# DIURNAL AND NOCTURNAL ROOST SITE FIDELITY OF DUNLIN (*CALIDRIS ALPINA PACIFICA*) AT HUMBOLDT BAY, CALIFORNIA

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Abstract.— Shorebird roosts are often considered traditional, on the basis of predictable occupancy by large numbers of birds over long periods. However, fidelity of individuals to roosts at fine spatial and temporal scales, particularly at night, has rarely been described. We compared diurnal and nocturnal use of high-tide roosts by radiotagged Dunlin (*Calidris alpina pacifica*) wintering (November–March) at Humboldt Bay, California. Despite high fidelity to the study area, fidelity to particular roosts was relatively low and highly variable. At night, Dunlin used fewer roosts, were more faithful to primary roosts, and moved shorter distances between successive roosts than during the day. Day and night roosts differed in location, habitat, and distance from tidal flats. At night, Dunlin made greater use of pasture, and less use of islands and manmade structures. Day and night strategies of high-tide space use by Dunlin may be related to differences in food availability or predation danger. Our results illustrate that notions of tradition and site fidelity are scale-dependent and that knowledge of space use across the full range of environmental conditions is necessary for appropriate management of shorebird habitat. *Received 25 January 2006, accepted 14 June 2006.*

Key words: *Calidris alpina pacifica*, Dunlin, nocturnal, pasture, roosts, site fidelity, tradition.

## Fidelidad a los Sitios de Descanso Diurnos y Nocturnos en *Calidris alpina pacifica* en la Bahía de Humboldt, California

Resumen.—Los sitios de descanso de las aves playeras son frecuentemente considerados como tradicionales debido a que éstos son ocupados prediciblemente por un gran número de aves durante períodos prolongados. Sin embargo, la fidelidad de los individuos a los sitios de descanso a escalas espaciales y temporales finas, particularmente durante la noche, rara vez ha sido descrita. Comparamos el uso diurno y nocturno de sitios de descanso durante los períodos de marea alta en individuos *Calidris alpina pacifica* marcados con transmisores de radio que se econtraban invernando entre noviembre y marzo en la Bahía de Humboldt, California. A pesar de que existió una alta fidelidad al área, la fidelidad a cada sitio de descanso fue relativamente baja y altamente variable. Durante la noche, las aves emplearon pocos sitios de descanso, fueron más fieles a los sitios principales y se movieron distancias más cortas entre sitios de descanso sucesivos que durante el día. Los sitios de descanso del día y la noche difirieron en su ubicación, hábitat y distancia a los planos mareales. Durante la noche, las aves emplearon más los pastizales, mientras que las islas y las estructuras hechas por el hombre fueron menos utilzadas. Las estrategias de uso del espacio durante las mareas altas en el día y la noche podrían estar relacionadas con diferencias en la disponibilidad de alimento o en el peligro de depredación. Nuestros resultados

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ilustran cómo las nociones de tradición y fidelidad al sitio dependen de la escala, y que es necesario contar con conocimiento acerca del uso del espacio a través del rango completo de condiciones ambientales para manejar el hábitat de las aves playeras adecuadamente.

ROOSTS ARE A conspicuous feature of the ecology of animals as diverse as birds, butterflies, bats, and pinnipeds. Roosts are often described as "traditional" because large numbers of individuals predictably congregate at the same location when they are not feeding or mating. While at roosts, individuals may spend a significant proportion of their daily activity budget resting, preening, and remaining vigilant for predators. Among birds, traditional roosts of wintering shorebirds (suborder Charadrii) are especially well known. In coastal areas, where tides predictably inundate primary foraging habitats, shorebirds coalesce into dense mixed-species flocks, which may number in the thousands (Hale 1980).

The idea that shorebird roosts are traditional is supported by observations at two scales: the population and the individual. At the population scale, large flocks representing a significant proportion of a local population may occur at the same site over long intervals. Long-term studies have reported shorebird use of specific roosts spanning decades (Burton et al. 1996; Rehfisch et al. 1996, 2003). Hale (1980) indicated that some roosts in England (e.g., Crossens roost on the Ribble marshes) have been used for more than a century. Thus, roosts appear to be traditional from the perspective of the population.

By contrast, a study of temporal variation in use of high-tide roosts by 14 nonbreeding shorebird species at Humboldt Bay, California, found that very few among 240 roosts were predictably used from week to week (Colwell et al. 2003). Rather, roosts fell on a continuum from traditional (used frequently by many birds) to ephemeral (used infrequently by few), and even the most-used roosts were occasionally unused. These observations suggest that roost use may be more dynamic than previously acknowledged, with high variation in the roosting behavior of individual shorebirds.

A second and stronger line of evidence for traditional roost use comes from studies of marked birds. Many studies have demonstrated strong nonbreeding site fidelity in shorebirds, at local to regional spatial scales (Pienkowski and Clark

1979; Smith et al. 1992; Rehfisch et al. 1996, 2003; Warnock and Takekawa 1996; Burton 2000; Drake et al. 2001; Shepherd 2001; Sanzenbacher and Haig 2002). After arriving in a wintering area, individuals move relatively short distances and may frequent a few roosts over intervals spanning days (Warnock and Takekawa 1996, Pearce-Higgins 2001, Leyrer et al. 2006) to years (Rehfisch et al. 1996, 2003). These findings suggest that roost use is traditional from the perspective of the individual as well.

Although generalizations about traditional roost use apply to many shorebird species, they are largely derived from diurnal observations, because of reliance on resighting or recapture of marked individuals (Pienkowski and Clark 1979; Rehfisch et al. 1996, 2003; Pearce-Higgins 2001). Although some studies have reported similar findings for day and night (Warnock and Takekawa 1996, Leyrer et al. 2006), others have reported differences in behavior, movements, and space use (Mouritsen 1992, 1994; Shepherd 2001; Sitters et al. 2001; Gillings et al. 2005; Rogers et al. 2006). In addition, diurnal mark–recapture studies cannot account for a bird's location every day, and observations are restricted to known locales. Telemetry may be required to locate all roosts in an estuary and monitor the influence of environmental factors such as weather, tide, and time of day (Rehfisch et al. 2003, Rogers 2003).

Spatial scale is fundamental to discussions of site fidelity. Individuals or populations with high site fidelity are often believed to be at greater risk from disturbance, contamination, or development (Rehfisch et al. 1996, 2003; Warnock and Takekawa 1996). Generally high winter site fidelity of shorebirds at scales of the home range or larger may not reflect fidelity to sites within an individual's home range, the scale at which disturbance and development typically occur. However, individual fidelity to specific roosts at a fine spatial scale has rarely been quantified.

Following investigation of roost use by the shorebird community at Humboldt Bay (Colwell et al. 2003), we initiated a study of individual Dunlin (*Calidris alpina pacifica*) to

improve understanding of the dynamics of shorebird roost use. This subspecies breeds in coastal western Alaska and winters from southern Alaska to the Pacific Coast of Mexico (Warnock and Gill 1996). The Dunlin is the most abundant wintering shorebird at Humboldt Bay, numbering in the tens of thousands and contributing >20% of observations at winter roosts (Colwell et al. 2003). However, recent population declines in *C. a. pacifica* highlight the need to better understand possible threats during the nonbreeding season (Brown et al. 2001). Resident populations of Dunlin on the Pacific Coast are relatively stable from December to March (Brennan et al. 1985), though occasional large midwinter movements from coastal to interior areas of California occur (Warnock et al. 1995).

During three consecutive winters from 2002 to 2005, we investigated fine-scale roost site fidelity of radiotagged Dunlin on Humboldt Bay. We compared diurnal and nocturnal high-tide behavior, habitat use, and spatial patterns of roosts. We described each bird's fidelity to high-tide roosts by examining the proportion of high tides spent at its primary roost, number of roosts used, and movements between consecutive high tides.

## Methods

*Study area.*—Humboldt Bay, located in coastal northern California (Fig. 1), is a site of international importance under the Western Hemisphere Shorebird Reserve Network (Harrington and Perry 1995). The bay is 22.5 km long and 7.2 km wide at its widest point, with a total area of 62.4 km$^2$ at mean high tide (Barnhart et al. 1992). Two uneven high and low tides occur every 24 h, with nocturnal high tides lower than diurnal high tides in winter. Humboldt Bay consists of three basins, the largest and northernmost of which is Arcata Bay (Fig. 1). Colwell et al. (2003) identified 124 winter roost sites on Humboldt Bay, including natural (mudflat, saltmarsh, islands, and beaches) and human-altered or created (jetties, riprap, wharfs, pier pilings, levees, floating rafts, and pastures) habitats.

*Field methods.*—We captured Dunlin using noose mats (Mehl et al. 2003) near the mouth of Jacoby Creek, a high-elevation tidal flat where dense flocks form before rising tides force them
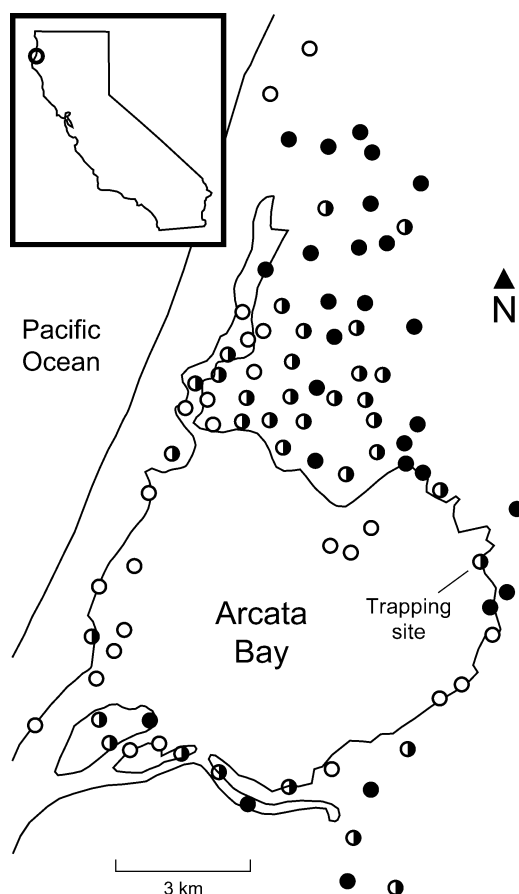


Fig. 1. Arcata Bay study area and locations of 86 high-tide roosts (open circle = day roost, filled circle = night roost, half-filled circle = day and night roost) used by radiomarked Dunlin during three successive winters of 2002–2005.

off the bay. Because of regular tide cycles, optimal trapping conditions occur at this site for four to five consecutive days every two weeks. Therefore, we staggered trapping attempts throughout the season, which resulted in "cohorts" of two to six radiotagged birds from each trapping period: four (21 December 2002 to 17 February 2003), six (24 November 2003 to 11 March 2004), and seven cohorts (2 December 2004 to 15 March 2005) in successive years of the study.

For each Dunlin, we measured length of exposed culmen (mm) and body mass (g). Female Dunlin are larger than males (Warnock and Gill 1996), but overlap in all morphometric characters prevents sexing of all individuals in the field. We sexed birds by culmen length

as follows: <37.7 mm = male; 37.7–39.8 mm = unknown sex; >39.8 mm = female (Page 1974). We released birds with low body mass (<48.0 g) unmarked. To understand age-related variation in behavior, we attempted to radiotag equal numbers of first-year and adult Dunlin. We aged birds by examining the innermost tertials or inner median wing coverts, which have buff-colored edges in first-year birds, and white or gray edges in adults (Page 1974).

We fitted each Dunlin with a unique combination of colored leg bands, a federal metal band, and a radiotransmitter. In year 1, we compared two methods of transmitter attachment. We attached five transmitters with Vetbond Tissue Adhesive (3M, St. Paul, Minnesota) to an area of plucked feathers on the lower back (Warnock and Warnock 1993). We attached six transmitters using a modified version of the figure-eight harness described by Sanzenbacher et al. (2000). We modified the harness by including a length of 2-mm thread, to ensure that it would eventually degrade through wear, thus freeing the individual. Subsequently, we modified the harness further, using elastic cord (0.5–1.0 mm) as the harness material, and we used this method to attach all transmitters in years 2 and 3. We sized and secured the elastic harness to the transmitters before capture, which greatly reduced handling time (usually <5 min). We monitored birds for 2–5 min in a holding cage to ensure proper attachment and then released them into the feeding flock. If the flock departed the site before we completed processing, we transported birds to the nearest known Dunlin roost for release.

The harness added 0.2 g to the 1.1-g transmitter (Holohil Systems, Carp, Ontario; model BD-2, battery life 4–5 weeks), for a total tag weight of 1.3 g (2.0–2.7% of body weight). We fitted 12 birds with transmitters equipped with a position-sensing mercury tip switch (model BD-2P; 1.7 g total tag weight; <3.2% of body weight), which doubles the pulse rate emitted when the top of the transmitter tips below horizontal in relation to the ground. Thus, birds can be categorized as "feeding" or "not feeding" without the need for visual confirmation (Shepherd 2001). In tests on captive Dunlin (Shepherd 2001), the tip switch most reliably indicated behavior when placed 1 cm above the uropygial gland, which is consistent with our radio-attachment methods. We limited our use of tip-switch transmitters to 12, because of their added weight and cost.

To focus efforts when Dunlin would most likely be at roosts, we tracked tagged Dunlin during a 2-h period bracketing predicted high tides, using National Oceanic and Atmospheric Administration data (see Acknowledgments). We defined "day" as the period from 30 min before sunrise to 30 min after sunset, and "night" as the remainder of the 24-h cycle. In previous coastal studies, Dunlin had small winter home ranges (24 km$^2$; Shepherd 2001) and >90% of within-year movements were <5 km (Rehfisch et al. 1996). Therefore, we concentrated tracking efforts around Arcata Bay and adjacent pastures, which constituted most of the potential roosting habitat within 10 km of the trapping site (Fig. 1). When we could not locate individuals within the study area, we occasionally traveled to likely roosting habitat west and south of Arcata Bay.

Before beginning the study, we identified a number of tracking "stations" that were easily accessible by car and provided adequate coverage of Arcata Bay. In a vehicle equipped with a roof-mounted magnetic omnidirectional antenna and TRX-2000S receiver (Wildlife Materials, Murphysboro, Illinois), we stopped at each station and scanned for all active frequencies of radiotagged Dunlin. We determined signal bearings using a hand-held, three-element Yagi antenna and compass, and made other stops along the route as necessary for triangulation. We took three bearings on an individual's location within 6–10 min, thus minimizing the likelihood of the bird moving between bearings. We plotted locations and bearings on a high-resolution (0.3-m pixel) aerial photo for later transcription into ARCVIEW geographic information system (GIS; ESRI, Redlands, California).

Using binoculars and a Leica 20–60× power spotting scope, we attempted to visually locate each bird detected by telemetry and estimated the number of Dunlin in the associated flock. We classified behavior in four categories: "roosting" when birds stood alert, loafed, or preened; "feeding" when birds actively foraged or moved about on the ground; "flying" when the signal clearly moved with an airborne flock; and "unknown" when we could not determine behavior. In rare cases, we recognized an individual by its color bands, and recorded its behavior. For birds fitted with tip-switch transmitters, a slow and steady pulse indicated roosting, whereas a fast or switching pulse rate indicated feeding. In all

other cases, we recorded the dominant behavior (>50% of individuals) of the associated flock. When both individual (color bands or tip switch) and flock behavior were available (*n* = 154 detections), dominant behavior of the flock correctly reflected individual behavior in >95% of cases.

An individual contributed a maximum of one data point per survey. When we detected a bird in multiple locations during a single survey (<10% of occasions), we used the first nonflying location. When we detected flying individuals, we attempted to follow the signal until the flock landed and used that location and subsequent behavior. We recorded as "flying" only birds that we never observed on the ground. Thus, we ensured that these detections represented sustained high-tide flying, and not short-term flushing or short-distance movements.

*Data summary and analysis.*—We used the GIS layer containing all nonflying high-tide detections from all three years to delineate Dunlin roosts within the study area. In most cases, we recognized clusters of detections as distinct roosts representing areas of continuous habitat separated from other roosts by unused or clearly unsuitable habitat such as roads or water. Where detection clusters did not conform to obvious habitat boundaries, we used the following subjective criterion based on personal experience with local Dunlin activity: if birds roosting in two spots were likely to act as a single flock (i.e., would flush together in response to a predator attack), we considered this a single roost. For example, we identified three islands in a manmade lake as one roost because of flock cohesion of birds on different islands. In two areas, limited road access prevented precise triangulation, requiring the combination of detections over a fairly large area into a single roost.

For spatial analysis, we derived a minimum convex polygon from the cluster of detections representing each roost. For each polygon, we then assigned a geometric center point from which to measure distances. We determined the shortest distance from each roost to the edge of the Humboldt Bay mudflat using the ANIMAL MOVEMENTS extension in ARCVIEW. We used Hawth's Tools in ARCGIS to measure inter-roost distances.

To each roost, we assigned one of six habitat categories: grazed pasture, ungrazed grassland, island, mudflat, saltmarsh, or manmade structure (pilings, oyster rafts, riprap, water pipes, trestles, and, in one case, a paved lumber yard). If a roost contained multiple habitats, we classified it by the substrate used most often by Dunlin at that site.

We calculated detection rates using only birds known, through subsequent detection, to be active. Higher diurnal detection rate and tracking effort resulted in a greater number of diurnal detections for most birds. The number of roosts an individual used was highly correlated with the number of detections, both day and night (Fig. 2). For statistical comparability, we limited the data to occasions when we detected a bird on both a diurnal high tide and the subsequent nocturnal high tide. Thus, number of detections varied among birds, but each individual had an equal number of diurnal and nocturnal detections. We analyzed roost fidelity of birds with at least 10 paired detections (*n* = 23). For both day and night, we assigned a primary roost to each bird—the site where that bird most often occurred during that period. We calculated fidelity to the primary roost as the proportion of all nonflying detections of that individual at its primary roost.

## Results

We radiotagged 58 Dunlin (11, 22, and 25 in successive years), including 40 males, 4 females, and 14 birds of unknown sex; 30 were juveniles and 28 were adults. Predators killed six Dunlin 1–19 days after release, three died of unknown causes (1–13 days), and three lost their radios because of attachment failure (11–16 days). We tracked the remaining 46 birds until their signals failed 1–38 days after capture.

We surveyed 96% (252 surveys) of diurnal and 65% (178 surveys) of nocturnal high tides during the study. We recorded 994 diurnal detections of 55 individuals and 679 nocturnal detections of 49 individuals. During high tide, Dunlin used 86 different roosts (Fig. 1), including grazed pasture (45 roosts), saltmarsh (20), manmade structure (9), mudflat (7), ungrazed grassland (4), and island (1).

*Fidelity to the study area.*—Dunlin showed high fidelity to Arcata Bay. Although some signal failures may represent medium- or long-distance movements by Dunlin, there was little evidence of regular movements in and out of the study area. On average, the detection rate of radiotagged Dunlin was 94% on diurnal
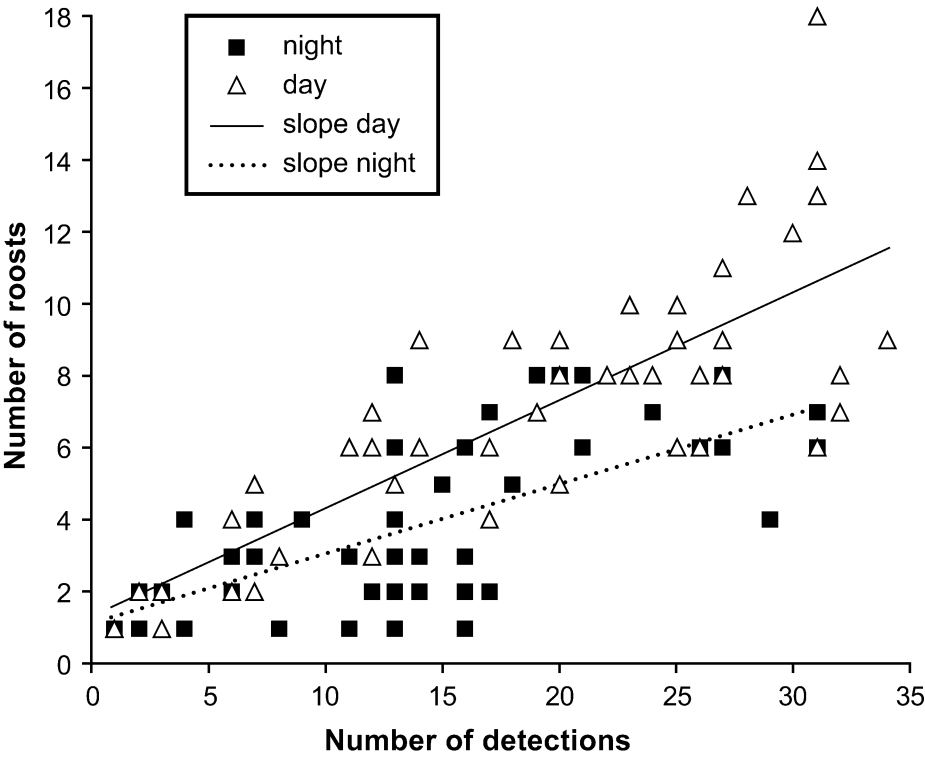
FIG. 2. Number of roosts increased with number of days tracked, both day ($r^2 = 0.694$) and night ($r^2 = 0.476$), but diurnal accumulation of roosts was faster and did not level off even after 30 tracking days.

surveys and 86% on nocturnal surveys. We relocated three birds (two adults and one juvenile) in the study area after absences of 7, 11, and 24 days, respectively. We detected a fourth bird (a juvenile) in South Humboldt Bay, ~14 km south of the study area, following a four-day absence; we did not detect it subsequently. Although we often tracked outside Arcata Bay to find missing birds, we detected only one other bird on these attempts. We found this adult bird 4 km south of the study area after a one-day absence and did not detect it subsequently.

*Roost fidelity.*—Within Arcata Bay, individual fidelity to specific roosts was low, particularly during the day, with birds using many roosts and frequently switching roosts on successive high tides (Table 1). The number of roosts used by individuals was positively correlated with number of detections (Fig. 2) for both day ($r^2 = 0.694$, $P < 0.0001$, $n = 55$) and night ($r^2 = 0.476$, $P < 0.0001$, $n = 49$). However, the slopes of these lines differed ($t = 4.00$, df = 100, $P < 0.001$), which indicates that Dunlin accumulated roosts faster

during the day than during night. Individuals used ≤18 different roosts during the day and continued to add new roosts even beyond 30 tracking days. At night, individuals used a maximum of eight roosts, and accumulation of roosts decreased conspicuously after 18 detections. Three birds with 11, 13, and 16 detections used only one night roost each.

In a paired comparison, Dunlin ($n = 23$) used fewer roosts at night than during the day (Table 1; Wilcoxon paired test: $z = 3.52$, $P < 0.001$). Eighteen individuals (78%) used more roosts during the day (in one case, eight times the number of night roosts the bird used); three individuals (13%) used more roosts at night. Considering only an individual's primary roost, Dunlin had higher fidelity to their nocturnal roosts than diurnal roosts (Table 1; Wilcoxon paired test: $z = 3.53$, $P < 0.001$). Seven birds did not have a clear diurnal primary roost, because of equal frequencies at two to four most-used roosts. At night, five birds had equal frequencies at two most-used roosts. Eleven birds (48%)

TABLE 1. Differences between diurnal and nocturnal roost use by Dunlin at Humboldt Bay, California.

|                                              | Day      | Night    |
|----------------------------------------------|----------|----------|
| **Roost use**                                |          |          |
| Total number of roosts used [a]              | 59.00    | 61.00    |
| Mean roost distance from bay (m)             | 989.90   | 1,666.10 |
| Mean number of roosts used [b]               | 7.10     | 4.50     |
| Mean fidelity to primary roost [b]           | 0.35     | 0.54     |
| Total primary roosts [b]                     | 11.00    | 19.00    |
| Mean primary roost distance from bay (m)     | 416.40   | 1,655.30 |
| Mean run at roost (days) [c]                 | 1.47     | 2.27     |
| Mean inter-roost distance (m) [d]            | 2,057.60 | 1,047.80 |
| **Habitat use [e]**                          |          |          |
| Pasture                                      | 0.38     | 0.76     |
| Saltmarsh                                    | 0.20     | 0.14     |
| Manmade structure                            | 0.18     | 0.01     |
| Island                                       | 0.18     | 0.01     |
| Mudflat                                      | 0.04     | 0.03     |
| Ungrazed grassland                           | 0.01     | 0.04     |
| **Behavior [f]**                             |          |          |
| Roost                                        | 0.81     | 0.54     |
| Feed                                         | 0.07     | 0.41     |
| Fly                                          | 0.07     | 0.02     |
| Unknown                                      | 0.05     | 0.03     |

[a] Day: $n$ = 958 detections (55 birds); night: $n$ = 650 detections (49 birds).
[b] $n$ = 23 birds with 10 or more paired day–night detections.
[c] Consecutive high tides at a specific roost. Day: $n$ = 632 runs (50 birds); night: $n$ = 284 runs (46 birds).
[d] Distance between consecutive high-tide locations. Day: $n$ = 35 birds with 10 or more paired day–day detections; night: $n$ = 21 birds with 10 or more paired night–night detections.
[e] Proportion of nonflying detections. Day: $n$ = 938 detections (55 birds); night: $n$ = 649 detections (49 birds).
[f] Proportion of all detections. Day: $n$ = 958 detections (55 birds); night: $n$ = 103 detections (10 birds with tip-switch transmitters).

used their nocturnal primary roost at least half the time, compared with only two birds (9%) during the day. Nineteen birds (83%) had higher fidelity to their nocturnal than to their diurnal primary roost.

Dunlin were more likely to switch roosts between consecutive diurnal high tides than at night. The average run (number of consecutive high tides a bird used a specific roost before switching) at night was 1.5× more than during the day (Table 1). Only 4% of diurnal runs (28 of 632) exceeded three consecutive high tides (maximum = 10 days), compared with 18% of nocturnal runs (51 of 284; maximum = 16 days). Dunlin moved greater distances between consecutive diurnal than nocturnal locations (Table 1; $t$ = 4.15, df = 38, $P < 0.0001$).

*Roost locations.*—Dunlin used different roosts night and day. Twenty-five roosts were used only by day, 27 only at night, and 34 both day and night (Fig. 1). On average, night roosts were farther from the tidal flats of Arcata Bay than day roosts (Table 1; $t$ = 2.32, df = 116, $P = 0.022$). Similarly, nocturnal primary roosts were farther from the tidal flats than diurnal primary roosts (Table 1; $t$ = 2.94, df = 23, $P = 0.007$). Only 2 of 23 birds (9%) had the same diurnal and nocturnal primary roost. On 96% of occasions (444 of 461 day–night pairs), individuals used different roosts at night than they had during the previous diurnal high tide. The mean distance moved between diurnal and successive nocturnal locations was 3,586.2 m ($n$ = 22 birds with ≥10 paired day–night detections), significantly greater than movements between consecutive diurnal (Table 1; $t$ = 5.05, df = 32, $P < 0.0001$) or nocturnal high tides ($t$ = 7.52, df = 38, $P < 0.0001$).

Diurnal and nocturnal habitat use were significantly different (Table 1; $\chi^2$ = 501.3, df = 5, $P < 0.001$). At night, Dunlin used pastures to a much greater extent, and used islands and manmade structures less often than during the

day. Thirteen of 19 (68%) nocturnal primary roosts were in pastures, compared with 4 of 11 (36%) diurnal primary roosts. In addition, Dunlin used different pastures night and day. Of the 4 diurnal primary roosts in pasture, only 1 was among the 13 nocturnal primary roosts in pasture. When individual Dunlin used pasture both during the day and on the successive nocturnal high tide, they switched roosts 95% of the time (142 of 150 day–night pairs).

*High-tide behavior.*—Time of day influenced high-tide behavior. Dunlin were more likely to feed during nocturnal than during diurnal high tides (Table 1). Also, Dunlin were more likely to be flying at dawn and dusk: 61% of all flying detections occurred within 2 h of sunrise or sunset. Dawn and dusk flying reflected two conspicuous Dunlin behaviors: individuals flying between diurnal and nocturnal roost sites, and sustained overwater flying by large flocks.

During diurnal high tides, tagged Dunlin occurred in flocks ranging from 1 to 10,000 individuals (mean = 2,015, $n$ = 560 flocks). Flying flocks (mean = 3,645, $n$ = 51) were larger than roosting (mean = 1,919, $t$ = 5.14, df = 58, $P$ < 0.0001, $n$ = 459) or feeding flocks (mean = 1,190, $t$ = 6.82, df = 86, $P$ < 0.0001, $n$ = 49). Flocks were larger in pastures (mean = 2,132, $n$ = 187) than in other habitats (mean = 1,689, $t$ = 3.16, df = 506, $P$ = 0.0008, $n$ = 321).

Although we could not conduct flock counts at night, several indirect lines of evidence suggested that flocks were smaller at night than during the day. Diurnal roost use was highly concentrated: among 59 diurnal roosts, 79% of detections occurred at just 10 roosts, and 2 of these each accounted for >18% of detections. By contrast, the top 10 night roosts accounted for 53% of detections, with 8% at the most-used roost. Eleven roosts constituted the diurnal primary roosts for all 23 birds, compared with 19 nocturnal primary roosts. On a per-survey basis, radiomarked Dunlin were distributed among more roosts at night than during the day: on average, 4.0 Dunlin were found at 2.7 roosts during the day and 3.7 roosts at night.

Anecdotal evidence also suggested smaller flocks at night. On dawn high tides, flocks seen approaching the bay from nocturnal pastures were always in the tens or low hundreds, and usually joined large flocks of 1,000–10,000 Dunlin near or over the bay. At dusk, Dunlin at large diurnal roosts broke off in small groups and flew toward nocturnal pasture roosts. On a number of occasions, we spotlighted pastures at night when radiomarked Dunlin were present and never flushed more than 5–10 birds.

*Age and sex.*—We found no differences between juvenile and adult Dunlin, day or night, in number of roosts used, fidelity to primary roost, average run of consecutive high tides at a roost, or behavior. However, there were significant age-related differences in habitat use, both day and night. Juveniles were less likely to use pasture than adults, both day (juveniles: 0.34, adults: 0.45; $\chi^2$ = 11.3, df = 1, $P$ < 0.001) and night (juveniles: 0.66, adults: 0.96; $\chi^2$ = 89.4, df = 5, $P$ < 0.001). Also, juveniles moved greater distances between consecutive nocturnal high tides (mean = 1,548.1 m) than adults (mean = 672.6 m; $t$ = 2.20, df = 12, $P$ = 0.048). Distances moved between consecutive diurnal high tides and between diurnal and successive nocturnal high tides were similar for adults and juveniles. The small number of females in our sample precluded analysis of sex effects.

## Discussion

*What is a roost?*—For shorebirds in coastal estuaries, a roost is generally considered a place where birds go to rest when primary intertidal foraging habitat is unavailable. Accordingly, we defined a "roost" as any location used by tagged Dunlin at high tide. During the day, flocks or individuals occasionally fed at high tide when the opportunity arose. At night, tip-switch transmitters indicated that incidence of high-tide foraging was substantially higher, though the small sample ($n$ = 10 birds) precludes broad conclusions from these data. Because our goal was to investigate the predictability of an individual's high-tide location, we included these locations in our analyses of "roosts."

*Roost use.*—We found striking differences between day and night in roost choice, fidelity to roosts, and distance moved between surveys. During the day, Dunlin were highly mobile, and spent only about a third of high tides at their primary roosts. The most mobile individual, an adult of unknown sex, used 18 different roosts in 32 diurnal high tides, switching roosts every 1.2 days and visiting its primary roost only four times. The cumulative curve of roosts over time did not reach an asymptote even after a month, which suggests very flexible use of roost sites.

During the day, Dunlin typically chose roosts directly adjacent to the intertidal mudflat, and they were generalists in regard to habitat.

At night, Dunlin were much more sedentary, though fidelity to specific roosts might still be characterized as moderate and highly variable. Average fidelity to the primary roost was 54%, and several birds showed complete fidelity to a single nocturnal roost. At night, accumulation of roosts clearly leveled off after 18 days, and no bird used more than eight roosts. Night roosts tended to be in pastures well away from the bay's edge, and Dunlin appeared to avoid common diurnal roosting habitats such as islands, pier pilings, and riprap.

The detection rate of radiomarked Dunlin was lower at night. This was perhaps the result of greater nocturnal use of terrestrial habitat, where terrain, structures, and vegetation were more likely to obstruct radio signals. Additionally, observers could not use visual clues to locate Dunlin flocks at night. However, if absences represent use of unknown roosts, different detection rates could potentially confound comparisons of roost fidelity and movements. To address this concern, we reanalyzed roost use with the assumption that each absence represented use of a different unknown roost. This naturally decreased fidelity to primary roost and increased number of roosts used, but the differences in both measures remained highly significant between day and night.

Differences between daytime and nighttime roost use by Dunlin may be related to foraging or antipredator strategies. Birds may forage in different habitats during day and night because of different foraging techniques or changing prey availability (Evans 1987, Mouritsen 1994, Shepherd 2001, Evans Ogden 2002). If birds roost near foraging areas (Furness 1973, Luís and Goss-Custard 2005, Rogers et al. 2006), this could result in the use of different roosts during day and night. Also, birds may forgo roosting if opportunities exist to continue feeding at high tide. The apparent increase in night feeding in the present study suggests that foraging influences nocturnal high-tide space use by Dunlin in Arcata Bay.

Type, abundance, and distribution of predators may vary with time of day, and so may the strategies shorebirds use to avoid them. During the day, Dunlin roost in large, tight flocks, thus reducing the danger for any single individual through cumulative vigilance and presence of numerous targets for predators (Cresswell 1994). At night, the benefit of large flocks is greatly reduced, because darkness prevents early visual detection of predators, which can easily detect and surprise a flock. Therefore, shorebirds tend to occur in smaller flocks at night (Evans Ogden 2002, Gillings et al. 2005), which is consistent with our observations.

In response to attacks by diurnal predators, such as Peregrine Falcons (*Falco peregrinus*) and Merlins (*F. columbarius*), roosting Dunlin flocks flush readily, often remaining airborne for several minutes or departing the roost altogether (J. Conklin pers. obs.). At night, Dunlin tend to freeze rather than flush when disturbed (Mouritsen 1992). Assuming equal predation pressure day and night, this behavioral difference would result in fewer nocturnal movements by Dunlin and predicts the nocturnal patterns we observed: higher fidelity to roosts, shorter distances moved, and lower incidence of high-tide flying. Alternatively, decreased nocturnal movements may simply reflect lower rates of predation or disturbance.

The increase in high-tide flying near dawn and dusk may also be related to predation risk. Sustained high-tide flying by Dunlin has been linked to the absence of safe, open-roosting habitat (Brennan et al. 1985, Dekker 1998, Hötker 2000). If antipredator strategies differ between day and night, dawn and dusk may be transitional times, when high-tide flying, despite its energetic cost, is preferable to roosting in a situation with high predation risk. Other Dunlin studies have reported crepuscular movements between diurnal and nocturnal habitats (Ruiz et al. 1989, Sanzenbacher and Haig 2002).

Rogers et al. (2006) demonstrated that roost-selection criteria differed between day and night. Great Knots (*C. tenuirostris*) and Red Knots (*C. canutus*) chose diurnal roosts on the basis of proximity to feeding areas and microclimate, but used safer, more distant roosts at night. Similarly, nocturnal roosts in our study were farther from the tidal flat, and birds moved great distances between diurnal and nocturnal roosts. In addition, Rogers et al. (2006) suggested that shorebirds are less able to constantly evaluate roost quality at night, because of decreased visibility. This would predict higher fidelity to nocturnal roosts, which is consistent with our findings.

*Is roost use traditional?*—Some facets of Dunlin roosting behavior support the notion that roosts are traditional. Seventy-nine percent of diurnal detections occurred at just 10 of 86 roosts, and 11 roosts constituted the primary roosts for all 23 birds. The high use of these roosts may span years; five were among the six top-ranked roosts used by this population in January–March 2002 (Colwell et al. 2003). In particular, the top-ranked Dunlin roost in that study (Klopp Lake) was the most-used roost in this study as well, and the diurnal primary roost of 7 of 23 birds. Thus, several roosts within Arcata Bay can be considered traditional from the perspective of the population. By contrast, the low fidelity to primary roosts and the fact that radiomarked birds used most roosts infrequently contradict the view of roosts as traditional. Rather than roosting at the same location every high tide, Dunlin demonstrated high variation in roost choice. This was especially true during the day, when only 2 of 23 birds used their primary roosts more than half the time.

Dunlin showed high fidelity to Arcata Bay, which is consistent with other studies reporting limited movements once shorebirds reach their wintering grounds (Pienkowski and Clark 1979; Smith et al. 1992; Rehfisch et al. 1996, 2003; Warnock and Takekawa 1996; Burton 2000; Drake et al. 2001; Shepherd 2001; Sanzenbacher and Haig 2002). In the present study, we tested whether this widely observed phenomenon held up when applied to roosts defined at the finest possible spatial scale. That it did not, especially during the day, emphasizes that site fidelity is scale-dependent.

However, our findings are specific to Dunlin wintering in Humboldt Bay. Fine-scale fidelity to roosts is likely to vary among species and sites, depending on availability of alternative roosts, predictability of food resources, and levels of disturbance and predation. For example, Red Knots had higher roost fidelity in tropical Mauritania than in the temperate Wadden Sea (Leyrer et al. 2006). Ideally, this comparative approach could be applied to estuaries worldwide, accompanied by foraging, disturbance, and mortality data. Ranking sites on a continuum from low to high fidelity would potentially reveal a wealth of knowledge for understanding ecology and future management of nonbreeding shorebirds.

*Pasture use.*—Grazed pasture was the most-used habitat type during high tide, accounting for 38% of diurnal and 76% of nocturnal detections. Four of 11 diurnal primary roosts and 13 of 19 nocturnal primary roosts were in grazed pasture. Several studies identified the importance of pastures as alternative foraging areas for wintering shorebirds (Townshend 1981, Rottenborn 1996, Colwell and Dodd 1997, Shepherd 2001, Evans Ogden et al. 2006); our results also emphasize the importance of pastures as roosting habitat. The persistence of agricultural fields may be crucial for supporting a resident winter Dunlin population in Humboldt Bay (Rottenborn 1996, Butler 1999, Shepherd and Lank 2004).

Pasture use was higher at night, which is consistent with Dunlin in the Fraser River Delta (Evans Ogden 2002, Shepherd and Lank 2004). However, mean peak tide during the present study was higher during the day (2.21 m) than at night (1.81 m). Mudflat remained available (peak tide < 1.6 m) during 21% of nocturnal high tides, compared with 5% of diurnal high tides. Conversely, saltmarsh habitat was inundated (peak tide > 2.4 m) on only 1% of nocturnal high tides, compared with 30% of diurnal high tides. Thus, pasture use was highest when availability of alternative habitat was greatest, which further emphasizes the effect of time of day on pasture use.

Juvenile Dunlin used pasture less than adults and accounted for nearly all nonpasture detections at night. Age-related spatial differences in Dunlin (Ruiz et al. 1989, Warnock 1990, Evans Ogden et al. 2006) may be explained by dominance, local experience, or tradeoffs between profitability and safety. In the Fraser River Delta, terrestrial habitats contributed more to juvenile than to adult Dunlin diets (Evans Ogden et al. 2006). Although our study was restricted to high tide, the reverse pattern of age-related pasture use suggests that different factors influence Dunlin in Arcata Bay.

*Conservation implications.*—Individual Dunlin used multiple high-tide roosts and had low fidelity to primary roosts. This suggests that Dunlin in Humboldt Bay are not limited by available roost sites. Even the most-used roosts in our study were often unused for many consecutive high tides, which is consistent with Colwell et al. (2003). This flexibility in roost use by individuals and the population may indicate that the loss of any given roost (e.g., because of development or human disturbance) would

have little detrimental effect on the local Dunlin population. However, the effect of time of day on roost choice illustrates that Dunlin require different roosts under different environmental conditions. Also, the availability of alternative roosts may make Dunlin less vulnerable to predation and human disturbance (Gill et al. 2001). The question of how many roosts can be lost before a measurable population effect is detected remains unknown. Our results emphasize that diurnal observations alone may misrepresent shorebird habitat requirements (Gillings et al. 2005), and that knowledge of habitat use across the full range of environmental conditions is necessary for appropriate management of shorebird habitat. In addition, it is critical that data used to assess possible effects of habitat loss be at a spatial scale appropriate to those effects.

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