) 2.127 (16.4%); (III) 1.144 (8.8%).

ilar to discriminant function 3, is highly correlated with decreasing wing aspect ratio and increasing wing area. Species or individuals scoring high on this component have rounded and broad wings. Principal component III (tail roundness factor) is correlated negatively with tail graduation and positively with the ninth-primary notch and wing loading. Significant differences were found among species for all factors using a one-way ANOVA ( $df = 3$  and

104): (PCI)  $F = 23.36$ ,  $P < 0.001$ ; (PCII)  $F = 28.04$ ,  $P < 0.001$ ; and (PCIII)  $F = 3.71$ ,  $P < 0.05$ ). The individuals of the four species are projected onto the first two components (Fig. 1).

*Relation between morphology and energetic condition.*—We correlated PC scores with fat-free body mass and energetic condition among and within each species. Among species, we found significant negative correlations between the wing-size factor (PCI) and both fat-free mass

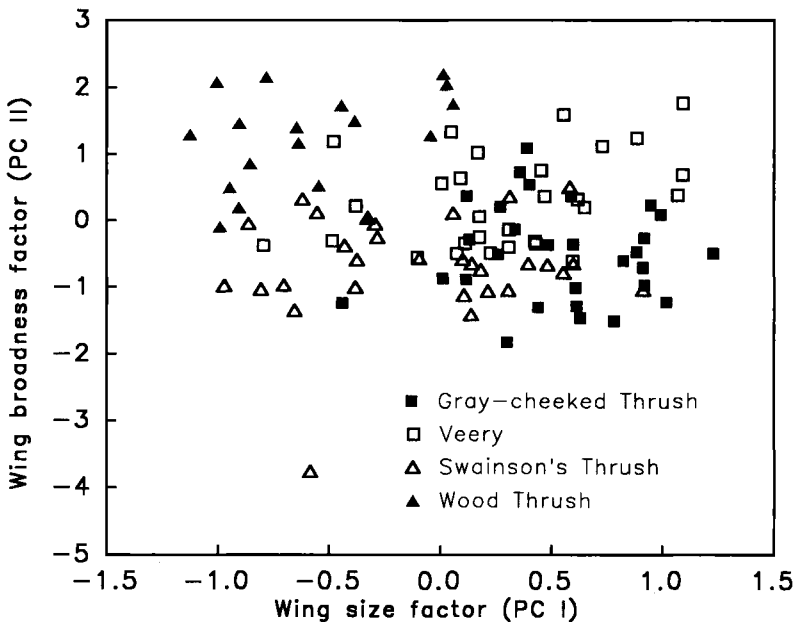


Fig. 1. Projections of individuals of four thrush species on rotated principal components I and II.

TABLE 3. Pearson's correlations of flight morphology (as described by principal-component scores) with fat-free mass and estimated fat among and within four thrush species.

	Principal components		
	I	II	III
<b>Among species</b>			
Fat-free mass	-0.489**	0.588**	-0.335**
Estimated fat	-0.643**	-0.090	0.286**
<b>Fat-free mass within species</b>			
Gray-cheeked Thrush	0.372*	0.147	0.255
Swainson's Thrush	0.506**	0.109	0.323*
Veery	0.455**	0.497**	0.229
Wood Thrush	0.521*	0.250	0.291
<b>Estimated fat within species</b>			
Gray-cheeked Thrush	-0.751**	0.269	0.150
Swainson's Thrush	-0.872**	-0.004	0.269
Veery	-0.769**	0.069	0.386*
Wood Thrush	-0.793**	-0.205	0.493*

\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; others not significant ( $P > 0.05$ ).

and estimated fat (Table 3). Smaller (body mass) species have longer, more pointed wings and lower amounts of fat (i.e. smaller energy stores). PCII (wing broadness factor) is significantly related to body size; larger species have relatively broader and more rounded wings (Table 3). PCIII (tail factor) has a significant, but relatively low, negative correlation with both fat-free mass and estimated fat. When mean PC scores are examined, the Gray-cheeked Thrush and Veery had higher scores on PCI (i.e. species with relatively longer wing and tail are smaller and carry less fat stores and, consequently, have reduced wing loading). Wood Thrushes, with their relatively large fat-free mass, are associated with more rounded and broader wings (higher score on PCII).

Within species, wing-size factor (PCI) had a significant positive relation with fat-free mass and a significant negative relation with estimated fat in every species. These relationships indicate that larger (greater fat-free mass) individuals, regardless of species, have longer and more pointed wings than do smaller individuals. Moreover, larger individuals with longer wings carried smaller energy stores. Whereas the wing-size factor (PCI) and fat-free mass was negative among species, the wing-size factor was negatively associated with energetic condition both among and within species. These results suggest that the amount of fat stores is related to wing shape.

*Scale relation between morphology and body size.*—Individuals with relatively larger wings had

relatively smaller fat stores both within and among species. This pattern could be explained in two ways: (1) wing size increases allometrically with body-size increase, whereas fat stores increase isometrically; (2) wing size increases isometrically with body mass, whereas fat stores increase at a slower rate. We examined scale relationships of fat-free mass with wing span and wing area to decipher how the variables body size, wing size, and energetic condition are associated with one another.

Wing span and wing area are expected to increase isometrically as the 0.33 and 0.67 power, respectively, of fat-free body mass for geometrically similar individuals (Greenewalt 1962, 1975, Alexander 1971, Rayner 1979). The regression analyses of fat-free mass with log-transformed wing span and with wing area revealed allometric relationships both among and within species (Fig. 2). The rate of increase of wing span and wing area with increasing fat-free mass were much higher than the expected isometric (0.33 and 0.67) relationship for each species and among the *Catharus* thrushes (Figs. 2 and 3). Among species, however, the slopes of the regression lines of fat-free mass with wing span and wing area were 0.19 ( $P < 0.001$ ) and 0.44 ( $P < 0.001$ ), respectively, and much lower than the expected 0.33 and 0.67 values. These analyses demonstrate that the rate of change of wing size with increasing body size deviates positively from an isometric relationship within each species, but deviates negatively among species.

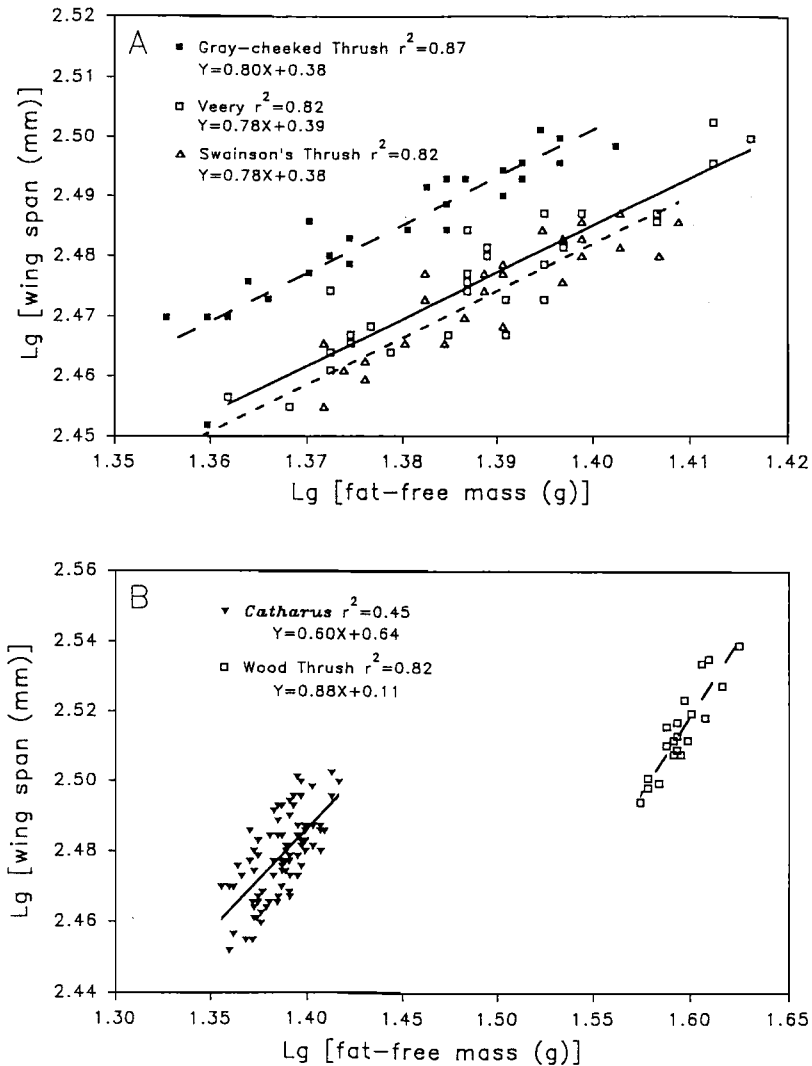


Fig. 2. Allometric relationship between wing span and fat-free mass. Lines fitted with least squares have expected slopes of 0.333. Comparison (A) among *Catharus* species and (B) between *Catharus* species and Wood Thrush. All correlations  $P < 0.001$ .

#### DISCUSSION

*Flight morphology.*—Long-distance migration selects for morphological features that reduce the cost of transport (e.g. Winkler and Leisler 1985). Differences among thrush species in flight morphology may have evolved in response to differences in migratory distance. *Catharus* thrushes, notably the Gray-cheeked Thrush, migrate further between wintering and breeding grounds than the Wood Thrush. Gray-cheeked Thrushes have relatively long, narrow, pointed wings, the lowest wing loading, and a relatively

high aspect ratio. Wing shape and size affect the energy cost of flight. Birds with long, pointed wings (high aspect ratio) generate more power at a lower cost than birds with short, rounded wings (low aspect ratio) because longer, pointed wings are more able to shed tip vortices that create drag because they must be pulled along by the bird (cf. Kerlinger 1989; see also Pennycuik 1968). Lower wing loading reduces induced drag and the bird is less costly to pull.

Wood Thrushes have relatively short wings, a short tail, small wing area, a low aspect ratio,

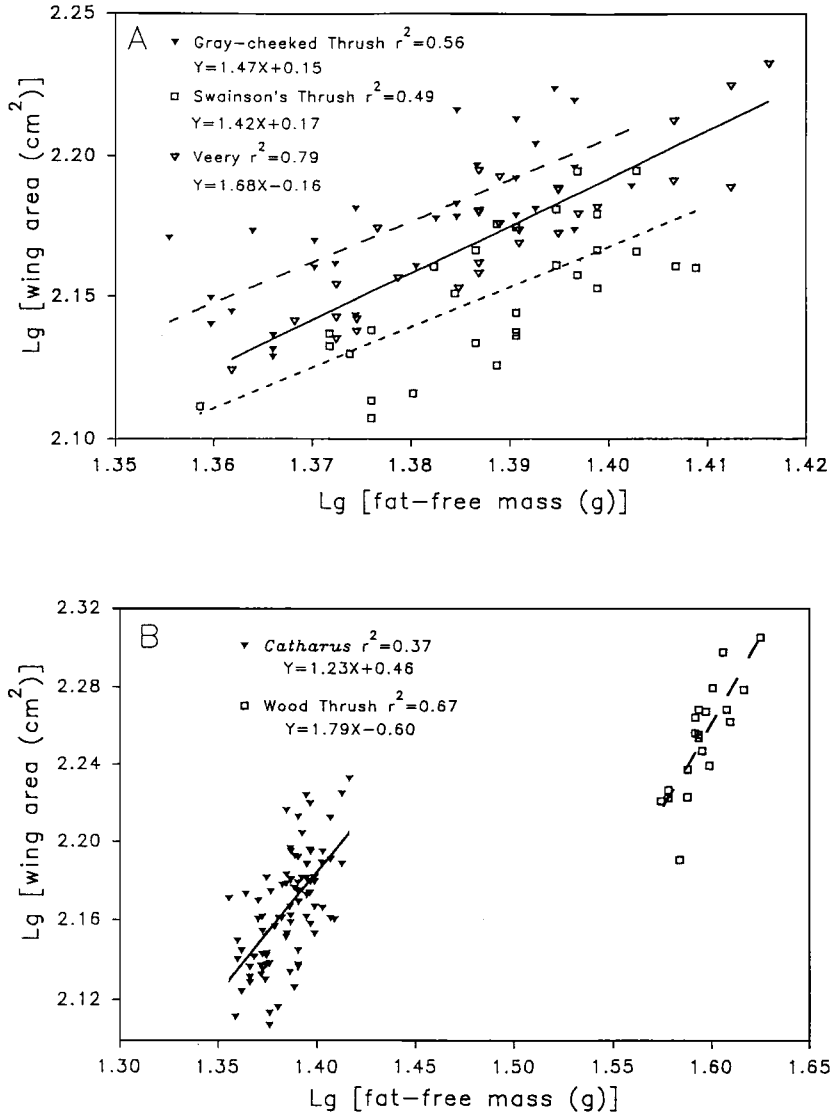


Fig. 3. Allometric relationship between wing area and fat-free mass. Lines fitted with least squares have expected slopes of 0.666. Comparison (A) among *Catharus* species and (B) between *Catharus* species and Wood Thrush. All correlations  $P < 0.001$ .

and greater wing loading—a flight morphology that could be tied to their shorter migration distance, as well as their propensity to forage on the ground (Holmes and Robinson 1988, Yong unpubl. data). The greater wing loading of Wood Thrushes results from the combined effect of larger body mass and smaller wing area. A low-aspect-ratio wing increases maneuverability and generates high power at low speeds, which would be advantageous during takeoff from the ground (Pennycuick 1983). The

same characterization applies to Swainson's Thrushes relative to the other *Catharus* thrushes examined.

However, the increased wing loading characteristic of the Wood Thrush and Swainson's Thrush should decrease maneuverability during flight, all else being equal. The loss of maneuverability because of high wing loading is compensated somewhat by relatively broad and rounded wings, which are best for slow flight (e.g. Chandler and Mulvihill 1992). Conversely,

the loss of maneuverability with increased wing length among Gray-cheeked Thrushes is compensated by relatively low wing loading. Lower wing loading in Gray-cheeked Thrush and Veery promotes rapid takeoff and maneuverability at slow speeds (Norberg 1990).

*Allometric relations and energetic demands.*—If wing span and wing area scale isometrically in relation to fat-free body mass, individuals with the same fat store per gram of body mass experience the same potential flight distance (Pennycuik 1968, Rayner 1979). The allometric relationships between wing morphology and fat-free mass among species probably results from the small wing size of Wood Thrushes in relation to body size. *Catharus* thrushes, especially the Gray-cheeked Thrush, have relatively larger wing span and wing area in relation to body size. Within each species, the positive allometric increase of wing span and wing area with body mass means that larger individuals have disproportionately large and long wings relative to their fat-free mass.

Morphological differences between sexes, age classes, or populations could produce the intraspecific allometric relationship between wing morphology and fat-free mass (cf. Chandler and Mulvihill 1992). For example, young passerines tend to have shorter and more rounded wings than adults (Alatalo et al. 1983; see also Mulvihill and Chandler 1990). Among some Old World warblers, Baggott (1986) found that younger birds and females had higher fat content during migration. Hedenstrom and Pettersson (1986) found that male Willow Warblers (*Phylloscopus trochilus*) had more pointed wings and carried less fat during the spring migration than females.

Because the relation between wing size and body mass is positively allometric in each species and negatively allometric among species, larger individuals and species with smaller body size do not consume as much energy as smaller individuals and species with larger body mass for the same migratory distance. Among *Catharus* thrushes, Gray-cheeked Thrushes and Veerys arrive at our study site with lower fat stores (6.57% and 4.71% fat-free mass, respectively) than Swainson's Thrushes (11.84% fat-free mass; unpubl. data). Similarly, larger individuals within species carry relatively less fat (Yong 1993). Larger individuals within a species or smaller thrush species will achieve longer flight distance for the same relative amount of stored

fat. This relationship between wing morphology and amount of stored fat is consistent with the relationship between morphology and the energy demands for flight.

Alternatively, smaller species (the Gray-cheeked Thrush and Veery) and larger individuals within species might have mobilized more of their energy stores during passage and arrived at a stopover site in poorer energetic condition than smaller individuals (and larger species). If so, larger individuals within each species should have stopped for a longer period because stopover length is related with energetic condition upon arrival (e.g. Moore and Kerlinger 1987, Kuenzi et al. 1991). We tested this possibility by examining the length of stay in relation to body size (fat free mass) of thrushes ( $n = 1,903$ ) captured over three springs at our study site (Yong 1993). Low correlations between fat-free mass and stopover length are not consistent with this alternative explanation (Gray-cheeked Thrush,  $r = 0.04$ ,  $n = 235$ ; Swainson's Thrush,  $r = 0.03$ ,  $n = 689$ ; Veery,  $r = -0.12$ ,  $n = 255$ ; Wood Thrush,  $r = -0.01$ ,  $n = 724$ ,  $P > 0.05$ ).

*Morphology, energetic condition and behavior.*—Morphological differences among species and the significant relation between flight morphology and energetic condition both among and within species suggest an effect of flight morphology on energy demands associated with long-distance migration. Species or individuals with relatively long, pointed wings are more efficient migrants, and the energy demand per unit distance travelled is lower. Reduced energy costs for flight means that: (1) less fat is required to negotiate a long-distance flight (e.g. cross Gulf of Mexico); and (2) less fat need be replenished during stopovers before migration is resumed.

Circumstantial evidence suggests that Gray-cheeked Thrushes and Veerys may adopt a longer, transoceanic route during spring passage between tropical winter quarters and temperate breeding areas (R. S. Mulvihill pers. comm.). The more efficient wing design of those two species would permit them to fly farther with the same fat store than either Swainson's Thrushes and Wood Thrushes.

Furthermore, a Gray-cheeked Thrush requires less stored fat, so devotes less time and energy to foraging, and may experience a shorter stopover, not to mention reduced risk of predation during stopover by virtue of less for-



aging activity. A shorter stopover may mean a faster migration (cf. Alerstam and Lindström 1990). Spring arrival data at our study site suggest that Gray-cheeked Thrushes and Veerys start spring migration later than Swainson's Thrushes (unpubl. data). Yet, passage times in Illinois, later in spring and closer to breeding grounds (Graber et al. 1971), indicate that the Swainson's Thrush does not arrive any sooner. Our banding data also reveal that average stopover length for both Gray-cheeked Thrushes and Veerys is 2.27 days, and is significantly shorter than Wood Thrush stopover of 3.16 days ( $t = 2.38$ ,  $df = 221$ ,  $P < 0.01$ ), which is another indicator of a faster pace of migration. Lower fat stores are not necessarily an indication of poor energetic condition, but rather may be indicative of different "strategies of migration" dictated by the relation between flight morphology and energetic demand.

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