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

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Abstract.—It has proven difficult to support the classic prediction of aerodynamic theory that highly migratory birds should have more pointed wings than less migratory birds. This study extends the search by testing for correlations between wing shape of *Calidris* sandpipers and a traditional migratory variable (total migration distance) as well as a novel variable (relative fuel load). Using phylogentically independent contrasts, it was determined that relative fuel load is a better predictor of wing shape than total migration distance. *Received 30 May 2002, accepted 22 April 2003.*

Resumen.— Hasta ahora ha sido difícil apoyar la predicción clásica de la teoría aerodinámica de que las aves altamente migratorias deberían tener alas más puntiagudas que las menos migratorias. Este estudio amplía la búsqueda mediante la puesta a prueba de la existencia de correlaciones entre la forma de las alas de playeros del género *Calidris* y una variable migratoria tradicional (distancia total de migración) y una variable nueva (carga relativa de combustible). Usando contrastes filogenéticamente independientes, se determinó que la carga relativa de combustible predice mejor la forma de las alas que la distancia total de migración.

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 of reduced drag (Savile 1956, Rayner 1988, Norberg 1990, Hedenström and Møller 1992, Pennycuick et al. 1994), but entail a reduction of other performance attributes such as take-off ability when escaping predators (Swaddle and Lockwood 1998). Wing shape should thus be a product of natural selection for an optimal balance between benefits of pointed wings, which increase with migratory behavior, and costs, which increase with higher predation risk. Aerial foraging technique and courtship displays can also be important factors that must be taken into account in ecomorphological studies of avian wing shape (Marchetti et al. 1995, Swaddle and Lockwood 1998). I examine the correlation between wing shape in *Calidris* sandpipers, a group of highly migratory birds with worldwide distribution and similar foraging and courtship behaviors, and three variables: two migratory flight variables and predation risk.

Previous studies have used total migration distance (median breeding range to median nonbreeding range) as a migratory flight variable to describe the potential selective pressure of migration on morphology. The longer the total journey a species makes, the greater the selection for pointed wing shape. A detailed study on the ecomorphology of passerines by Winkler and Leisler (1992) found a correlation between migration distance and a multivariate representation of wing morphology, but phylogenetic history was not controlled for. Two more recent phylogenetically controlled comparisons have demonstrated that migratory species have more pointed wings than nonmigratory species (Mönkkönen 1995, Lockwood et al. 1998), whereas others have failed to detect differences (Mulvihill and Chandler 1990, Keast 1996). Only one study has shown a relationship between migration distance and wing shape comparing migratory species (Marchetti et al. 1995).

Those studies have not attempted to account for differences in flight lengths during migration. Species may take different length flights between stopovers, which Piersma (1987) described as "hop, skip, and jump" tactics. Those differences may be due either to factors such as ecological barriers forcing long flights or differences in the spacing of preferred foraging habitats along the migration route. For example, Red Knots (scientific names in Table 2) take long "jumps" between relatively rare large mudflat areas rich in gastropod prey (Piersma 1987).

Flight distance is important because longer

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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 cost of flight (Pennycuick 1972, Norberg 1990). Another cost is the increased time required for foraging and thus an increase in total time taken to migrate (Alerstam and Lindström, 1990). The prediction is that species with higher relative fuel loads (mass – lean body mass / lean body mass) during migration have higher flight costs, and natural selection should then have acted to produce more efficient wing shape (i.e. pointed) than birds with low departure fuel loads. Thus, relative fuel load (a product of flight distance) can be used as another migratory flight variable rather than total migration distance.

Relative fuel load may also affect wing shape through a reduced ability to escape predators. Quick take-off from the ground, which is important in shorebird escape from predators (Rudebeck 1950, Page and Whitacre 1975, Cresswell 1993), is aided by rounded wing tip shape (Swaddle and Lockwood 1998). Increased mass, due to fuel storage, of migrant Least and Western sandpipers (Burns and Ydenberg 2002), as well as some passerines (Kullberg et al. 1996, 2000; Lind et al. 1999), slows their escape. Individual migrant birds therefore pay a cost when they carry greater fuel loads at migration fueling sites. That effect may occur interspecifically as well, in that species that carry higher relative fuel loads are also more at risk than species with lower relative fuel loads. The two opposing hypotheses for the effect of relative fuel load on wing shape are that (1) high relative fuel load will select for pointed wings to increase long-distance flight efficiency, and (2) high relative fuel load will select for rounder wings to increase escape ability.

Here I test for a relationship between the wing shape of *Calidris* sandpipers and two migratory flight variables (total distance and relative fuel load) and a predation risk variable (relative fuel load). All analyses are phylogenetically controlled to account for the evolutionary relatedness of the species within that genus.

## METHODS

The choice of *Calidris* species depended on two factors: courtship display types and availability of relative fuel-load data. The species differ in migration distance and relative fuel load but do not differ greatly in foraging technique. Most *Calidris* species have acrobatic courtship displays as well (Székely et al. 2000), which can be defined as displays having steep dives, climbs, twists, and turns. To control for that last potential selective force on wing shape, three species with nonacrobatic courtship displays (Pectoral Sandpiper [*C. melantos*], Buff-breasted Sandpiper [*Tryngites subruficollis*], and Ruff [*Philomachus pugnax*]) were removed from the analysis. Of the remaining 17 *Calidris* species and 3 close relatives, sufficient relative fuel-load data (see criteria below) were available for 9 species

To analyze wing shape, Lockwood et al.'s (1998) method of size-constrained components analysis was used. That method, related to principal components analysis, constrains the first component (C1) to size, whereas the subsequent components describe shape. Lengths of eight distal primary feathers were measured (to 0.01 cm with vernier callipers) on the right wing of 2 to 26 museum skins of 8 *Calidris* sandpiper species and 3 subspecies of *C. canutus (canutus, islandica,* and *rufa)*. For species with wide geographic distributions, only specimens from populations for which relative fuel-load data were available were used. For instance, Little Stint specimens and migration data are all from the African wintering population rather than the Indian population. To control for effects of moult on wing shape, all specimens were nonmoulting adults. Values were log-transformed to meet the assumption of normality and were standardized to equal unit variances.

I interpreted the first shape component as wing pointedness (C2) (Table 1). All other shape components, such as wing convexity (C3), explained a much lower percentage of the shape variation and were not correlated with any variable under study here; therefore, they will not be examined further. That shape component corresponds with the wing pointedness examined in other studies of wing shape with higher values of wing pointedness indicating more tapered wing tips. No differences were detected between genders within species (all $P > 0.10$), so data were pooled.

Total migration distance is the difference in kilometers between median breeding range and median nonbreeding range. Latitude and longitude for medians were determined from range maps provided in species accounts (Table 2), and surface distance between medians determined using a web-based distance calculator (see Acknowledgments). Distance was log-transformed to meet assumptions of normality.

Relative fuel load was quantified using masses of birds caught at migration fueling sites (see Appendix). Data from different years for the same site were combined. Relative fuel load is mass at fueling site minus tropical winter mass all divided by tropical winter mass. Tropical winter mass is the lowest mean mass of a sample of the species during the nonmigratory season (Zwarts et al. 1990). Thus, relative fuel load is

TABLE 1. Size-constrained components analysis of wing shape based upon primary feather length (P1–P8 refers to primaries 1 to 8, starting at the distal primary). C1 is constrained to representing size, C2 is interpreted as wing pointedness, and C3 as wing convexity.

| | Factor loading | | |
|---|---|---|---|
| Variable | C1 | C2 | C3 |
| P1 | 0.337 | 0.465 | –0.173 |
| P2 | 0.343 | 0.4 | –0.152 |
| P3 | 0.352 | 0.238 | –0.157 |
| P4 | 0.353 | 0.139 | 0.007 |
| P5 | 0.351 | 0.007 | 0.266 |
| P6 | 0.355 | –0.185 | 0.499 |
| P7 | 0.361 | –0.364 | 0.396 |
| P8 | 0.375 | –0.618 | –0.667 |
| Percent of total variance explained | 98.1 | 1.3 | 0.3 |
| Percent of shape variance explained | – | 72.7 | 13.6 |

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 *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.

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. I used Baker's (1992) phylogeny and Borowik and McLennan's (1999) phylog-

TABLE 2. Data and sources for migration and morphology variables for *Calidris* sandpipers. Size and wing shape values are from size-constrained components analysis and thus do not have units. Sample size for wing measurements are in parentheses under size.

| Species | Mean fueling mass (g)* | Tropical winter mass (g) | Total migration distance (km) | Size | Wing pointedness |
|---|---|---|---|---|---|
| Curlew Sandpiper (*C. ferruginea*) | 64.9 | 48.8[a] | 10,977[b] | 2.489 (6) | 0.100 |
| Dunlin (*C. alpina pacifica*) | 61.0 | 48.4[c] | 2,505[d] | 1.467 (6) | –0.021 |
| Least Sandpiper (*C. minutilla*) | 24.8 | 20.9[e] | 6,288[e] | –2.513 (26) | –0.423 |
| Little Stint (*C. minuta*) | 26.2 | 20.6[f] | 8,485[b] | –2.137 (5) | 0.181 |
| Red Knot (*C. canutus canutus*) | 162.2 | 125[b] | 9,611[b] | 5.449 (3) | 0.304 |
| Red Knot (*C. canutus islandica*) | 173.0 | 133[b] | 3,510[b] | 5.259 (3) | 0.316 |
| Red Knot (*C. canutus rufa*) | 157.5 | 124.9[g] | 13,179[h] | 5.904 (2) | 0.257 |
| Red-necked Stint (*C. ruficollis*) | 32.6 | 25.6[i] | 9,112[j] | –1.516 (9) | 0.440 |
| Semipalmated Sandpiper (*C. pusilla*) | 27.3 | 21.9[k] | 8,475[l] | –1.958 (14) | –0.002 |
| Western Sandpiper (*C. mauri*) | 27.6 | 22[k] | 7,663[j] | –1.716 (26) | –0.004 |
| White-rumped Sandpiper (*C. fuscicollis*) | 43.1 | 32.4[m] | 12,908[n] | 1.500 (6) | 0.165 |

*See Appendix for individual fueling site data.

References: [a] Elliott et al. 1976, [b] Cramp 1983, [c] Holmes 1966, [d] Warnock and Gill 1996, [e] Cooper 1994, [f] Pearson 1987, [g] Harrington 2001, [h] Piersma and Davidson 1992, [i] Melville 1981, [j] Hayman et al. 1986, [k] P. D O'Hara unpubl. data, [l] Gratto-Trevor 1992, [m] Harrington et al. 1991, [n] Parmelee 1992 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, $R^2 = 0.04$, $P = 0.55$).

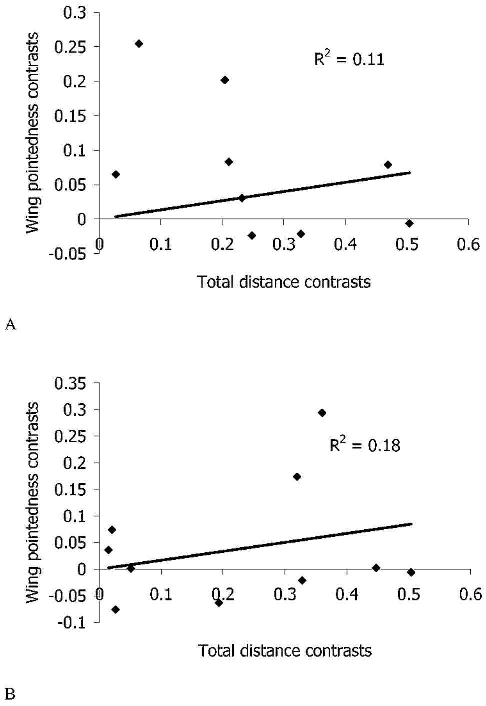

FIG. 1. Wing pointedness of *Calidris* sandpipers is not correlated with total migration distance for either phylogeny: (A) Baker (1992), $P = 0.34$; (B) Borowik and MacLennan (1999), $P = 0.20$.

## 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

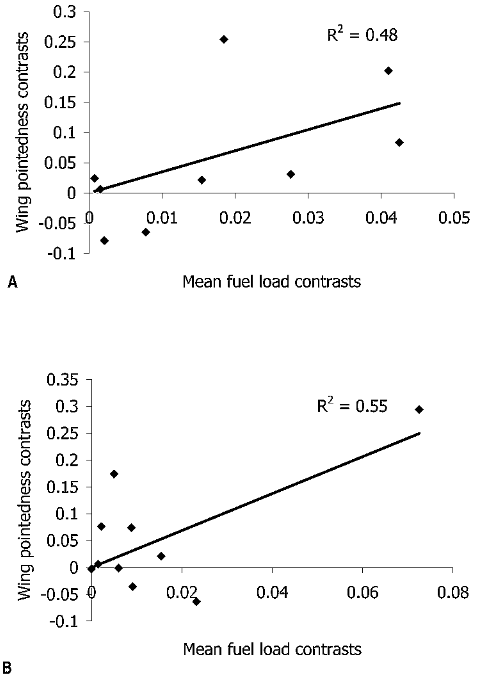

FIG. 2. Wing pointedness of *Calidris* sandpipers is significantly positively correlated with migratory fuel load for the Baker (1992) phylogeny (A) ($P = 0.027$) and the Borowik and MacLennan (1999) phylogeny (B) ($P = 0.009$).

total migration distance. However, that does not mean that total distance is an unimportant selective pressure on shorebird wing morphology because their wings are already considered long and pointed compared to less migratory groups of birds (Cramp 1983).

I also simultaneously tested an alternate hypothesis for the effect of relative fuel load on wing shape. If high relative fuel load increases risk of predation, relative fuel load should be negatively correlated with wing pointedness because round wing shape facilitates escape take-off flights (Swaddle and Lockwood 1998). My study found no evidence that interspecific differences in relative fuel load affect predation risk. However, predation risk is highly complex and depends on many variables including predator community and habitat type. Those extra factors must be considered before making any further conclusions about the effect of predation risk on wing shape. Unfortunately, there are no other independent measures of predation risk available for the birds in this study.

The positive correlation between size and relative fuel load for the Borowik and McLennan (1999) phylogeny may be a result of a spurious correlation (see above), a true ecological outcome, or the result of problems with the assumptions behind relative fuel load. For instance, larger species may migrate in longer flights than smaller species for ecological reasons beyond the scope of my inquiry. However, the result could also be explained by problems with Castro and Myers' (1989) prediction that flight range is the same for a given relative fuel load for different-sized species of similarly shaped shorebirds. Older flight-range estimates (McNeil and Cadieux 1972, Davidson 1984) predict that larger species can fly farther than small species with the same relative fuel load. That implies that large species are more efficient in long distance flight and that required relative fuel load is not equivalent for different species traveling the same distance. However, Castro and Myers' (1989) equation takes factors such as basal metabolic rate and as such may be a better predictor of flight range than other equations. At this time there is no empirical evidence supporting or refuting Castro and Myers' (1989) equation, so my results must be viewed with caution.

Confirming the long-held assumption that pointed wings are selected for by long distance migration has proven to be a more complex endeavor than originally conceived many decades ago. The data used here are not ideal but can be considered a useful preliminary analysis of a new hypothesis. Total migration distance was not correlated with wing shape in *Calidris* sandpipers, but relative fuel load was and so appears to have a relatively greater effect on wing shape than total distance. Both variables should be taken into account to better determine their relative importance in determining the wing morphology of migrant birds.

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R. Ydenberg, B. Crespi, and S. Wardrop all made helpful contributions to the development of this manuscript. Distance between medians determined using a web-based distance calculator available online at www.wcrl.ars.usda.gov/cec/java/lat-long.htm.

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Appendix. Mean body masses (g) and sample sizes (*n*) 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) | *n* | 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 | Morroco | 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 |
| | 23.2 | 276 | Venezuela | Thomas 1987 |
| | 25.0 | 69 | Canada | Alexander and Gratto-Trevor 1997 |
| Little Stint | 23.0 | 261 | Morroco | Cramp 1983 |
| | 29.6 | 85 | Kenya | Cramp 1983 |
| | 24.8 | 170 | Bahrain | Hirschfeld et al. 1996 |
| | 29.0 | 1,524 | Kenya | Pearson 1987 |
| | 24.6 | 195 | Mauritania | Fletcher 1989 |
| Red Knot (*canutus*) | 172.8 | 147 | South Africa | Summers and Waltner 1978 |
| | 167.8 | 768 | Germany | Dick et al. 1987 |
| | 146.0 | 279 | Mauritania | Piersma 1989 |
| Red Knot (*islandica*) | 172.2 | 1,972 | Norway | Evans 1992 |
| | 175.9 | 173 | England | Johnson 1985 |
| | 175.9 | 203 | Iceland | Morrison 1972 |
| | 176.9 | 46 | Iceland | Piersma et al. 1999 |

APPENDIX. Continued.

| Species | Mean body mass (g) | *n* | Fueling site location | Reference |
|---|---|---|---|---|
| Red Knot (*islandica*) | 190.8 | 223 | Iceland | Gudmundsson et al. 1991 |
| | 183.0 | 472 | Iceland | Morrison 1972, Gudmundsson et al. 1991, and Piersma et al. 1999 |
| | 135.8 | 1,398 | Iceland | Wilson and Morrison 1992 |
| Red Knot (*rufa*) | 149.4 | 264 | Argentina | Harrington 2001 |
| | 161.2 | 1,322 | USA | Harrington 2001 |
| | 161.9 | 908 | USA | Harrington 2001 |
| Red-necked Stint | 29.3 | 151 | Hong Kong | Melville 1981 |
| | 34.3 | 358 | Australia | Barter 1984 |
| | 34.2 | 4,156 | Australia | Rogers et al. 1996 |
| Semipalmated Sandpiper | 28.1 | 102 | USA | Murray and Jehl 1964 |
| | 30.9 | 2,502 | USA | Dunn et al. 1988 |
| | 28.2 | 22,875 | Canada | Gratto-Trevor 1992 |
| | 24.8 | 56 | Suriname | Gratto-Trevor 1992 |
| | 29.8 | 229 | USA | Page and Salvadori 1969 |
| | 26.3 | 90 | Canada | Alexander and Gratto-Trevor 1997 |
| | 26.2 | 723 | Canada | Alexander and Gratto-Trevor 1997 |
| | 25.9 | 66 | USA | Lyons and Haig 1995 |
| | 25.3 | 969 | USA | Lyons and Haig 1995 |
| | 27.0 | 107 | Canada | Gratto 1983 |
| Western Sandpiper | 27.3 | 2,371 | Canada | Butler et al. 1987 and Butler unpubl. data |
| | 28.8 | 737 | Canada | Butler et al. 1987 |
| | 30.3 | 311 | USA | Warnock and Bishop 1998 |
| | 25.6 | 44 | USA | Warnock and Bishop 1998 |
| | 26.2 | 118 | USA | Warnock and Bishop 1998 |
| White-rumped Sandpiper | 48.3 | 83 | Canada | Harrington et al. 1991 |
| | 43.5 | 104 | Brazil | Harrington et al. 1991 |
| | 45.8 | 452 | USA | Harrington et al. 1991 |
| | 34.7 | 367 | Venezuela | Thomas 1987 |