

## SEX RATIOS OF DUNLIN WINTERING AT TWO LATITUDES ON THE PACIFIC COAST<sup>1</sup>

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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

diferencias entre sexos en los patrones de movimientos estacionales. Ambas poblaciones presentaron un sesgo general hacia los machos (Fraser 5 61% machos, Bolinas 5 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 R<sub>1</sub>

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

calculated asymptotic standard errors for all estimates and report sex ratios as the percent of males  $\pm$  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 ( $\% \text{ ME} = 100\% [s_{\text{within}}^2 / (s_{\text{within}}^2 + s_{\text{among}}^2)]$ ).

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 per-

cent 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  $\pm$  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 duFis

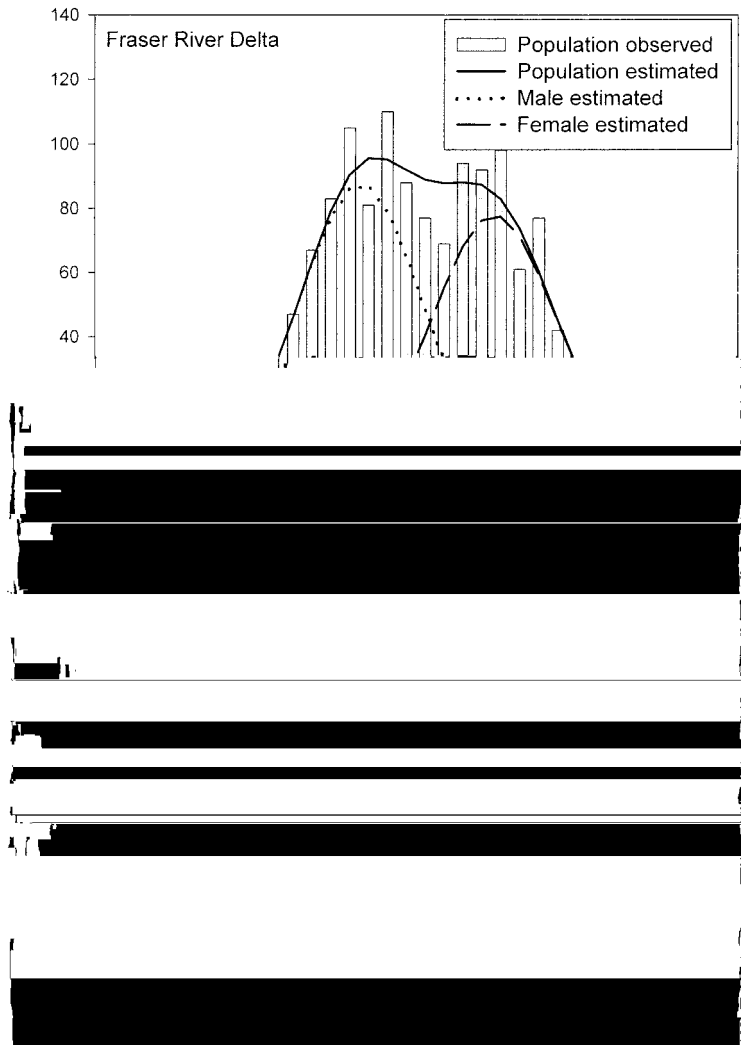


FIGURE 1. Culmen distribution of Dunlin (males, females, and overall population) from the Fraser River Delta, British Columbia, estimated using mist-netted and reference samples (observed), and from Bolinas Lagoon, California estimated using the mist-netted sample (observed) and Bayesian prior probabilities.

During winter (December through February), there were an estimated 65  $\pm$  9% males in the Fraser Delta and 62  $\pm$  3% males in Bolinas ( $z = 1.0$ ,

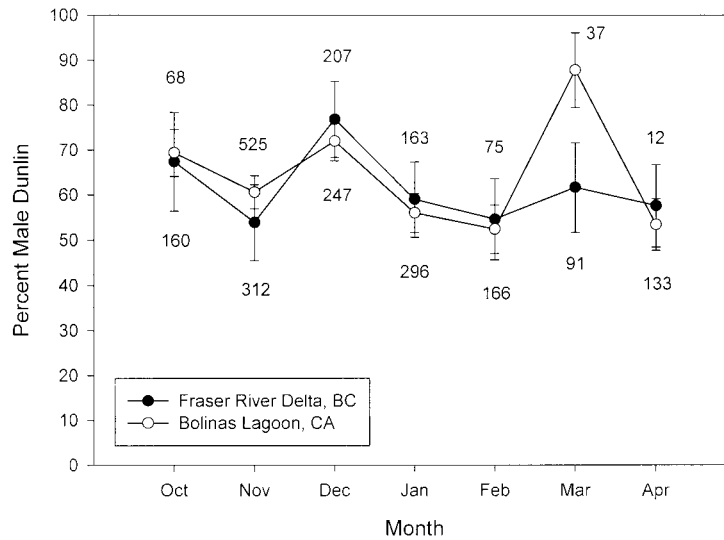


FIGURE 2. Monthly percent male Dunlin (including standard errors and sample sizes) for the Fraser River Delta, British Columbia, and Bolinas Lagoon, California (Fraser River Delta sample corrected for sex differences in habitat use).

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 ( $P \leq 0.09$ ), 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 pop-

ulation 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.

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

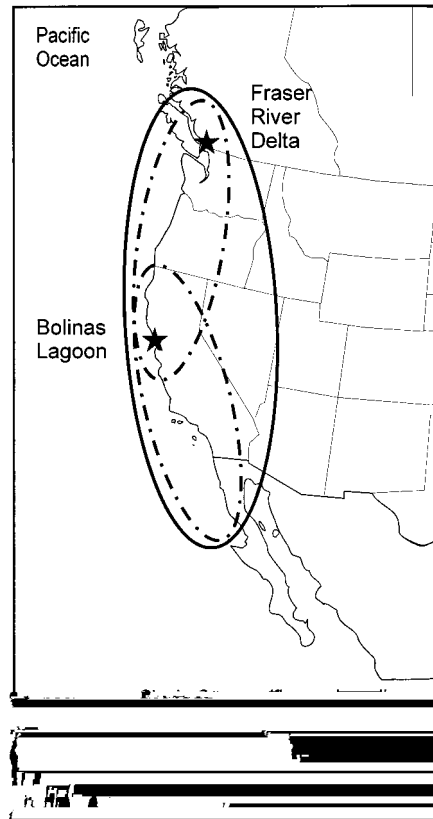


FIGURE 3. Hypothesized patterns of latitudinal clines in sex ratio (more males at higher latitude ends of each oval) in Dunlin wintering along the Pacific coast. Pattern 1 (solid line) may result if there is a latitudinal cline in sex ratio occurring in *C. a. pacifica* as a whole, and pattern 2 (dashed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

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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