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SEX RATIOS OF DUNLIN WINTERING AT TWO LATITUDES ON THE PACIFIC COAST[1]

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Abstract. Latitudinal clines in sex ratio during the nonbreeding season occur in some shorebirds of the Scolopacidae. We compared populations of nonbreeding Dunlin (*Calidris alpina pacifica*) from two latitudes along the Pacific flyway: the Fraser River Delta, British Columbia, and Bolinas Lagoon, California, to determine whether, and to what degree, they exhibited sex ratios consistent with a latitudinal cline. Dunlin are plumage monomorphic, so we used a maximum likelihood model to estimate overall and monthly sex ratios for each population based on culmen length distributions. Sex ratios in the Fraser River Delta were corrected for sex differences in habitat use. Monthly sex ratios were similar at the two sites but varied throughout the winter, likely reflecting differences in seasonal movement patterns between the sexes. Both populations showed an overall bias toward males (Fraser = 61% males, Bolinas = 65% males). Since there is no evidence to support the possibility of a skew toward males in *C. a. pacifica* as a whole, our data are consistent with some form of latitudinal cline in the sex ratio of *C. a. pacifica.* However, additional data from the Oregon coast, southern California, and Mexico are required to resolve this question. We also tested the hypothesis that mean body size within each sex is larger at the higher-latitude site (Fraser River Delta), but this did not appear to be the case.

Key words: Calidris alpina, *Dunlin, latitudinal cline, maximum likelihood model, morphometric measurement error, sex ratio, shorebirds.*

Proporción de Sexos de *Calidris alpina pacifica* en Dos Latitudes de la Costa Pacífica

Resumen. Durante la época no reproductiva, algunas aves playeras de la familia Scolopacidae muestran variaciones latitudinales de tipo clinal en la proporción de sexos. Comparamos poblaciones no reproductivas de *Calidris alpina pacifica* de dos latitudes a lo largo del corredor de vuelo del Pacífico: (1) el delta del Río Fraser, British Columbia y (2) la Laguna Bolinas, California para determinar si presentaban (y en qué grado) proporciones de sexos acordes con una clina latitudinal. Debido a que el plumaje en *C. a. pacifica* es monomórfico, utilizamos un modelo de máxima probabilidad para estimar la proporción de sexos (general y mensual) de cada población con base en distribuciones de la longitud del culmen. Las proporciones de sexos para el delta del Río Fraser fueron corregidas de acuerdo a diferencias entre sexos en el uso de hábitat. Las proporciones de sexos fueron similares entre los sitios mes a mes, pero variaron a lo largo del invierno, probablemente reflejando

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diferencias entre sexos en los patrones de movimientos estacionales. Ambas poblaciones presentaron un sesgo general hacia los machos (Fraser = 61% machos, Bolinas = 65% machos). En general, no existe evidencia que apoye la existencia de un sesgo hacia los machos en *C. a. pacifica*, de manera que nuestros datos son consistentes con alguna forma de variación latitudinal de tipo clinal en la proporción de sexos en estas aves. Sin embargo, para contestar esta pregunta son necesarios datos adicionales de la costa de Oregon, el sur de California y México. También pusimos a prueba la hipótesis de que el tamaño corporal promedio de cada sexo es mayor en el sitio de mayor latitud (delta del Río Fraser), pero esto no apareció ser cierto.

INTRODUCTION

Latitudinal clines in sex ratio during the nonbreeding season are common in birds (Ketterson and Nolan 1983, Belthoff and Gauthreaux 1991). In species known to exhibit the phenomenon, females, which are usually the smaller sex, typically overwinter farther from the breeding grounds than males (Ketterson and Nolan 1976, 1979, Belthoff and Gauthreaux 1991). Three principal hypotheses have been put forward to explain this difference in winter range (reviewed by Ketterson and Nolan 1983). First, the ‘‘body-size’’ hypothesis proposes that the larger sex could winter at higher latitudes due to superior fasting endurance and thermal efficiency. Second, the ‘‘dominance’’ hypothesis proposes that the dominant sex will migrate to ‘‘optimal’’ wintering habitats, and the subdominant sex will be forced to either undergo longer and more costly migrations or occupy less suitable habitats. Third, the ‘‘arrival-time’’ hypothesis proposes that the sex that benefits most by arriving on the breeding grounds earlier will winter closer to the breeding grounds.

Myers (1981) tested these hypotheses using data on shorebird species with different patterns of winter distribution of the sexes, with both male and female-biased sexual size dimorphism, and with different mating systems and patterns of arrival on the breeding grounds. Conclusions about the relative importance of each hypothesis can be drawn if they lead to testable predictions, such as in those species in which males are smaller than females, but precede them to the breeding grounds. Myers found that males wintered north of females in all species for which males arrived first on the breeding grounds, regardless of which sex was larger. Latitudinal clines in sex ratio were not observed in species that arrived on the breeding grounds together. Myers concluded that information on breeding ground arrival schedules was ‘‘both necessary and sufficient’’ to predict whether and how sexes would segregate latitudinally.

The North American Pacific Coast subspecies of Dunlin (*Calidris alpina pacifica*) breeds in Alaska and winters in significant numbers from the Fraser River Delta in southwestern British Columbia to southern Baja California (Warnock and Gill 1996). Estuaries in that range support tens of thousands of wintering and migrating Dunlin each year (Paulson 1993, Page et al. 1999). During the nonbreeding season, most Dunlin are found in coastal and adjacent agricultural habitats, although some spend part or all of the season inland in freshwater wetlands and agricultural habitats in the Willamette Valley, Oregon, and the Central Valley, California (Strauch 1967, Shuford et al. 1998). Dunlin males arrive first on the breeding grounds, defend breeding territories, and are smaller than females (Holmes 1971, Warnock and Gill 1996, R. E. Gill, unpubl. data).

The arrival-time hypothesis predicts that male Dunlin will winter farther north than females, whereas the body-size and dominance hypotheses make the opposite prediction. If the pattern observed in other species by Myers (1981) is general, we expect that the Dunlin population wintering in the Fraser Delta will be male-biased relative to more southerly sites. However, following the logic of the body-size and dominance hypotheses, we might also expect to find within-sex differences in body size, with larger birds wintering in the Fraser Delta. To our knowledge, the latter possibility has not previously been examined in this context for shorebirds.

Information on population sex ratios at different wintering latitudes is needed to test these predictions. Ideally, sex would be determined unequivocally using a molecular sexing technique (Baker et al. 1999), but the costs for large data sets are not trivial, and appropriate samples are not available from long-term data sets originating before the techniques were available. Sex of Dunlin, which are plumage monomorphic, is often assigned based on culmen length (MacLean and Holmes 1971, Pienkowski and

Dick 1975, Prater et al. 1977). However, geographically distinct groups of Dunlin also vary in culmen length (Warnock and Gill 1996, Engelmoer and Roselaar 1998). Differences in size and, in particular, culmen size, have been used to identify the breeding origin, wintering sites, and migration routes of different groups and subspecies of Dunlin and other shorebirds (Pienkowski and Dick 1975, Browning 1977, Engelmoer and Roselaar 1998). Therefore, the use of culmen length criteria from one population to determine the sex of individuals in another population could lead to errors in the assessment of sex ratio. We studied two nonbreeding populations of *C. a. pacifica*: one near 49°N latitude on the Fraser River Delta, British Columbia, and one near 38°N latitude on Bolinas Lagoon, California. We estimated the sex ratios of these two populations using a maximum likelihood mixture analysis of culmen length distributions derived from local populations. We used the ratios estimated to determine whether, and to what degree, the pattern was consistent with a latitudinal cline, and we investigated within-sex differences in body size.

METHODS

REFERENCE SAMPLE POPULATION

A reference sample of culmen lengths for Dunlin of known sex was created from Dunlin collected on the Fraser Delta mudflats from November through March 1992–1995 (n = 182). We measured culmen length (from the tip to the margin between mandible and feathers at the center of the upper mandible) to the nearest 0.1 mm. Sex was determined by dissection. Page's (1974) data collected from California museum specimens of Dunlin were used as the reference data for Bolinas Lagoon.

MIST-NETTED SAMPLE POPULATIONS

Dunlin were captured at night in mist nets, banded, measured, and released in the Fraser Delta from October through May 1978–1979 (n = 1316), and in Bolinas from October through April 1979–1992 (n = 1179), as part of two separate studies. Dunlin in the Fraser Delta were captured on mudflats, while Dunlin in Bolinas were caught in tidal marshes. We measured culmen length to the nearest 0.1 mm and inferred each bird's age based on its plumage (Page 1974, Prater et al. 1977).

SEX RATIO ESTIMATION

We used a maximum likelihood mixture model (Schnute and Fournier 1980, Smith and Jamieson 1989) to estimate the population sex ratio (proportion of males) in the Fraser Delta and Bolinas during the entire nonbreeding season (October through April), during winter (December through February), and by month. We used culmen length as the only discriminating criterion. Although wing length and mass have been used to discriminate between sexes in *C. a. pacifica* (Brennan et al. 1984), we chose not to include these variables. Both mass and wing length are known to vary seasonally, and wing length exhibits more variation than culmen length between live and museum specimens (Pienkowski and Dick 1975, Prater et al. 1977, Atkinson et al. 1981, Freed et al. 1996). In fact, Greenwood (1979), examining post-mortem shrinkage of Dunlin skins, detected significant shrinkage in wing length and no change in culmen length.

Mixture analysis is routinely used in fisheries investigations to separate sex and age classes (Schnute and Fournier 1980, Smith and Jamieson 1989, Smith and Botsford 1998). For our application, the distribution of culmen lengths in the population was modeled as an overlapping mixture of normally distributed male and female culmen lengths. Five parameters are required to describe the distribution: mean and SD of culmen lengths for each sex, and the proportion of one sex in the distribution of culmen lengths. Given a reference sample of individuals of known sex (e.g., by dissection), the model estimates the mean size and SD of males and females in the reference and ''unknown'' samples together, as well as the proportion of one sex.

We used the mixture model in two ways. For the Fraser Delta, all five parameters were estimated simultaneously, using culmen length data from both the reference sample and the unknown sample. For Bolinas, we had available only the means, SDs and sample sizes of a reference sample from California museum specimens (Page 1974). We accepted these as a reference since Greenwood (1979) detected no post-mortem shrinkage in the culmen lengths of Dunlin. Thus, we used a Bayesian approach by formally including the uncertainty (SE) in the point estimates of the means and SDs for the Bolinas population (Walpole et al. 1998). We calculated asymptotic standard errors for all estimates and report sex ratios as the percent of males ± SE.

We tested the goodness-of-fit of our predictions to sampled data using the chi-square diagnostic and judged that five outliers be removed. We compared the estimated sex ratios of the Fraser Delta and Bolinas samples using *z*-tests, and we used chi-square goodness-of-fit tests to determine whether the sex ratios were significantly different from 1:1.

MEASUREMENT ERROR

Culmen length measurements vary both within and among observers (Barrett et al. 1989, Lougheed et al. 1991). Dunlin used in our study were measured by several different observers, so to determine whether there might be biases among samples, the culmen lengths of eight Dunlin were measured three times each by four of the observers involved in collecting the data. We tested for measurement variation among samples using nested ANOVA, and calculated the overall percent measurement error (% ME) using Bailey and Burns' (1990) formula (% ME = 100% $[s^2_{\text{within}}/(s^2_{\text{within}} + s^2_{\text{among}})]$).

There was significant variation in culmen length measurements between the observers that measured the Fraser Delta reference and mist-netted samples (0.3 mm, $F_{8,32} = 6.5$, $P < 0.001$), with one always recording smaller measurements than the other. Therefore we applied a correction factor to the Fraser Delta data. Culmen length measurements were not significantly different between the Fraser Delta and Bolinas observers ($F_{8,80} = 1.5$, $P = 0.2$), and the overall measurement error was 0.7%.

CAPTURE BIAS

Sex differences in habitat use have been reported for several species of shorebirds (Townshend 1981, Puttick 1984, Warnock 1994, McCloskey and Thompson 2000). Sex-specific habitat-use data were collected in the Fraser Delta using radio-telemetry during the 1995–1996 nonbreeding season (P. Shepherd, unpubl. data). Both male and female Dunlin use agricultural habitats adjacent to the mudflats in the Fraser Delta, predominantly at night when predation risk decreases; however, males appear to use agricultural habitats more often than females (P. Shepherd, unpubl. data). There was a marginally significant correlation between culmen length and the percent of time Dunlin were absent from the mudflats at night ($r = -0.31$, $n = 37$, $P = 0.06$), with male (shorter-billed) Dunlin absent 15.1 ± 7.5% more often than female (longer-billed) Dunlin (taking tide stage into account). Since the mist-netting for our Fraser Delta sample took place at night on the mudflats, we corrected the estimated sex ratio. We did this by multiplying the percentage of males by 115.1% and adding the variance in this correction factor (7.5%) to the total variance of the percentage of males. Warnock et al. (1995) also found some habitat segregation between the sexes in Bolinas, but it was on a seasonal rather than a daily scale and is accounted for in the month-to-month sex ratio data reported below. Therefore no correction was made to the Bolinas data.

BODY SIZE

Culmen length is highly correlated with body size in Dunlin ($P < 0.001$), so it was used as an index of body size (Engelmoer and Roselaar 1998, Shepherd, unpubl. data). ANOVA was used to compare the culmen lengths of the Fraser Delta reference sample for each sex by season: fall (October and November), winter (December through February), and spring (March and April). No seasonal differences were found for either males ($F_{2,62} = 0.1$, $P = 0.9$) or females ($F_{2,114} = 1.4$, $P = 0.3$), so the samples were pooled for further analyses. Culmen lengths of adult and juvenile Dunlin were compared, separately by sex, using *t*-tests. No age differences were found for either males ($t_{16} = -0.5$, $P = 0.7$) or females ($t_{19} = -0.1$, $P = 0.9$), so age classes were pooled. We used one-tailed *z*-tests to determine whether the estimated mean culmen lengths of Dunlin in the Fraser Delta were larger than those in Bolinas, separately by sex. We report mean culmen lengths ± SE below.

RESULTS

SEX RATIOS

The mixture model estimated the overall (October through April) nonbreeding percentage of males in the Fraser River Delta to be 53 ± 3% (Fig. 1). When corrected for sex differences in habitat use, the percentage of males in the Fraser Delta was estimated at 61 ± 8%. This was lower than, but not significantly different from, the 65 ± 3% males estimated for Bolinas Lagoon ($z = -0.5$, $P = 0.6$, Fig. 1).

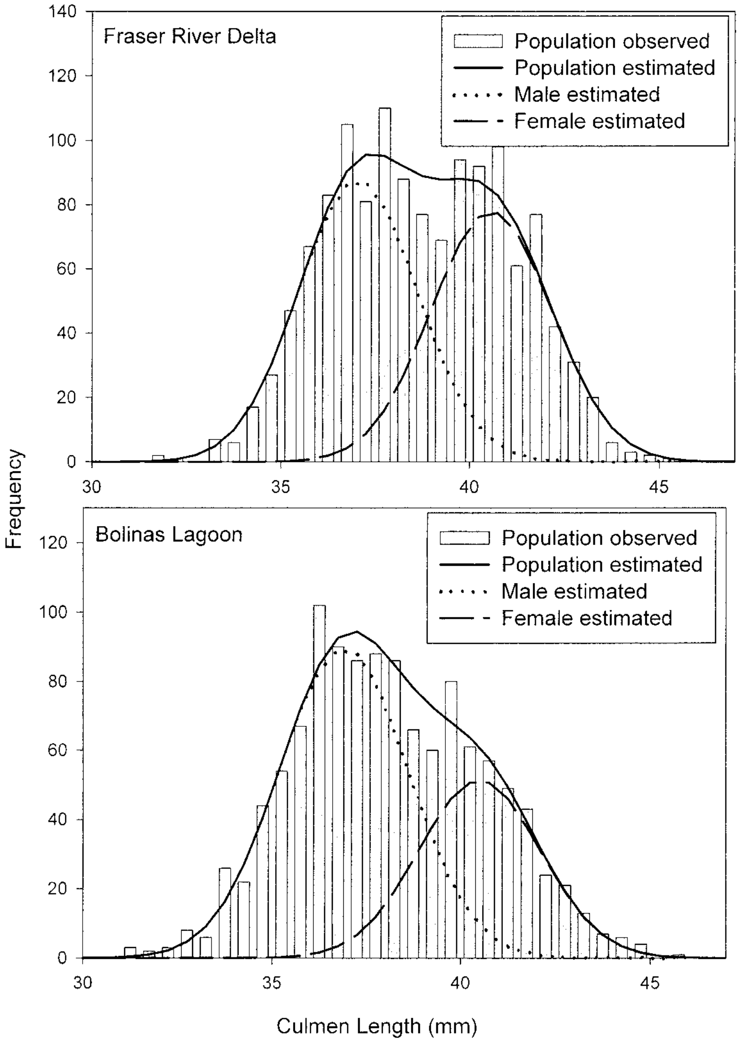

FIGURE 1. Culmen distribution of Dunlin (males, females, and overall population) from the Fraser River Delta, British Columbia, estimated using mist-netted and reference samples (observed), and from Bolinas Lagoon, California estimated using the mist-netted sample (observed) and Bayesian prior probabilities.

During winter (December through February), there were an estimated 65 ± 9% males in the Fraser Delta and 62 ± 3% males in Bolinas ($z = 1.0$, $P = 0.3$). Sex ratios at both sites were significantly male-biased overall ($\chi^2_1 > 33$, $P < 0.001$) and in winter ($\chi^2_1 > 34$, $P < 0.001$). Sex ratio patterns varied throughout the nonbreeding season, but varied similarly for the two sites (Fig. 2). The probability that sex was correctly assigned by our model was 88%.

BODY SIZE

After correcting for observer bias, the mean culmen length of male Dunlin in the Fraser Delta (37.0 ± 0.1 mm) was estimated to be about 0.2 ± 0.1 mm larger ($z = 1.3$, $P = 0.09$) than the mean for Bolinas (36.8 ± 0.1 mm). There was no difference between sites in female mean culmen lengths (40.6 mm, $z = 0$, $P = 0.5$).

DISCUSSION

Sex ratios of nonbreeding Dunlin were significantly male-biased in the Fraser River Delta, both overall (October–April) and during winter (December–February), but not more so than sites farther south. Buchanan et al. (1986) found an overall male bias similar to that of the Fraser

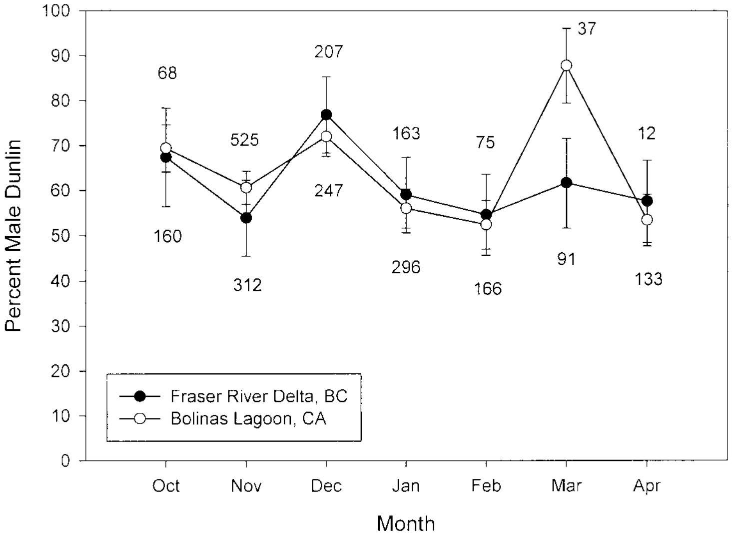

FIGURE 2. Monthly percent male Dunlin (including standard errors and sample sizes) for the Fraser River Delta, British Columbia, and Bolinas Lagoon, California (Fraser River Delta sample corrected for sex differences in habitat use).

Delta (62%) in Dunlin samples from several sites in Washington. Our data also show male biases in the Bolinas Dunlin population overall and in winter, findings supported by those of Page (1974). Since males predominate in the Fraser Delta, Bolinas, and in Washington, we must ask whether there is a sex ratio bias in the entire *C. a. pacifica* subspecies, and if not, then ask where are the remaining females during the nonbreeding season?

If there were a sex ratio bias favoring males in the entire *C. a. pacifica* subspecies, we would expect to find unmated males on the breeding grounds in summer or remaining on the wintering grounds during the breeding season, neither of which has been reported (Paulson 1993, D. Schamel pers. comm.). Alternatively, we might expect males to have higher survivorship than females, but this is not true for *C. a. pacifica* (Warnock et al. 1997, P. C. Shepherd, unpubl. data). We corrected for sex differences in habitat use in the Fraser Delta that would have resulted in a bias toward capturing more females. All else being equal, since smaller males are likely to be more maneuverable than females, we would expect to catch more females. The opposite is true, so a trapping sex bias does not account for our results.

The body-size and dominance hypotheses predict that we should find the remaining females north of the Fraser Delta. However, too few Dunlin winter north of the delta for this to account for the difference (Paulson 1993, Warnock and Gill 1996). These hypotheses also predict that we should find larger individuals in the Fraser Delta. There was some indication that this may have been true of male Dunlin ($P = 0.09$), but the statistical results were equivocal and we found no difference in female mean culmen length between sites. We therefore do not have convincing evidence, either within or among the sexes, to support the body-size or dominance hypotheses.

The arrival-time hypothesis predicts that we would find the remaining females south of Bolinas. We examined data from 25 *C. a. pacifica* skins from the Museum of Vertebrate Zoology at the University of California at Berkeley and 13 skins from the Natural History Museum of Los Angeles County. We found a 1:1 winter sex ratio in birds collected from a number of sites south of Bolinas over a number of years beginning in the 1890s. Small samples of Dunlin trapped in San Diego, California ($n = 25$) and La Paz, Mexico ($n = 5$) since 1989 were determined to be male-biased using our mixture model (B. Kus and R. Carmona, pers. comm.). There are sites south of Bolinas that support large numbers of Dunlin (Warnock and Gill 1996, Page et al. 1999), but the necessary data on population numbers and proportions of females are currently unavailable.

Within-latitude habitat segregation between the sexes does not appear to explain the male bias we found in the Fraser Delta and Bolinas Dunlin populations. Buchanan et al. (1986) suggested that such segregation might have occurred at two of their study sites in Washington. They also detected some variation in sex ratios among their four main study sites, although they still found an overall male bias. Radio-telemetry data collected in the Fraser Delta indicated that habitat segregation between the sexes occurred on a daily scale (P. Shepherd, unpubl. data), so we corrected for this in our analysis. Warnock et al. (1995) also found some habitat segregation between the sexes in Bolinas, but it was on a seasonal rather than a daily scale. They found that male Dunlin were more likely than females to make one-way, mid-season movements to agricultural and wetland habitats up to 140 km inland, and this difference is reflected in the month-to-month sex ratio results presented here.

We suggest one final possibility. Our results could reflect a latitudinal cline in sex ratio within two partially overlapping wintering populations, with males wintering north of females within each population (Fig. 3). This would produce what appears to be a weak cline over the species' range. Twenty-nine of 32 resightings of Dunlin marked with picric acid in the Yukon-Kuskokwim Delta (the more northerly breeding site) occurred in Canada and the northwestern United States, while 22 of 24 resightings of Dunlin marked on the Alaska Peninsula (the more southerly breeding site) occurred in California (R. Gill, pers. comm.). Thus, our data may reflect a latitudinal cline in sex ratio within each of two nonbreeding populations, with partial overlap obscuring the segregation within populations. This hypothesis predicts that we would find female-biased populations between southern Washington and northern California, and from southern California into Mexico. At present, the data required to test this hypothesis are not available. The Mexico data cited above neither support nor reject the hypothesis, since the sample sizes are very small.

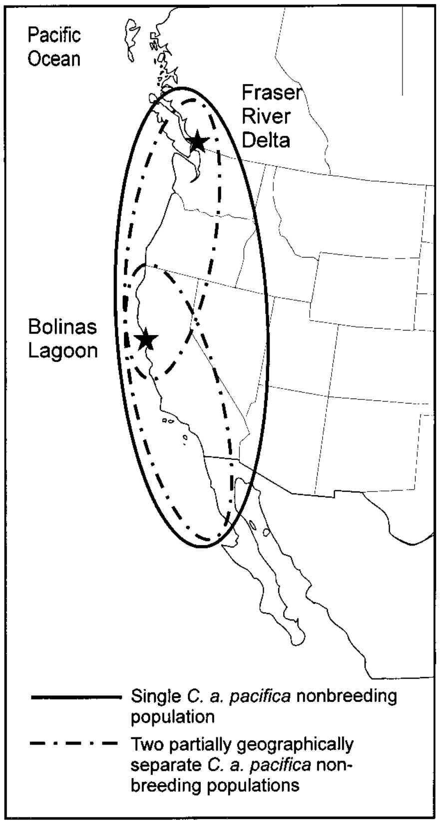

FIGURE 3. Hypothesized patterns of latitudinal clines in sex ratio (more males at higher latitude ends of each oval) in Dunlin wintering along the Pacific coast. Pattern 1 (solid line) may result if there is a latitudinal cline in sex ratio occurring in *C. a. pacifica* as a whole, and pattern 2 (dashed line) may result if there are latitudinal clines in sex ratio occurring in two partially geographically separate populations of *C. a. pacifica.*

The seasonal pattern of sex ratios (Fig. 2) is consistent with partially overlapping populations. The percentage of females was higher at both the Fraser Delta and Bolinas in November, perhaps reflecting the movement of females to sites farther south. Buchanan et al. (1986) found a comparable pattern at the site for which they had the most complete data set (Nisqually, Washington). The proportion of female Dunlin in the Fraser Delta increased in late winter and early spring, but at the same time the total numbers of birds increased (Shepherd 2001), suggesting that females moved into the delta in late winter and early spring. In March, when the number of birds in the Fraser Delta reached the spring maximum, the proportion of males once again increased. At Bolinas, the total numbers of Dunlin decreased along with the percentage of males in late winter and early spring (Warnock 1994). This could have been due to early northward movements of males (Paulson 1993), or disproportionate movements of males inland with the advent of heavy rains (Warnock et al. 1995).

We conclude that some form of latitudinal cline in sex ratio occurs in *C. a. pacifica.* However, additional data from the Oregon coast, southern California, and Mexico are required to determine the location of the missing females and to confidently document the pattern of clinal variation.

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