

STRUCTURE OF A WINTERING DUNLIN POPULATION¹

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Abstract. We have documented structure on two different scales for the Dunlin (*Calidris alpina*) population wintering at Bodega Bay, California in 1986-1987. Within a night roost, significantly more juvenile birds were captured at the center vs. periphery between October and December. In addition, there was a significant difference in the mean size of birds among areas of the roost during November, with birds at the center being largest.

Structure also developed during the winter on a scale which separated the entire population at Bodega Harbor into two groups. In late winter, large numbers of Dunlins left the area late in the day and returned in early morning, apparently roosting elsewhere. As a result, the number of Dunlins at the night roost declined in winter much more than the daytime population size at Bodega Bay. These roughly crepuscular movements were not evident earlier, in the fall, and did not correspond closely to tidal cycles. The resultant fragmentation of the population into "resident" and "mobile" groups was reflected in physiological differences between groups. Those birds which remained in the harbor day and night (residents) weighed less, had lower amounts of body fat, and were delayed in molt schedule in March relative to (mobile) birds which left at night.

While the ecological significance of structure on both scales remains unknown, evidence from this and previous studies suggests that it may be a relatively common phenomenon with important implications for studies of avian populations.

Key words: Movement patterns; roost structure; molt schedule; physiological condition; Dunlin; *Calidris alpina*.

INTRODUCTION

There is abundant evidence that the dispersion of wintering shorebirds (suborder Charadrii) is not random with respect to age and sex. Latitudinal gradients and differences in the timing of migration by age and sex have been well documented for many species (Page et al. 1979, Myers 1981, Morrison 1984, Pienkowski and Evans 1984). Elements of spatial structure also emerge on much smaller scales. The Eurasian Oystercatcher *Haematopus ostralegus*, for example, is known to form feeding and roosting flocks whose age and sex composition differ over very short distances (Goss-Custard and Durrell 1984, Swennen 1984). It appears that these local oystercatcher populations are structured by social dominance, whereby larger and older birds in-

fluence the distribution, activities, diet, and condition of smaller and younger individuals.

Among shorebirds, various forms of spatial structure have been found within local populations of the Dunlin *Calidris alpina* (Have et al. 1984; B. Kus, pers. comm.), Bar-tailed Godwit *Limosa lapponica* (Smith 1975), Eurasian Curlew *Numenius arquata* (Townshend 1981), and Sanderling *Calidris alba* (L. M. Gordon and J. P. Myers, pers. comm.). The mechanisms that structure these populations may include age- and sex-related differences in dominance, experience, feeding efficiency, or vulnerability to predators. Here, we describe structure within a population of shorebirds that differs substantially from previous accounts.

STUDY SITE AND METHODS

Our primary study site was Bodega Harbor, located at Bodega Bay, California (Fig. 1). The harbor is approximately 320 ha in area, 70% of which is exposed during moderate low tides. A diverse group of invertebrate species occurs across the

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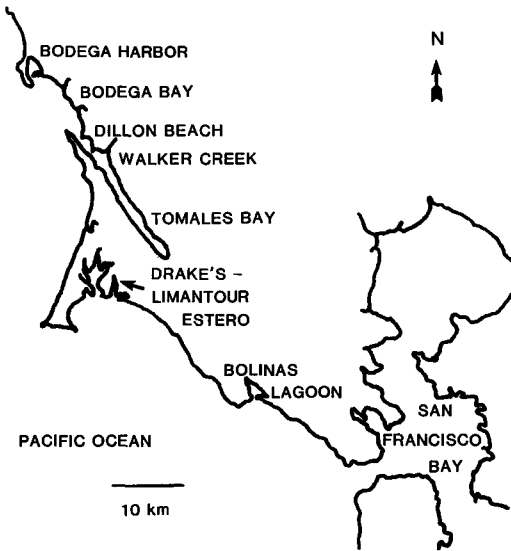


FIGURE 1. Map of California coast between Bodega Harbor and northern San Francisco Bay.

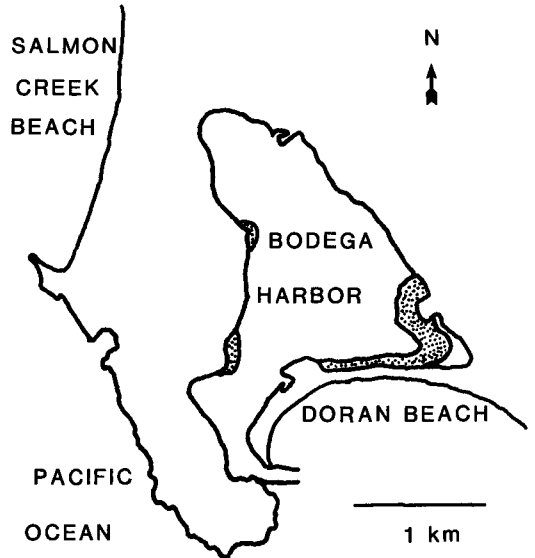


FIGURE 2. Map of Bodega Harbor. *Salicornia* marsh is shown as stippled area.

tidal sandflats and serves as the primary food resource for thousands of wintering shorebirds (for further detail, see Standing et al. 1975, Connors et al. 1981, Ruiz 1987).

The closest similar tidal habitat for most wader species from Bodega Harbor is at Estero Americana, Dillon Beach, and Walker Creek delta, roughly 4–12 km southeast, bordering Bodega Bay and Tomales Bay (Fig. 1). Farther south, other suitable habitat occurs at the southern end of Tomales Bay, within esteros on the Point Reyes Peninsula, and on tidal flats of Bolinas Lagoon and northern San Francisco Bay; these sites are 25–75 km from Bodega Harbor. To the north, no extensive coastal wetlands/sandflats occur until Humboldt Bay (280 km away).

Approximately every 2 weeks from July 1983 to June 1987 we counted the numbers of each shorebird species in Bodega Harbor within 1.5 hr of low tide. Counts were scheduled to coincide with low tides between 0.4–0.7 m above mean lower low water. During March 1987, we also counted Dunlins at 2- to 4-hr intervals from dawn until dusk; three dates were chosen to examine diurnal changes in abundance under different tidal regimes, and the flux of birds entering and leaving the harbor was monitored. Between two and four observers participated in counts, and four to eight individuals monitored bird movements in and out of Bodega Harbor.

During evening high tides, our observations

indicated that over 95% of the Dunlins present within Bodega Harbor and on the two outer beaches roosted in a small *Salicornia* marsh (stippled area in the southeast corner of the harbor, Fig. 2). We trapped birds at this roost site with mist nets from October to April 1985–1987. Nets were set at three locations (each ca. 150 m apart), and birds were flushed out of the immediate surrounding vegetation. All birds were weighed to the nearest 0.5 g and banded immediately at capture. The bill, wing, and tarsus were measured for each bird, and birds were aged as either juvenile (first-year) or adult (older than 1 year) based on plumage as described in Page (1974). Most birds were individually color-banded and released within the harbor. On some evenings, we held birds captive (in covered laundry baskets that were kept in dark rooms) and weighed them repeatedly throughout the night to determine rates of weight loss. Additional data were obtained from birds caught while feeding during the day in 1985–1986.

We determined the presence of color-marked individuals within Bodega Harbor throughout 1986–1987 by using 15–60× telescopes. From February to April 1987, an effort was also made roughly every 2 weeks to locate marked birds in Tomales Bay and local fields where other shorebird species had been observed previously. The pattern of pre-nuptial molt was recorded for both marked and unmarked birds in March, assigning

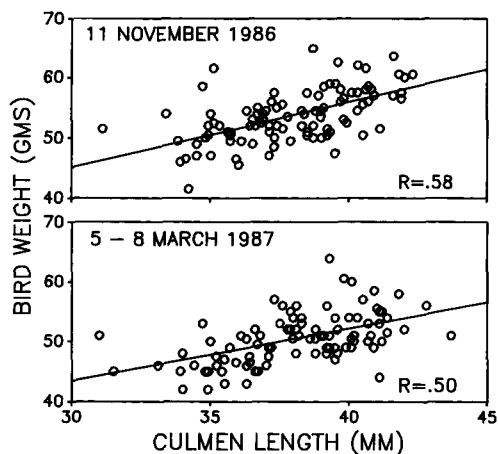


FIGURE 3. Regression of weight at capture vs. culmen length for Dunlins netted in Bodega Harbor on two separate nights.

a molt score based on the appearance of the darkening breast (0 for white underparts to 5 for a complete black patch).

Dunlins were also collected by shotgun while feeding on exposed tidal flats in Bodega Harbor during 1985–1986. These birds were used to examine diet, weight, and lipid content. For the latter, birds without their digestive tracts were dried at 60°C and extracted for 24 hr with hexane using a Soxhlet apparatus (Evans and Smith 1975); lipid content was calculated as the difference between dry weight before and after extraction.

We adjusted individual weights to take account of size variation among individual Dunlins; we used analysis of covariance (Sokal and Rohlf 1981) to standardize weights, using exposed culmen length as the independent variable. Dunlins are sexually dimorphic for size (Hayman et al. 1986), and the regression of weight on culmen length explained roughly 25% of the variation in weight among individuals (Fig. 3). Using a bill length (exposed culmen) of 38.5 mm to separate males ($\bar{x} = 37.02$, $SD = 1.73$, $n = 76$) from females ($\bar{x} = 40.37$, $SD = 1.70$, $n = 68$) collected at Bodega Bay, the fit of this regression appears similar for both sexes; thus, the two sexes were not treated separately in the analyses.

RESULTS

STRUCTURE WITHIN THE ROOST

Dunlins captured at the night roost in Bodega Harbor were not distributed in a random manner

among the three net sites. The middle net had the most juvenile birds on four of the five nights of trapping, comprising 62% of the entire sample as opposed to 23% and 39% at the outside nets (Table 1). A Friedman two-way analysis of variance indicates a significant difference (Friedman statistic = 6.40, $df = 2$, $P = 0.041$) in the age ratio of birds among nets when ranking the nets for each of the five nights; when pooling all five nights together, there was also a significant difference in age distribution among net sites ($\chi^2 = 8.71$, $df = 2$, $P < 0.02$).

For November 1986, there was a significant difference in the size of birds among nets ($F = 3.26$, $df = 2$, 92 , $P = 0.04$) with larger birds being most abundant at the center net. As already mentioned, Dunlins are sexually dimorphic for size, so these results suggest that juvenile females comprised a greater proportion of the birds at the middle vs. outside nets. During the 1985–1986 season, and later in the 1986–1987 season, too few birds were captured at some net sites for similar comparisons.

ACTIVITY PATTERNS

The seasonal abundance of Dunlins in Bodega Harbor, as determined by daytime counts at low tide, is shown in Figure 4. Individuals begin to return from breeding grounds in mid-October, the population size rapidly climbs to a peak of 3,000–6,000 individuals by late November, declining soon thereafter to approximately 1,500–2,000 birds until late March. The population declines through April, and the last individuals leave in early May.

At dusk, Dunlins coalesced into flocks of 10–500 birds which flew back and forth at the edge of the marsh vegetation, eventually breaking into smaller groups which entered the marsh and formed a dispersed roost. The nature of roost formation changed seasonally; in late winter, we observed flocks of 10–300 birds coalesce at dusk and then fly southeast out of the harbor from February to April of both years. Trapping became much more difficult during this period, because the roost size diminished out of proportion to changes in the daytime population and fluctuated unpredictably.

In March 1987, it appeared that a population of approximately 200–400 birds remained all day and night within Bodega Harbor, but most Dunlins present in the daytime roosted elsewhere, returning to the harbor on a daily basis. The

TABLE 1. Variation in the age structure of Dunlins among capture locations in Bodega Harbor at night. Shown are the ratios of juveniles (HY) to adults (AHY) for three net locations on each of five different nights from October to December 1986.

	Net 1		Net 2		Net 3	
	HY/AHY	(n)	HY/AHY	(n)	HY/AHY	(n)
28 October	0.56	(25)	0.93	(15)	0.69	(13)
11 November	0.62	(34)	0.77	(35)	0.44	(30)
13 November	0.58	(33)	0.67	(40)	0.64	(58)
25 November	0.39	(31)	0.58	(33)	0.72	(32)
23 December	0.67	(33)	0.83	(23)	0.75	(5)
All five nights	0.23	(156)	0.62	(146)	0.39	(137)

majority of birds in this latter group entered the harbor in large flocks near dawn, with smaller groups continuing to arrive until early afternoon; at that time, the process was reversed with small flocks leaving first, followed by a large exodus at dusk.

Figure 5 shows the diurnal fluctuation of Dunlin abundance at Bodega Harbor for 3 days. The magnitude of actual fluctuations, especially of evening departure, is underestimated due to major changes occurring at times of darkness or low light. Nevertheless, it can be seen that much of the movement in and out of Bodega Harbor is crepuscular and did not closely track the tidal cycle. In fact, birds were usually seen entering the harbor at dawn regardless of tidal condition, and it was not unusual to observe flocks of departing birds before and during midday low tides. Most of the arriving and departing birds flew out of Bodega Harbor, over Doran Beach, and followed the eastern shore of Bodega Bay, but we did not discover their destination during our visits to surrounding coastal and inland sites.

Dunlins often arrived in mixed flocks with Western Sandpipers (*C. mauri*). These mixed-species flocks exhibited crepuscular movement patterns that were similar to those of Dunlin

flocks in the spring at Bodega Harbor. These mobile groups of birds contained color-banded individuals, indicating that many birds had roosted in Bodega Harbor earlier in the year. Arriving birds usually joined a resident flock of conspecifics immediately and, therefore, could not be identified as to age or sex.

CONDITION OF BIRDS

The size-adjusted weights of Dunlins sampled during the day diverged from those at night as the 1985–1986 season progressed (Fig. 6A). From November to January, weights differed by only 1–2 g, but this difference increased to 5 g in Feb-

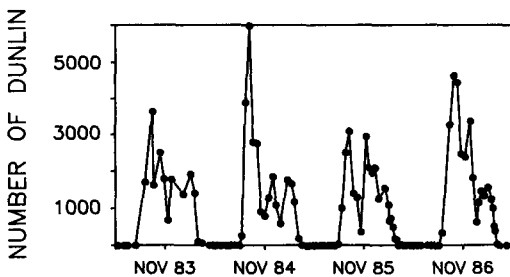


FIGURE 4. Number of Dunlins at Bodega Harbor on low-tide counts (1983–1987).

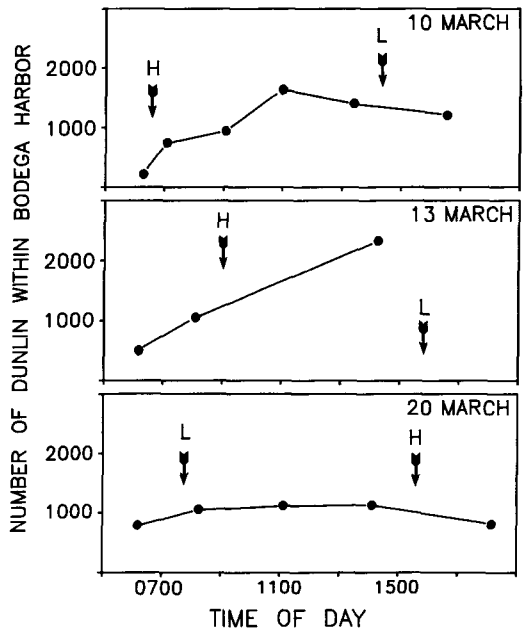


FIGURE 5. Diurnal variation in the number of Dunlins at Bodega Harbor for 3 days. Arrows indicate the times of low (L) and high (H) tides; first count on each day was taken at dawn.

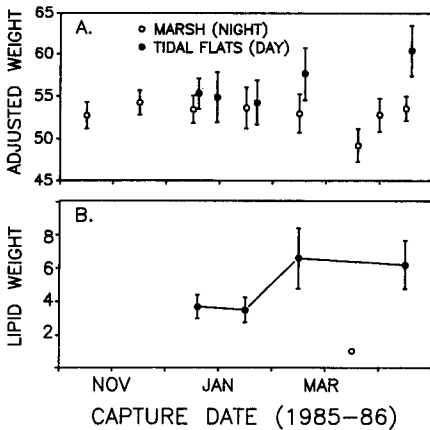


FIGURE 6. The adjusted weight (A) and lipid weight (B) of Dunlins from Bodega Harbor during the 1985-1986 season. For adjusted weights, the means and 95% comparison intervals are shown; the means and 95% confidence intervals are given for lipid weights. Open circles denote birds netted at night, and closed circles represent daytime captures. [Sample sizes for each figure from left to right are as follows: Above = 36, 43, 34, 28, 10, 15, 13, 17, 9, 23, 23, 43, 9; Below = 18, 8, 8, 9, 8.]

ruary and to 7 g by April; in the latter comparison, this represents a significant difference (ANCOVA, $P < 0.05$) despite the small sample size.

Although lipid data are not available for day and night samples on the same date, data in Fig-

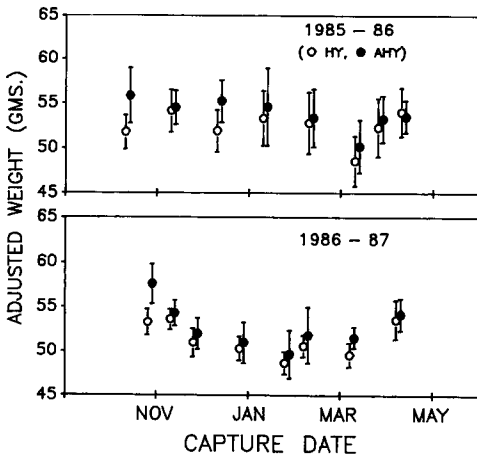


FIGURE 7. Adjusted weights for adult and juvenile Dunlins netted from 1985 to 1987 at Bodega Harbor. The mean and 95% comparison interval is shown separately for adults (AHY) and juveniles (HY) on each sampling date. [Sample sizes for each figure from left to right are as follows: Above = 26, 10, 17, 26, 17, 16, 10, 5, 8, 9, 12, 11, 9, 14, 15, 30; Below = 37, 16, 59, 39, 30, 25, 42, 15, 39, 11, 53, 8, 44, 53, 17, 24.]

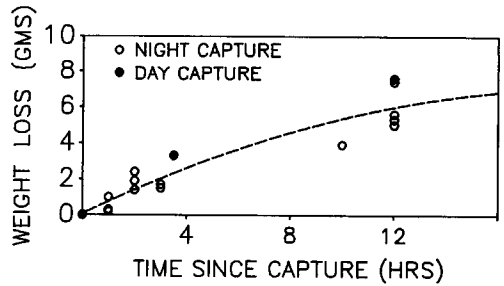


FIGURE 8. Rate of weight loss for Dunlins captured at night (open circles) and during the day (closed circles). The dashed curve represents a least squares regression for all points.

ure 6B indicate that the differences observed in body weight actually reflect large differences in fat reserves: a 7- to 10-g difference in wet weight for day vs. night samples was accompanied by a fourfold difference in fat reserves.

The demographic composition of birds from day vs. night collections appeared very similar, such that age or sex does not explain group differences. Since the regression of size on weight does not appear different for males and females (Fig. 3), sex is essentially taken into account when standardizing for size in the analysis of covariance. That age is not responsible for observed differences is seen in Figure 7, as adult birds were only slightly heavier than juveniles.

It also seems that diurnal weight fluctuations cannot explain such large differences. Importantly, the magnitude of day vs. night weight differences was small for three consecutive samples and then increased with no changes in the site or time of collection. As the night sample was collected routinely 2-3 hr after birds had stopped feeding, the rate of weight loss in captive birds was not rapid enough to account for these differences (Fig. 8). The weight loss of birds captured during the day and night suggests that 1-2 g may be lost between sample times (see also Lloyd et al. 1979, Pienkowski et al. 1979, Davidson 1981); we suspect this is an overestimate, because the stress and elevated temperature involved in captivity may accelerate rates of weight loss.

MOLT SCHEDULE

For the period of 12-16 March 1987, the molt scores of marked and unmarked Dunlins feeding in Bodega Harbor are summarized in Figure 9. The distribution of molt scores for unmarked birds was bimodal with most birds relatively ad-

vanced in molt. Marked birds observed under the same conditions had a unimodal distribution for molt score which corresponded to the lower mode for the unmarked birds. Most marked birds had been recently trapped in the night roost, while unmarked birds included both resident Dunlins and birds from the mobile population.

Using Dunlins that were marked and released at Walker Creek, a similar comparison of marked vs. unmarked birds indicated that both were unimodal for a high molt score at this site (Fig. 9); this was also the case for marked and unmarked birds at Bolinas Lagoon (N. Warnock and G. Page, unpubl. data). It is apparent from the similarity in molt schedules between marked and unmarked Dunlins at these nearby sites that the differences between Bodega Harbor groups were not simply an artifact of being marked.

DISCUSSION

We have presented data that indicate spatial structure in a population of shorebirds on two scales. Within night roosts, Dunlins were distributed nonrandomly with respect to age and sex. To our knowledge, structure at a roost has only been reported once for the Charadrii. In an unpublished thesis, Whitlock (1979, as cited by Ydenberg and Prins 1984) found that adult Common Redshanks (*Tringa totanus*) displaced juveniles from downwind positions during the day. Such roost structure is probably widespread among shorebirds. It is well-known for other avian groups (Orians 1961; Meanly 1965; Swingland 1977; Caldwell 1981; Weatherhead 1983, 1985), and is thought to arise when particular positions are more advantageous than others in reducing the risk of predation or heat loss, with access to preferred sites being mediated by age- or sex-biased dominance (see especially Swingland 1977 and Weatherhead 1983). We doubt that Dunlins' positions within their dispersed roost at Bodega Harbor carry meaningful costs or benefits with respect to thermal regime, and we have no data on the relative predation risk by position. It seems unlikely, however, that predation risk was higher at the center of the roost area, or that the juvenile birds that occurred there would have aggressively displaced older individuals. Thus, such explanations do not seem applicable here.

While we cannot explain the structure observed within the roost, we recognize its practical importance for biologists attempting to obtain

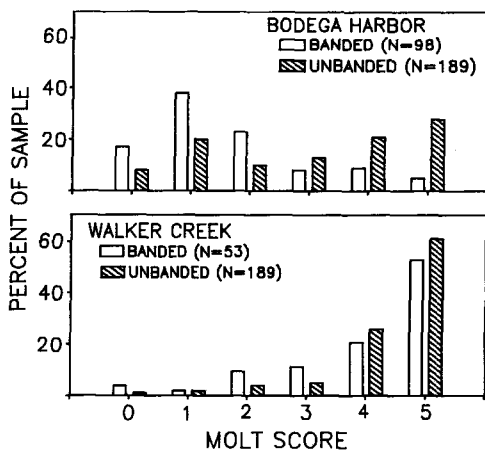


FIGURE 9. Frequency distribution of molt scores for banded and unbanded Dunlins at Bodega Bay (above) and Walker Creek (below). [See text for explanation of molt scores.]

population data from limited sampling. In the present case, even relatively large sample sizes ($n > 100$) gave us markedly different age ratios depending on net location within the roost (Table 1). Such structure in any population will require careful, spatially distributed, sampling schemes to gain meaningful estimates of population data.

Dunlins that fed in Bodega Harbor during the day also exhibited structure, dividing into two groups. Activity data show that approximately 75% of the Dunlins left the harbor at night in March 1987. A comparison of weights and molt schedules indicates that day vs. night samples came from two statistically different groups, suggesting that respective groups were somewhat cohesive without much interchange between them. Furthermore, we believe that the collection of daytime birds may actually have underestimated weight differences between groups, due to the possible presence of resident birds (of low weight) in daytime collections.

The Dunlins feeding in Bodega Harbor from November to January appeared to all remain and roost locally at night, although a quantitative confirmation of this pattern (such as the dusk-dawn observations made in March) has not yet been made. Nonetheless, the relative lack of Dunlins roosting at Bodega Bay in March, the sighting of many previously marked birds in the mobile flocks upon arrival, and the improbability of missing an exodus of 75% of the Dunlin population each day offer compelling evidence

for the change in roosting patterns between early and late winter.

Although crepuscular movement such as that exhibited by the mobile group is relatively common for charadriiforms at inland sites (Hamilton 1959, Swingbrood 1964, Brooke 1972, Atkinson 1976) and for passeriforms (Aldous 1944, French 1967, Davis and Lussenhoop 1970, Bray et al. 1975, Weatherhead 1985), it appears unusual for coastal waders, whose movements are usually related to tidal cycle and the accompanying changes in food availability (Burger et al. 1977, Connors et al. 1981, Burger 1984, Myers 1984). For the few individual days examined quantitatively, an association with tidal fluctuations was weak, if present at all; on many other days, we observed Dunlin flocks leaving Bodega Harbor at or before low tides. Nevertheless, body condition and molt schedule data indicate that differences existed in the food resources experienced by mobile vs. resident birds, since mobile individuals were in better condition despite a presumably greater energy expenditure in daily flights. For this reason, movement schedules may be a response to superior food resources that became available elsewhere on a schedule somewhat independent of the tidal regime at Bodega Harbor. While it is possible that a lag in the timing of tides at alternate coastal sites makes movement more profitable than remaining in Bodega Harbor, this too should be predictable based upon tidal cycle and would not result in the consistent crepuscular timing of movement.

We surmise that the mobile Dunlins were moving inland on a daily basis in late winter to feed in fields and nontidal drainage systems to supplement their food intake, as observed in other wader species (Atkinson 1976, Elphink 1979, MacLennon 1979, Townshend 1981, Goss-Custard and Durrell 1984). Occasional inland sightings of Marbled Godwits (*L. fedoa*) that were color-marked at Bodega Harbor and of unmarked Dunlins in flocks, and the absence of coastal sightings of Bodega Harbor birds despite a substantial search effort in Tomales Bay and Bolinas Lagoon, lend support to this possibility. Furthermore, the activity pattern of insect and annelid prey in this habitat may be nocturnal or crepuscular (Gerard 1967, Dugan 1981) and thus responsible for the observed timing of shorebird movement.

In April 1985, an unusually large recruitment of Dungeness crabs, and their subsequent

predation on tidal invertebrates, caused a dramatic decline in the abundance of shorebird prey in Bodega Harbor (Ruiz 1987). It is not clear whether the existence and/or size of the mobile group of Dunlins is a response to the resultant poor food resources. For example, Townshend (1981) has shown that in the Eurasian Curlew population at the Tees Estuary, United Kingdom, a small subgroup with a strong male bias regularly used nearby fields to feed, and during severe weather, when prey availability was reduced, these birds returned to the estuary until the weather relented. As utilization of such alternate habitat for feeding appears widespread (as above), it seems clear that many species behave like the Eurasian Curlew with some individuals specializing in the use of alternate habitat and others using it only opportunistically. Thus, the situation at Bodega Bay may simply represent an extreme example of opportunism in response to prolonged prey depletion.

While we observed similar population structures to develop in the seasonal movement patterns of both Dunlins and Western Sandpipers, no comparable data are available prior to the crab recruitment for these species. It is interesting, however, that other species exhibited a qualitatively similar pattern both before and after this event. From July to November/January 1983–1987, Marbled Godwits roosted at night within the harbor. After midwinter, the entire roost flock departed from the harbor soon after forming at dusk, flying south in the same direction as the departing Dunlins and returning at dawn. We observed a similar seasonal pattern for Black-bellied Plovers (*Pluvialis squatarola*), Willets (*Catoptrophorus semipalmatus*), and Semipalmated Plovers (*Charadrius semipalmatus*). The fact of crepuscular movement for other species before and after the crab settlement event suggests that movement (and perhaps structure) of the Dunlin population is a regular component of Dunlin ecology at Bodega Harbor regardless of annual changes in food conditions.

As food resources continue to recover in Bodega Harbor following the 1985 crab invasion, we can determine whether the formation of subgroups in the Dunlin population is a temporary, opportunistic response to food resources or a relatively persistent feature. The age and sex composition of the mobile group, though elusive, may offer clues about the mechanism of formation and the ecological and evolutionary sig-

nificance of such complex local population structure. Further interpretation of this phenomenon must await new data along these lines. Nevertheless, it is clear that spatial structure exists on several levels within shorebird populations and must be given serious consideration in the sampling design and interpretation of ecological studies.

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