

## ROOSTING BEHAVIOR OF PREMIGRATORY DUNLINS (*CALIDRIS ALPINA*)

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**ABSTRACT.**—We studied roosting behavior of Dunlins (*Calidris alpina*) during late summer along the coast of the Yukon-Kuskokwim Delta, Alaska, in relation to tidal cycle, time of day, time of season, and occurrence of predators. Within Angyoyaravak Bay, peak populations of 70,000–100,000 Dunlins occur each year. The major diurnal roost sites were adjacent to intertidal feeding areas, provided an unobstructed view of predators, and were close to shallow waters used for bathing. At one site studied intensively, roosting flocks formed at high water consistently during the day but rarely at night. On about 75% of the days, Dunlins also came to the roost at dawn and dusk when the tide was low. The size of the roosting flock, the length of time birds spent at the roost site, and behavior at the roost site were highly variable throughout the season and significantly affected by both tide level and time of day. Roosting behavior changed significantly between early and late August, as Dunlins underwent heavy wing and body molt, and began premigratory fattening. The reaction of Dunlins to potential predators, the formation of roosting flocks in response to light cues, and seasonal changes in social behavior at the roost site suggested that communal roosting behavior may be related not only to the risk of predation but also to behavior during migration. Received 9 July 1990, accepted 5 August 1991.

FEW investigators have examined the roosting behavior of shorebirds in light of either the physical factors that govern it or the benefits that might accrue (for review, see Myers 1984, Hockey 1985). Postbreeding Dunlins (*Calidris alpina*) roost in large flocks and feed on expansive intertidal mudflats of the Yukon-Kuskokwim Delta, Alaska, from July until early October (Holmes 1971, Gill and Handel 1990). At this time they are in transition from the breeding period, during which they defend dispersed nesting and feeding territories (Holmes 1966a, b, 1970, Pitelka et al. 1974), to the wintering period, during which they are highly social, and most commonly feed and roost in flocks along the coast (Storer 1951, Page 1974, Page and Whitacre 1975, O'Connor 1981, Brennan et al. 1985, Ruiz et al. 1989).

While on the Yukon-Kuskokwim Delta, Dunlins complete prebasic molt (Holmes 1971) and prepare for a transoceanic migration to wintering areas in southeastern Asia and California (Gill and Handel 1990, in prep.). We expected that their feeding and roosting schedule would be dictated primarily by physical factors, such as the tidal cycle, that affect the profitability of foraging (Heppleston 1971, Prater 1972, Burger et al. 1977, Hartwick and Blaylock 1979, Kelly and Cogswell 1979, O'Connor 1981, Zwartz et

al. 1990). We examined the patterns of formation and dispersal of roosting, premigratory Dunlin flocks to determine what factors might influence roosting behavior during this important part of their annual cycle.

### METHODS

*Behavior of roosting flocks.*—Between 2 August and 19 September 1980 we studied Dunlins at the mouth of the Tutakoke River, Alaska (61°15'N, 165°38'W). This river empties into Angyoyaravak Bay, a large, shallow bay covering extensive mud and sand flats on the central Yukon-Kuskokwim Delta (Fig. 1). Adjacent coastal meadows are characterized by numerous shallow ponds and salt-tolerant vegetation (e.g., *Carex ramenskii*, *Elymus arenarius*, *Potentilla egedii*, *C. rariflora*, and *Calamagrostis canadensis*). Coastal habitats have been described in detail by others (Harris 1966, Jackson 1981, Holmes and Black 1973).

From a 3-m observation tower at this site, we monitored the formation, behavior, and dispersal of one or more daytime roosting flocks on 26 days, and noted the presence or absence of roosting flocks on an additional 13 days. During systematic censuses we counted all birds at the roost every 30 min and recorded instantaneous behavior (Altmann 1974) for each individual when the flock was small (usually <500 birds). In larger flocks we subsampled behavior by selecting two to eight groups of 100 birds without replacement from different parts of the flock until an average of 22% of the flock was sampled (range = 8–

64%). When distinct parts of the flock were engaged in different behaviors, we sampled each part of the flock separately. Behaviors were categorized as: flying, running, feeding, bathing, preening, standing, or sleeping (resting with bill tucked into back or scapular feathers). Between counts we recorded the size of all arriving and departing flocks and intrusions of potential predators.

On seven nights we checked to determine if Dunlins were present at the roost site. On one night we went by boat to outer mudflats to see if Dunlins were feeding.

*Aerial surveys.*—Eleven aerial surveys were conducted at high water along the coast of Angyoyaravak Bay on: 7 July 1977; 16 July and 6 September 1978; 12 July, 2 August, 27 August, 20 September and 30 September 1979; 7 September and 4 October 1980; and 3 October 1981 (for details, see Gill and Handel 1990). Two observers recorded all shorebirds and plotted the locations of all roosts. Because species of small sandpipers could not easily be distinguished from the air, we estimated their relative seasonal abundance from ground counts (see Gill and Handel 1990).

*Availability of intertidal habitat.*—A pole calibrated at 3-cm intervals was placed on the bank of the Tutakoke River with the zero datum at the estimated height of the mean lower low water in the bay. From this we recorded tide height at the start of each 30-min ground count to correlate movements of birds to and from the roost site with availability of intertidal habitats. To estimate the area exposed to birds feeding at various tide levels, we mapped several points at the mud/water interface at 0.6-m tide increments. We then used aerial photographs to draw approximate contour lines and measured (by planimeter) the amount of mudflats within each contour interval.

*Data analysis.*—The daylight period was defined as 30 min before sunrise to 30 min after sunset, and was divided into three equal time periods each day. Daylight decreased steadily throughout the postbreeding season from about 18.0 h on 2 August to about 14.5 h on 19 September 1980 (U.S. Department of Commerce 1979). Each roosting flock was assigned to the morning, midday or evening period according to when flock size peaked. Similarly, each flock was classified as reaching its peak size nearer to high or low water. Median arrival time and median departure time were defined for each flock as the time when 50% of the peak flock had arrived at or departed from the roost, respectively. We defined the mean duration of roosting for each flock as elapsed time between median arrival and median departure time. The study period was divided into four 10-day intervals: 1–10 August, 21–30 August, 1–10 September, 11–20 September. Differences in peak size were tested with ANOVA in relation to the following factors: (1) seasonal period, (2) daylight period, and (3) high water vs. low water. Mean duration of roosting flocks was tested with multiple linear regression for significant relationships with

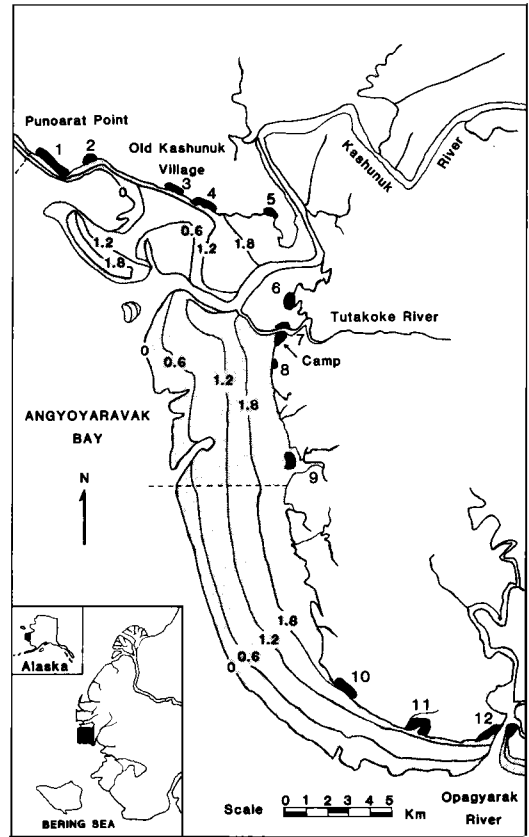


Fig. 1. Location of Tutakoke River study site within Angyoyaravak Bay on central Yukon-Kuskokwim Delta, Alaska. Approximate topography of intertidal flats shown in 0.6-m contour intervals. Area between dashed lines mapped from ground; remainder derived from aerial photography. Dark, shaded areas show major roost sites used by Dunlins during 11 aerial surveys between July and September from 1977–1981. Numbered roost sites cross-referenced in Table 1 and Figure 3.

date, time of day, height of high water, predicted height of previous and following low waters, time after sunrise, and time before sunset.

We tested the proportions of birds engaged in each behavior within each flock, summed over all 30-min counts, with Kruskal-Wallis ANOVA to determine if behavior varied among flocks with: (1) seasonal period, (2) daylight period, or (3) high water vs. low water. For flocks formed at high water, the proportions of birds engaged in each behavior were also tested with Kruskal-Wallis ANOVA to see if roosting behavior varied significantly with time in relation to high water. Flocks of fewer than 100 birds were excluded from all behavioral analyses.

To assure a valid characterization of Dunlin be-

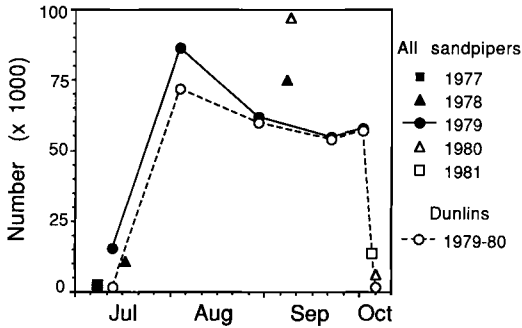


Fig. 2. Seasonal and interannual variation in number of Dunlins and other small sandpipers using Angyoaravak Bay on 11 aerial surveys during post-breeding period. Proportion of sandpipers using bay that were Dunlins estimated from ground censuses throughout 1979 and in October 1980.

havior at roosts during staging, we: (1) sampled at several series of tides throughout the season; (2) made several all-day counts to examine the interaction of tide height with time of day; and (3) observed behavior at a second major roost within the bay for comparison. A few limitations should be noted. We could not collect data from the early staging period (late July) or just before the birds' migration (late September). We also were unable to conduct simultaneous ground counts at major roosts within the bay to examine interactions during a given tidal cycle. Finally, we were not equipped to monitor behavior and locations of Dunlins at night.

All statistical analyses followed recommendations by Sokal and Rohlf (1981) and Conover (1980), using SPSS (1990) software. Values are presented as means  $\pm$  standard errors unless stated otherwise. Significance testing was done at the 0.05 level.

## RESULTS

**Tidal cycle.**—Tides at Angyoaravak Bay were semidiurnal and occurred about 1 h later each day (U. S. Department of Commerce 1979). Height of high water averaged  $2.1 \pm 0.04$  m (range = 1.6–2.7,  $n = 39$ ) above zero datum and did not vary significantly with time of day. Lower low water always occurred at night or in the morning and averaged  $-0.3 \pm 0.33$  m (range =  $-0.7$  to  $0.2$ ,  $n = 10$ ). Higher low water occurred at midday or in the evening and averaged  $0.4 \pm 0.06$  m (range = 0.0–0.9,  $n = 18$ ). About 130 km<sup>2</sup> of mud and sand flats were exposed at the zero datum (mean lower low water), and the amount of exposed intertidal decreased linearly at a rate of about 50 km<sup>2</sup>/m of

TABLE 1. Size and frequency of occurrence of roosting flocks of small sandpipers at 12 primary roost sites in Angyoaravak Bay during 11 aerial surveys from mid-July to early October, 1978–1981 (see Fig. 1 for location of roost sites).

| Site | Number of surveys when flock present | Size of flock when present |              |
|------|--------------------------------------|----------------------------|--------------|
|      |                                      | $\bar{x} \pm SE$           | Range        |
| 1    | 9                                    | 11,700 $\pm$ 4,000         | 500–40,000   |
| 2    | 6                                    | 6,100 $\pm$ 4,300          | 300–27,500   |
| 3    | 4                                    | 12,100 $\pm$ 4,800         | 4,500–26,000 |
| 4    | 10                                   | 11,600 $\pm$ 3,900         | 600–32,500   |
| 5    | 7                                    | 1,800 $\pm$ 1,400          | 25–10,000    |
| 6    | 2                                    | 4,000 $\pm$ 3,000          | 1,000–7,000  |
| 7    | 10                                   | 5,100 $\pm$ 2,600          | 200–21,500   |
| 8    | 2                                    | 1,620 $\pm$ 1,380          | 240–3,000    |
| 9    | 6                                    | 1,650 $\pm$ 570            | 120–3,500    |
| 10   | 10                                   | 3,000 $\pm$ 1,100          | 160–10,000   |
| 11   | 5                                    | 2,100 $\pm$ 830            | 350–4,500    |
| 12   | 11                                   | 2,200 $\pm$ 620            | 70–6,500     |

tide height (Fig. 1). All intertidal flats were covered at a tide level of 2.6 m.

**Seasonal use of roost sites in Angyoaravak Bay.**—During 11 aerial surveys of Angyoaravak Bay between mid-July and early October 1978–1981, populations of small sandpipers peaked in August and early September each year at 75,000 to 100,000 birds (Fig. 2). From ground censuses during 1979, we (Gill and Handel 1990) found that most of the sandpipers were Dunlins, Western Sandpipers (*Calidris mauri*), and Rock Sandpipers (*C. pillocnemis*). The number of Dunlins estimated using the bay in 1979 rose from about 1,700 in mid-July to a peak of about 72,000 in early August. By late August, numbers had declined to about 55,000 birds, which remained until our departure in late September (Fig. 2). By early October of both 1980 and 1981, most small sandpipers had departed. Only about 1,800 Dunlins remained in the bay during a ground count on 4 October 1980 (Fig. 2).

Twelve sites within the bay hosted roosting flocks of at least 2,000 small sandpipers during one or more aerial surveys (Fig. 1). Seasonal use of individual sites was highly variable in terms of both size of roosting flock and frequency of occurrence during the surveys (Table 1). However, combining sites into the following four general areas of the bay produced more consistent counts: Punoarat Point area (sites 1–2); northern shore near Old Kashunuk Village (3–5); central part of the bay around the Tutakoke

River (6-9); and southern part of the bay near the Opagarak River (10-12). Roost sites along the north edge of the bay at Punoarat Point and near Old Kashunuk Village were used consistently by the largest numbers of sandpipers (Fig. 3). Up to 80,000 sandpipers were found in these areas in flocks of up to 40,000 birds. The main roost sites were along cut banks of the bay, where the substrate was solid and sparsely vegetated. Shallow ponds adjacent to the roosting areas were used for bathing.

We recorded up to 30,000 sandpipers in the central part of the bay roosting in flocks of up to 21,500 birds, mainly at the mouth of the Tutakoke River (Fig. 3). There birds roosted mainly on mudflats adjacent to graminoid meadows. On windy days Dunlins sometimes took shelter along the banks of sloughs, in small channels, or behind vegetated islands on the mudflats. Up to 3,500 birds roosted on dry, exposed mudflats at the mouth of a slough 6 km south of the Tutakoke River (Fig. 1, site 9). The three roost sites at the southern edge of the bay near the Opagarak River collectively hosted up to 16,000 sandpipers (Fig. 3). The areas used for roosting were cut banks similar to those at the north end of the bay.

*Use of Tutakoke River roost site.*—During 1980, Dunlins roosted at the mouth of the Tutakoke River on 38 of 39 days we were present. A roosting flock formed during 43 of the 44 (98%) high-water cycles checked during daylight hours, but during only 2 of 6 (33%) high-water cycles checked at night (Table 2). The size of the roosting flock during diurnal high tides averaged  $3,143 \pm 351$  birds ( $n = 28$ ) and did not vary significantly with time of day. On the two nights we found Dunlins roosting at the site, we heard large numbers of them vocalizing and estimated that several thousand birds were present. During the day, the amount of time during which Dunlins were present at the roost site varied, ranging from 2.0 to 10.0 h over the 28 high-water cycles we monitored. The amount of time between median arrival and median departure was much less variable and averaged  $3.4 \pm 0.23$  h (it did not vary significantly with time of day; Table 2). Between early August and late September, the average time between median arrival and median departure at the roost site during high-water cycles declined steadily from 4.1 to 3.0 h. This seasonal decline in duration with date was nearly significant statistically ( $r = -0.36$ ,  $P = 0.059$ ). The duration at

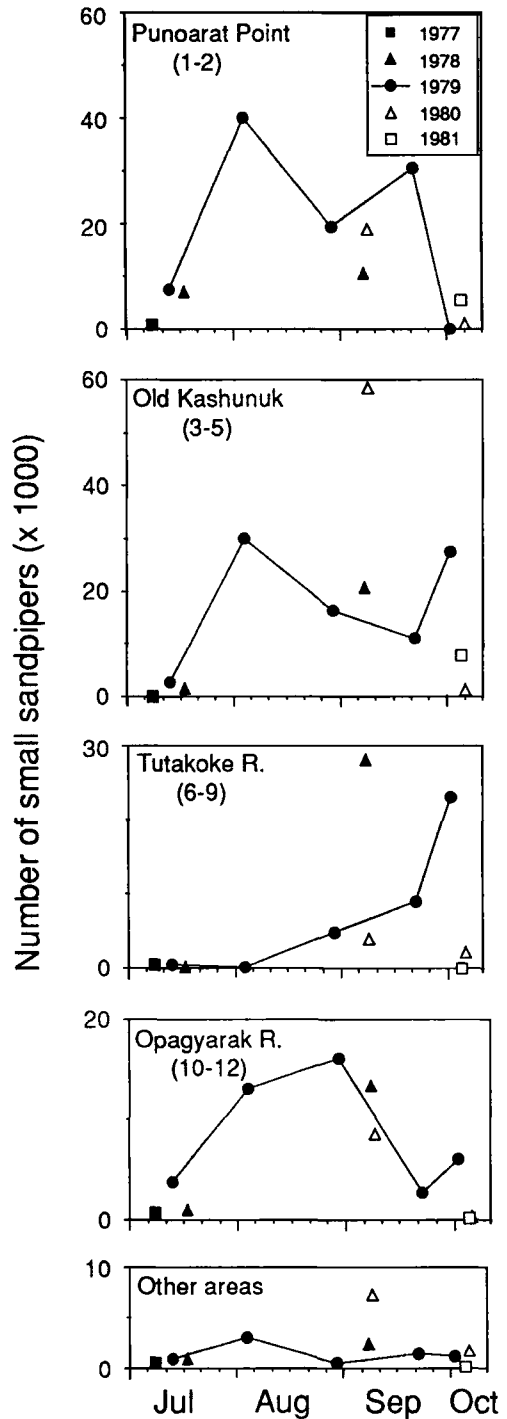


Fig. 3. Seasonal and interannual variation in number of postbreeding small sandpipers at 12 primary roost sites within four areas (as well as "other areas") of Angyoaravak Bay. Locations of particular roost sites (referenced by numbers in parentheses) shown on Figure 1.

TABLE 2. Occurrence of Dunlins at the Tutakoke River roost site at different tide stages and times of day.

| Tide stage and time of day | Percent of days roost occupied ( <i>n</i> ) <sup>a</sup> | Peak size of flock<br>$\bar{x} \pm SE$ ( <i>n</i> ) | Hours at roost <sup>b</sup><br>$\bar{x} \pm SE$ ( <i>n</i> ) |
|----------------------------|--|---|--|
| High water                 |  |   |  |
| Morning                    | 100% (13)  | 3,732 $\pm$ 798 (8)                                 | 3.2 $\pm$ 0.57 (8)   |
| Midday                     | 94% (16)   | 2,578 $\pm$ 634 (10)                                | 3.6 $\pm$ 0.38 (10)  |
| Evening                    | 100% (15)  | 3,236 $\pm$ 414 (10)                                | 3.4 $\pm$ 0.28 (10)  |
| Night                      | 33% (6)  | Undetermined  | Undetermined   |
| Low water                  |  |   |  |
| Morning                    | 78% (27)   | 1,103 $\pm$ 315 (10)                                | 1.3 $\pm$ 0.22 (9)   |
| Midday                     | 0% (18)  | —   | —  |
| Evening                    | 75% (20)   | 2,314 $\pm$ 559 (9)                                 | 1.6 $\pm$ 0.22 (9)   |
| Night                      | 0% (1)   | —   | —  |

<sup>a</sup> *n* = number of days roost site checked for presence of roosting flock.

<sup>b</sup> Number of hours between median arrival time and median departure time.

high-water roosts was slightly more strongly correlated with height of high water ( $r = 0.38$ ,  $P < 0.05$ ), which itself was highly negatively correlated with date ( $r = -0.60$ ,  $P < 0.01$ ). No other variables, including height of previous or following low water, time of day, time after sunrise, or time before sunset, contributed significantly towards explaining variation in time spent at the roost site.

Roosting flocks also formed at the Tutakoke River site during 78% of the morning low-water cycles we checked ( $n = 27$ ), but the flocks were significantly smaller ( $P < 0.01$ ) than those formed during morning high-water cycles (Table 2). Dunlins were present during low water from 1.5 to 7.5 h. The time at the roost between median arrival and median departure averaged  $1.3 \pm 0.22$  h, significantly less than the time Dunlins spent at the roost in the morning when the tide was high ( $P < 0.05$ ). A similar phenomenon occurred during evening low-water cycles, although these flocks were not significantly smaller than those that formed during evening high water (Table 2). We never found Dunlins at the roost during low-water periods at midday ( $n = 18$ ) or at night ( $n = 1$ ).

At 2300 on 23 August, when there was no discernible moonlight, we went by boat to mudflats at the mouth of the Tutakoke River on a receding tide to see if Dunlins fed at night. A flock of 4,500 Dunlins, which had been at the Tutakoke roost site during high water, had departed by 2230. On the mudflats we heard Dunlins calling, and we spotlighted several that were feeding. We heard several others calling as they flew past to outer mudflats as the tide receded.

Observations at the roost at Punoarat Point

confirmed that the patterns of roost formation and dispersal we observed at Tutakoke were not unique. At Punoarat Point large flocks formed on all six diurnal high-water cycles that occurred when we were there. We also recorded them twice at dawn and once at dusk during low water. Dunlins did not roost at Punoarat Point during high water on either of two nights.

*Formation and dispersal of roosting flocks.*—The timing of formation of roosting flocks varied greatly from day to day, but was strongly influenced by both tide level and daylight. On days when high water occurred in the morning and evening, roosting flocks formed during the two high-water cycles, and no Dunlins were present during the midday low water. Use of the roost site varied over a typical four-day period in early September (Fig. 4). During this period, the timing of high water shifted from the morning and evening to midday and night. At all times of day, peak occupation of the roost site usually occurred just before high water. Arrival during morning high-water cycles was more closely related to the timing of sunrise than to tide level. As the morning high water peak shifted later each day, the time spent by Dunlins at the roost increased. Similarly, the timing of sunset affected the evening use of the roost. Although the timing of high water shifted later each night, Dunlins continued to disperse just after sunset, regardless of the stage of tide. By the time high water occurred close to midday (Fig. 4, bottom), roosting flocks formed at sunrise, at the midday high water, and at sunset.

Because of the influence of sunrise, Dunlins arrived at the roost at lower tide levels in the morning than during midday or evening. Over eight morning high-water cycles, one-half the

roosting flock had arrived by the time the tide had risen to  $1.4 \pm 0.23$  m, at which time 45% of the intertidal flats were still exposed. At mid-day and in the evening, they waited until the tide had reached  $1.9 \pm 0.11$  m ( $n = 10$ ) and  $2.0 \pm 0.12$  m ( $n = 10$ ), respectively, when only about 22% of the flats remained uncovered. Departures from high-water roosts were similar at all times of day in relation to the amount of exposed intertidal flats. Half the Dunlins had left the roost by the time the tide averaged  $1.5 \pm 0.06$  m and about 40% of the flats were exposed.

Roost-site use over a typical four-day period with midday and night high-water cycles illustrates the interactive effects of high water, sunrise, and sunset during this tidal regime (Fig. 5). Roosting flocks consistently formed at sunrise, at the midday high water, and just before sunset, although the number of Dunlins was highly variable. No Dunlins were found at the roost site during high water on the single night (28 August) we checked during this period (Fig. 5). As the evening low water got progressively closer to the time of sunset, the size of the evening roosting flock decreased.

Movements to and from the roost during low-water periods were keyed closely to the timing of sunrise and sunset (Fig. 6). During formation of 10 morning low-water roosting flocks, birds began to arrive during the half hour before sunrise, and peak numbers (43%) of the Dunlins arrived at sunrise (Fig. 6, top). Most (56%) of the Dunlins left the roost from 0.5 to 1.5 h after sunrise. During evening low-water cycles, the rate of arrival was gradual before sunset, after which it dropped abruptly (Fig. 6, bottom). Few birds left the roost before sunset. A mass exodus usually occurred during the 1.5 h after sunset, regardless of the stage of tide.

*Turnover at the roost.*—On average,  $81 \pm 2.5\%$  of the Dunlins counted at the roost were present when the flock reached its peak size ( $n = 47$  flocks). This ranged from a high of 100%, for a flock in which no birds left the roost before all had arrived, to a low of 45%, for a flock in which more than twice the number of Dunlins actually visited the roost as were there when the flock reached its peak size. During almost every 30-min census period, Dunlins left the roost while others arrived. These included birds that came to the roost as the flock was just being formed, stopped for a few moments, and then left. They also included birds that left the roost after the flock had been intact for several hours but be-

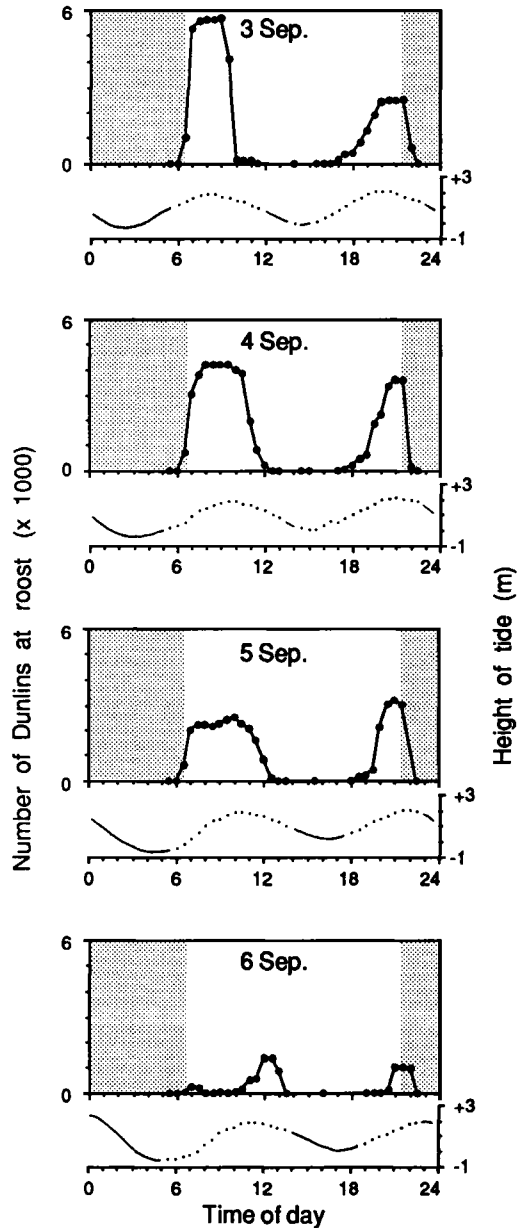


Fig. 4. Number of Dunlins at Tutakoke roost site over a four-day period (3–6 September 1980) when high water occurred in morning and evening. Occupation of roost shown in relation to periods of darkness (shaded areas) and tide height (lower graphs). Dots on lower graphs indicate measured tide height during each census. Solid lines indicate values interpolated from tide tables.

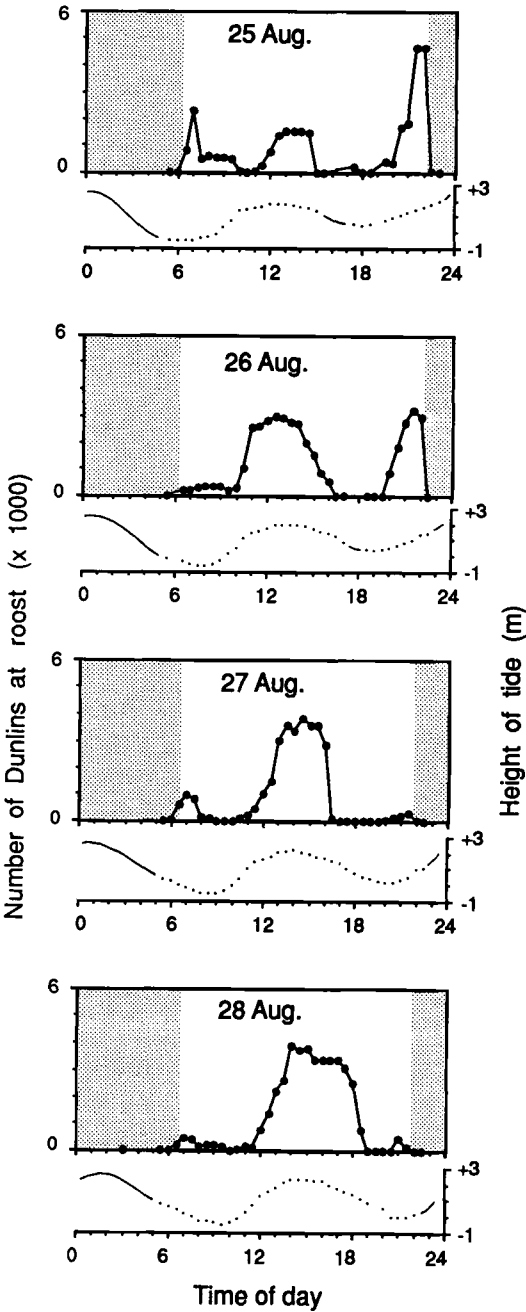


Fig. 5. Number of Dunlins at Tutakoke roost site over a four-day period (25-28 August 1980) when high water occurred at midday and at night. Occupation of the roost shown in relation to periods of darkness (shaded areas) and tide height (lower graphs). Dots on lower graphs indicate measured tide height during each census. Solid lines indicate values interpolated from tide tables. No Dunlins present during single high-water cycle checked at night during this period (28 August, 0300).

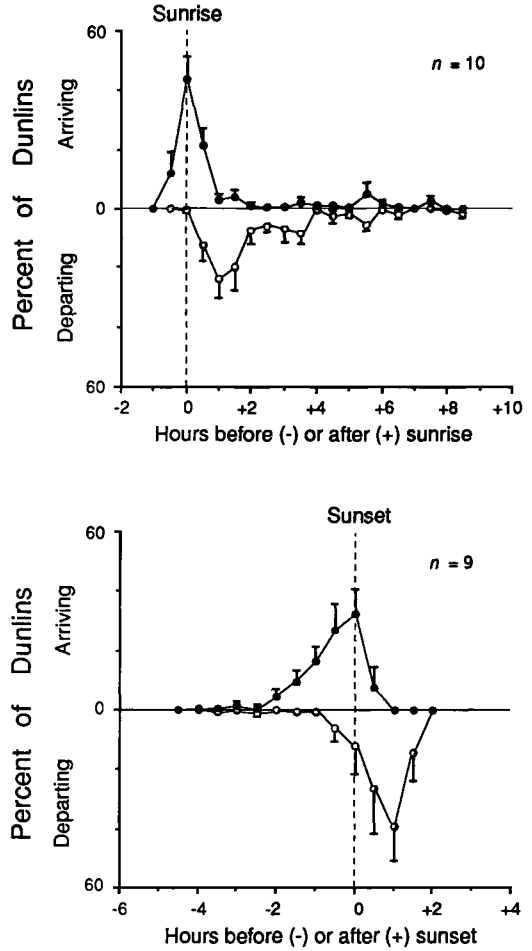


Fig. 6. Percent of Dunlins arriving at and departing from Tutakoke roost in relation to time of sunrise (top) and sunset (bottom) during low-water cycles. Data given as  $\bar{x} \pm SE$ .

fore feeding areas were exposed. Without individually marked birds we could not determine how many of those individuals that left the roost early returned later to stay. The turnover rate within roosting flocks did not vary significantly with time of day or between low- and high-water cycles. It was significantly correlated with the number of birds that visited the roost; the more Dunlins that visited the roost the higher the proportion that stayed ( $r = 0.38$ ,  $P < 0.01$ ).

*Behavior at roost site.*—Sleeping was the predominant behavior at the Tutakoke roost site, and comprised 77% of all behavior recorded for the 47 flocks monitored. Preening (10%) and

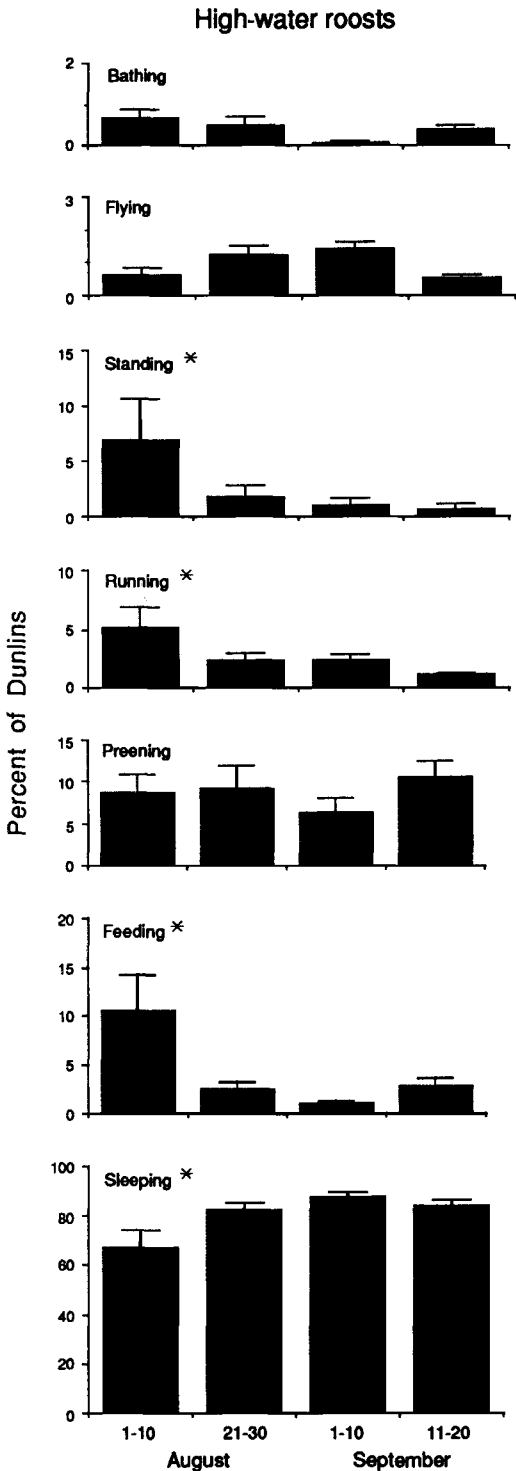


Fig. 7. Seasonal variation in behavior of Dunlins at roost during high-water cycles. Asterisks indicate behaviors that changed significantly between early August and later in season ( $P < 0.05$ ). Data presented

feeding (5%) were the next most common activities, followed by running (3%) and standing (3%). Few Dunlins were recorded flying (1%) or bathing (<1%). Behavior changed as the season progressed and also was affected by the stage of the tide. Among the 27 roosting flocks monitored during high-water cycles, there was no significant diurnal variation in Dunlin behavior. There was, however, significant seasonal variation in the proportion of birds standing, running, feeding, and sleeping among the four 10-day periods monitored ( $P < 0.05$ ). The greatest change occurred between early August and later in the season, when birds became less active at the roost site and spent more time sleeping (Fig. 7).

During early August, Dunlin behavior at high-water roosts in relation to the stage of tide varied greatly among flocks (Fig. 8). Later in the season, the proportion of birds that ran and slept at the site was influenced significantly by tide stage ( $P < 0.05$ ). The proportion of Dunlins running was highest at the early stages of flock formation and then steadily declined (Fig. 8). The proportion sleeping was greatest near the time of high water, after which most birds had settled in at the roost but before they were preparing to depart.

Dunlin behavior at the roost during morning low-water cycles also varied seasonally (Fig. 9). The greatest change recorded was in the proportion of Dunlins preening, which increased significantly from  $5 \pm 0.6\%$  in early August to  $15 \pm 2.4\%$  later in the season ( $P < 0.05$ ). The increase in the proportion of birds flying and the decrease in running between these two periods (Fig. 9) were suggestive, but not significant statistically (both  $P = 0.08$ ). During early August, behavior at morning low-water roosts was similar to that at high-water roosts. Later in the season, Dunlins behaved differently during morning low-water cycles than during high-water cycles. During this period, significantly fewer birds slept ( $67 \pm 7.2\%$  vs.  $85 \pm 1.5\%$ ) and more were recorded preening ( $15 \pm 2.4\%$  vs.  $9 \pm 1.2\%$ ) and standing ( $2 \pm 0.7\%$  vs.  $1 \pm 0.2\%$ ) during morning low water than during high water ( $P < 0.05$ ). The proportion that fed at the roost during morning low water was highly

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as  $\bar{x} \pm SE$  for each 10-day period. Sample sizes for four periods are 4, 5, 8, and 10 flocks, respectively.



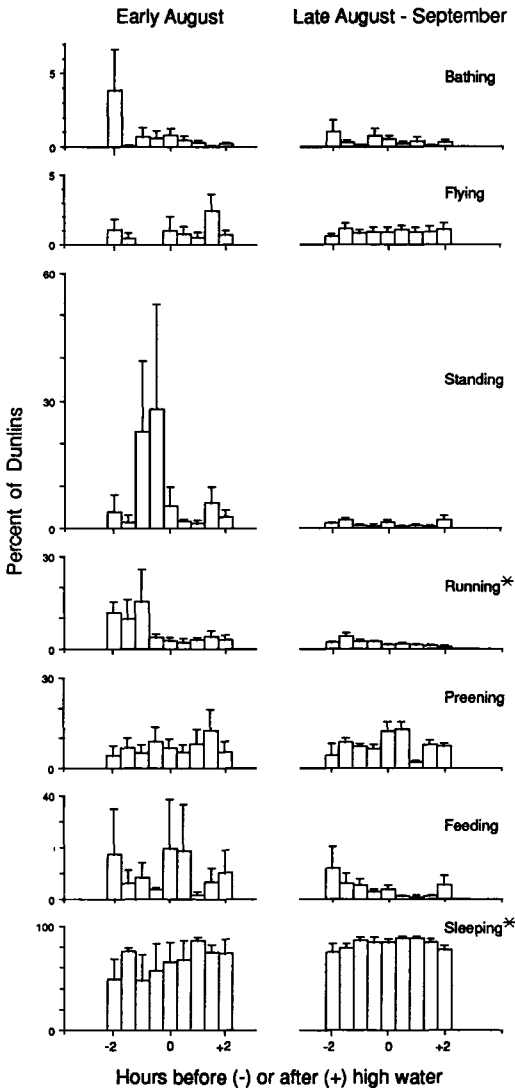


Fig. 8. Behavior of Dunlins at Tutakoke roost during high-water cycles during early August ( $n = 4$  flocks) and later in season ( $n = 23$  flocks) in relation to tide stage. No significant differences among tide stages in any behavior during early August. Asterisks indicate those behaviors late in season that varied significantly among tide stages ( $P < 0.05$ ).

variable late in the season ( $12 \pm 5.9\%$ ) and nearly greater statistically ( $P = 0.06$ ) than that recorded during high water ( $2 \pm 0.4\%$ ).

We monitored behavior of Dunlins in flocks that formed during low-water cycles in the evening only during the middle of the season. Behavior was highly variable and did not differ significantly between late August and early

September (Fig. 9). Significantly more Dunlins were recorded running at the roost during evening low water ( $7 \pm 3.5\%$ ) than during high water ( $2 \pm 0.3\%$ ) late in the season ( $P < 0.05$ ). Dunlins spent significantly less time preening during evening low-water ( $6 \pm 1.2\%$ ) than morning low-water cycles ( $P < 0.05$ ).

*Aerial flocking behavior at roosts.*—Dunlins were disturbed at the roost site 83 times during 250.5 h of observation. Most disturbances ( $n = 53$ ) were by predators, particularly Parasitic Jaegers (*Stercorarius parasiticus*,  $n = 26$ ), Glaucous Gulls (*Larus hyperboreus*,  $n = 9$ ), and Mew Gulls (*L. canus*,  $n = 7$ ). Dunlins also responded to arctic foxes (*Alopex lagopus*), Northern Harriers (*Circus cyaneus*), Short-eared Owls (*Asio flammeus*), and Long-tailed Jaegers (*S. longicaudus*). Bar-tailed Godwits (*Limosa lapponica*) that flew low over the roosting flock accounted for 22 disruptions; 8 were caused by four other nonpredatory bird species.

When an avian predator appeared in the vicinity of the roost, the typical response was for the entire roosting flock to rise as a tight group, circle over the roost site at a height of 30 to 50 m, and realight after the predator had left. When the roosting flock was in the early stages of formation or late stages of departure, part or all of the flock sometimes left the roosting area. Active mobbing was recorded infrequently. Northern Harriers were mobbed on three of four visits to the roost, one juvenile Parasitic Jaeger was mobbed as it made several feeble attempts to chase Dunlins, and one juvenile Mew Gull was mobbed as it flew low over the Tutakoke River. On four occasions we observed avian predators flying through the area with no response from the Dunlins: twice for Parasitic Jaegers, and once each for a Northern Harrier and a Peregrine Falcon (*Falco peregrinus*).

Roosting Dunlins reacted differently to arctic foxes than to avian predators. Generally, only those Dunlins closest to the fox moved. They flew a short distance to another part of the roosting flock. On two of five occasions, Dunlins did not move.

We observed no predation during 1980, but on 5 August 1979 we saw an adult Glaucous Gull on the Tutakoke River swallowing a Dunlin. We also observed a pair of Parasitic Jaegers attempt to take a small bird away from a Glaucous Gull. Either bird may have been one of the large number of Dunlins that we had captured the previous day. On 22 August 1979 we ob-

served a Parasitic Jaeger capture a lone Western Sandpiper in the air and try, unsuccessfully, to take another.

On 74 other occasions, the roosting flock arose suddenly, flew around the roost site in a tight, whirling formation, and then realighted at the roost site in the apparent absence of any predator or other bird. Such whirling flights were visible for long distances (>10 km). On at least two occasions, two or more of the major roosts in the bay were in the air simultaneously. The frequency of whirling flights increased steadily from 0.23 flights/h in early August to 0.40 flights/h in late September.

DISCUSSION

Roosting behavior of Dunlins staging on the Yukon-Kuskokwim Delta in late summer was highly variable throughout the season. The tidal cycle was the most important factor governing attendance and behavior at roosts, but the influence of daylight was also unexpectedly important. Some behavior variability was related to seasonal requirements for molt and migration. Other variability was related to less predictable changes in conditions at the roost site.

*Effect of tidal cycle.*—The dominating effect of tidal cycle on roosting behavior confirmed our initial predictions. Most studies of coastal shorebirds have reported close relationships between tides and movements to and from feeding areas, primarily because of the effect of tide level on availability of prey and foraging space (Evans 1976, Burger et al. 1977, Connors et al. 1981, O'Connor 1981, Cramp and Simmons 1983, Burger 1984, Myers 1984, Zwarts et al. 1990). Although roosting during high water is a common phenomenon among coastal shorebirds, certain species continue to feed by shifting to inland areas either regularly or seasonally during periods when food requirements are not being met on intertidal areas alone (Goss-Custard 1969, Heppleston 1971, Burger 1984). Dun-

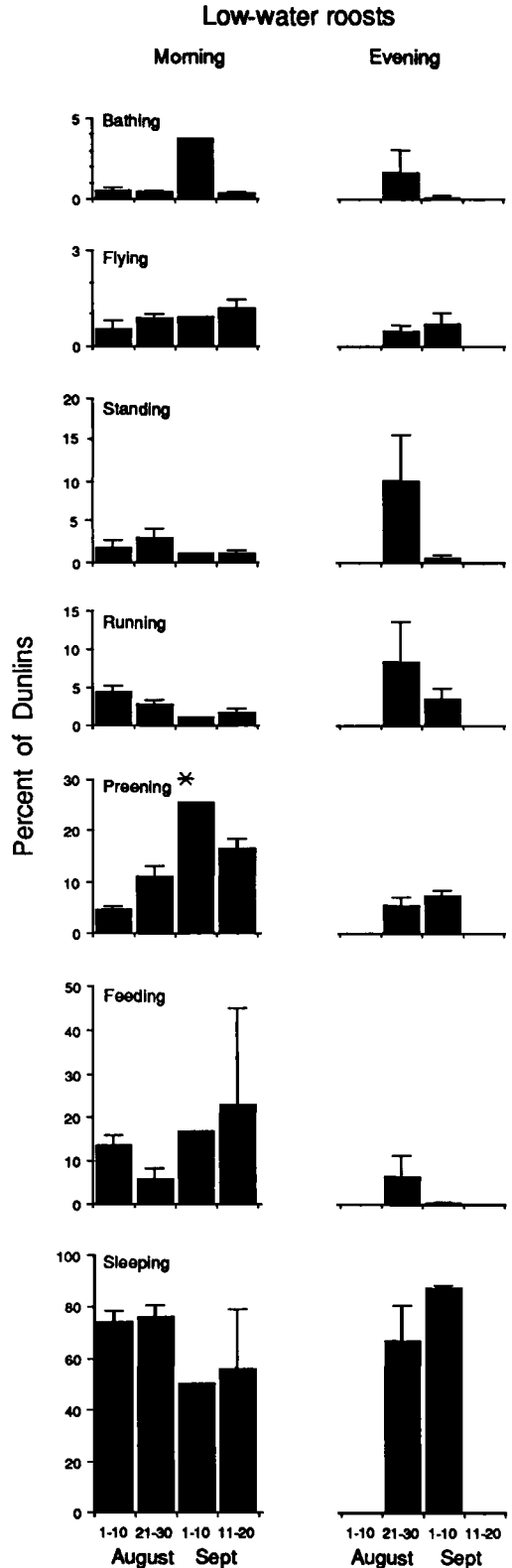


Fig. 9. Seasonal variation in behavior of Dunlins at Tutakoke roost during low-water cycles in morning and evening. Asterisk indicates a significant increase in preening at morning roosts between early August and later in season ( $P < 0.05$ ). Data presented as  $\bar{x} \pm SE$  for each 10-day period. Sample sizes for four periods are 2, 4, 1 and 2 morning roosting flocks, and 0, 6, 3 and 0 evening roosting flocks, respectively.

lins wintering in Great Britain have been recorded feeding just above the high-water line or in adjacent salt marshes during high-water cycles (Hale 1980:149). We found no evidence of Dunlins foraging on vegetated habitats during high water, although a small proportion of the birds regularly fed at the roost site itself. Food resources on coastal meadows in arctic and subarctic Alaska decline sharply as summer progresses, and this decline is probably an important determinant of the timing of Dunlins' shift to intertidal foraging areas after breeding (Holmes 1966b, 1970, 1971).

Dunlins departing from evening high-water roosts flew predominantly in the direction of main feeding areas as the tide receded, and our single venture out to the mudflats at night confirmed that at least part of the population foraged at night. Nocturnal foraging has been recorded in Dunlins in Great Britain, Sweden, Africa, and California (Mascher 1966, Evans 1976, Zwarts et al. 1990, N. Warnock pers. comm.). Dunlins wintering in Great Britain fed less extensively at night than by day; fewer birds were observed at night on the preferred daytime feeding areas and those occurring at night usually fed for less of the tidal cycle than by day (Evans 1976). In Africa, as Dunlins prepared for spring migration, densities on intertidal foraging areas at night were consistently lower than those during the day, but the time spent feeding at night increased during the period of premigratory fattening (Zwarts et al. 1990). The importance of nocturnal foraging in shorebirds has been largely neglected, and its frequency, seasonal occurrence, relative efficiency, and energetic contribution (compared to diurnal foraging) need further study (but see Dugan 1981, Goss-Custard 1984, Puttick 1984, Myers et al. 1985, Robert et al. 1989, Zwarts et al. 1990).

*Effect of daylight.*—Because Dunlin feeding activity in other areas had been found to follow primarily a tidal rather than diurnal periodicity (Pienkowski et al. 1979), crepuscular movements to and from the roost regardless of the stage of tide were unanticipated. Not only did dawn and dusk influence the formation and dispersal of roosting flocks at low water, when we had expected Dunlins to be foraging on intertidal flats, but interactions of the timing of sunrise and sunset with the timing of high water also served to extend the amount of time Dunlins spent at typical high-water roosts.

Crepuscular formation of roosts is typical of

shorebirds using inland habitats (e.g. Hamilton 1959, Swinebroad 1964, Brooke 1972, Atkinson 1976, Myers and Myers 1979, Myers 1980) and has been documented for a few species of coastal-dwelling shorebirds (e.g. Goss-Custard 1969, Hartwick and Blaylock 1979, Hockey 1985, Myers et al. 1985). Dunlins wintering in central California roost at night, as well as during diurnal high waters (Blick 1980, Ruiz et al. 1989). At Bodega Bay, the roosting pattern varied between early winter, when the entire population appeared to use local nocturnal roosts, and late winter, when a portion of the population left the bay at dusk apparently to feed on alternate food sources (probably inland) and returned to the bay at dawn (Ruiz et al. 1989).

We found no evidence that Dunlins on the Yukon-Kuskokwim Delta fed on coastal meadows at night. Although we never determined the destination of the Dunlins that left the roost site at dusk on incoming tides, the fact that Dunlins occupied the Tutakoke roost site on two of six nights checked during high water suggests that on other nights they were probably flying to an alternate roost site. From flight directions and synchronous movements of the departing birds, we infer that Dunlins flew to an area of mudflats that was not going to be submerged at high water, to some unknown roost site inland, or to join a roosting flock in the northern part of the bay. On one occasion Dunlins at the Punoarat Point roost site also flew inland as a flock at dusk. Despite extensive searches of coastal meadows up to 5 km inland, we never found concentrations of droppings or molted feathers to indicate where Dunlins might have roosted.

During nocturnal high tides it may have been advantageous for Dunlins to roost at sites other than those occupied regularly during the day to decrease risk of predation by ground predators. Foxes have been postulated to be important predators of European populations of wintering shorebirds (Townshend 1984) and may be important on coastal staging areas as well. Arctic foxes on the Yukon-Kuskokwim Delta and elsewhere are most active during crepuscular and nocturnal periods (M. Anthony, pers. comm.; Kavanau and Ramos 1975). Pre-roost gatherings at dusk may enable Dunlins to travel quietly as a flock to different night roosts so that they can: (1) avoid advertising the location of their night roost by traveling under cover of darkness; and (2) roost in a tight formation to

increase their probability of detecting an attacking predator (cf. Zahavi 1971). Ground predators would likely have a lower success rate when searching for clumped prey (Tinbergen et al. 1967, Vine 1973, Bertram 1978).

Dunlins wintering on the Dutch Wadden Sea also came to their high-water roost at dusk when water levels were still low; weight differences among different captures suggested that individuals that came to the roost early were heavier than those that came later, just before high water (Goede and Nieboer 1983). African Black Oystercatchers (*Haematopus moquini*) also leave foraging areas at mid-tide to join roosts for the night (Hockey 1985). Their nocturnal roosts are usually silent and less approachable than roosts formed during the day, suggesting that reducing risk of predation was an important function of roost formation at night. In Great Britain, nocturnal Dunlin roosts were larger and suffered less disturbance than equivalent roosts during the day (D. H. Worrall in Cramp and Simmons 1983:363). These findings support the idea of there being a trade-off between the requirement to feed and the benefits of coming to the roost at dusk. Dunlins on the Yukon Delta may have partially compensated for loss of potential feeding time during the evening low water by feeding more extensively during the morning low water, which was always the lower of the two. Intertidal foraging should have been more profitable during lower tides (Evans 1981).

Why some Dunlins also regularly came to the Tutakoke roost during low water at sunrise is puzzling. Such behavior has not been reported for other shorebird species. Most of the birds at sunrise roosts arrived along the coast and departed to mudflats. Although we do not know if these birds had been feeding or roosting before they arrived, they did not appear to be satiated. More fed at the roost site at low water than at high water, even though intertidal flats were exposed around the roost site during all but the most extreme high-water periods.

Morning low-water roosting flocks may have been formed by Dunlins that had remained at nocturnal roost sites until dawn rather than going out to feed when mudflats became available. Morning tides in this series were the lowest available in late summer and allowed much longer foraging bouts than at other times during the staging period. Gathering at the coastal roost site at sunrise may have enabled individuals to

coalesce into flocks before flying to feed. Shorebirds foraging in certain-sized groups have been shown to be less vulnerable to predation (Page and Whitacre 1975, Kus et al. 1984).

*Seasonal variability in roosting behavior.*—Dunlins staging on the delta begin prebasic molt of flight and body feathers during July (Holmes 1971). By late August, most birds are completing primary molt and are undergoing heavy body molt (Holmes 1971, Gill and Handel, in prep.). Dunlins build lipid deposits steadily from early September until their departure in late September or early October (Gill and Handel, in prep.). The significant changes we recorded in roosting behavior between early August and later in the staging period coincided with changes in physiological requirements. During molt, an increase in thermoregulatory cost is probably incurred from decreased insulation (Payne 1972). Growing feathers are highly vascularized and increased surface area is exposed to heat loss during cool temperatures (Payne 1972).

Behavior that increases insulation or minimizes heat loss may benefit Dunlins undergoing molt as temperatures decline in late summer at subarctic latitudes. The increase in sleeping and decrease in running, standing and feeding at the roost site during high-water cycles late in the season presumably reduced energetic costs for thermoregulation. Sleeping with the bill tucked in scapular feathers and standing on one leg, which was the predominant behavior of Dunlins at the roost, conserves heat (Mitgård 1978, Lustick 1985, Klaassen 1990). Dunlins wintering in tropical Africa will lie down while sleeping when substrate temperature exceeds ambient air temperature (Klaassen 1990). This behavior was never seen in Alaska. Because it is likely that the air was always warmer than the mudflats during the staging period, standing would have been the more heat conservative posture.

The increase in preening and bathing at morning low-water roosts during this same period coincided with increased requirements of plumage maintenance during molt. Dunlins also sacrificed potential foraging time during low-water cycles at midday and in the evening to maintain their plumage during this period. As they departed from the roost on receding tides, they routinely flew first to shallow ponds adjacent to the roost site to bathe and preen before flying out to mudflats to feed. Wind-resistant plumage can be extremely important for shore-

birds, because it is difficult to compensate behaviorally for thermoregulation on open mudflats (Kersten and Piersma 1987).

In Africa, Dunlins significantly increased feeding time during the estimated four-week period of intense premigratory fattening before spring migration (Zwarts et al. 1990). Although there was a slight increase in diurnal feeding time as daylength increased, the greatest increase in feeding time occurred during nocturnal periods of low water (Zwarts et al. 1990). For Dunlins staging in Alaska, the suggestive (but not statistically significant) steady seasonal decrease in time spent at the roost during diurnal high waters may indicate that a similar phenomenon has been occurring. This seasonal effect is difficult to distinguish from the influence of tide level, because the height of diurnal high waters during our study also showed a strong seasonal decline. Later in the season, Dunlins may have spent less time at roosting areas during the day simply because intertidal flats were exposed for longer periods.

Decreasing daylength was an additional factor that may have affected seasonal changes in the roosting and feeding schedule of Dunlins on the delta. During our study, daylight decreased from about 18.0 h in early August to 14.5 h in late September, and was about 12.5 h in early October when the Dunlins probably departed. By comparison, Dunlins in Africa, whose nocturnal foraging schedule changed significantly before spring migration, experienced a slight increase in daylight from 12.5 h to 13.5 h (Zwarts et al. 1990). Foraging at night may also become particularly important for Dunlins on the delta immediately before departure, when daylight is greatly reduced and energy demands due to premigratory fat deposition and thermoregulation are high.

*Influence of predators.*—Potential predation was a strong influence on roosting behavior in that almost half (42%) of all flocks we monitored were disrupted one or more times by predators. Most predators attempted to isolate an individual bird from the airborne flock, a common hunting behavior on wintering areas (Kus et al. 1984, Boyce 1985, Buchanan et al. 1988, Bijlsma 1990). The predator-evasion flocking responses that we observed were similar to those described for Dunlins by Buchanan et al. (1988) as flashing behavior. Although we witnessed only one certain instance of predation, Page and Whitacre (1975) estimated that diurnal raptors

killed 21% of the Dunlins foraging on a California lagoon one winter, and presented evidence that such predation was a major factor selecting for flocking behavior among shorebirds. In Scotland, similar high rates of mortality (16–20%) for Redshanks (*Tringa totanus*) and Ruddy Turnstones (*Arenaria interpres*) were attributed to raptor predation, although mortality of Dunlins there appeared to be much less (4%; Whitfield 1985).

*Effect of wind.*—Dunlin roosting behavior was also influenced by wind speed and direction. On days of winds greater than 25 km/h, Dunlins tended to form large, compact roosting flocks or to disperse into cracks on the mudflats or behind low vegetated islands and pieces of driftwood. Roosting Dunlins wintering in Great Britain have also been recorded crowding together in high winds and always facing into the wind (D. H. Worrall in Cramp and Simmons 1983:363). Wind has a strong effect on the insulative quality of plumage (Robinson et al. 1976), and heat loss in Dunlins is thought to be accelerated by wind (Evans 1976). Communal roosting may have afforded some thermal benefits because wind speed is lower in the middle of shorebird roosts than at the edge (Whitlock 1979 in Ydenberg and Prins 1984).

Strong winds also affected attendance at particular roost sites. During a period of steady 25–30 km/h winds from the N and NW, and for up to two days afterwards, the number of Dunlins roosting was greatly depressed at the Tutakoke site, which offered little protection from winds from that direction. Sightings of color-banded birds confirmed that some interchange occurred among roost sites within the bay throughout the summer. The high variability in turnover within a particular roosting flock suggested that birds may come to a roost site to “test” the conditions there. The more birds present, the more likely others were to remain. The flexibility to use several traditional roost sites interchangeably, depending on local roosting or feeding conditions, may allow Dunlins to minimize energetic expenditures during a period of high demands.

Only once during late summer over the five years we spent in the area did we encounter winds strong enough to hold the tide in during a low-water cycle so as to preclude feeding on intertidal areas within the entire bay.

*Premigratory behavior.*—The increase in whirlwind flights of Dunlins at the roost in the absence

of predators coincided with fat deposition preparatory to fall migration. These flights were similar to those described for Black-tailed Godwits (*Limosa limosa*) by Piersma (1983), who hypothesized that social stimulation within the flocks may serve to synchronize migration. Increased lipid levels of Dunlins staging in Sweden were also thought to be related to the "migratory mood" of the birds and their attendant increase in "migratory unrest activities" (Mascher 1966). Swinebroad (1964) suggested that circling flights of flocks of inland shorebirds preparing to roost at dusk may have been related to a lowering of threshold sensitivity to certain external stimuli, and may have been an indicator of impending migration.

On the delta, Dunlins usually departed the roost site in small flocks (<50 birds) when going to daytime feeding areas and when leaving at dusk. An increase in vocalizations accompanied the increase in activity as birds prepared to depart. Departing birds generally gave one to three prolonged "preep" calls with an ascending end note, and departure of one or a few birds usually stimulated a stream of others to follow in the same direction. Hartwick and Blaylock (1979) also noted specific vocalizations among American Black Oystercatchers (*Haematopus bachmani*) moving from roosts to feeding areas and Swinebroad (1964) described increases in vocalizations among inland shorebirds before they flew from one roost site to another. This roost departure behavior is similar to that observed for Dunlins departing from the Alaska Peninsula during fall migration (R. E. Gill, Jr., in prep.) and for Dunlins migrating in spring from western Africa (Piersma et al. 1990). Migrating in structured flocks may benefit Dunlins in terms of both aerodynamic efficiency and navigational accuracy (Piersma et al. 1990).

Consistent formation of roosting flocks at dusk may have added significance in terms of migration. Dunlins migrating from the Alaska Peninsula in fall depart between dusk and midnight (R. E. Gill, Jr., in prep.), and those migrating in spring from western Africa departed predominantly in the late afternoon, close to sunset (Piersma et al. 1990). Departure during crepuscular periods may allow integration of multiple navigational cues, including visual landmarks, light polarization, magnetic cues, and stars (Piersma et al. 1990). Crepuscular departures also might be beneficial energetically, because atmospheric conditions at night may

be better for migrants powered by flapping flight (Kerlinger and Moore 1989). In addition, nocturnal migrants might have lower thermoregulatory demands because of decreased solar radiation, and might result in arrival at their destination during more profitable diurnal foraging periods (Piersma et al. 1990). Communal-roosting behavior responsive to light cues, thus, may provide a critical mechanism for aiding migration.

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