

Latitudinal clines in sex ratio, bill, and wing length in Least Sandpipers

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ABSTRACT. Differential distribution of nonbreeding Least Sandpipers (*Calidris minutilla*) according to sex, bill, and wing length was documented using capture data from six locations between California and Ecuador. The distribution of age classes did not vary with latitude. Females, which are slightly larger than males, migrated further south. Wing length increased toward the south for both males and females, which is consistent with the notion that longer wings are adaptive for longer migrations. Bill length also increased in both sexes from north to south. A latitudinal cline in prey burying depth may underlie the clines in bill length as well as in sex ratio.

SINOPSIS. Clino latitudinal en la tasa de sexos, y tamaño del pico y el ala en *Calidris minutilla*

La distribución diferencial por sexo, tamaño del pico y del ala fue documentada para individuos migratorios de *Calidris minutilla*, utilizando datos de captura de seis localidades entre California y Ecuador. La distribución de las edades no varío con la latitud. Las hembras, que son algo más grande que los machos, migran más al sur. El tamaño del ala incrementó con los muestreos más al sur, en ambos sexos, lo que es consistente con la noción de que las alas más largas son adaptaciones para migraciones más lejanas. El tamaño del pico también incrementó de norte a sur en ambos sexos. Un clino latitudinal, en la profundidad a la cual se entierran las presas, pudiera ser la explicación al clino en tamaño del pico y en la tasa de sexos de estas aves.

Key words: *Calidris minutilla*, differential migration, Least Sandpiper, resource partitioning, Western Sandpiper

The annual migrations of birds have fascinated humans for millennia and still raise many unanswered questions at both the proximate and ultimate levels. A particularly intriguing aspect of migration is the spatial separation of individuals according to age or sex during the nonbreeding season. Such differential migration is common among migratory birds, but the underlying factors remain poorly understood (Cristol et al. 1999).

A number of hypotheses have been developed to explain patterns of differential distribution (Cristol et al. 1999). According to the body size hypothesis, larger individuals are better suited to survive the colder and less predictable climates at higher latitudes because they can endure longer periods of fasting (Ketterson and Nolan 1976). Alternatively, dominant individuals may monopolize areas closer to the breeding grounds

to lower migration costs (dominance hypothesis; Gauthreaux 1978). The arrival time hypothesis predicts that individuals that benefit most from early arrival should winter closest to the breeding grounds (Ketterson and Nolan 1976; Myers 1981).

These three hypotheses do not make predictions about changes in morphology with latitude. Choice of nonbreeding sites might, however, be a function of wing or bill length, as opposed to body size per se, which would nonetheless result in sex ratio clines in sexually dimorphic species. Long wings are generally considered adaptive for longer migrations (Hamilton 1961; Lockwood et al. 1998; O'Hara 2002). A cline in bill length in a migratory shorebird has previously been attributed to changes in food availability across latitudes (resource partitioning hypothesis; Elnor and Seaman 2003; Nebel 2005; Nebel et al. 2005).

Here, I present data on intraspecific differences in nonbreeding distribution with regard to the sex, age, and morphology of Least Sandpipers (*Calidris minutilla*). This small shorebird breeds in the subarctic tundra and in the marshy habitat

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in the boreal forest region of North America, and winters along the Pacific and Atlantic coasts between the northern United States and northern Chile and central Brazil, respectively (Cooper 1994). Published sex ratio estimates exist from only two nonbreeding sites. In California, the sex ratio was slightly female-biased (Page 1974), while, in Suriname, females outnumbered males by about 6:1 (Spaans 1976). These reports suggest that female Least Sandpipers may migrate further south than males, but more data are needed to establish whether differential migration occurs in this species. To achieve this, I collected data on sex and age ratios as well as bill and wing length of Least Sandpipers at six sites across their nonbreeding range and combined these with data from one published account.

METHODS

Data were collected at the following locations and times: Bodega Bay (38.2°N, 123.0°W; November–December 2000), Tomales Bay (38.1°N, 122.6°W; November–December 2000), San Francisco Bay, California, USA (37.5°N, 122.3°W; November–December 2000); Costa del Este, upper Bay of Panama, Republic of Panama (09.0°N, 79.3°W; January–February 2002); San Pablo (02.1°S, 80.5°W; November–February 1991–1999) and Punta Carnero/Ecuasal Lakes at Mar Bravo, Ecuador (02.3°S, 80.5°W; November–February 1991–1999). When testing for variation in sex and age ratios with latitude, I included estimates from Suriname obtained by Spaans (1976). He provided data for Least Sandpipers caught near Paramaribo (06.0°N, 55.5°W; December 1970–March 1973) and near Wageningen and Nickerie, Suriname (06.0°N, 57.0°W; December 1971 and November 1972).

Least Sandpipers were captured in mist-nets and measured using standard procedures. Bill length was measured with calipers and individuals with exposed culmens of <17.5 mm and >18.6 mm were classified as males and females, respectively (Page 1974). Sexing criteria were developed based on a sample of 89 museum specimens in breeding plumage collected in California, British Columbia, and Alaska. Measurements were similar to those taken by Jehl (1970) on individuals breeding at Churchill, Manitoba, Canada.

Flattened and straightened wings were measured with a hand-held ruler. At one site, measurements of the flattened and straightened wing were regressed against those of the flattened, but not straightened, wing. Using the slope and constant of this regression, wing length measurements from Ecuador were transformed, where the flattened but not straightened wings were measured. Age (adult or first-year) was determined using plumage characteristics (Prater et al. 1977). No information on age was available for birds captured in Panama.

General linear models were used to test for variation in the dependant variable (proportion of females, proportion of first-year birds, bill length, and wing length) with latitude, which was treated as a continuous independent variable. Proportions were arcsine-transformed prior to analysis to stabilize variance.

Data collected at San Pablo, Ecuador, represented the most comprehensive sample and were used to assess variation in sex and age ratios among years. To do so, the frequency of males and females and adults and first-year birds, respectively, were compared using 2×2 contingency tables. All analyses were performed using Systat version 11.

RESULTS

I found that the proportion of females increased significantly from north to south ($F_{1,6} = 8.28$, $P = 0.028$; Fig. 1A). In contrast, no relationship was found between the proportion of first-year birds and latitude ($F_{1,5} = 0.004$, $P = 0.95$; Fig. 1B). Sex and age ratios as well as sample sizes are given in Table 1. The proportion of birds of unknown sex and age was 0.37 and 0.13, respectively. Individuals of unknown sex were not included in the analyses. I used sex and age ratios collected over nine consecutive years at San Pablo, Ecuador, to assess variation among years. The proportion of females to males did not differ among years (Pearson $\chi^2_8 = 9.05$, $P = 0.34$; Fig. 2), but the proportion of first-year birds to adults varied significantly (Pearson $\chi^2_8 = 52.06$, $P < 0.001$; Fig. 2).

Because the proportion of first-year birds did not vary with latitude, I pooled both age classes in the analyses of morphometric variables with latitude. Length of bill increased from north to south for both males ($F_{1,60} = 4.92$, $P = 0.03$) and females ($F_{1,321} = 13.65$, $P < 0.001$; Fig. 3A).

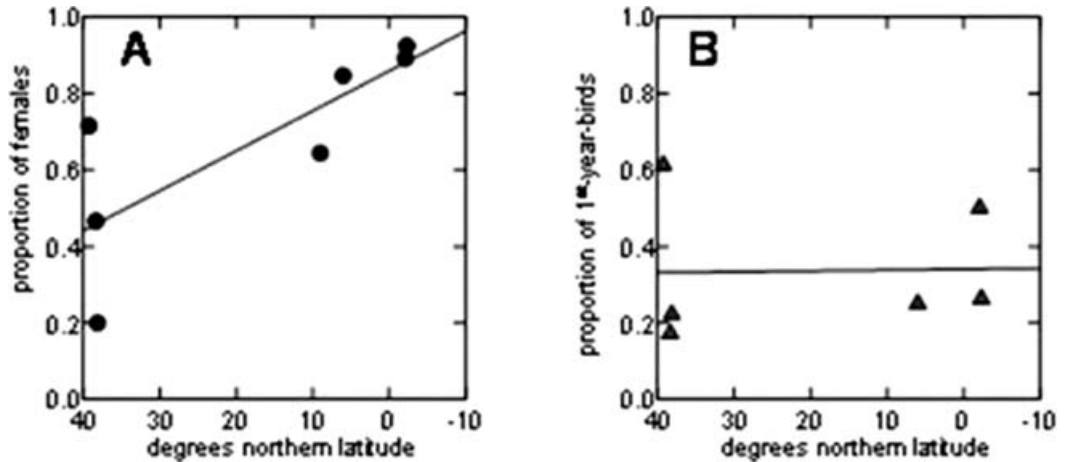


Fig. 1. The proportion of nonbreeding female Least Sandpipers increased linearly with decreasing latitude (A), but no change was detected in the proportion of first-year birds (B).

Similarly, length of wing increased from north to south for males ($F_{1,58} = 38.93$, $P < 0.001$) and females ($F_{1,288} = 16.23$, $P < 0.001$; Fig. 3B).

DISCUSSION

I documented latitudinal clines in sex ratio, and bill and wing length in nonbreeding Least Sandpipers. The proportion of females increased from California south toward Ecuador, and significant increases in bill and wing length from north to south were observed for both females and males. No significant variation in sex ratio was observed over nine consecutive years in Ecuador, suggesting that this ratio does not vary with year. Similarly, no change in age ratio with latitude was detected. However, the proportion of first-year birds to adults varied significantly among years in Ecuador. It is therefore possible

that a latitudinal trend in age ratio was masked by collecting data in different years.

Female Least Sandpipers are larger than males (Cooper 1994) and migrate further south, which is in contrast to the prediction of the body size hypothesis (Ketterson and Nolan 1976). Assuming that the larger sex dominates the smaller sex, the dominance hypothesis predicts higher proportions of females at more northern sites (Gauthreaux 1978), which again is in contrast to the pattern I observed. Male Least Sandpipers establish territories and arrive on the breeding grounds before the females (Miller 1983), and males winter further north, which is in accordance with the arrival time hypothesis (Ketterson and Nolan 1976; Myers 1981). However, in the Western Sandpiper (*Calidris mauri*), a congener with similar distribution patterns and life history (Wilson 1994), birds in central

Table 1. Number and proportion of female and first-year Least Sandpipers captured at each study site.¹

Study site	Proportion of females (<i>N</i>)	Proportion of first-year birds (<i>N</i>)
Bodega Bay, California, USA	0.46 (28)	0.17 (35)
Tomales Bay, California, USA	0.71 (7)	0.61 (18)
San Francisco Bay, California, USA	0.20 (5)	0.22 (9)
Costa del Este, upper Bay of Panama	0.64 (14)	n/a
Paramaribo & Nickerie, Suriname	0.85 (39)	0.25 (24)
San Pablo, Ecuador	0.89 (284)	0.50 (387)
Punta Carnero/Mar Bravo, Ecuador	0.92 (66)	0.26 (80)

¹Numbers in parentheses indicate the number of individuals for which sex and age, respectively, was determined. Data from Suriname are from Spaans (1976).

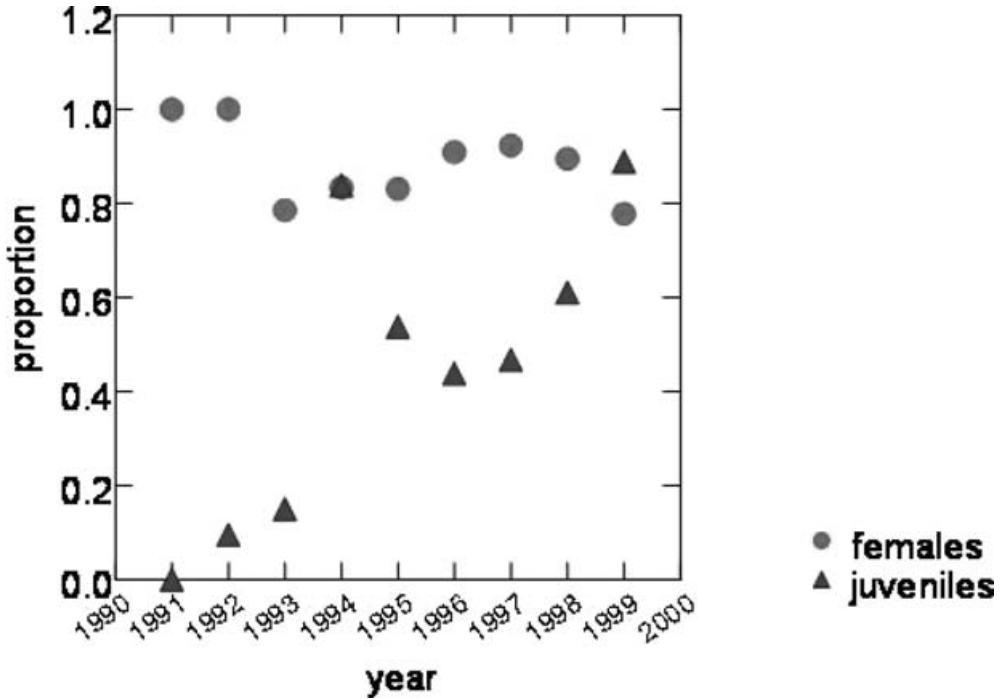


Fig. 2. The proportion of first-year Least Sandpipers captured at San Pablo, Ecuador, varied among years, but the proportion of females did not. See Results for statistical details. Sample sizes ranged from four to 93 ($\bar{X} = 36$).

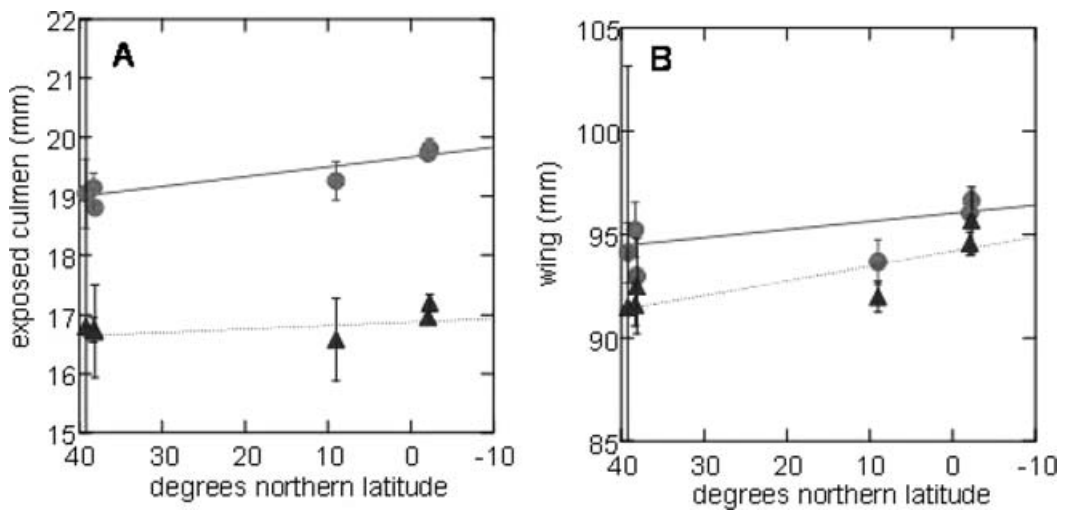


Fig. 3. Bill length (\pm 95% CI) increased from north to south for female (\bullet – solid line) and male (\blacktriangle – stippled line) Least Sandpipers (A). Wing length (\pm 95% CI) also increased from north to south for both males and females (B).

Mexico initiate northward migration two to three weeks earlier than those in central California (Fernández et al. 2001) and six to seven weeks earlier than those in British Columbia (Butler et al. 1987). This difference in migration chronology is likely to offset the longer migration distance (Nebel et al. 2002). No comparable data on latitudinal differences of departure timing are currently available for Least Sandpipers, but a similar adjustment of departure timing to offset longer migrations seems possible.

I found that wing length of Least Sandpipers increased with latitude. Longer and more pointed wings are considered adaptive for longer migratory flights because an increase in wing length and area facilitates longer periods of sustained flight (Hamilton 1961). The trend of longer, higher aspect ratio wings in migrants has been supported by studies of intraspecific (Chandler and Mulvihill 1990; Marchetti et al. 1995) as well as interspecific variation (Yong and Moore 1994; Mönkkönen 1995; Lockwood et al. 1998) in migratory behavior. The observed increase in wing length in individual Least Sandpipers that migrate further south is consistent with this trend.

For both male and female Least Sandpipers, bill length increased from north to south. Bill length was used to assign sex, and a change in bill length with latitude has the potential to bias the correct sex determination. The sex ratio cline could potentially be confounded by females being incorrectly classified as males at northern sites, or males as females at southern sites. The sample of birds used to establish the sexing criteria was collected primarily during spring migration at the northern end of the nonbreeding range and on the breeding grounds (Page 1974). It is, therefore, not possible to infer whether this sample is representative of the entire population. Bill measurements of individuals sexed using either molecular techniques or by gonadal inspection and collected at the northern and the southern end of the nonbreeding range are needed to ascertain whether the morphology-based sexing criteria need to be refined to account for latitudinal variation in average bill length. Currently, the possibility that the cline in sex ratio is confounded by incorrect sexing as a result of latitudinal clines in bill length cannot be excluded.

An increase in average bill length with latitude was also documented in male and female

Western Sandpipers (O'Hara 2002; Nebel 2005). This pattern has been associated with resource partitioning between the sexes resulting from a postulated latitudinal cline in the relative abundance of epi- vs infaunal intertidal invertebrate prey (Elner and Seaman 2003; Nebel 2005; Nebel et al. 2005). Foraging behavior of Western Sandpipers on a tropical mudflat in the Bay of Panama changed with increasing sediment temperature from pecking toward more probing (Nebel and Thompson 2005). Probe-to-peck ratios can serve as indicators for change in relative prey abundance at different sediment depths (Sutherland et al. 2000) and the observed increase in probe-to-peck ratios was interpreted to reflect an increase in invertebrate burying depth, mitigating the effects of high temperatures and desiccation at the sediment surface (Nebel and Thompson 2005). Air temperatures increase with proximity to the equator by 0.4°C for every degree of latitude (Piersma et al. 2005), and so does intertidal sediment temperature (Piccolo et al. 1993). Intertidal invertebrates are able to adjust burying depth in response to changes in local sediment temperature (Brown 1960; Emson et al. 2002). Conceivably, the average burying depth of intertidal invertebrates increases in response to the higher temperatures closer to the equator, resulting in a latitudinal change in the relative availability of epi- vs infaunal shorebird prey.

Like their congeners, Least Sandpipers feed on intertidal invertebrates during the nonbreeding season (Cooper 1994). A cline in the relative availability of epi- vs infaunal prey would, therefore, favor longer-billed individuals at more southern latitudes. I documented such a bill length cline both between the sexes as well as within females, but data concerning the burying depth of invertebrates at different latitudes are needed. Nonetheless, the postulated latitudinal cline in relative food availability resulting in resource partitioning between the sexes offers a novel, and potentially far-reaching, explanation as to why long-billed individuals tend to migrate further south than short-billed conspecifics.

No variation in the proportion of first-year birds to adults with latitude was observed, but I did detect variation among years at San Pablo, Ecuador. Variation in age ratios on the nonbreeding grounds has been attributed to variation in breeding success, which in turn is thought to vary with the abundance of lemmings

(Underhill et al. 1989). Lemming populations undergo population cycles every three to five years (Predavec et al. 2001) and, in years of high lemming abundance, lemmings constitute a prime source of food for predators such as arctic foxes (*Alopex lagopus*) and Long-tailed Jaegers (*Stercorarius longicaudatus*). In years following lemming peaks, the high predator populations can severely impact nesting shorebirds (Underhill et al. 1989). Lemming abundance, however, varies substantially across the Arctic and nesting success is also known to show spatial variation (McCaffery and Ruthrauff 2004). Without precise knowledge of the breeding locations of the individuals caught at San Pablo, Ecuador, variation in age ratios as a function of lemming population cycles needs to be viewed with caution.

In summary, I have shown that female Least Sandpiper migrated further south than males and that, for both males and females, wing and bill length increased at southern latitudes. No trend in age ratios was detected. I speculate that latitudinal variation in mean ambient temperature may predispose birds with longer bills to migrate to hotter and more southern sites. This resource partitioning hypothesis requires further testing, but potentially explains the striking latitudinal cline in sex ratio in this and possibly other closely related species.

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