The Auk 120(1):55–61, 2003

APPARENT SURVIVAL RATES OF WESTERN SANDPIPER (*CALIDRIS MAURI*) WINTERING IN NORTHWEST BAJA CALIFORNIA, MEXICO

Guillermo Fernández,[1,4] Horacio de la Cueva,[1] Nils Warnock,[2,3,5]
and David B. Lank[2]

[1] *Centro de Investigación Científica y de Educación Superior de Ensenada, Km 107 Carretera Tijuana-Ensenada, Ensenada, Baja California, Mexico;*
[2] *Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada, and*
[3] *Environmental and Resource Sciences, University of Nevada, Reno, Nevada 89512, USA*

Abstract.—To estimate annual apparent local survival, we collected capture–resighting data on 256 individually marked male Western Sandpipers (*Calidris mauri*) wintering at Estero de Punta Banda, Mexico, between 1994–1997. A hierarchical modeling approach was used to address the effect of age class and year on survivorship rates. The best-fit model included a constant apparent survival probability ($\phi = 0.489$; 95% CI = 0.410–0.569), but several models fit nearly as well, and averaging among the top five, to account for model uncertainty, suggested that adults had somewhat higher values than juveniles ($\phi = 0.490 \pm 0.051$ vs. 0.450 ± 0.067). Detection probability was substantially higher for adults than for juveniles ($p = 0.741$ vs. $p = 0.537$). Those apparent survival estimates are low compared with those from other studies of Western Sandpipers at breeding and other nonbreeding locations, and substantially lower than the true survivorship rates expected for small sandpipers in general. We interpret these results as indicating that this site is of below average quality for nonbreeding male Western Sandpipers. *Received 16 October 2001, accepted 12 September 2002.*

Resumen.—Para estimar la supervivencia local aparente, se colectaron datos de captura-avsitamiento de 256 machos individualizados de *Calidris mauri* que invernaron en el Estero de Punta Banda, México, entre 1994–1997. Se utilizo un enfoque de modelación jerárquica para determinar el efecto de la edad y año en la tasa de sobrevivencia. El modelo que mejor se ajusta incluye una probabilidad de sobreviencia aparente constante ($\phi = 0.489$; 95% CI = 0.410–0.569), pero varios modelos tienen un ajuste similar y un promedio de los cinco mejores modelos, dado la incertidumbre del modelo, sugiere que los adultos tienen valores relativamente mayores a los juveniles ($\phi = 0.490 \pm 0.051$ vs. 0.450 ± 0.067). La probabilidad de avistamiento fue sustancialmente mayor en adultos que en juveniles ($p = 0.741$ vs. $p = 0.537$). Las estimaciones de supervivencia aparente fueron bajas en comparación a otros estudios de *C. mauri* durante en la época reproductiva y no reproductiva, y sustancialmente menores a las tasas de supervivencia verdaderas esperadas para un calidrido en general. La interpretación de estos resultados indican que este sitio esta por debajo de la calidad promedio para los machos de *C. mauri* durante la época no reproductiva.

Migratory birds make repeated annual decisions about site settlement on both breeding and nonbreeding grounds. Each year a fraction of surviving individuals return to sites occupied in previous years. The accumulation of capture histories, and the widespread distribution of capture–recapture software to analyze such data (Lebreton et al. 1992) have lead to a proliferation of estimates of apparent annual survival rates for migratory birds. Apparent survival rates measure the probability that an individual will both survive over a time period, and if alive, return to a site it previously occupied.

In this study, we estimate apparent survival rates of male Western Sandpipers (*Calidris mauri*) wintering at an isolated estuary in northwestern Baja California, Mexico. Western

---

[4] Present address: Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada. E-mail: gjf@sfu.ca

[5] Present address: Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970, USA.

Sandpipers are one of the most common western hemisphere shorebirds (Morrison et al. 2000), with a global population on order of 3–3.5 million birds (Bishop et al. 2000). The species breeds primarily in the western subarctic of Alaska, and winters primarily along the Pacific coast from California to Peru, and the Atlantic coast from New Jersey to Surinam (Wilson 1994), with males predominating at more northerly latitudes (Page et al. 1972, Harrington and Haase 1994, Buenrostro et al. 1999, Nebel et al. 2002). Western Sandpipers exhibit return rates and apparent annual survivorship rates of 50% or higher to breeding territories (Holmes 1971, Sandercock et al. 2000) and specific wintering areas (Rice 1995, Fernández et al. 2001, O'Hara 2002). Like other shorebirds, Western Sandpipers may defend small feeding territories under appropriate ecological conditions during the nonbreeding season (Tripp and Collazo 1997, Johnson et al. 2001, G. Fernández pers. obs.), but, in general, their nonbreeding population structure consists of broadly overlapping home ranges (Warnock and Takekawa 1996). As is typical of migratory shorebirds, the species spends only approximately 2–3 months on the breeding grounds, and most annual mortality probably occurs on migration or during the nonbreeding season (Evans 1991) when predation can account for loss of substantial fractions of local populations (Page and Whitacre 1975, Cresswell and Whitfield 1994), and density-dependent mortality due to interference, competition for food, or both also may occur (Goss-Custard 1977). We tested whether age and annual variation affected apparent survival and resighting rates.

Apparent annual survival estimates have been made primarily from data at breeding sites, and we know much less about rates based on survival and return to nonbreeding sites (Sherry and Holmes 1995, 1996; Warnock et al. 1997; Robertson and Cooke 1999; Johnson et al. 2001). Sandercock and Jaramillo (2002) propose that generating parameters such as apparent survival rates based on nonbreeding data may in certain cases produce more reliable estimates. Here, we compare our apparent survival rates with those estimated on the breeding grounds, and from other nonbreeding sites, and consider the prospects for interpreting apparent survivorships with respect to age-specific site-fidelity decisions and relative habitat qualities.

METHODS

We studied nonbreeding Western Sandpipers at the Estero de Punta Banda ("Punta Banda", 31°52'N, 116°37'W), an isolated 20 km^2 coastal wetland located on the northwest west coast of the Baja California peninsula, 13 km south of Ensenada. We trapped birds at several locations within the estuary (Buenorostro et al. 1999), but consider return rates to the area as a whole in this study. Shorebirds feed and roost on extensive mudflat and marsh areas. Maximal monthly population size of Western Sandpipers was estimated from the combination of monthly surveys of the entire estuary conducted on low falling tides, and from counts at major feeding sites (Buenrostro et al. 1999). Western Sandpipers were captured with mist nets on high rising spring tides during four winters, from October to March of 1994–1995 ("1994"), September to April of 1995–1996 ("1995") and 1996–1997 ("1996"), and November to March of 1997–1998 ("1997"). Each bird was sexed based on culmen measurements (males <24.2 mm, females >24.8 mm; Page and Fearis 1971), and aged as a juvenile (<1 year old) or adult based on plumage coloration of inner median coverts and tertial feathers, and wear of primaries (Page et al. 1972). Birds with culmen of intermediate size were considered unknown and discarded from the survival analysis.

From 1994–1997, 664 individuals were color marked. Birds were captured throughout the fall, winter, and spring (September, 3%; October, 8%; November, 35%; December, 10%; January, 19%; February, 16%; and March, 9%). Twenty-six birds of unknown sex were omitted from the survival analysis. Marked birds were resighted, using spotting scopes, during 1–4 h scanning surveys of Western Sandpiper flocks made on high–low spring tides throughout each season. Resighting effort varied among years ($\bar{x}$ = 40, SE = 10 days, n = 4 years; Table 1), averaging 3 (±1), resightings bird^{-1} year^{-1}.

In preliminary analyses, the resighting data were initially reduced to the presence or absence of individuals during monthly intervals. It soon became evident that individuals used Punta Banda for different durations and seasons, including birds which regularly stopped for short periods during migration, and whose residence time was independent with respect to trapping month (Fernández et al. 2001). In this article, to minimize effects of transient birds, we restricted the analysis to wintering resident individuals that were (1) banded during December–February, or (2) resighted primarily during those months. Eighteen percent of birds in this later category were first banded outside December–February. We report results for males only because females represented <20% of birds captured (see below). Of 527 males color-banded between 1994–1997, 49% (256/527) were included in the analysis (n = 117 adult and 139 juveniles).

TABLE 1. Population structure and annual number of wintering Western Sandpipers (December–February), at Estero Punta Banda, Baja California, Mexico.*

Year	Population size $\bar{x}$ ± SE	Number banded	Percent adults	Percent males	Resighting days	Total number of field days
1994	2,700 ± 423	299	46	87	13	35
1995	1,757 ± 361	81	51	81	39	54
1996	1,522 ± 228	179	40	74	49	76
1997	2,050 ± 600	79	49	81	31	43

* Twenty-six birds of unknown sex were excluded.

To estimate apparent annual survival rates, we further reduced the data to a bird's presence or absence each year. Apparent survival rate (ϕ, also termed "local" survival) is the probability that a bird alive in winter *i* remained available for resighting until winter of next year *i* + 1 (i.e. survived through that interval and did not permanently emigrate from the study area). Detection rate (*p*) is the probability that a bird alive and associated with the study area in year *i* was detected in year *i* . We estimated apparent survival and detection rates using the program MARK (White and Burnham 1999) following the information-theoretic approach discussed by Burnham and Anderson (1998).

A global model that included age and annual variation in ϕ and *p* was developed. For the models that considered age effect, apparent survival was calculated for (1) the first winter to the second winter season of life, for birds first captured as juveniles, and (2) subsequent winter-to-winter years of life, using post-first-year data for juveniles merged with data for birds caught as adults. Goodness-of-fit to that global model was calculated using a bootstrap method that generated a distribution of expected deviances under the assumptions of no heterogeneity and full independence (*n* = 1,000 simulations). That procedure tested whether or not our data met the assumptions of mark–recapture methods. An overdispersion factor ($\hat{c}$) was calculated using deviance estimate for the actual data divided by the average deviance for the simulated data sets. If overdispersion was detected (>1), relative model fit was assessed with a modified version of Akaike's Information Criterion (AIC) that included correction factors for overdispersion and small sample size (quasi-AIC_c, $QAIC_c$).

We proceeded to improve model fit by fitting nested models with reduced number of parameters. Factorial models that included interactions among factors (e.g. age × time) and main effects models (e.g. "additive" model: age + time) were constructed by using dummy variables in design matrices (White and Burnham 1999). All models were constructed using the logit-link function. Models selected with AIC_c are the best approximating models for the data that consider some tradeoff number of parameters, sampling variance, and bias (Burnham and Anderson 1998). Models were selected if the difference in AIC_c from the best-fit model was ≤ 2. To obtain annual estimates of ϕ and $\hat{p}$, model parameters were weighted by Akaike weights (*w*), and model averaging was used to calculate parameters and unconditional variance that include model uncertainty (Burnham and Anderson 1998). Resighting effort was used as a covariate to explain variation in detection probability.

RESULTS

Between December and February each year, 1,500-3,500 Western Sandpipers occurred at Punta Banda (Table 1). We captured similar proportions of juveniles and adults each year ($\bar{x}$ = 47% adults, SE = 2; Table 1), and 4× as many males as females ($\bar{x}$ = 81% males, SE = 2; Table 1), as expected at this latitude (S. Nebel et al. unpubl. data). Due to our limited sample sizes for females, we restricted our survivorship analyses to males.

Goodness-of-fit tests based on bootstrap sim-ulations indicated that the model $\phi_{age \times t}$, $p_{age \times t}$ was an acceptable global model (51.6% of 1,000 simulated data sets had a deviance larger than that observed in the actual data set). We did not detect overdispersion in our data set ($\hat{c} = 0.967$). One model had delta AIC_c values of 0.0 (Table 2). Apparent survival probability (ϕ) was constant and detection probability (*p*) was age-specific. However, equally approximating models for the data included age, or time, or constant dependence in ϕ, and annual variation and a constant difference between ages, or age and year had additive effect, or constant dependence in *p*. The model with resighting effort as a covariate did not explain variations in detection probability ($\Delta AIC_c = 12.26$).

The approximating models produced estimates of apparent survival rates ranging between 0.469–0.489, and estimated detection probabilities of 0.390–0.610 for juveniles and 0.651–0.819 for adults (Table 3). We used a model averaging approach to calculate parameters averaged across all the models. Apparent survival rate of juveniles was 8% lower than those of adults, and the probability of resighting was 18% higher among adults (Table 3).

DISCUSSION

Three aspects of our results are noteworthy. First, the difference in apparent survivorship between age classes was small. Following a strict model-selection approach, ϕ did not differ between age classes. However, the levels of model uncertainty were relatively high, and estimates from averaging five potential models that fit our data approximately equally well suggest that adults had higher apparent survivorship estimates than juveniles in both years (Table 3). We conclude that the difference in ϕ between age groups, although present, is of small magnitude.

This is a striking conclusion in part because we expect substantially lower rates for juveniles in both the true survivorship and philopatry components of ϕ. Studies of nonbreeding shorebirds have found that juveniles are more susceptible to predation than adults (Kus et al. 1984, Whitfield et al. 1986, Bijlsma 1990, Cresswell and Whitfield 1994), are disadvantaged in competition for food or space (Goss-Custard 1977, Cresswell 1994, Hockey et al. 1998), have lower apparent survivorship (Warnock et al. 1997), and lower true survivorship (Evans 1991, Thompson and Hale 1993, Peach et al. 1994). Thus, current research consistently shows or implies a lower true survivorship component of ϕ for juveniles. For male Western Sandpipers at Punta Banda, we also expect higher rates of permanent emigration by juveniles than adults, which would also lower juvenile ϕ values. Nonbreeding Western Sandpipers segregate among latitudes by sex and age class (Nebel et al. 2002). Young males are disproportionately represented in the northern end of the nonbreeding range, which includes Punta Banda. To the extent that the latitudinal trend in age ratios reflects southward movement of some males between their first and subsequent seasons, as opposed to arising entirely from a latitudinal trend in relative true survivorship of the age classes, we expect higher juvenile than adult permanent emigration from Punta Banda. Instead, we found little difference between age classes in ϕ.

TABLE 2. Akaike Information Criterion (AIC_c) values* for maximum-likelihood models of apparent survival (ϕ) and detection probability (p) of male Western Sandpipers (n = 117 adults and 139 juveniles).

	Model for p				
Model for ϕ	$a \times t$	$a + t$	t	a	c
$a \times t$	10.24	9.63	6.50	7.45	5.84
$a + t$	7.62	3.43	3.47	4.59	3.25
t	5.55	**1.37**	4.68	3.22	4.64
a	5.79	2.05	2.22	**1.63**	**0.68**
c	3.78	**0.13**	3.59	**0.00**	2.07

* AIC_c are expressed as deviations from the best-fit model. Best-fit ($\Delta AIC_c = 0$) and best-approximating models for the data ($\Delta AIC_c \leq 2$) are shown in boldface type; a is age effects (adult vs. juvenile), t is time or annual variation, c is constant, × denotes a model with interaction, and + denotes an additive or main-effects model.

One explanation is that there is only a small age-class performance difference between adults and those juveniles that have survived to the December–February marking period. That implies that most differential juvenile mortality would occur after fledgling, on migration, at stopovers (e.g. Dierschke 1998), or early after

TABLE 3. Apparent survival (ϕ) and resighting rate (p) of male Western Sandpipers wintering at Estero Punta Banda, Baja California, Mexico in 1994–1997.

		Age	
Model	Year	Juveniles	Adults
		ϕ_c, p_{a+t}	
Apparent survival	Pooled	0.489 ± 0.040	0.489 ± 0.040
Resighting	1994–1995	0.610 ± 0.090	0.819 ± 0.074
	1995–1996	0.390 ± 0.126	0.655 ± 0.100
	1996–1997	0.393 ± 0.104	0.651 ± 0.115
		ϕ_c, p_a	
Apparent survival	Pooled	0.469 ± 0.036	0.469 ± 0.036
Resighting	Pooled	0.537 ± 0.083	0.741 ± 0.072
		$\hat{\phi}, \hat{p}$ [a]	
Apparent survival	1994–1995	0.450 ± 0.067	0.490 ± 0.051
	1995–1996	0.461 ± 0.084	0.502 ± 0.065
	1996–1997	0.500 ± 3.777	0.540 ± 3.761
Resighting	1994–1995	0.636 ± 0.107	0.755 ± 0.089
	1995–1996	0.535 ± 0.151	0.672 ± 0.101
	1996–1997	0.508 ± 2.144	0.646 ± 2.825

[a] Annual estimates were calculated via model averaging (mean ± unconditional SE).

arrival at nonbreeding locations. However, the nonbreeding season performance differences in foraging ability and susceptibility to predation between adults and juveniles listed above make that unlikely to be a complete explanation.

The second interesting aspect of our data is that the ϕ values of 0.47–0.49 found for the Punta Banda birds are lower than other estimates for Western Sandpipers. Those include 0.62 and 0.57 for males, and 0.59 and 0.55 for females, for birds breeding at Nome, Alaska, in 1993 and 1994, respectively (Sandercock et al. 2000); return rates, which underestimate ϕ, of 0.58 for males and 0.49 for females breeding in the northern Yukon–Kuskokwin Delta, Alaska, in 1966–1969; 0.56 and 0.61 for mixed sex samples of adults and juveniles, respectively, overwintering at Cabo Rojo, Puerto Rico (Rice 1995); and 0.54 for males and 0.62 for females overwintering at Chitré, Panama (O'Hara 2002). Our estimate is also substantially lower than the level of true survivorship needed to sustain a breeding population of Semipalmated Sandpipers (*Calidris pusilla,* ~0.80; Hitchcock and Gratto-Trevor 1997), a species with demographics likely comparable to those of Western Sandpipers. Low values of ϕ suggest that male Western Sandpipers wintering at Punta Banda have below-average survival rates, below average annual site-fidelity, or both. One qualification on this conclusion is that ϕ has meaning only with respect to a defined area, and lower values will be obtained for studies done on smaller scales relative to interannual dispersal distances. Because our capture histories summarize birds caught throughout the estuary, we do not believe that this accounts for our results.

Our finding of only a small difference in apparent survivorships between age classes occurred not because juvenile ϕ was unusually high, but because the adult ϕ was unusually low, due to higher levels of annual adult mortality or higher levels of permanent emigration than found at other sites. Both possibilities imply that Punta Banda is a below-average nonbreeding site for adult male sandpipers, and that adults should be underrepresented in the population. Consistent with that hypothesis, the age ratio as measured by the banding samples is about half juveniles and half adults, which under-represents adults relative to what we expect from the birds' basic demography (c.f. Semipalmated Sandpipers, Hitchcock and Gratto-Trevor 1997). Furthermore, residency patterns of transient and wintering birds at Punta Banda were independent of age, trapping month, or year, and older birds were more likely to depart earlier and switch their residency pattern, from wintering to transient (Fernández et al. 2001), suggesting less attachment to Punta Banda as a nonbreeding site. Assuming that the true survivorship of juveniles is lower than that of older birds, and apparent survivorship at Punta Banda is not greatly different for both age classes, the site-fidelity rate of birds returning to Punta Banda in their second year of life must in fact be higher than that of birds banded as adults. To put it differently, individuals may have a greater propensity to disperse to a new site in their third or subsequent years than do birds returning after their juvenile season.

Our third intriguing finding was that although the detection rate was relatively high, we had a higher probability of not detecting birds marked as juveniles in subsequent years when they were in fact still alive, suggesting temporary emigration or other behavioral differences. Spatial segregation of cohorts of birds and biased resighting efforts can lead to biased detection and survival rates (Pradel et al. 1995). Spatial segregation of juveniles and adults does exist among sites within Punta Banda (Buenrostro et al. 1999). However, within this estuary and within age classes, we believe that there was sufficient mixing of birds such that differential resighting probabilities when summarized across three months were minimal. Punta Banda is not a large estuary, and during falling tides most of Western Sandpipers concentrate at one area. Our resighting efforts centered on that site and visibility was excellent. Thus, we believe that birds marked as juvenile males were genuinely temporarily absent in a subsequent year (e.g. their first "adult" season) more frequently than those marked as adults. Conversely, birds marked as adults and subsequently failed to return in subsequent years more often than did those marked as juveniles, due to permanent emigration or death. The former might occur if adults had sufficiently greater experience in evaluating sites to make "seeking greener pastures" more profitable than benefiting from the presumed advantages of local familiarity that favor site-fidelity in general (e.g. Baccetti et al. 1999), which may have operated more strongly in younger birds. As with a low overall local survival rate, that result also implies that Punta Banda is a below average nonbreeding site for older male Western Sandpipers.

From a comparative study of sparrows, Sandercock and Jaramillo (2002) suggested that rates of site-fidelity on the breeding grounds were likely to be lower than that on nonbreeding grounds, due to compromises attributable to mate, nesting, and additional ecological considerations associated with reproduction. We agree that this is plausible, but suggest that the opposite may also be the case. The additional constraints on breeding site settlement decisions relative to nonbreeding site settlement may increase, rather than decrease site-fidelity. As a data base of apparent survival rates from different species, sites, ages and sexes accumulate, careful comparisons among them may provide novel information not only on minimal annual survival rates, but also on relative site quality and the behavioral ecology of birds' breeding and nonbreeding site-fidelity.

ACKNOWLEDGMENTS

Numerous individuals assisted with the capture and resighting of color-banded Western Sandpipers, in particular, A. Buenrostro, Y. Sandoval, F. Becerril, E. Sánchez, and L. Enriquez. We thank F. Cooke, L. Oring, and R. E. Elner, R. W. Butler for their input and support. We are grateful to P. Shepherd, P. D. O'Hara, and F. Delgado for their advice during data analyses, interpretation, and for allowing us to cite unpublished data. This project was funded by the Canadian Wildlife Service (CWS) Latin American Program, CWS/NSERC Chair in Wildlife Ecology at Simon Fraser University, Centro de Investigación Científica y de Educación Superior de Ensenada, NSERC grants to D. B. L. and F. Cooke, and a graduate fellowships to G. F. from the Consejo Nacional de Ciencia y Tecnología (CONACYT, Mexico). We thank C. Schwarz for discussions about interpretations of ϕ, and E. Cam, C. Gratto-Trevor, G. W. Pendleton, B. K. Sandercock, R. C. Ydenberg, and an anonymous reviewer for constructive comments on earlier drafts of this paper.

LITERATURE CITED

BACCETTI, N., L. SERRA, G. CHERUBINI, AND A. MAGNANI. 1999. Timing to attachment to wintering site as revealed by experimental displacements of Dunlins (*Calidris alpina*). Journal für Ornithologie 140:309–317.

BIJLSMA, R. G. 1990. Predation by large falcons on wintering waders on the Banc d'Arguin, Mauritania. Ardea 78:75–82.

BISHOP, M. A., P. M. MEYERS, AND P. F. MCNELEY. 2000. A method to estimate migrant shorebird numbers on the Copper River Delta, Alaska. Journal of Field Ornithology 71: 627–637.

BUENOROSTRO, M. A., N. WARNOCK, AND H. DE LA CUEVA. 1999. Wintering Western Sandpipers *Calidris mauri* at Estero de Punta Banda, Baja California, México. Wader Study Group Bulletin 88: 59–63.

BURNHAM K. P. AND D. R. ANDERSON. 1998. Model Selection and Inference: A Practical Information-theoretic Approach. Springer, New York.

CRESSWELL, W. 1994. Age-dependent choice of Redshank (*Tringa totanus*) feeding location: Profitability or risk? Journal of Animal Ecology 63:589–600.

CRESSWELL, W., AND D. P. WHITFIELD. 1994. The effects of raptor predation on wintering wader populations at the Tyninghame Estuary, southeast Scotland. Ibis 136:223–232.

DIERSCHKE, V. 1998. High profit at high risk for juvenile Dunlins *Calidris alpina* stopping over at Helgoland (German Bight). Ardea 86:59–69.

EVANS, P. R. 1991. Seasonal and annual patterns of mortality in migratory shorebirds: Some conservation implications. Pages 346–359 *in* Bird Population Studies (C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, Eds.). Oxford University Press, Oxford.

FERNÁNDEZ, G., H. DE LA CUEVA, AND N. WARNOCK. 2001. Phenology and length of stay of transient and wintering Western Sandpipers at Estero Punta Banda, Mexico. Journal of Field Ornithology 72:509–520.

GOSS-CUSTARD, J. D. 1977. The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). Journal of Applied Ecology 14:721–739.

HARRINGTON, B., AND B. HAASE. 1994. Latitudinal differences in sex ratios among nonbreeding Western Sandpiper in Puerto Rico and Ecuador. Southwest Naturalist 39:188–189.

HITCHCOCK C. L., AND C. GRATTO-TREVOR. 1997. Diagnosing a shorebird local population decline with a stage-structured population model. Ecology 78:522–534.

HOCKEY, P. A. R., J. K. TURPIE, AND C. R. VELÁSQUEZ. 1998. What selective pressures have driven the evolution of deferred northward migration by juvenile waders? Journal of Avian Biology 29: 325–330.

HOLMES, R. T. 1971. Density, habitat and the mating system of the Western Sandpiper (*Calidris mauri*). Oecologia 7:191–208.

JOHNSON, O. W., P. L. BRUNER, J. J. ROTELLA, P. M.

Johnson, and A. E. Burner. 2001. Long-term study of apparent survival in Pacific Golden Plovers at a wintering ground on Oahu, Hawaiian Islands. Auk 118:342–351.

Kus, B. E., P. Ashman, G. W. Page, and L. E. Stenzel. 1984. Age-related mortality in a wintering population of Dunlin. Auk 101:69–73.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypothesis using marked animals: A unified approach with case studies. Ecological Monographs. 62:67–118.

Morrison, R. I. G., R. E. Gill, Jr., B. A. Harrington, S. Skagen, G. W. Page, C. L. Gratto-Trevor, and S. M. Haig. 2000. Population estimates of Nearctic shorebirds. Waterbirds 23:337–352.

Nebel, S., et al. 2002. Western Sandpipers (*Calidris mauri*) during the nonbreeding season: Spatial segregation on a hemispheric scale. Auk 119: 922–928.

O'Hara, P. 2002. The role of feather wear in alternative life history strategies of a long-distance migratory shorebird, the Western Sandpiper (*Calidris mauri*). Ph.D. dissertation, Simon Fraser University, Burnaby, British Columbia.

Page, G., and B. Fearis. 1971. Sexing Western Sandpipers by bill length. Bird-Banding 42:297–298.

Page, G., B. Fearis, and R. M. Jurek. 1972. Age and sex composition of Western Sandpipers on Bolinas Lagoon. California Birds 3:79–86.

Page, G., and D. F. Whitacre. 1975. Raptor predation on wintering shorebirds. Condor 77: 73–83.

Peach, W. J., P. S. Thompson, and J. C. Coulson. 1994. Annual and long-term variation in the survival rates of British Lapwings *Vanellus vanellus*. Journal of Animal Ecology 63:60–70.

Pradel, R., E. Cooch, and F. Cooke. 1995. Transient animals in a resident population of Snow Geese: Local emigration or heterogeneity? Journal of Applied Statistics 22:695–710.

Rice, S. M. 1995. Residency rates, annual return rates and population estimates of Semipalmated and Western sandpipers at the Cabo Rojo Salt Flats, Puerto Rico. M.S. thesis, University of Puerto Rico, Mayaguez.

Robertson, G. J., and F. Cooke. 1999. Winter philopatry in migratory waterfowl. Auk 116:20–34.

Sandercock, B. K., and A. Jaramillo. 2002. Annual survival rates of wintering sparrows: Assessing demographic consequences of migration. Auk 119: 149–165.

Sandercock, B. K., D. B. Lank, R. B. Lanctot, B. Kempenaers, and F. Cooke. 2000. Ecological correlates of mate fidelity in two Arctic-breeding sandpipers. Canadian Journal of Zoology 78: 1948–1958.

Sherry, T. W., and R. T. Holmes. 1995. Summer versus winter limitation of populations: What are the issues and what is the evidence? Pages 85–120 *in* Ecology and Management of Neotropical Migratory Birds (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.

Sherry, T. W., and R. T. Holmes. 1996. Winter habitat quality, population limitation, and conservation of Neotropical–Neartic migrant birds. Ecology 77:36–48.

Thompson, P. S., and W. G. Hale. 1993. Adult survival and numbers in a coastal breeding population of Redshank *Tringa totanus* in northwest England. Ibis 135:61-69.

Tripp, K. J., and J. A. Collazo. 1997. Non-breeding territoriality of Semipalmated Sandpipers. Wilson Bulletin 109:630–642.

Warnock, N., G. W. Page, and B. K. Sandercock. 1997. Local survival of Dunlin wintering in California. Condor 99:906–915.

Warnock, S. E. G., and J. Takekawa. 1996. Wintering site fidelity and movement patterns of Western Sandpipers *Calidris mauri* in the San Francisco Bay estuary. Ibis 138:160–167.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked individuals, version 2. Bird Study 46 (Supplement):120-139.

Whitfield, D. W., A. D. Evans, and P. A. Whitfield. 1986. The impact of raptor predation on wintering waders. Pages 674–687 *in* Acta XIX Congressus Internationalis Ornithologici (H. Oueilet, Ed.). National Museum of Natural Science, Ottawa, Ontario.

Wilson, H. E. 1994. Western Sandpiper (*Calidris mauri*). *In* The Birds of North America, no. 90 (A. Poole and F. Gill, Eds). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Associate Editor: A. Powell