WESTERN SANDPIPERS (*CALIDRIS MAURI*) DURING THE NONBREEDING SEASON: SPATIAL SEGREGATION ON A HEMISPHERIC SCALE

Silke Nebel,[1,12] David B. Lank,[1] Patrick D. O'Hara,[1] Guillermo Fernández,[1]
Ben Haase,[2] Francisco Delgado,[3] Felipe A. Estela,[4] Lesley J. Evans Ogden,[1]
Brian Harrington,[5] Barbara E. Kus,[6] James E. Lyons,[7] Francine Mercier,[8]
Brent Ortego,[9] John Y. Takekawa,[10] Nils Warnock,[11] and Sarah E. Warnock[11]

[1]*Department of BioSciences, Simon Fraser University, 8888 University Drive, Burnaby,
British Columbia V5A 1S6, Canada;*
[2]*℅ FEMM, casilla 0901, 11 905 Guayaquil, Ecuador;*
[3]*C. Meliton Martin, N 32-94, Chitré, Herrera, Republic of Panamá;*
[4]*Asociación Calidris, Kra 24F oeste 3-110, Cali, Colombia;*
[5]*Manomet Center for Conservation Sciences, P.O. Box 1770, Manomet, Massachusetts 02345, USA;*
[6]*U.S. Geological Survey, Western Ecological Research Center, San Diego Field Station, 5745 Kearny Villa Road,
Suite M, San Diego, California 92123, USA;*
[7]*Department of Zoology, North Carolina State University, Raleigh, North Carolina 27695-7617, USA;*
[8]*Parks Canada, 24 Eddy Street, Hull, Quebec K1A 0M5, Canada;*
[9]*Texas Parks and Wildlife Department, 2805 North Navarro, Suite 600B, Victoria, Texas 77901, USA;*
[10]*U.S. Geological Survey, Western Ecological Research Center, San Francisco Bay Estuary Field Station,
P.O. Box 2012, Vallejo, California 94592, USA; and*
[11]*Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970, USA*

ABSTRACT.—The nonbreeding distribution of Western Sandpipers (*Calidris mauri*) was documented using 19 data sets from 13 sites along the Pacific and Atlantic coasts of the Americas. Western Sandpipers showed latitudinal segregation with regard to sex and age. Females wintered farther south than males. A ''U'' shaped pattern was found with respect to age, with juveniles occurring at higher proportions at both the northern and southern ends of the range. Distribution of sexes might be affected by differences in bill length and a latitudinal trend in depth distribution of prey. For age class distribution, two different life-history tactics of juveniles might exist that are related to the higher cost of feather wear for juveniles compared to adults. Most juveniles complete three long-distance migrations on one set of flight feathers whereas adults complete two. Juveniles may winter either far north, thereby reducing feather wear induced by ultraviolet light, migration, or both, or far south and spend the summer on the nonbreeding area. *Received 30 October 2001, accepted 8 July 2002.*

RESUMEN.—Determinamos la distribución de *Calidris mauri* durante la época no reproductiva utilizando 19 bases de datos de 13 sitios localizados en las costas del Pacífico y Atlántico del Continente Americano. *Calidris mauri* presentó una distribución latitudinal diferencial por sexo y edad. Las hembras invernan más al sur que los machos. Encontramos un patrón en forma de U con respecto a la edad, con una mayor proporción de juveniles en los extremos norte y sur del intervalo. La distribución de los sexos puede estar en función a la diferencia en la longitud del pico y el patrón latitudinal en la profundidad de las presas. La distribución de las edades puede estar relacionada a un mayor costo en el desgaste de las plumas en juveniles en relación a los adultos. Los juveniles que se reproducen ensu primer verano llevan a cabo tres migraciones con un juego de plumas mientras que los adultos solo dos. En juveniles pueden existir dos tácticas de historias de vidas diferentes donde los juveniles invernan más al norte y se reproducen en el primer verano, reduciendo así el desgaste de las plumas producido por la luz ultravioleta y/o la migración, o invernan más al sur y veranear en áreas no reproductivas.

''DIFFERENTIAL MIGRATION'' REFERS to either differences in timing of migration or to spatial distribution of age or sex classes within a species during the nonbreeding season (Myers 1981a, Gauthreaux 1982, Ketterson and Nolan 1983, Hockey et al. 1998, Turpie 1994, Cristol et al. 1999). According to a recent review, that tac-

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[12] E-mail: snebela@sfu.ca

tic occurs in the majority of migratory bird species (Cristol et al. 1999).

The Western Sandpiper (*Calidris mauri*) is well suited for the study of differential migration. It is one of the most common shorebirds in North America, with the latest total population estimate being 3.5 million (Bishop et al. 2000, Morrison et al. 2001). Most of the population breeds in western Alaska, whereas during the nonbreeding season, its range extends along the American Pacific coast from southern Canada to Peru, and, to a lesser extent, along the east coast of the Americas (Wilson 1994). During winter, the largest concentrations occur in western central Mexico and in Panama (Morrison and Ross 1989; Morrison et al. 1993, 1994, 1998, 2001). No subspecies are recognized (Wilson 1994).

Recently, a latitudinal difference in Western Sandpiper life-history tactics was discovered. Most juveniles wintering in California and western Mexico gain fat and migrate north in their first spring (N. Warnock and G. Fernández unpubl. data). In contrast, nearly all juvenile Western Sandpipers wintering at Chitré, Panama, do not undergo hyperphagia, prepare for northward migration, or molt into significant amounts of alternate plumage. Instead, they spend their yearling summer in predominantly basic plumage on the nonbreeding grounds (O'Hara et al. 2002). We assume that the difference between those sites reflects a latitudinal trend within Western Sandpipers, with higher propensity to oversummer the farther south the birds winter. Across shorebird species, a higher propensity to oversummer occurs in those with longer migratory flights (Summers et al. 1995, Hockey et al. 1998).

Females are more abundant towards the southern part of the nonbreeding area (Page et al. 1972, Harrington and Haase 1994, Naranjo et al. 1994, Buenrostro et al. 1999), but no information on the distribution of age classes is documented. Here, data are combined from sites across the entire nonbreeding range, allowing us to present an account of the nonbreeding sex and age distribution and to suggest possible explanations for the observed patterns.

METHODS AND STUDY SITES

We used 19 data sets gathered from 13 locations (Table 1). To restrict comparisons to residents, only birds caught between November and February were included in the analyses. All sandpipers were caught with mist nets, and we assumed capture did not produce a bias towards a sex or age class that would vary among sites. Sex was assigned on the basis of bill length (Page and Fearis 1971). Given that Page and Fearis (1971) analyzed birds collected in California only, the method was verified by internally sexing over 250 Western Sandpipers from Panama and British Columbia, of which only one was misidentified using bill length (C. G. Guglielmo pers. comm.). Juveniles (birds in their first winter) were distinguished from adults on the basis of plumage (Prater et al. 1977) at all sites except Florida, which was not included in the age analysis. Second-winter birds, if recognized, were treated as adults. By comparing bill lengths of adults and juveniles on fall migration in the Fraser River Delta, British Columbia, we demonstrated that juvenile bill lengths were full adult length on southward migration (mean bill length of juvenile males: 22.65 mm, $n = 590$, adult males: 22.55 mm, $n = 857$, $t = -1.02$, df = 1 and 445, $P = 0.31$; juvenile females: 26.75 mm, $n = 847$, adult females: 26.80 mm, $n = 342$, $t = 0.91$, df = 1 and 187, $P = 0.36$). This demonstrates that using bill length to assign sex in juveniles will not create a bias towards males. As a measure of migration distance, we calculated the Great Circle Route (in kilometers, see Acknowledgments) from the breeding grounds, represented by Nome, Alaska (Wilson 1994), to the nonbreeding site. Migration distance correlated tightly with latitude ($r^2 = 0.92$, $P < 0.001$).

Statistical Analysis.—Relative proportions of each age and sex class were analyzed as a function of distance from breeding grounds, using analysis of covariance (ANCOVA). Class frequencies were modeled as binomial probabilities, using a linear model with a logit link function. Preliminary analysis indicated overdispersion in the data (reflecting strong heterogeneity in sample size), so we used a quasi-likelihood adjustment by rescaling the parameter estimates using model deviance divided by the model degrees of freedom. Relative proportions of all age and sex classes were arcsin transformed prior to analysis to stabilize variance. Analyses of variance were performed using GENMOD, SAS, version 8.1 (SAS Institute 2001).

RESULTS

In the northwestern part of the wintering range (Canada, United States, and Mexico) the proportion of males was higher than that of females, whereas south of Mexico that pattern was reversed (Table 1). The proportion of females increased linearly with distance from Nome (Fig. 1). The slope of that relationship did not differ between ages ($\chi^2 = 0.00$, $P = $

TABLE 1. Sample locations, distance from Nome, Alaska (km), sample sizes and proportions of female and juvenile Western Sandpipers at 13 locations.

Location	Years of data collection	Distance from Nome (km)[a]	Number of birds	Percent females	Percent juveniles	Source
British Columbia, Fraser River Delta	'78–79, '98, '00	3,037	32	0.19	0.91	1, 2
California, different locations	'57–58, '68–93, '00	4,149	407	0.28	0.56	2, 3, 4, 5
Mexico, Punta Banda	'93–98	4,942	582	0.17	0.57	6
Mexico, Bahia Santa Maria	'99–01	5,965	1,383	0.28	0.16	7
Texas, different locations	'72, '81–84, '95–00	6,185	112	0.17	0.07	2, 8
South Carolina, Georgetown	'91–93	6,532	67	0.55	0.55	9
Florida, Marco Island	'86–89	7,133	66	0.24		10
Costa Rica, central Pacific coast	'74–80, '85–88	8,556	143	0.58	0.32	2
Puerto Rico, Cabo Rojo Salt Flats	'89–94	8,613	42	0.95	0.50	11
Panama, Chitré	'95–98	8,986	584	0.59	0.33	12
Venezuela, Araya Peninsula	'84–86	9,490	584	0.58	0.37	13
Colombia, Punta Soldado	'84–96	9,547	35	0.69	0.48	2, 14
Ecuador, Santa Elena Peninsula	'91–99	9,965	512	0.81	0.75	15

[a] Distance measured as Great Circle Route.

Sources: 1 = L.J. Evans Ogden, 2 = Banding Office, 3 = B.E. Kus, 4 = S. Nebel, 5 = J.Y. Takekawa and S. Warnock, 6 = G. Fernández, H. de la Cueva and N. Warnock, 7 = G. Fernández, 8 = B. Ortego, 9 = J. Lyons, 10 = T. Below, 11 = B. Harrington, 12 = P.D. O'Hara and F. Delgado, 13 = F. Mercier, 14 = F.A. Estela, 15 = B. Haase.
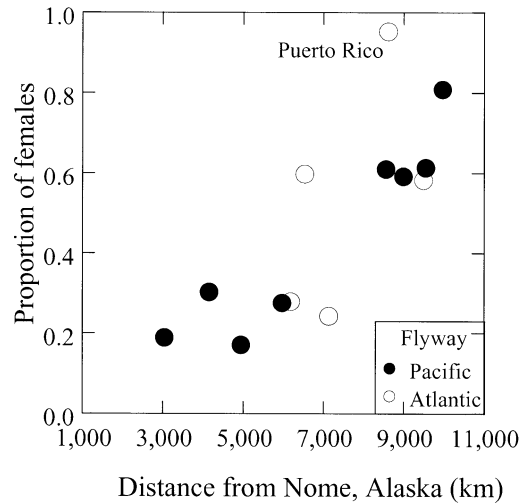

FIG. 1. Proportion of female Western Sandpipers increased linearly with distance from breeding grounds, centered at Nome, Alaska ($\chi^2 = 128.42$, df = 1, $P < 0.001$).

0.99). However, between Mexico and Panama, sex ratios were more female skewed for juveniles than adults (Fig. 2).

In contrast, no differences were detected in the slope of the proportion of adults and migration distance between males and females ($\chi^2 = 0.79$, $P = 0.383$), nor differences between intercepts ($\chi^2 = 1.58$, df = 1, $P = 0.209$). When we pooled sexes, there was no evidence of a simple linear trend in age-ratio with distance from the
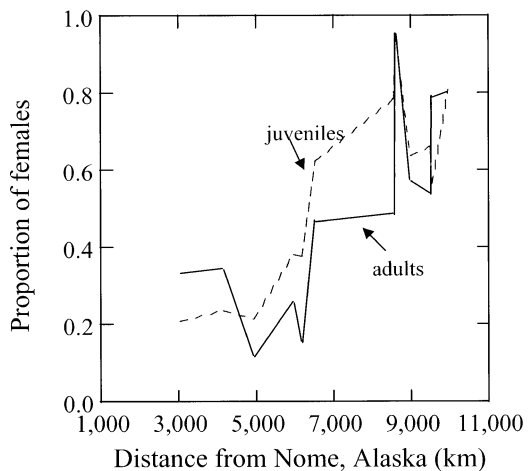

FIG. 2. Proportion of female Western Sandpipers was greater among juveniles than among adults for a given distance ($\chi^2 = 8.18$, df = 1, $P = 0.004$).
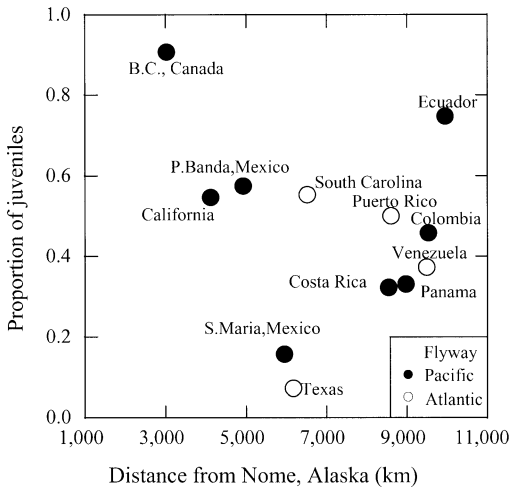
FIG. 3.   Age ratio of Western Sandpipers captured at 12 locations. Proportion of juveniles versus latitude described a ''U'' shaped pattern ($F = 5.08$, df = 1 and 22, $P < 0.005$).
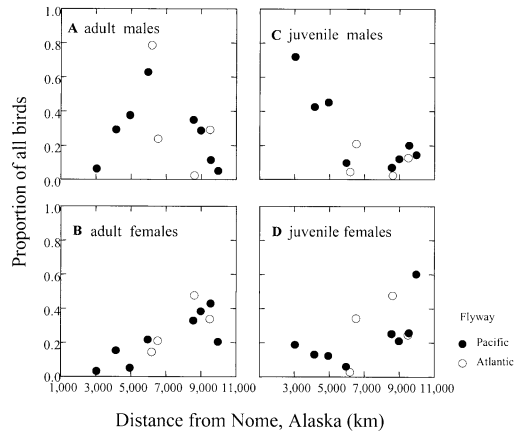

FIG. 4.   Distribution for the four age and sex classes of Western Sandpipers. For each site, proportions of the four graphs add up to one. (A) Proportions of adult males peaked at intermediate distance from Nome (quadratic model: $P = 0.043$, $r^2 = 0.50$, F change from adding a quadratic term: $P = 0.02$); (B) proportions of adult females increased with distance from Nome (linear model: $P = 0.002$, $r^2 = 0.64$); (C) proportions of juvenile males decreased with distance from Nome (quadratic model: $P < 0.001$, $r^2 = 0.90$, F change from adding a quadratic term: $P < 0.001$); (D) proportions of juvenile females increased with distance from Nome (linear model: $P = 0.044$, $r^2 = 0.35$).

breeding grounds ($\chi^2 = 0.04$, df = 1, $P = 0.85$). However, a model where age-ratio was a function of distance and distance-squared (accounting for the ''U'' shape) was supported by the data (distance: $\chi^2 = 36.48$, df = 1, $P < 0.001$; distance^2: $\chi^2 = 37.05$, df = 1, $P < 0.001$). At sites relatively close and relatively distant from the breeding grounds, the proportion of juveniles in the sample was higher than observed at intermediate distances, resulting in a ''U'' shaped distribution (Fig. 3).

In the north, the proportion of the population that were adult males increased with distance from Nome, peaking at an intermediate distance, and decreasing further south (Fig. 4A). The proportion of adult females increased linearly with distance from the breeding grounds (Fig. 4B). Proportions of juvenile males formed a ''U'' shaped pattern with distance (Fig. 4C). Juvenile females showed a linear increase in proportions with distance (Fig. 4D); in contrast to adult females, proportions were somewhat higher at the northern end of the range. Results were not notably influenced by excluding data from the Atlantic Flyway.

DISCUSSION

Western Sandpipers showed latitudinal segregation with regard to sex and age classes during the nonbreeding season. As in previous studies, females wintered farther south than males. We found a ''U'' shaped pattern with respect to age: juveniles occurred at higher proportions at both the northern and southern ends of the range. That pattern could be produced by disproportionately high mortality of juveniles wintering in the center of the range, but this seems unlikely. Alternatively, some males may shift their wintering grounds farther south as they age, whereas some females shift farther north, despite substantial annual nonbreeding ground site fidelity (O'Hara 2002).

Given the tight relationship between migration distance and latitude, we include both in our discussion despite the small difference in statistical fit. However, whereas the proportion of females in Puerto Rico seems high for its latitude, it fits well with other data points when plotted against migration distance.

There has been considerable effort put into explaining differential migration patterns, primarily by testing single-factor hypotheses (see Cristol et al. 1999). We suggest that a useful ap-

proach involves considering trade-offs between differential costs and benefits among classes of birds with respect to three aspects: (1) performance at the nonbreeding site, (2) intraspecific interactions, and (3) ''cross-seasonal interactions'' with the breeding season (Myers 1981b).

Performance at the nonbreeding site.—Body-size differences may interact with local climate to produce differential distributional optima, principally by sex (Ketterson and Nolan 1976). That is based on a physiological argument: larger individuals can survive longer periods of fasting and are therefore thought to be better suited to survive colder or less predictable climates, typically found at higher latitudes. That prediction has not been supported with unequivocal empirical evidence for shorebirds (Myers 1981a, Shepherd et al. 2001) or any other bird species (Cristol et al. 1999). In Western Sandpipers, members of the larger sex, females, winter farther south. This hypothesis cannot account for the distribution found.

Western Sandpipers feed on invertebrate prey items during the nonbreeding season (Wilson 1994). They use several different modes of feeding, but pecking (with the bill just touching the substrate surface) and probing (when the bill is more deeply inserted) is most common (Sutherland et al. 2000). Female Western Sandpipers have longer bills than males (on average, 12%), whereas other structural measurements differ only slightly (between 0 and 5%; Cartar 1984). The difference in bill length is likely related to habitat use, mode of feeding (Harrington 1982, Durrell 2000), or both. A longer bill may be better suited for probing and probing may be a more profitable feeding mode farther south. That could be caused by a latitudinal gradient in temperature affecting burying depth of invertebrates.

Intraspecific interactions.—Asymmetrical interactions among age and sex classes can produce habitat segregation (Marra 2000) and might produce geographical segregation (''dominance hypothesis''; Gauthreaux 1978). Dominant individuals may benefit by monopolizing areas closer to the breeding grounds, thereby lowering ''migration costs''. If we assume that the larger sex dominates the smaller sex, and that adults dominate juveniles (but see Komers and Komers 1992), we would expect to find higher proportions of females and adults at more northern sites, in contrast to the patterns observed.

Cross-seasonal interactions.—Factors other than maximizing overwinter survivorship may influence nonbreeding distributions (Myers 1981b). In particular, a sex or age class that benefits more from earlier arrival on the breeding grounds will gain by wintering closer to the breeding grounds (''arrival time hypothesis''; Ketterson and Nolan 1976, Myers 1981a). Because males are the primary territory holders in Western Sandpipers and arrive on the breeding grounds before females (Holmes 1971, Warnock and Bishop 1998), this hypothesis predicts the general pattern we observed with respect to sex. However, Western Sandpipers wintering at Punta Banda, Mexico, initiate northward migration two to three weeks earlier than those in central California (Fernández et al. 2001), which could offset the longer distance. Similar differences occur in other shorebird species (Turpie 1994), which may make that effect less important.

A multifactor hypothesis.—None of these single-factor hypotheses completely account for the patterns seen in Western Sandpipers (see Cristol et al. 1999). The pattern of males wintering farther north and females farther south might relate to bill-length differences, which allow females to better exploit resources at greater depths. Ambient temperature increases closer to the equator which might affect burying depth of intertidal invertebrates. Females might prefer southern latitudes due to higher predictability of environmental conditions (Ketterson and Nolan 1976, Lovvorn 1994).

For the ''U'' shaped pattern in the distribution of juveniles, we suggest an explanation based on work by O'Hara et al. (2002). Molt tactic and feather wear might account for the latitudinal differences in juvenile migration behavior through their influence on migratory flight performance. Adult Western Sandpipers molt flight feathers following each southward migration, and then perform northward and southward migration on those feathers. Juveniles, on the other hand, retain flight feathers grown in June of their hatching year until late summer of their second year of life (Prater et al. 1977). Juveniles that migrate thus make three migratory flights on that set of feathers.

Juveniles wintering farther north may benefit by avoiding additional primary wear associat-

ed with longer migration distances or induced by higher intensity of ultraviolet light closer to the equator. For juveniles wintering farther south, feather wear is less of a consideration, because they oversummer and will have molted new primaries prior to their first northward migration in their second spring. Additionally or alternatively, intraspecific competition might play a role, with adults excluding juveniles from the nonbreeding site in the center of the distribution.

We suggest that latitudinal trends in environmental variability, ultraviolet light intensity, and temperature affecting burying depth of invertebrates interact with body size and bill-length differences as well as age-specific molting schedules, creating different optima in nonbreeding distribution depending on age and sex of individual Western Sandpipers. Whatever the causes, our findings have important implications for conservation of the species as well as for the study of survivorship. When creating protected areas for a population of conservation concern, it is important to know whether both sexes occur in similar numbers in these areas, because otherwise the effective population size will be smaller than the actual one (Ridley 1996).

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