

RELATIONSHIP OF *CALIDRIS* SANDPIPER WING SHAPE WITH RELATIVE FUEL LOAD AND TOTAL MIGRATION

A CLASSIC PREDICTION of aerodynamic theory is that highly migratory birds should have more pointed wings than less migratory or nonmigratory birds. More pointed wings are more efficient during long-distance flight because

flights are more costly per unit distance, in terms of energy and water use, than short flights (Klaassen 1996). Longer flights require more fuel in the form of fat and protein. That adds extra body mass, which increases the metabolic

Calidris species here differ in lean mass from 20 to 133 g, but shorebirds of a wide range of sizes (25–428 g) are predicted to have the same flight range per relative fuel load because of their similar body morphology (Castro and Myers 1989). Thus, according to Castro and Myers (1989), a 20% relative fuel load should exert the same demands on the tiny Least Sandpiper as it does on the much larger Red Knot.

In an effort to reduce the likelihood of sampling bias in estimation of mean relative fuel load, data for migration fueling sites had to meet a number of criteria. First, mean masses at a minimum of three sites, separated by either geography or season, were used for each species. Those values were averaged to determine mean relative fuel load. Second, reported masses had to be for adults of both genders caught over at least a two-week period with a sample size >30. The two-week time criterion was used because stopover masses in the literature often include birds just about to depart and just arriving. Using data over a length of time decreases the likelihood that a sample will be biased to either heavy or light birds. Relative fuel load was arcsin transformed to meet assumptions of normality.

the percentage of total body mass that is added specifically for migration. Fueling site masses are not departure masses but are from birds at different stages of fattening. I assume that the mean of those masses of birds at different stages will be correlated with mean final departure mass. Although the migration mass data used here are not ideal for the purpose of my analysis, the data available are an appropriate starting point for analysis of this new hypothesis. Ultimately, direct measures or estimates of departure fuel load for each species at many sites would be desirable.

Differences in size between species can affect flight dynamics but should not affect the analysis. The

Correlations between variables were analyzed using the method of phylogenetically independent contrasts (Felsenstein 1985, Garland et al. 1992) because *Calidris* sandpiper species are not independent data points because of their common ancestry. Contrasts were obtained for size, wing shape, and migration variables using COMPARE 4.4 software (Martins 2001). The *Calidris* phylogeny continues to be revised, so two separate phylogenies were used to test the robustness of any relationship to different

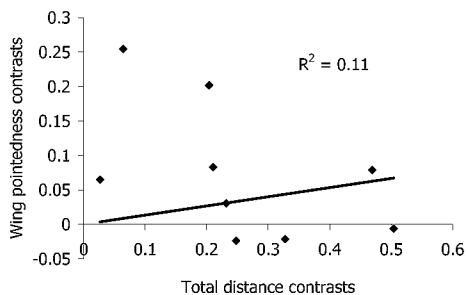
Phylogenetic hypotheses are shown in the Appendix. The first hypothesis is based on the phylogeny of *Calidris* species in the genus *Calidris* (Martins 2001). The second hypothesis is based on the phylogeny of *Calidris* species in the genus *Calidris* (Martins 2001).

eny (maximum-likelihood and maximum-parsimony trees were the same). Baker's (1992) phylogeny does not include Little Stints so that species was left out of the analysis using that tree. The phylogeny of *C. canutus* subspecies is from Tomkovich (1992). All branch lengths were set to unity. Standard deviations of the contrasts were not significantly correlated with traits in any case, indicating that the data and branch lengths were adequately standardized (Garland et al. 1992). Regression through the origin was used to test for correlations among the three morphology contrasts and the two migration contrasts (Garland et al. 1992). The method of independent contrasts creates $N-1$ contrasts from the original data set; thus in the analysis, there are 9 data points using the Baker (1992) phylogeny and 10 using the Borowik and McLennan phylogeny (1999). Correlations were analyzed with SYSTAT 10 (SPSS, Chicago, Illinois).

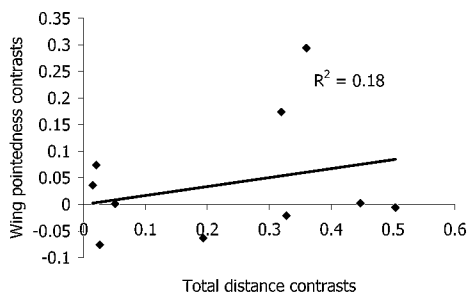
RESULTS

The correlation between wing pointedness and migration of *Calidris* sandpipers depends upon which migratory flight variable is used but is similar for the two phylogenies. There was no significant correlation between wing pointedness (C2) and total migration distance (Fig. 1), but wing pointedness and relative fuel load were significantly positively correlated for both phylogenies (Fig. 2). Size (C1) was not correlated with either wing-shape variable or total distance but was positively correlated with relative fuel load (Baker phylogeny, $R^2 = 0.39$, $P = 0.036$; Borowik and McLennan phylogeny, $R^2 = 0.40$, $P = 0.050$). Relative fuel load includes a measure of size (lean mass) in its denominator; thus, it is possible that there is a spurious correlation between relative fuel load and size caused by compounding ratios (Atchley et al. 1976).

To test whether Castro and Myers (1989) flight-range estimates affect the interpretation of the data, body size (C1) was regressed against the residuals of the relative fuel load and wing pointedness relationship presented in Figure 2. If flight range and body size are linked, we would expect the analysis to overestimate the selective pressure of fuel load on wing shape of the largest species, and vice versa for the smallest species. However, there is no evidence that larger species had a greater effect on the results (smaller residuals) or smaller species a lesser effect (larger residuals) because there is no relationship between residuals and body size (Baker phylogeny, $R^2 = 0.01$, $P = 0.77$; Borowik and McLennan phylogeny, $R^2 = 0.04$, $P = 0.55$).



A



B

FIG. 1. Wing pointedness of *Calidris* sandpipers is not correlated with total migration distance for either phylogeny: (A) Baker (1992), $P = 0.34$; (B) Borowik and McLennan (1999), $P = 0.20$.

DISCUSSION

The data support the hypothesis that wing shape in *Calidris* sandpipers is partially selected for by the cost of relative fuel loads carried during migratory flights. Although the result using Borowik and McLennan's (1999) phylogeny is strongly influenced by one contrast, the result from Baker's (1992) phylogeny suggests the relationship is robust. The hypothesis that the distance between the start and end of a migration should correlate with wing pointedness was not supported.

Relative fuel load takes into account that the extra fuel mass required for long flights is more energetically and metabolically demanding per unit distance than that needed for short flights (Klaassen 1996). The positive correlation between relative fuel load and wing pointedness indicates that *Calidris* wing shape is adapted to the selective pressure of the demands of carrying large relative fuel loads during migration. Relative fuel load thus appears to have a relatively greater effect on *Calidris* wing shape than

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APPENDIX. Mean body masses (g) and sample sizes () from studies capturing and weighing shorebirds at fueling sites. Data from all sites for each species were averaged to calculate mean fueling mass.

Species	Mean body mass (g)		Fueling site location	Reference
Curlew Sandpiper	69.1	186	Bahrain	Hirschfeld et al. 1996
	70.6	107	Netherlands	Smit and Wolff 1981
	65.5	435	France	Cramp 1983
	59.0	91	France	Cramp 1983
	55.8	366	Morocco	Cramp 1983
	77.1	257	South Africa	Elliot et al. 1976
	57.0	75	Kenya	Elliot et al. 1976
Dunlin	64.1	82	USA	Warnock and Gill 1996
	57.2	190	USA	Warnock and Gill 1996
	61.6	38	USA	Holmes 1966
Least Sandpiper	23.6	318	Canada	Cooper 1994
	27.2	55	Canada	Page and Salvadori 1969

APPENDIX. C

			M a	n	F a g	R
S			a (g)		a	
R K	(islandica)		190.8	223	I a	G a . 1991
			183.0	472	I a	M 1972, G a . 1991, a
R K	(rufa)		135.8	1,398	I a	P a a . 1999
			149.4	264	A g a	W a M 1992
			161.2	1,322	USA	Ha g 2001
			161.9	908	USA	Ha g 2001
R -	S		29.3	151	H g K g	M 1981
			34.3	358	A a a	Ba 1984
S	Sa		34.2	4,156	A a a	R g a . 1996
			28.1	102	USA	M a a J 1964
			30.9	2,502	USA	D a . 1988
			28.2	22,875	Ca a a	G a -T 1992
			24.8	56	S a	G a -T 1992
			29.8	229	USA	Pa g a Sa a 1969
			26.3	90	Ca a a	A a a G a -T 1997
			26.2	723	Ca a a	A a a G a -T 1997
			25.9	66	USA	L a Ha g 1995
			25.3	969	USA	L a Ha g 1995
			27.0	107	Ca a a	G a 1983
W	Sa		27.3	2,371	Ca a a	B a . 1987 a B . a a
			28.8	737	Ca a a	B a . 1987
			30.3	311	USA	Wa a B 1998
			25.6	44	USA	Wa a B 1998
			26.2	118	USA	Wa a B 1998
W -	Sa		48.3	83	Ca a a	Ha g a . 1991
			43.5	104	B a	Ha g a . 1991
			45.8	452	USA	Ha g a . 1991
			34.7	367	V a	T a 1987