JOURNAL OF AVIAN BIOLOGY 36: 191–202, 2005

Life history varies with migratory distance in western sandpipers *Calidris mauri*

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O'Hara, P. D., Fernández, G., Becerril, F., de la Cueva, H., and Lank, D. B. 2005. Life history varies with migratory distance in western sandpipers *Calidris mauri*. – J. Avian Biol. 36: 191–202.

The propensity of migratory waders to remain on the non-breeding grounds during the arctic breeding season ("oversummer") in their first biological year of life ("juveniles") may be latitude, and thus migratory distance dependent. We compared the extent of preparation for northward migration of western sandpipers *Calidris mauri* spending the non-breeding season in México and Panamá during 1995–1998. During winter residency and premigratory periods, we measured body mass and scored the extent of dull basic versus bright alternate breeding plumage of captured juveniles and adults (second biological year or older), and obtained additional plumage scores from observations of uniquely colour banded birds. Nearly all western sandpipers in México prepared for northward migration by increasing body mass and moulting into breeding plumage. In Panamá, most adults prepared for migration, but few, if any, juveniles did so. Patterns of body mass and breeding plumage development do not generally support the hypothesis that oversummering by juveniles results directly from less efficient foraging or from resource competition with adults. We suggest instead that costs directly associated with migratory distance *per se* influence the life history strategies of sandpipers spending the non-breeding seasons at different latitudes. This latitudinal difference should interact with the well documented sex-ratio cline in non-breeding distribution (male western sandpipers predominating in northern parts of the range and females in southern parts). This suggests that females have more conservative life histories, prioritizing first year survivorship, relative to males that instead weight first-year breeding opportunities.

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Bird migration involves the fundamental tradeoff between obtaining a higher survivorship probability by remaining resident at a familiar site versus the potential reproductive and/or survivorship benefit from moving to exploit seasonally available feeding or nesting resources elsewhere (Fretwell 1980, Greenberg 1980, Gauthreaux

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1982, Sillett and Holmes 2002). Some species of migratory waders forego northward migration and breeding in their first year or years of life, opting instead to remain resident on the non-breeding grounds ("oversummering" in reference to the boreal summer; e.g. Johnson and Johnson 1983, McNeil et al. 1994, Summers et al. 1995, Hockey et al. 1998, O'Hara et al. 2002). Among species, either or both body size and longevity, and wing moult strategy in combination with migration distance, correlate with variation in the propensity to oversummer (Summers et al. 1995). Proximate and ultimate explanations for this behaviour in younger birds include: lower foraging proficiencies (Hockey et al. 1998), inadequate development of immunocytological systems (McNeil et al. 1994), breeding probabilities being sufficiently less profitable (Summers et al. 1995), and improved conditions for wing moult and lower risks associated directly with migration itself, including those related to flight feather condition and flight performance (O'Hara et al. 2002).

It is difficult to evaluate the relative selective importance of these mechanisms based on interspecific comparisons of data currently available. Using within species comparisons, Summers et al. (1995) showed that in three out of four species of waders, a higher proportion of the non-breeding season population oversummered in South Africa than in England, suggesting that the large difference in migration distance altered the selective balance for or against migration in the first year. However, the huge difference in migration distance and small number of species involved limits the interpretation of these patterns.

The western sandpiper *Calidris mauri*, a small scolopacid wader, migrates between breeding grounds in western and northern Alaska and eastern Siberia, and non-breeding grounds along the west coast of the Americas ranging from Oregon to Peru, and southern New Jersey to Surinam along the east coast (Wilson 1994). The species is partially segregated by sex and age on the non-breeding grounds, with males disproportionately farther north, and older birds disproportionately in the center of the range (Nebel et al. 2002). Some birds migrate north and attempt to breed in their first spring of life (Ruthrauff 2002, D. Schamel, B. Sandercock unpubl. data). Northward migration by these birds is a particularly interesting phenomenon in this species because migrating young birds (second biological year) must complete three migratory journeys on the same set of primary feathers they grew as chicks on the breeding grounds. O'Hara et al. (2002) suggested that differential feather wear associated with migration distance might influence whether or not young western sandpipers migrate northward in their first spring.

In this paper we present evidence that oversummering behaviour in western sandpipers is latitude-dependent. First we compared preparation for migration between adults and juveniles (individuals in their first non-breeding season, approx. August to April) at sites in México and Panamá. We used rates of mass gain and extent of prealternate (prenuptial) moult into bright breeding plumage as indices of preparation for migration and breeding. Using these plumage indices, we also estimated the proportion of juveniles that defered their first spring migration and instead oversummer as young adults. Secondly, we explored variation in mass as an indirect measure of foraging proficiency and/or competitive subordination as a potential mechanism accounting for deferred migration in juvenile and young western sandpipers. We did this by comparing mass variation during the 'boreal winter' residency seasons (approx. 1 September to 1 February), and premigratory periods (from 1 February to the end of March), between age categories in Panamá and in México. Juveniles maintaining lower mass during the residency period would be consistent with the notion that younger less experienced birds are poorer foragers than adults, resulting in an inability to prepare adequately for migration. Also consistent with this hypothesis is the prediction that juvenile mean mass would be adversely affected by increasing adult foraging intensity during the premigratory period.

Materials and methods

Data collection

Data were collected in Panamá and México from 1 September to 1 May 1995–1996, 1996–1997, and 1997–1998. Non-breeding western sandpipers were studied at the Estero de Punta Banda (31°52′N, 116°37′W), an isolated 20 km^2 coastal wetland located on the northwest coast of the Baja California peninsula, 13 km south of Ensenada. In Panamá, data were collected at two beaches near Chitré, province of Herrera, (8°0′N, 80°50′W), where we have banded and recaptured western sandpipers for 14 non-breeding seasons. In both countries, we captured birds in mist nets, recorded body mass and culmen length (see Prater et al. 1977), and scored the degree of bright breeding body ('contour') plumage acquired during prealternate moult. Each individual was banded with a USGS aluminum band. Birds were categorized as juvenile (0–10 months: fledging to onset of first spring premigratory period), or older (11+ months), based on plumage (Page et al. 1972, Prater et al. 1977) and/or banding history. We assigned sex based on culmen length (Page and Fearis 1971: males $<$ 24.3 mm, females $>$24.7 mm). Since we found little or no significant effects in our analyses associated with sex, we included birds of unassigned sex (culmen lengths within 24.3–24.7 mm) in our final analyses.

Plumage scores

The prebasic moult of western sandpipers into basic (dull non-breeding) contour plumage occurs on the non-breeding grounds between August and December, and the pre-alternate moult into bright breeding (alternate) contour plumage occurs between February and May, in preparation for northward migration (Wilson 1994). The breeding plumage includes variable numbers of rufous-centred or rufous-edged contour feathers (crown, cheeks, mantle, upper scapulars, and tertials) and coverts (Prater et al. 1977). In Panamá, we scored the contour plumage coloration during prealternate moult in the spring for recaptured (previously aged) individuals as follows: 1 = no rufous anywhere, 2 = trace of rufous on any tract such as the mantle, upper scapulars, tertials, or crown, 3 = traces of rufous on more than one tract, 4 = presence of rufous in three or four tracts, 5 = rufous on lower scapulars and other tracts, and 6 = full alternate plumage, with rufous throughout all previously mentioned tracts. In México, because of a low recapture rate, we scored the contour plumage coloration of individually-colour banded birds during prealternate moult through observation with a 15–40x spotting scope during spring (from March to April), using the following ordinal scale: 1 = bird in basic plumage, with uniform grayish-brown upper parts, and whitish eyebrow, 2 = black-tipped tertials and lower scapular feathers, 3 = rufous fringed tertials and lower scapular feathers, 4 = more intense rufous of scapular and tertial feathers, some marked with rufous basally, and covert feathers also somewhat rufous, 5 = mantle feathers fringed with rufous, ear coverts just starting to show rufous colour, and black streaks ('chevrons') appearing in the breast, and 6 = alternate plumage almost complete, crown feathers fringed with rufous, and chevrons visible on the breast. At both sites, we scored plumage coloration rather than intensity of moult, and thus we did not distinguish between juveniles that may have moulted into a second basic-like plumage versus those that did not moult at all.

Timing and rate of moult analyses

We examined annual and within year variation in the rate and timing of prealternate moult into bright breeding plumage among sex-age categories within sites, and we compared sex-age dependent variation between sites. Although our methods for categorizing plumage coloration varied between sites, this should not affect our conclusions since our study focused on differences between age categories within sites. For individuals captured or resighted more than once per year at each site, only the latest moult score observation was used in the analyses (i.e. no replicates per individual per year). Plumage scores were treated as ordinal response variables and analyzed using logistic regression models (Wald χ^2, two-tailed $\alpha = 0.05$) with a cumulative logit link function (proc 'LOGISTIC'; SAS 1999). To visualize trends (Fig. 2 and 4), we fitted linear or curvilinear relationships to our data applying least squares methods or cubic splines with four degrees of freedom respectively (S-Plus 2001).

Plumage scores were collected in México during March and April of the last two years of this study, constraining our comparisons between sites to these periods. Since our sample sizes differed considerably between sites (México: n = 177, Panamá: n = 5372), we were concerned about the differential probability of obtaining a type II statistical error, or failure to reject a false null hypothesis for between-site comparisons. Because we tested for age-sex associated differences within sites using a logistic regression and a cumulative logit link function (i.e. moult scores were treated as a multinomial response), we found it difficult to test for power. Instead we tested whether or not we would have obtained similar results with similar sample sizes by: (1) multiplying our sample in México to reflect sample size in Panamá, and (2) randomly subsampling our data from Panamá (10,000 iterations) to test sets of the same sample size as those obtained in México (n = 177), and reanalyzed each subset for age-sex association in plumage scores. Although most juveniles in México migrate in their first spring, there are some that appear to defer their first migration until the following spring. Since some do migrate in their first spring, we expected significant association with age, but not as strong as that shown in Panamá.

We used plumage scores to estimate the proportion of each age class preparing for migration primarily because of our familiarity with breeding plumage (versus any other indicator of migratory preparedness, such as site-specific mass gain). At both sites, adults appeared to moult at similar rates. We estimated "predicted proportions" of both age categories at each site with different plumage scores (Fig. 2 and 4) using proc LOGISTIC (model statement output 'PRED'; SAS 1999). We categorized individuals with a plumage score of four or higher by 1 April as those preparing for migration, since 1 April appears to be close to spring migration departure and is a date included in almost all the data sets. It should be emphasized that this likely will be an under-estimate of the proportion actually departing from each site, as predicted plumage scores continued to increase well into April.

Mass analyses

To examine patterns of mass change, we divided each non-breeding season into a winter "residency" and a spring "premigratory" period. Residency was the period from the onset of our field work at each site each year through to the start of the premigratory period. The premigratory period began on 1 February, at which time mass started to increase and the alternate plumage became visible (Fig. 1–4). This timing was consistent among years. We analyzed patterns of temporal variation separately for each period, and in order to visualize trends we applied cubic spline curves with four degrees of freedom (S-Plus 2001). Within sites, masses were compared among sex-age categories and years with an ANCOVA (proc 'MIXED'; SAS 1999), using data from each individual only once per year (i.e. no replicates per individual per year). We included exposed culmen length (proxy for structural size) as a covariate in these analyses to help control for size variation, and we included culmen length interactions with age and sex, allowing for possible variation in scaling between mass and structural size among sex-age categories. Models were reduced to their most parsimonious form using Type III SS ($\alpha = 0.05$). All least squares means (lsmeans statement in proc 'MIXED'; SAS 1999) and slopes (estimate statement in proc 'MIXED'; SAS 1999) are reported with standard errors. We made all pair-wise post-hoc comparisons using CONTRAST and LSMEANS statements in proc MIXED (SAS 1999). The t-values are reported with degrees of freedom as subscripts, and F-values with numerator and denominator degrees of freedom as subscripts. Power analyses are also reported for age comparisons within sites ($1-\beta$).

Results

Differences between age categories in preparation for migration

México

Western sandpipers became heavier over the course of the premigratory periods (Fig. 1). There were no significant differences in temporal patterns between age classes (all age and age interaction terms: $P > 0.39$) and mass gain did not differ between sex categories (all sex × day interaction terms: $P > 0.20$). In all three years, the rate of mass gain was significantly greater than zero (Table 1), but rates varied among years (date × year, $F_{2,157} = 8.81$, $P = 0.0002$), with the highest rate in 1996–97. However, power was very low for detecting differences in mass gain between age categories ($1-\beta = 0.159$).

In both seasons during which plumage data were collected in México, prealternate moult into bright breeding plumage progressed with time between the

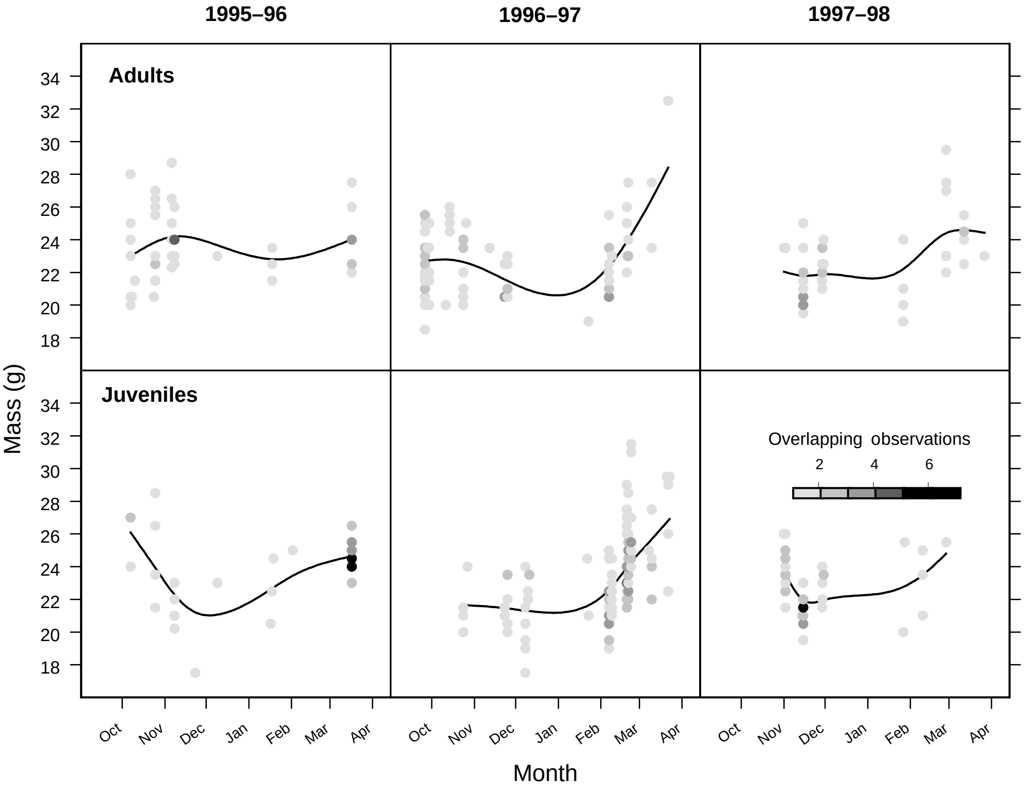

Fig. 1. Mass variation in adults and juveniles (both sexes) wintering in México. Colour of circle represents sample size for overlapping observations (see scale in legend: darker symbols represent greater numbers). A cubic smoothing spline curve is in black (Materials and methods).

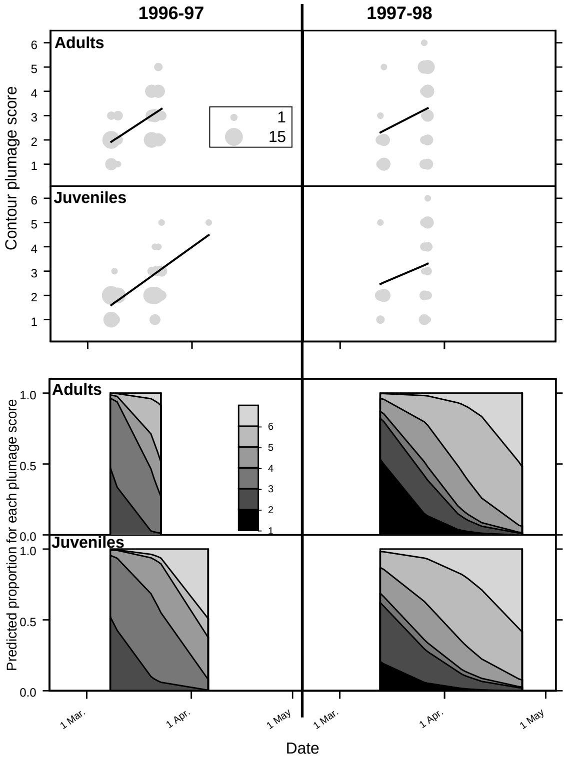

Fig. 2. Contour plumage scores for México in both age classes. Higher values indicate more alternate plumage (see methods). Area of circle represents sample size for overlapping observations (see legend). Lines were fitted using Least squares method (Materials and methods).

end of February (approximately) and migratory departure in the spring (Fig. 2; Wald $\chi^2 = 96.5$, df = 1, $P < 0.0001$). The rates did not differ by age class (age × date: Wald $\chi^2 = 0.28$, df = 1, $P = 0.60$), or sex (sex × date: Wald $\chi^2 = 0.09$, df = 1, $P = 0.77$), in either season. Rates of change in plumage scores were also consistent between the two seasons (season × date: Wald $\chi^2 = 0.13$, df = 1, $P = 0.72$). Although there is a likelihood of a type II error (i.e. not detecting a true difference between age categories) due to low sample size, we could not estimate power for age associated plumage scores (see Materials and methods). Instead, we multiplied our dataset from México to match our Panamanian sample size. This artificially enlarged dataset produced significant age associated plumage scores (age × date: Wald $\chi^2 = 8.34$, df = 1, $P = 0.004$), but the association was not as strong as that detected in Panamá (see below). This suggests that different proportions of each age class prepare for migration in México, but that the difference between age categories is substantially lower in México than in Panamá.

We found it difficult to estimate predicted proportion of individuals in México with a plumage score of four or higher during the 1996–97 season because of the low sample size during and after 1 April (Fig. 2). Furthermore, the small sample of juveniles with high plumage scores observed after 1 April strongly influenced our results. Nevertheless, before 1 April during this season, adults and juveniles appeared to moult at similar rates. Stronger evidence for similar plumage scores between age categories comes from our second season of observations, where approximately 70–80% of both adults and juveniles present on 1 April had a plumage score of four or higher.

Panamá

In contrast to México, adults and juveniles in Panamá strongly diverged in mass and plumage patterns over the course of the premigratory periods (Fig. 3 and 4). There was a significant age difference in mass gain with date, with adults gaining mass while juveniles did not (Table 2; age × date: $F_{1,3966} = 122.3$, $P < 0.0001$). However, this age-dependent difference was not completely consistent among years (age × date × year: $F_{2,3966} = 37.0$, $P < 0.0001$), as neither age category showed significant mass gain 1997–98. There was some evidence for differential weight gain between sex categories among years (sex × date × year: $F_{1,3961} = 3.48$, $P = 0.031$), but the lack of difference between age categories within sexes was consistent within and among years ($P > 0.075$).

In all three years, adults moulted their contour feathers extensively into alternate plumage during premigratory periods, while all but a few juveniles did not (Fig. 4; age × date: Wald $\chi^2 = 331.4$, df = 1, $P < 0.0001$). However, as with mass gain, the magnitude of age-dependent difference varied among years (Fig. 4; age × date × year: Wald $\chi^2 = 86.2$, df = 2, $P < 0.0001$) with considerably less difference in 1997–98, when fewer adults showed as extensive an amount of breeding plumage. Nevertheless, in all three years adults had significantly higher plumage scores than juveniles (Fig. 4), which was consistent between sex categories (all sex × day and higher interaction terms: $P > 0.41$). Furthermore, in our subsampled randomization (each iteration with $n = 177$), we found that 9075 out of 10 000 replications showed significant age variation with higher plumage scores in adults.

From our predicted proportions of plumage scores (Fig. 4), we estimated that approximately 55–65% of the adult populations present on 1 April had scores of four or higher during the first two non-breeding seasons (1995–96 and 1996–97). During the 1997–98 season however, a considerably smaller proportion of adults appeared to preparing for migration as quickly, with only 40–45% adults having scores of four or higher. In all three seasons, a very small proportion of juveniles had high plumage scores on 1 April (Fig. 4; <5%), however, during 1995–96 and 1996–97, juvenile proportions with scores greater than four were higher earlier in the premigratory period, suggesting that juveniles with higher plumage scores might be leaving the area (i.e. had

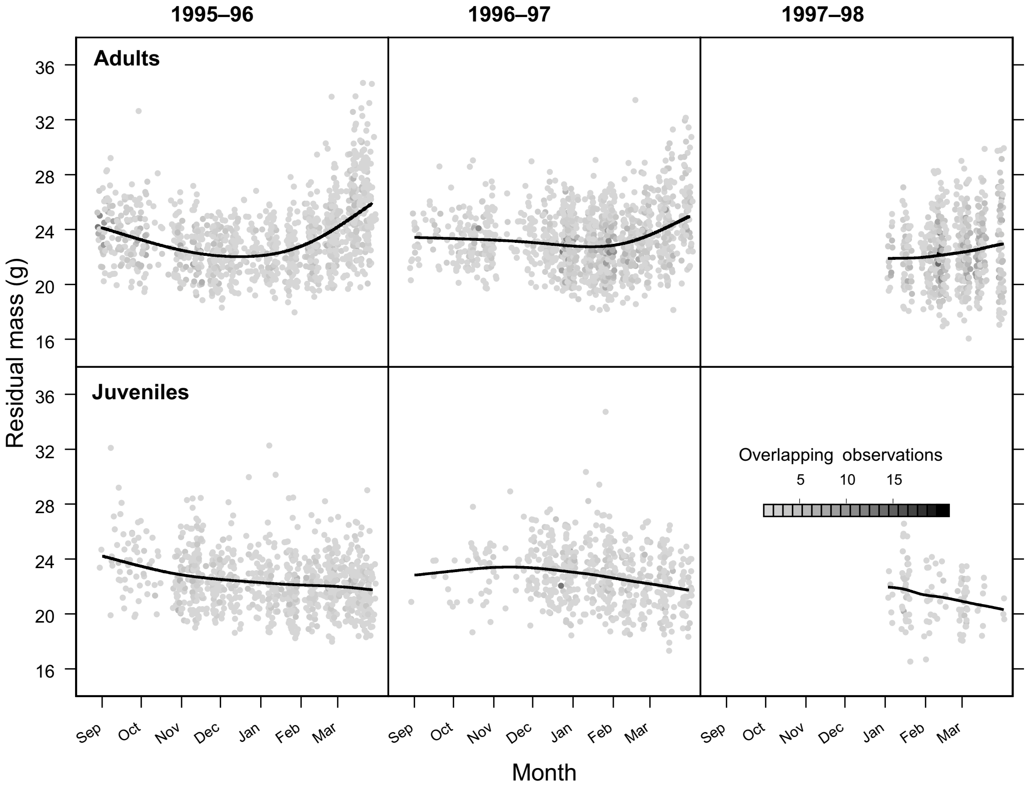

Fig. 3. Juvenile and adult masses (g) through the non-breeding season and the premigratory preparatory period for all three years in Panamá. Colour of circle represents sample size for overlapping observations (see legend: darker symbols represent greater numbers). A cubic smoothing spline curve is in black (Materials and methods).

departed on their northward migration). Conversely, in the final non-breeding season (1997–98), proportions of juveniles with scores of four and higher increased to approximately 5% of the juvenile population present on 1 April and continued to increase afterward.

Age-dependent migration versus residency decisions

Poorer foraging in juveniles as a result of inexperience or competitive subordination may play a role in determining migration in the first spring, and we examined our mass data for evidence of maintenance of lower juvenile mean mass (than adults) during the residency and premigratory periods. In general, mass decreased during the winter residency period in México, for both age categories (Fig. 1). There was no difference in mean mass or rates of mass loss between sexes in either adult or juvenile age categories ($P > 0.70$). Increasing power by pooling over sex categories, we found that juvenile mass loss was significantly greater than for adults ($F_{1,164} = 5.40$, $P = 0.021$: juvenile slope $= -0.049 \pm 0.013$ $g \times d^{-1}$, $n = 185$; adult slope $= -0.011 \pm 0.008$ $g \times d^{-1}$, $n = 153$). Age dependent variation in mass change during the non-breeding season may be due largely to the considerable difference in mass between age categories at the start of the 1995–96 non-breeding season, increasing estimated juvenile mass at the beginning of the non-breeding season in the pooled data (Fig. 1; $F_{1,164} = 4.97$, $P = 0.027$). However, least squares mean masses during the residency period (controlling for time of capture and rate of mass loss as well as culmen length) did not differ between age categories ($t = 0.73$, $P = 0.47$; lsmeans: juveniles $= 22.98 \pm 0.26$ g; adults $= 22.75 \pm 0.18$ g).

In Panamá, the population mean mass also declined during the residency period, and these rates varied annually ($F_{2,4751} = 12.41$, $P < 0.0001$, 1995–1996: -0.012 $g \times d^{-1}$, $t = 13.5$, $P < 0.0001$; 1996–1997: -0.008 $g \times d^{-1}$, $t = 20.7$, $P < 0.0001$; 1997–1998: -0.043 $g \times d^{-1}$, $t = 2.87$, $P = 0.0041$). Although females were disproportionately heavier than males by approximately 0.31 g (relative to culmen length: $F_{1,4751} = 39.2$, $P < 0.0001$), mass loss during the residency period was consistent between males and females among years ($F_{1,4747} = 1.23$, $P = 0.27$). Overall, there was no age-dependent difference in rates of mass loss during the residency period ($F_{1,4750} = 0.02$, $P = 0.90$), nor in

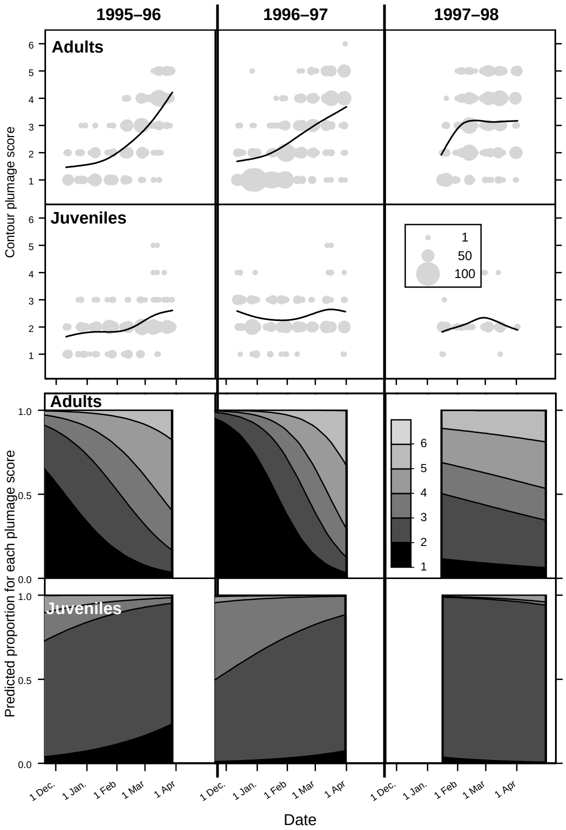

Fig. 4. Contour plumage scores for adults and juveniles of both sexes in Panamá. Higher values indicate more alternate plumage (see Materials and methods). Area of circle represents sample size for overlapping observations (see legend). Age differences in rates of moult varied among years, but differences were significant for all three years (1995–96: Wald $\chi^2 = 898.6$, df = 1, $P < 0.0001$; 1996–97: Wald $\chi^2 = 869.4$, df = 1, $P < 0.0001$; 1997–98: Wald $\chi^2 = 42.79$, df = 1, $P < 0.0001$). A cubic smoothing spline curve is in black (Materials and methods).

intercepts at the beginning of the period ($F_{1,4751} = 2.71$, $P = 0.10$).

Juveniles may also maintain lower mass during the premigratory period in Panamá as adult foraging intensity increases. We tested for changes in rates of mass loss within the juvenile category between residency and premigratory periods in Panamá. Overall, rates of juvenile mass change did not vary between these periods ($F_{1,2582} = 0.21$, $P = 0.64$) and this was consistent among years ($F_{2,2580} = 2.27$, $P = 0.10$). However, intercepts differed between periods and the size of this difference varied with season ($F_{2,2581} = 9.91$, $P < 0.001$). In 1995–1996 least squares mean mass increased by 0.54 g in juveniles but in 1996–1997 decreased by 0.34 g, while there was no significant change in 1997–1998, possibly due to the relatively small sample size for juveniles that year (Table 3). Although juvenile mean mass may have been affected by increased foraging intensity in adults during the premigratory period, this possible effect was not consistent among our study years.

Discussion

Our results suggest that migration distance influences the probability of deferred migration in young western sandpipers and are consistent with the hypothesis of a similar effect on young waders of other species (Summers et al. 1995). In México, both adult and juvenile western sandpipers prepared for northward migration (during the spring season). Both age classes gained substantial mass and approximately 70–80% of all individuals present 1 April had acquired colorful alternate plumage during the premigratory period (Fig. 1 and 2). Adults in Panamá, gained mass significantly during premigratory periods in the first two years of this study (Fig. 3), and approximately 55–65% of adults present had moulted into a contour plumage score of four or higher by 1 April (Fig. 4). However, in the final year (1997–98), adults did not show a significant gain in mass during the premigratory period and only 40–45% of those present 1 April had a plumage score of four or higher. In contrast, juveniles in Panamá did not gain mass significantly during any of the premigratory periods and 5% or less of those present on 1 April had a plumage score of four or more.

Our major conclusion partly depends on a lack of significant differences between age categories in México, and is therefore susceptible to type II errors (failure to reject a false null hypothesis). Low power in our mass

Table 1. Mass change (g × day^{-1} ± SE) while controlling for culmen length (proxy for structural size) during the premigratory period in México for all three years (sample sizes in parentheses). Slopes did not vary between sexes or age classes, but did vary significantly among years (see Results). Pairwise comparisons indicate that mean mass change (‘Mean Slope’) varies significantly between 1995–96 and 1996–97 ($t = 4.20$, $P < 0.0001$), but not between 1995–96 and 1997–98 ($t = 1.52$, $P = 0.13$), nor between 1996–97 and 1997–98 ($t = 1.68$, $P = 0.094$). Mean slopes for all three years were significantly greater than zero (1995–96: $t = 2.06$, $P = 0.041$; 1996–97: $t = 7.58$, $P < 0.0001$; 1997–98: $t = 3.11$, $P = 0.002$).

	1995–96	1996–97	1997–98
Juveniles	0.029 ± 0.015 (25)	0.086 ± 0.014 (86)	0.009 ± 0.060 (6)
Adults	0.011 ± 0.018 (11)	0.120 ± 0.025 (24)	0.068 ± 0.021 (15)
Mean slope	0.025 ± 0.012	0.100 ± 0.012	0.052 ± 0.018

Table 2. Mass change (g × day^{-1} ± SE) while controlling for culmen length (proxy for structural size) during the premigratory period in Panamá for all three years. Slopes varied between age classes and among years but did vary significantly among sexes (see Results). *A posteriori* tests indicate that adults slopes were significantly greater than zero in the first two years, but not in the last (1995–96: $t = 15.4$, $P < 0.0001$; 1996–97: $t = 12.5$, $P < 0.0001$, and 1997–98: $t = 0.21$, $P = 0.83$). In juveniles, the slope was significantly different from zero only in the first year (1995–96: $t = 2.30$, $P = 0.022$; 1996–97: $t = 1.12$, $P = 0.26$, and 1997–98: $t = 0.22$, $P = 0.83$). There was no age difference in mass gain rates in the final year ($t = 0.27$, $P = 0.79$).

	1995–96	1996–97	1997–98
Juveniles	−0.014 ± 0.006 (509)	−0.008 ± 0.007 (284)	0.002 ± 0.008 (156)
Adults	0.075 ± 0.005 (800)	0.060 ± 0.005 (715)	−0.001 ± 0.002 (1553)

analyses demands that we temper our conclusions, allowing for a potential age difference in mass gain in México. Nevertheless, age-specific differences in mass gain are much clearer in Panamá, which is consistent with the latitude dependent hypothesis for migration northward in the first spring. Artificially inflated sample sizes for the plumage score comparisons in México further support this reinterpretation, suggesting that there is an age-dependent difference in prealternate plumage coloration, but that a far lower proportion of juveniles in Panamá moult into a bright breeding plumage than in México. Also, our analysis of 10 000 random subsamples of Panamá plumage scores indicated that there was a strong age-dependent difference despite considerable variation among individuals.

We conclude that a major life history difference exists between juvenile birds spending the non-breeding season at these locations. Those in northern México migrate and presumably attempt to breed in their first spring of life, and migratory preparation and possibly departure dates are similar between age categories. Juveniles in Panamá, however, either depart on their first migration a month or more later than adults, or oversummer and make their first northward migration and breeding attempt in their second spring. We are aware of only one previous study documenting a regular presence of oversummering western sandpipers on the non-breeding grounds. Smith and Stiles (1979) documented small numbers of western sandpipers less than 5% of the winter population – oversummering in one year at a small estuary (approximately 10°2′ N latitude) on the Pacific Coast of Costa Rica (but see also Pereira Perez 1990). Data from another non-breeding site in Venezuela (approximately 10°25′N latitude) are inconclusive (McNeil et al. 1994).

This study provides an example of intraspecific variation in life-history strategy associated with non-breeding season latitude. Since the breeding range spans a relatively narrow latitudinal and longitudinal range (Wilson 1994), non-breeding latitude serves as a reasonable measure of migration distance. Thus, in this case, a greater proportion of juvenile waders deferred northward migration from the non-breeding site more distant from breeding areas. Although our conclusion and that of Summers et al. (1995) are based on data collected at only two geographic areas, the proportional differences in migration distances, and other potential confounding ecological differences, are considerably smaller in our study. In addition to providing a more detailed example than Summers et al. (1995), we have shortened the distance over which a difference in migration propensity has been detected. The approximate one-way migration distances to the breeding grounds (e.g. wetlands surrounding Nome, AK) are ca. 5000 km from Punta Banda, and 10,000 km from Chitré. Thus, the difference between migrating to and from Punta Banda or Chitré is approximately 10,000 km (two times the difference of 5,000 km), whereas the differences in round-trip migration distances for waders in England versus South Africa may exceed 20,000 km.

We expect to find some "migratory divide" or a cline in propensity to migrate, at non-breeding sites between northern Baja California and Panamá. Consistent with this, at Bahia Santa Maria, approximately 1000 km south of our site in Baja California, approximately 20% of juveniles do not prepare for migration (Fernández et al. 2004). Of particular note, young males appear less likely to migrate from this site than young females.

Age-dependent migration versus residency decisions

We suggest that the propensity to migrate in the first spring season may be a function of some age-dependent

Table 3. Least squared mean mass (g × day^{-1}) for juveniles captured in Panamá during residency and premigratory periods, controlling for culmen length and measurement date. Differences varied annually (see Results) with significant differences occurring in the first two years of the study (1995–96: $F_{1,2583} = 10.9$, $P = 0.0010$, 1996–97: $F_{1,2583} = 6.05$, $P = 0.014$, 1997–98: $F_{1,2583} = 2.88$, $P = 0.090$).

Non-breeding periods	1995–96	1996–97	1997–98
Residency	22.13 ± 0.072 (800)	22.88 ± 0.073 (780)	21.53 ± 0.226 (80)
Premigratory	22.67 ± 0.123 (509)	22.54 ± 0.108 (284)	20.89 ± 0.448 (156)
Difference	0.538 ± 0.163	−0.341 ± 0.139	−0.641 ± 0.378

differential cost that increases with migratory distance (i.e. flight) and associated costs in some species of waders, such as the western sandpiper. Sillett and Holmes (2002) calculated that the daily probability of mortality for a small passerine was 15 times higher during migratory as opposed to residency seasons, which is indicative of the costs of migration in that species at least. Alternatively, some age-dependent ecological factor associated with tropical versus subtropical non-breeding sites may be involved, rather than factors related to flight distance *per se*.

What selective processes might operate to produce this pattern in western sandpipers? O'Hara (2002) proposed that increased feather wear associated with longer migrations may help select for oversummering in younger birds farther south. Adult western sandpipers make two trips on a set of primaries grown following southward migration. By contrast, juveniles migrating in their first spring have to complete three full migratory journeys on the same set of primary feathers grown while they were chicks on the breeding grounds, potentially resulting in extensive feather wear. Other wader species avoid this situation by having evolved a juvenile "supplemental" wing moult (*sensu* Prater et al. 1977) or "partial primary wing" moult (*sensu* Gratto and Morrison 1981) during their first non-breeding season, but there is no evidence for this in western sandpipers, despite considerable opportunity to have observed it (O'Hara et al. 2002, G. Fernández and B. Haase unpubl. data). Higher flight costs and predation danger associated with extensive feather wear may thus select against migration in the first spring. The magnitude of differential feather wear between age classes appears to differ with migration distance (O'Hara 2002), providing a simple, intuitive mechanism to account for the latitudinal difference in age of first northward migration.

Hockey et al. (1998) suggested that lower juvenile foraging proficiency was a major factor selecting for deferred migration. The hypothesized mechanism is that lower efficiency leads to slower accumulation of migratory reserves resulting in later arrival on the breeding grounds, and later arrival would lead to reduced likelihood of successful breeding. The effect of this age differential in efficiency should increase in magnitude with longer migratory distances. While we do not have direct measures of foraging efficiency, we suggest that our data on seasonal patterns of mass for western sandpipers do not generally support predictions from this hypothesis. If juveniles were poorer foragers, we might expect them to have lower mean mass during the residency period. During the premigratory period in México, we might expect juveniles to prepare for migration more slowly than adults. If greater resource limitation in Panamá were to explain differences in the juvenile proportion migrating, we would expect juvenile mean mass to decline as adult foraging intensifies during the premigratory period. However, we found no age-dependent variation in mean mass at either of our sites during the residency periods (Fig. 1 and 3), and only a slight non-significant drop in juvenile mass between residency and premigratory mass gain periods for adults in two out of three years in Panamá (Table 3). More importantly, there was no evidence for age-dependent rates of mass gain in México, contrary to what might be expected under the foraging efficiency hypothesis (Fig. 1). There was also no age difference in the extent or rate of breeding plumage development in Mexico (Fig. 2), which may be used as an honest signal of a bird's relative body condition (Piersma and Jukema 1993, Fitzpatrick 1994, Piersma et al. 2001). Nevertheless, evidence for age-dependence in rates of migration (which may be a function of poorer foraging and lower rates of mass gain during stopovers) might come from breeding studies documenting later arrival and/or later nest initiation for young birds attempting breeding (for e.g. see Ruthrauff 2002).

Theoretically, resident non-breeding birds should maintain an optimal body mass, where fat load reflects a trade-off between the risk of predation and the risk of starvation (Lima 1985, McNamara and Houston 1990). This possible tradeoff limits our ability to interpret our mass patterns. Juveniles may have maintained masses similar to adults by spending a higher proportion of their daily time budget foraging, thereby taking greater risks to maintain their masses. If so, they should suffer higher within-season mortality. Alternatively, one could suggest that juveniles meet foraging requirements more similarly to adults in México than in Panamá. In Panamá, the perceived risk of predation may be sufficiently high and the risk of starvation sufficiently low that western sandpipers maintain a body mass with little or no fat reserves, whereas in northern México, birds maintain a small reserve, which is the common pattern for mudflat feeding waders at temperate sites (e.g. Castro et al. 1992). This suggested latitudinal variation in mass is inconsistent with our data. However, O'Hara (2002) has shown that within sex-age categories, individuals are structurally larger in Panamá than in México. Differences in preparation for migration could thus occur if obtaining resources at our sites in Panamá was more differentially costly to juveniles than to adults than at our site in México. This may be due to larger sizes of individuals spending the non-breeding season in Panamá and presumably increased resource requirements to adequately prepare for migration. Nevertheless, in general, we have little evidence for age differences in foraging ability that might affect migratory versus residency decisions.

We have correlative evidence that resource levels, in general, can affect probability of migration, and that age classes respond consistently to variation in resource levels. The third season of this study, 1997–1998, was a season with an exceptionally strong El Niño/Southern Oscillation (ENSO) event, with widespread effects throughout most of the eastern Pacific (for reviews see Chavez et al. 2002, Fiedler 2002). This ENSO affected populations of several taxa including macrophytes (Carballo et al. 2002), invertebrates (Raimondi et al. 2002), tidal pool fish (Davis 2000), and seabirds (Vandenbosch 2000, Gjerdrum et al. 2003). It was also exceptional throughout most the non-breeding range of the western sandpiper, except for our site in México. In Panamá, rates of moult and mass gain by adults were lower than in other years (Fig. 3 and 4), with a lower proportion of adults present 1 April with a plumage score of four or higher. In Ecuador, rates of mass gain for western sandpipers and other species of waders were also lower than in other seasons (O'Hara 2002). This suggests that the lack of age-dependence in Panamá during the premigratory period was due to large-scale global variation affecting sites throughout most of the non-breeding range, rather than sampling error (i.e. movement of individuals among sites). It appears that climatic variables affecting productivity modulated the migratory preparation of adults in this year.

Demographic implications

The difference in age of first migration creates alternative life history strategies for birds spending their first non-breeding season at different latitudes. If lifetime fitnesses are similar for individuals throughout the non-breeding range, then those spending their first non-breeding season farther north may have higher annual reproductive success, but lower longevity, relative to those spending their first season farther south. Estimates of local annual survivorships from our two sites are consistent with such a trend (O'Hara 2002, Fernández et al. 2004). Alternatively, fitnesses may not be equal, if for example, dominance displacement occurs over this range of latitudes (e.g. Gauthreaux 1982), and lifetime fitness differs as a function of juvenile non-breeding latitude.

Western sandpipers distribute themselves non-randomly with respect to sex and age during the non-breeding season. Males predominate in the north and females in the south, for both adults and juveniles, and young birds are disproportionately represented towards the extremes, and underrepresented in the centre of the range (Nebel et al. 2002). The latitudinal difference in age of first migration may thus translate, at the population level, into differences in life histories between the sexes, with females disproportionately delaying their first breeding season (but see Fernández et al. 2004). There is a male bias among western sandpipers on the breeding grounds, with some males failing to obtain mates (Lanctot et al. 2000, but also shown in semipalmated sandpipers; Gratto-Trevor 1991). The surplus of males could reflect a higher proportion of young males than young females attempting to breed in their first spring (among non-breeding sites across latitudes). Therefore, there may be a general difference between sexes in life history strategies.

Causes of variation in migration distances

Less clear is what determines where a bird spends its first non-breeding season, which would consequently strongly bias an individual towards one or the other life history. We have identified two correlates: sex and body-size. We can argue from the geographical distributions that selection may be stronger on males than on females for attempting to breed in their first year, thus shifting the male non-breeding distribution northward from one that might have been determined solely by ecological optima, especially if there is a cost associated with longer migrations (O'Hara 2002). Benefits from experience with territory acquisition, which is primarily a male activity (Lanctot et al. 2000), may help account for this difference.

Body size also varies with non-breeding latitude. Females, which are larger, are disproportionately represented farther south, as previously noted. But it is also the case that larger birds within each sex are found farther south, even among young birds (O'Hara 2002). If body size affects optimal migration speed or distance, this might be causally related to determining the non-breeding distribution.

We have documented a latitude-dependent difference in life history strategies with two correlated traits (mass gain and prealternate moult scores), and considered ecological factors associated with it. We know little, however, of the causes determining a juvenile bird's first non-breeding location. We may be documenting classical population differences associated with differences in geographical breeding range, e.g. a "leap-frog" system, in which birds from the extreme of the breeding range, farthest from non-breeding areas, migrate to the opposite extreme of the non-breeding range (Alerstam and Högstedt 1980, Greenberg 1980). While no clines in body size have been described from the breeding grounds, relevant data are sparse. This scenario predicts genetic population differentiation between life-history variants. Conversely, individuals may make a condition-dependent developmental decision to breed in their first versus their second spring, and migration distance may be a derivative, correlated consequence of this. Young hatching late in the season might be competitively disadvantaged, and therefore opt for a later age of first breeding. Or birds with suboptimal or damaged flight feathers might opt for shorter migration distances, which thereby shapes their subsequent life history.

O'Hara (2002) has documented clearly that wear increases with migratory distance and that migratory versus residency behaviour of adults can be modified with experimentally simulated primary feather wear.

In short, we do not know whether breeding birds segregate non-randomly with respect to non-breeding areas, or vice-versa, or whether migratory distance in some way reflects body "condition/state" of an individual. Neither do we know what role chance events play during a bird's first migration, nor whether individuals would alter their pre-migratory preparation if experimentally transported to different latitudes. These questions all represent fruitful directions for future research.

Acknowledgements – Funding was provided through the Centre for Wildlife Ecology at Simon Fraser University, the Latin American Programme of the Canadian Wildlife Service, Centro de Investigación Científica y de Educación Superior de Ensenada, NSERC grants to Fred Cooke, Graduate Fellowships at SFU to P.D. O'H., and scholarships from the Consejo Nacional de Ciencia y Tecnología (CONACYT, Mexico) to G. F. and F. B. We thank Drs. R. W. Elner, R. Butler, R. C. Ydenberg, F. Moore, P. Battley and 2 anonymous reviewers for valuable comments that helped improve this manuscript. The Smithsonian Tropical Research Institute and J. Christy provided crucial logistical support for field work in Panamá (including procuring suitable permits for research within Panamá), and the first author would like to thank the community of Playa El Agallito (Panamá) for their hospitality and help in capturing western sandpipers. As well, numerous individuals assisted with the capture and resighting of birds in Punta Banda, in particular, A. Buenrostro, Y. Sandoval, E. Sánchez, L. Enriquez and Nils Warnock.

References

Alerstam, T. A. and Högstedt, G. 1980. Spring predictability and leap-frog migration. – Ornis Scand. 11: 196–200.

Carballo, J. L., Olabarria, C. and Osuna, T. G. 2002. Analysis of four macroalgal assemblages along the Pacific Mexican coast during and after the 1997–98 El Nino. – Ecosystems 5: 749–760.

Castro, G., Myers, J. P. and Ricklefs, R. E. 1992. Ecology and energetics of sanderlings migrating to four latitudes. – Ecology 73: 833–844.

Chavez, F. P., Pennington, J. T., Castro, C. G., Ryan, J. P., Michisaki, R. P., Schlining, B., Walz, P., Buck, K. R., McFadyen, A. and Collins, C. A. 2002. Biological and chemical consequences of the 1997–1998 El Nino in central California waters. – Prog. Oceanogr. 54: 205–232.

Davis, J. L. D. 2000. Changes in a tidepool fish assemblage on two scales of environmental variation: seasonal and El Nino Southern Oscillation. – Limnol. Oceanograph. 45: 1368–1379.

Fernández, G., O'Hara, P. D. and Lank, D. B. 2004. Tropical and subtropical western sandpipers (Calidris mauri) differ in life history strategies. – Ornitología Neotropical (suppl) 15: 385–394.

Fiedler, P. C. 2002. Environmental change in the eastern tropical Pacific Ocean: review of ENSO and decadal variability. – Mar. Ecol. Prog. Ser. 244: 265–283.

Fitzpatrick, S. 1994. Colorful migratory birds-evidence for a mechanism other than parasite resistance for the maintenance of good genes sexual selection. – Proc. R. Soc. Lond. B 257: 155–160.

Fretwell, S. 1980. Evolution of migration in relation to factors regulating bird numbers. – In: Keast, A. and Morton, E. S. (eds). Migrant birds in the neotropics: ecology, behavior, distribution and conservation. Smithsonian Institute, Washington, DC, pp. 417–427.

Gauthreaux, S. A. 1982. The ecology and evolution of avian migration systems. – In: Farner, D. S. and King, J. R. (eds). Avian Biology. Academic Press, New York, pp. 93–168.

Gjerdrum, C., Valle AMJ, C., Cassady, St., Clair, C., Bertram, D., Ryder, J. and Blackburn, G. 2003. Tufted puffin reproduction reveals ocean climate variability. – Proc. Nat. Acad. Sci. 100: 9377–9382.

Gratto, C. L. and Morrison, R. I. G. 1981. Partial postjuvenile wing moult of the semipalmated sandpiper *Calidris pusilla*. – Wader Study Group Bull. 33: 33–37.

Gratto-Trevor, C. L. 1991. Parental care in semipalmated sandpipers *Calidris pusilla*: brood desertion by females. – Ibis 133: 394–399.

Greenberg, R. 1980. Demographic aspects of long-distance migration. – In: Keast, A. and Morton, E. S. (eds). Migrant birds in the neotropics: ecology, behavior, distribution and conservation. Smithsonian Institute, Washington, DC, pp. 493–504.

Hockey, P. A. R., Turpie, J. K. and Velásquez, C. R. 1998. What selective pressures have driven the evolution of deferred northward migration by juvenile waders? – J. Avian Biol. 29: 325–330.

Johnson, O. W. and Johnson, P. M. 1983. Plumage-molt-age relationship in "over-summering" and migratory lesser golden-plovers. – Condor 85: 406–419.

Lanctot, R. B., Sandercock, B. K. and Kempenaers, B. 2000. Do male breeding displays function to attract mates or defend territories? The explanatory role of mate and site fidelity. – Waterbirds 23: 155–164.

Lima, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. – Oecologia 66: 60–67.

McNamara, J. M. and Houston, A. I. 1990. The value of fat reserves and the tradeoff between starvation and predation. – Acta Biotheretica 38: 37–61.

McNeil, R., Tulio Diaz, M. and Villeneuve, A. 1994. The mystery of shorebird over-summering: a new hypothesis. – Ardea 82: 143–152.

Nebel, S., Lank, D., O'Hara, P., Fernández, G., Haase, B., Delgado, F., Estela, F., Evans Ogden, L., Harrington, B., Kus, B., Lyons, J., Mercier, F., Ortego, B., Takekawa, J., Warnock, N. and Warnock, S. 2002. Western sandpipers (*Calidris mauri*) during the non-breeding season: spatial segregation on a hemispheric scale. – Auk 119: 922–928.

O'Hara, P. D. 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. Biological Sciences, Simon Fraser University, Burnaby.

O'Hara, P. D., Lank, D. B. and Delgado, F. S. 2002. Is the timing of moult altered by migration? Evidence from a comparison of age and residency classes of western sandpipers (*Calidris mauri*) in Panamá. – Ardea 90: 61–70.

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

Page, G. W. and Fearis, B. 1971. Sexing western sandpipers by bill length. – Bird Banding 4: 82–88.

Pereira Perez, A. I. 1990. Ecologia de la alimentacion de los correlimos (Aves: Scolopacidae) de una playa fangosa del Golfo de Nicoya, Costa Rica. – Thesis dissertation. Biologia, Ciudad Universitaria "Rodrigo Facio" Costa Rica, San Jose, Costa Rica.

Piersma, T. and Jukema, J. 1993. Red breasts as honest signals of migratory quality in a long-distance migrant, the bar-tailed godwit. – Condor 95: 163–177.

Piersma, T., Mendes, L., Hennekens, J., Ratiarison, S., Groenewold, S. and Jukema, J. 2001. Breeding plumage honestly signals likelihood of tapeworm infestation in females of a long-distance migrating shorebird, the bar-tailed godwit. – Zoology 104: 41–48.

Prater, A. J., Marchant, J. H. and Vuorinen, J. 1977. Guide to identification and ageing of Holarctic Waders. – British Trust for Ornithology, Tring, Herts.

Raimondi, P. T., Wilson, C. M., Ambrose, R. F., Engle, J. M. and Minchinton, T. E. 2002. Continued declines of black abalone along the coast of California: are mass mortalities related to El Nino events? – Mar. Ecol. Progr. Ser. 242: 143–152.

Ruthrauff, D. 2002. Seasonal and age-related trends in the reproductive output of western sandpipers (*Calidris mauri*) at Kanaryaraq, Alaska. – M.Sc. dissertation. Department of Wildlife, Humboldt State University, Arcata, California.

SAS. 1999. SAS Systems for Windows. Version 8.0. – SAS Institute Inc., Cary, N.C.

Sillett, T. and Holmes, R. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. – J. Anim. Ecol. 71: 296–308.

Smith, S. M. and Stiles, F. G. 1979. Banding studies of migrant shorebirds in northwestern Costa Rica. – Stud. Avian Biol. 2: 41–47.

S-Plus. 2001. Academic Site Licence Edition Release 2. Version 6.0. – Lucent Technologies Inc.

Summers, R. W., Underhill, L. G. and Prys-Jones, R. P. 1995. Why do young waders in southern Africa delay their first migration to the breeding grounds? – Ardea 83: 351–357.

Vandenbosch, R. 2000. Effects of ENSO and PDO events on seabird populations as revealed by Christmas Bird Count data. – Waterbirds 23: 416–422.

Wilson, W. H. 1994. Western sandpiper. – The Birds of North America 90: 1–20.

(*Received 30 December 2003, revised 14 May 2004, accepted 23 May 2004.*)