

SEASONAL VARIATION IN DIURNAL AND NOCTURNAL DISTRIBUTIONS OF NONBREEDING SHOREBIRDS AT NORTH HUMBOLDT BAY, CALIFORNIA¹

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Abstract. Recent studies of nocturnal foraging by shorebirds (Charadriiformes: Charadrii) suggest that many species feed at night. Much of this research has been qualitative and/or restricted to a small portion of the annual cycle (e.g., a few nights or one season) making it difficult to evaluate the extent to which nocturnal foraging varies seasonally. Consequently, we examined seasonal variation in abundance and distribution of diurnal and nocturnal foraging shorebirds from 10 Jan 1992-10 Jan 1993 at North Humboldt Bay, California.

Shorebirds foraged primarily during the day. Overall, day/night frequency of occurrence (percent of censuses with birds) was 87%/48%. In fall, frequency of occurrence of shorebirds differed less between day and night (day/night: 82%/64%) than during spring (day/night: 79%/14%) or winter (day/night: 100%/42%). Moreover, nocturnal abundance of Marbled Godwit (*Limosa fedoa*), Willet (*Catoptrophorus semipalmatus*), dowitchers (*Limnodromus scolopaceus* and *L. griseus*), and Black-bellied Plover (*Pluvialis squatarola*) peaked in fall, whereas diurnal abundance of these species peaked in winter (Marbled Godwit, Black-bellied Plover, and dowitchers) or spring (Willet).

Taxa varied in day/night patterns. For Scolopacids, diurnal abundance significantly exceeded nocturnal abundance. However, abundance of American Avocet (*Recurvirostra americana*), Black-bellied Plover, and Semipalmated Plover (*Charadrius semipalmatus*) did not differ significantly between day and night. Our results suggest that a researcher's choice of season or taxa may influence observed patterns of diurnal and nocturnal distributions of shorebirds considerably.

Key words: shorebirds; nocturnal foraging; seasonal variation; nonbreeding distributions; Humboldt Bay.

INTRODUCTION

The extent to which birds forage at night has received considerable attention (McNeil 1991, McNeil et al. 1993). Increasing evidence suggests that many shorebird species (Charadriiformes: Charadrii) of several families forage at least occasionally at night throughout the year and across a broad range of latitudes (Dodd 1995). However, the relative frequency with which shorebirds forage nocturnally is largely unknown (sensu Robert et al. 1989, Mouritsen 1994).

Robert et al. (1989) suggested that shorebirds forage regularly at night in response to the periodicity and availability of tidally influenced feeding habitat. However, research conducted mainly at northern latitudes suggests that shorebirds are predominately diurnal feeders. Accounts of shorebirds not foraging at night (Feare 1966, Hartwick and Blaylock 1979, Puttick 1979,

Goss-Custard et al. 1977, Baker 1981, Barnard and Thompson 1985, Zwarts et al. 1990) or to a limited extent (Heppleston 1971, Evans 1976, Tree 1979, Pienkowski 1982, Hockey 1984, Pienkowski et al. 1984, Maron and Myers 1985, Zwarts et al. 1990, Manseau and Ferron 1991) are frequent in the literature. Moreover, evidence suggests that nocturnal foraging by shorebirds at northern latitudes is confined principally to winter (Goss-Custard 1969, Heppleston 1971, Pienkowski 1982, Stenzel et al. 1976, Evans and Harris 1994). The ecological explanation for this pattern has been that shorebirds at northern latitudes are forced to feed at night in winter because energy requirements cannot be met during periods of short day length (Goss-Custard 1969, Heppleston 1971, Goss-Custard et al. 1977, Puttick 1984, P. R. Evans 1988).

However, shorebirds forage extensively at night in the tropics (McNeil and Robert 1988, Robert and McNeil 1989, Robert et al. 1989, Swennen 1990, Zwarts et al. 1990, Rompré and McNeil 1994), where for most of the year day length is longer and temperatures are warmer than at

¹ Received 26 June 1995. Accepted 9 February 1996.

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northern latitudes (Robert et al. 1989). Studies conducted at southern and northern latitudes indicate that shorebirds also forage at night during spring (Burger 1984, Swennen 1990, Zwarts 1990, Zwarts et al. 1990, Rompré and McNeil 1994) and fall (Manseau and Ferron 1991; Mouritsen 1992, 1994; Rompré and McNeil 1994).

Protection and management of shorebird populations requires complete knowledge of their activity patterns during both day and night. However, it is difficult to evaluate the extent to which distributions of foraging shorebirds vary between day and night. Few studies (Zwarts et al. 1990, Robert et al. 1989, Manseau and Ferron 1991, Mouritsen 1994, Rompré and McNeil 1994) quantified abundance and/or frequency of occurrence of shorebirds on feeding grounds during both day and night. In addition, few studies observed shorebirds for more than a few nights (Dodd 1995). Only one study (Rompré and McNeil 1994) quantified both diurnal and nocturnal abundance of a foraging shorebird for more than one season. In this paper, we compare diurnal and nocturnal foraging patterns of several species of shorebirds in a northern latitude, coastal bay for a year. Our objectives are to: 1) examine day/night variation in abundance of foraging birds and frequency of occurrence of birds; and 2) assess seasonal and interspecific variation in day/night patterns of birds.

STUDY AREA AND METHODS

We studied shorebirds from 10 January 1992–10 January 1993 at the Arcata Marsh Project in North Humboldt Bay, Humboldt County, California (Fig. 1). North Humboldt Bay is the largest of three basins comprising Humboldt Bay with approximately 12.2 km² of exposed tidal mud flat at mean low tide (Costa and Stork 1984). Local tides are characterized by two uneven high and low tides each 24 hours. Gerstenberg (1972) and T.J. Evans (1988) provide detailed descriptions of the study area.

We established four 20 × 50 m study plots (marked with four 5 × 5 cm wooden corner stakes) on high elevation mud flats (Gerstenberg 1972, 1979; Evans and Harris 1994) within 50 m of the shoreline in areas of high shorebird use (Dodd, pers. observ.) (Fig. 1). For each plot, we censused twice within a 24-hour period each week: once during daylight and once during darkness on successive rising tides. We censused dur-

ing rising tides because shorebirds foraged along the advancing tide edge eventually congregating near the shoreline, which allowed close observation. We censused only one plot within a 24-hour period. Within each week, we randomly chose a 24-hour period in which to census a plot from 24-hour periods that had tides of sufficient magnitude so the water reached the plot both in darkness and in daylight. However, these tidal conditions did not occur for four to seven days on 13 occasions in mid-winter and summer. Consequently, we conducted additional censuses during other weeks. This resulted in a fairly even sampling effort across the year and from all hours of a 24-hour period (Dodd 1995). We categorized (a priori) censuses by season based on migratory patterns of shorebirds in the Humboldt Bay area (Gerstenberg 1979, Harris 1991) as follows: 1) fall: 1 July–30 November ($n = 85$); 2) winter: 1 December–17 March ($n = 50$); 3) spring: 18 March–8 May ($n = 29$); and 4) summer: 9 May–30 June ($n = 22$).

We conducted day censuses between nautical sunrise and nautical sunset and night censuses between nautical sunset and nautical sunrise. We considered nautical sunrise and nautical sunset to occur when we could and could not see, respectively, channel markers located 100 m away for day censuses and 50 m away for night censuses. Overall, 3.5% of censuses (three day and ten night) began or ended within 15 minutes of nautical sunrise or sunset. We conducted each census for 45 minutes beginning when the edge of the rising tide crossed the corner stake of a plot.

We observed birds with binoculars from a vehicle parked 21–51 m away on dikes. We arrived at observation points at least 30 minutes before a census to minimize disturbance to birds. At night, we verified observations by briefly (three to five seconds) illuminating plots with a 400,000 candlepower spotlight (Black Max Q-beam, Brinkmann Corp., Dallas, TX) covered with a red snap-on filter (Brinkmann Corp.). We used a red filter because it reduced spotlight glare and did not startle birds as often as unfiltered light (Dodd, unpubl.). However, during foggy conditions, we used an amber filter because amber-filtered light best penetrated fog. We illuminated plots immediately after we had recorded data on species, abundance, and behavior (see below) of birds. Additionally, we illuminated a plot whenever we: 1) heard, but could not see shorebird(s)

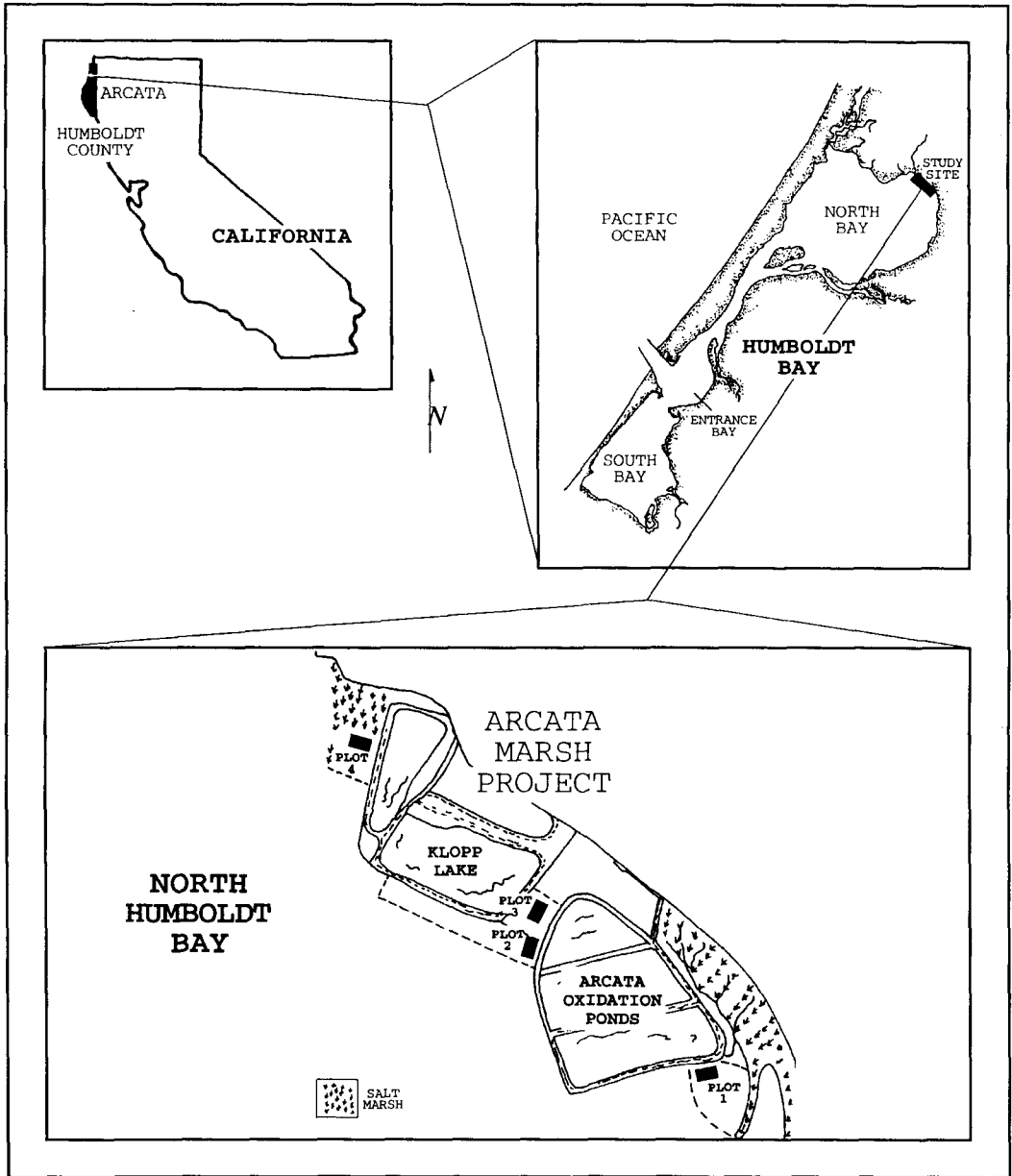


FIGURE 1. Location of four 20 × 50 m plots (shaded rectangles) within North Humboldt Bay, Humboldt County, California. Dashed lines represent four areas encompassing plots.

or 2) had not detected shorebirds for five to seven minutes.

For each census, we recorded the maximum number of foraging birds of each species. We also categorized behaviors of nonfeeding birds as fol-

lows: 1) loafing; 2) comfort movements including bathing and preening; and 3) other (e.g., alert and agonistic behavior).

At night, we had difficulty identifying some closely related species. Consequently, we com-

bined observations of Western and Least Sandpipers (*Calidris mauri* and *C. minutilla*, respectively) into the group "small sandpipers" and Long-billed and Short-billed Dowitchers (*Limnodromus scolopaceus* and *L. griseus*, respectively) into the group "dowitchers". In subsequent analyses we refer to these groups as species.

To evaluate whether or not data from plots were representative of surrounding mud flats, we recorded the presence of shorebirds on four areas (area 1 = 1.8 ha, area 2 = 3.7 ha, area 3 = 1.5 ha, area 4 = 2.3 ha) encompassing plots (Fig. 1). Additionally, at night, we recorded whether or not we heard shorebirds calling from any location on mud flats encompassing plots. We noted the species and approximate location of vocalizing birds; we disregarded calls coming from known shorebird roosts and from birds flying overhead.

DATA SUMMARY AND ANALYSIS

Data Summary. We omitted summer observations from analyses because we observed few shorebirds during this period (Dodd 1995). Additionally, we removed July–September censuses ($n = 51$) from analyses of Dunlin (*Calidris alpina*) because this species is a late fall migrant and usually does not arrive at Humboldt Bay until late September (Gerstenberg 1972, Dodd 1995). With the exception of American Avocet (*Recurvirostra americana*), we used plot data for analyses of all species because plot and area data obtained similar day/night and seasonal patterns of frequency of occurrence. For American Avocet, we used area data (instantaneous day and night counts [$n = 133$] of foraging birds) because data from plots did not represent the surrounding mud flat (Dodd 1995). We examined day/night patterns of foraging shorebirds using two response variables: frequency of occurrence and foraging abundance.

Frequency of Occurrence. For each species, we determined seasonal (fall, winter, and spring) percent of day and night censuses in which at least one shorebird occurred on plots.

Foraging Abundance. To reduce temporal dependence (of abundances) among multiple censuses conducted close in time (Hurlbert 1984), we calculated monthly averages summarized from data on the abundance of foraging shorebirds for each plot. However, seasonal intervals divided

the months of March and May. Consequently, we averaged counts from 1–8 May and all of April together, whereas we averaged counts from 1–17 March and 18–31 March separately. Excluding summer, this produced averages for each species per plot for 11 day and 11 night monthly-intervals (see Dodd 1995 for distribution of counts among plots and monthly intervals). A problem with averaging data across monthly intervals was that we conducted only one census for plots 3 and 4 during 1–17 March and 18–31 March, respectively. We used observed values (rather than means) for these data points. Hereafter, all references of abundance are to foraging individuals.

Comparisons of Day/Night and Seasonal Patterns. For each species, we compared day/night and seasonal abundances using nonparametric (rank-transformation; Conover 1980, Dowdy and Wearden 1991) two-factor ANOVA (Hintze 1992). We used day/night, season (fall, winter, and spring) and the interaction term (day/night \times season) as main effects; and ranked abundance (monthly-interval means) as the response variable. We used nonparametric ANOVAs because data did not meet assumptions of normality and homogeneity of variances (Dowdy and Wearden 1991). We used a relatively conservative alpha level of significance of <0.01 because we conducted a separate comparison for each species.

RESULTS

OVERALL PATTERNS.

We observed 12 and 11 species during day and night censuses, respectively (Table 1). A few uncommon species occurred exclusively in the day (Long-billed Curlew, *Numenius americanus*; Wilson's Phalarope, *Phalaropus tricolor*; and Baird's Sandpiper, *Calidris bairdii*) or night (Lesser Yellowlegs, *Tringa flavipes* and Killdeer, *Charadrius vociferus*). Most shorebirds (93% of diurnal observations and 99% of nocturnal observations) observed on plots foraged. We observed nearly seven times as many shorebirds during the day (22,180) than at night (3,237). Moreover, shorebirds occurred in a greater proportion of day censuses (87%) than night censuses (48%) (Table 2). However, frequency of occurrence of shorebirds differed less between day and night during fall (day/night: 82%/64%)

TABLE 1. Occurrence, number of birds, and behaviors of shorebird species observed on plots from 10 Jan 1992–10 Jan 1993 ($n = 186$ paired [day and night] censuses).

Species	Occurrence ^b		Number birds ^c		Percent of birds ^a							
	Day	Night	Day	Night	Foraging		Loafing		Comfort movement		Other	
					Day	Night	Day	Night	Day	Night	Day	Night
American Avocet	93	45	883	1,213	98.3	97.0	0.8	2.9	0.8	0.0	0.1	0.0
Marbled Godwit	100	11	2,618	37	81.0	100.0	2.6	0.0	13.1	0.0	3.3	0.0
Willet	67	5	824	7	62.0	100.0	20.9	0.0	16.7	0.0	0.4	0.0
Dowitchers	59	20	1,571	159	93.6	100.0	6.1	0.0	0.2	0.0	0.2	0.0
Black-bellied Plover	18	22	47	23	34.0	100.0	66.0	0.0	0.0	0.0	0.0	0.0
Semipalmated Plover	10	17	21	43	100.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
Dunlin	62	18	4,447	736	86.9	99.3	10.6	0.0	2.2	0.7	0.3	0.0
Small sandpipers	80	32	11,752	1,015	100.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
Killdeer	0	1	0	1	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
Long-billed Curlew	4	0	10	0	80.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0
Greater Yellowlegs	5	2	5	2	100.0	50.0	0.0	0.0	0.0	0.0	0.0	50.0
Lesser Yellowlegs	0	1	0	1	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
Baird's Sandpiper	1	0	1	0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Wilson's Phalarope	1	0	1	0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Shorebirds ^d	144	79	22,180	3,237	93.0	98.7	3.8	1.1	2.7	0.1	0.5	0.0

^a For each species, percent of number of birds exhibiting each behavior.

^b Total number of censuses in which each species occurred.

^c For each species, total number of shorebirds observed during 186 day and 186 night censuses.

^d All species of shorebirds included.

than during winter (day/night: 100%/42%) or spring (day/night: 79%/14%).

INDIVIDUAL SPECIES PATTERNS

We confined subsequent analyses to the eight most numerous and frequently occurring species on plots and areas.

Frequency of Occurrence Patterns. Most species occurred primarily during the day during fall (six of eight species), winter (seven of eight species), and spring (seven of eight species) (Table 2). However, Semipalmated Plover (*Charadrius*

semipalmatus) occurred only at night on plots in spring (Table 2). Six of eight species occurred at night mainly during fall (Table 2). Moreover, seven of eight species called at night from mud flats during a greater proportion of fall than spring or winter censuses (Fig. 2). By contrast, during the day, five of eight species' occurrences peaked in winter (Table 2).

Comparisons of Day/Night and Seasonal Patterns. For five of eight species, day abundance significantly exceeded night abundance (Tables 3, 4). A significant interaction between day/night and seasonal effects resulted for Marbled God-

TABLE 2. Temporal (day/night and seasonal) variation in frequency of occurrence of shorebirds on plots. For each species, values are the percent of censuses in which at least one shorebird occurred on plots.

Species	Fall ($n = 85$)		Winter ($n = 50$)		Spring ($n = 29$)		Total ^a ($n = 164$)	
	Day	Night	Day	Night	Day	Night	Day	Night
American Avocet ^b	77.6	60.0	79.6	63.2	69.0	32.1	76.7	56.2
Marbled Godwit	55.3	12.9	74.0	0.0	55.2	0.0	61.0	6.7
Willet	25.9	4.7	58.0	2.0	55.2	0.0	40.9	3.1
Dowitchers	29.4	22.4	56.0	2.0	20.7	0.0	36.0	12.2
Black-bellied Plover	9.4	24.7	16.0	2.0	6.9	0.0	11.0	13.4
Semipalmated Plover	10.6	16.5	2.0	2.0	0.0	6.9	6.1	10.4
Dunlin ^c	73.5	32.4	56.0	8.0	31.0	10.3	54.9	15.9
Small sandpipers	55.3	21.2	56.0	22.0	17.2	10.3	48.8	19.5
Shorebirds ^d	82.4	63.5	100.0	42.0	79.5	13.8	86.7	48.2

^a Summer censuses ($n = 22$) excluded.

^b Area data used instead of plot data. Number of censuses: fall = 85; winter = 49; spring = 28 (night), 29 (day); total = 163 (day), 162 (night).

^c Early fall censuses excluded. Number of censuses: fall = 34; total = 113.

^d All species of shorebirds included.

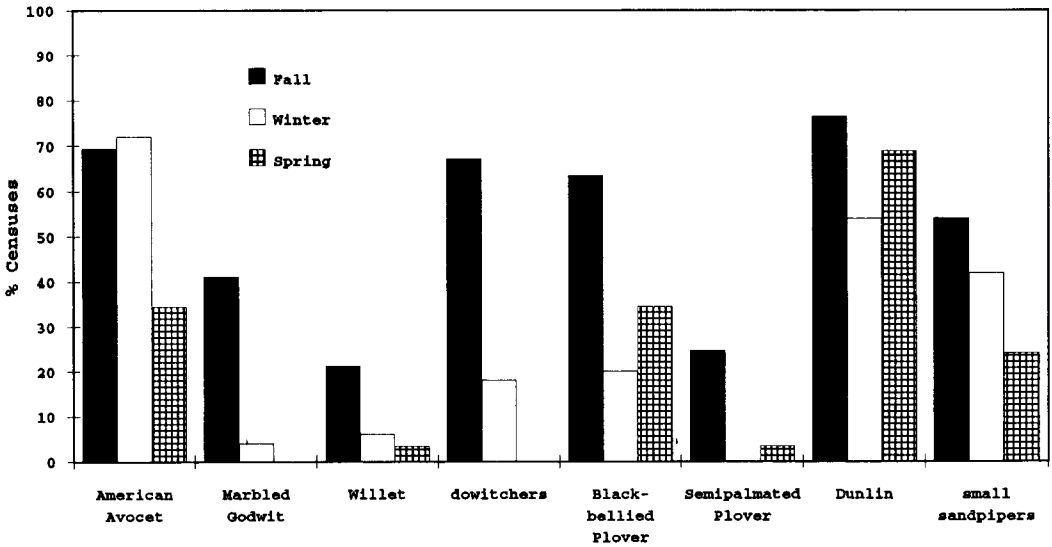


FIGURE 2. Seasonal variation in nocturnal vocalizations by the eight most abundant species. Histograms indicate the percent of fall, $n = 85$ (Dunlin: $n = 34$), winter ($n = 50$), and spring ($n = 29$) censuses in which birds on mud flats encompassing plots called at night.

wit (*Limosa fedoa*), Willet (*Catoptrophorus semipalmatus*), dowitchers, and Black-bellied Plover (*Pluvialis squatarola*) (Table 3). Nocturnal abundance of these species peaked in fall, whereas diurnal abundance peaked in either winter (Marbled Godwit, Black-bellied Plover, and dowitchers) or spring (Willet) (Table 4). For Marbled Godwit, Willet, and dowitchers, day abundance exceeded night abundance in fall, winter, and spring. In addition, Black-bellied Plover foraged in greater abundance in day than at night, with the exception of fall when night abundance exceeded day abundance. However, overall day and night abundance of Black-bellied Plover did not differ significantly (Table 3).

INTERSPECIFIC VARIATION

Day/night patterns of shorebirds varied among taxa. For members of the family Charadriidae (plovers) and Recurvirostridae (American Avocet), abundance did not differ significantly between day and night (Table 3). By contrast, all members of the family Scolopacidae (sandpipers) foraged in significantly greater abundance in the day than at night (Tables 3, 4). A comparison of day/night ratios of abundance and occurrence among taxa suggests American Avocet and plovers were relatively more nocturnal than sandpipers (Table 5). Among Scolopacids, smaller-bodied species (Dunlin and small sandpipers)

were relatively more nocturnal than larger-bodied species (Marbled Godwit and Willet).

DISCUSSION

This study quantifies substantial interspecific and temporal (seasonal) variation in the distribution of day and night feeding shorebirds at a temperate latitude site. Shorebirds foraged principally during the day. However, day/night patterns varied seasonally. Nocturnal foraging by shorebirds of most species predominated in fall (Tables 2–4; see also Fig. 2). By contrast, during the day, a few species occurred more frequently and in greater abundances in winter.

It is difficult to compare our results with other studies because most researchers restricted observations to a single season and/or did not quantify abundance or occurrence of shorebirds between day and night. However, our findings generally contradict those reported elsewhere. For example, other studies conducted at northern latitudes have found that shorebirds foraged at night more frequently and in higher numbers during winter periods (Goss-Custard 1969, Heppleston 1971, Pienkowski 1982, Evans and Harris 1994).

Our results also differ from patterns reported for studies conducted at southern latitudes. For example, Robert et al. (1989) reported that shorebirds wintering in northeastern Venezuela fed more often and in greater numbers at night.

TABLE 3. Comparison of diurnal and nocturnal abundances (response variable) of eight shorebird taxa presented as results of nonparametric two-factor ANOVAs with day/night, season (fall, winter, and spring), and the interaction term (day/night \times season) as main effects.

Species	Source of variation	df	F	P-value
American Avocet*	Day/night	1	2.62	0.11
	Season	2	1.57	0.21
	Day/night \times season	2	1.21	0.30
	Error	80		
Marbled Godwit	Day/night	1	115.01	<0.0001
	Season	2	0.17	0.84
	Day/night \times season	2	9.48	0.0002
	Error	82		
Willet	Day/night	1	93.22	<0.0001
	Season	2	3.41	0.04
	Day/night \times season	2	6.71	0.002
	Error	82		
Dowitchers	Day/night	1	27.50	<0.0001
	Season	2	2.65	0.08
	Day/night \times season	2	9.67	0.0002
	Error	82		
Black-bellied Plover	Day/night	1	0.18	0.67
	Season	2	4.54	0.013
	Day/night \times season	2	6.24	0.003
	Error	82		
Semipalmated Plover	Day/night	1	1.79	0.18
	Season	2	4.58	0.013
	Day/night \times season	2	0.54	0.58
	Error	82		
Dunlin	Day/night	1	20.81	<0.0001
	Season	2	3.87	0.03
	Day/night \times season	2	2.48	0.09
	Error	58		
Small sandpipers	Day/night	1	19.84	<0.0001
	Season	2	4.70	0.012
	Day/night \times season	2	2.03	0.14
	Error	82		

* Area data used instead of plot data.

Robert et al.'s study occurred during a three-month winter period, so a complete evaluation of seasonal variation was not possible. Recently, Rompré and McNeil (1994) compared the proportion of Willets foraging in the day and night from October–May in northeastern Venezuela. Willets foraged as often at night as during the day, with the exception of fall (October and November) when they fed more at night. In our study, nocturnal abundance of Willets also peaked in fall, but day abundance exceeded night abundance during all seasons.

Other southern and northern latitude studies have reported shorebirds foraging at night during migratory periods. For example, Zwarts et al. (1990) compared densities of several shorebird species during spring on a 6.9 ha area in the day and a 2.5 ha area at night on the Banc d'Arguin,

Mauritania. Most species (including Dunlin and Black-bellied Plover) foraged at higher densities during the day, although nocturnal densities of Red Knot (*Calidris canutus*) and Bar-tailed Godwit (*Limosa lapponica*) exceeded diurnal densities during their premigration period. Manseau and Ferron (1991) compared abundance of Semipalmated Sandpiper (*Calidris pusilla*) between day and night on four 50 \times 50 m plots at the Bay of Fundy during a fall migratory stopover. More Semipalmated Sandpipers occurred in the day than at night. Recently, Mouritsen (1994) compared diurnal and nocturnal densities of Dunlin in September and October on a mud flat and a *Corophium*-bed at the Danish Wadden Sea. Interestingly, diurnal densities exceeded nocturnal densities on the mud flat, but the reverse occurred on the *Corophium*-bed. Mourit-

TABLE 4. Mean (\pm SE) abundance (prior to rank transformation) and total number of birds of each species on plots.

Species	Day/night	Mean* \pm SE (total number ^b)			
		Fall	Winter	Spring	
American Avocet ^c	day	21.93 \pm 6.32 (1,404)	38.36 \pm 12.62 (989)	25.10 \pm 8.20 (561)	
	night	24.55 \pm 8.14 (1,604)	49.83 \pm 14.93 (1,750)	11.75 \pm 10.22 (212)	
Marbled Godwit	day	4.91 \pm 2.36 (406)	24.73 \pm 8.44 (1,352)	20.78 \pm 12.92 (362)	
	night	0.44 \pm 0.15 (37)	0.00 \pm 0.00 (0)	0.00 \pm 0.00 (0)	
Willet	day	0.59 \pm 0.20 (50)	4.96 \pm 2.12 (277)	11.49 \pm 7.07 (184)	
	night	0.05 \pm 0.03 (5)	0.03 \pm 0.03 (2)	0.00 \pm 0.00 (0)	
Dowitchers	day	4.78 \pm 2.04 (403)	16.89 \pm 4.05 (967)	2.69 \pm 1.69 (100)	
	night	1.89 \pm 0.91 (149)	0.14 \pm 0.14 (9)	0.00 \pm 0.00 (0)	
Black-bellied Plover	day	0.08 \pm 0.05 (7)	0.18 \pm 0.09 (8)	0.04 \pm 0.04 (1)	
	night	0.27 \pm 0.07 (22)	0.03 \pm 0.03 (1)	0.00 \pm 0.00 (0)	
Semipalmated Plover	day	0.23 \pm 0.11 (19)	0.04 \pm 0.04 (2)	0.00 \pm 0.00 (0)	
	night	0.28 \pm 0.12 (24)	0.21 \pm 0.21 (10)	0.33 \pm 0.28 (9)	
Dunlin ^d	day	39.23 \pm 18.71 (1,308)	39.48 \pm 16.89 (2,268)	7.51 \pm 4.19 (289)	
	night	13.96 \pm 10.79 (454)	0.92 \pm 0.54 (49)	8.77 \pm 7.03 (227)	
Small sandpipers	day	99.83 \pm 25.94 (8,682)	44.62 \pm 15.25 (2,094)	20.89 \pm 17.36 (976)	
	night	9.81 \pm 4.67 (876)	1.32 \pm 0.92 (66)	2.79 \pm 2.34 (71)	

* For each species, averages of counts of foraging birds on each plot in day and night per monthly-intervals. Number of monthly-interval means: 44 day and 44 night divided into 20 (fall), 16 (winter), and 8 (spring).

^b Total number of foraging birds per source of variation.

^c Area data used instead of plot data. Number of monthly-interval means: 43 day and 43 night divided into 20 (fall), 15 (winter), and 8 (spring).

^d Early fall censuses excluded. Number of monthly-interval means: 32 day and 32 night divided into 8 (fall), 16 (winter), and 8 (spring).

sen (1994) argued that greater prey availability at night on the *Corophium*-bed explained this finding.

Despite methodological differences among studies, one generality emerges from studies conducted at northern latitudes: nocturnal foraging is less prevalent than diurnal foraging and it varies throughout the annual cycle. However, there is less agreement regarding the season in which nocturnal foraging becomes more common. We suspect that differing methodologies as well as differences among locations contribute to variation in these patterns.

CAUSES OF SEASONAL VARIATION

Two non-mutually exclusive hypotheses have been proposed to explain seasonal variation in nocturnal foraging patterns of shorebirds (see McNeil 1991). The "supplemental" hypothesis postulates that shorebirds forage at night when diurnal intake of prey is not sufficient to meet daily energetic requirements (e.g., mid-winter periods at northern latitudes, Heppleston 1971). By contrast, the "preferential" hypothesis posits that shorebirds forage at night to avoid diurnal predators (Robert et al. 1989, Morrier and McNeil 1991) or to take advantage of increased prey activity at night (Dugan 1981, Pienkowski 1983b,

Pienkowski et al. 1984, Evans 1987, Robert and McNeil 1989, Mouritsen 1994). The following observations offer insight into the explanatory power of these two hypotheses in Northern California.

First, shorebirds typically go through a complete body molt during fall, whereas spring mi-

TABLE 5. Taxonomic comparisons of day and night abundance and frequency of occurrence of shorebirds on plots, presented as ratios of day/night values.

Taxa	Ratio Day/night	
	Mean abundance ^a	Frequency of occurrence ^b
Family Charadriidae:		
Semipalmated Plover	0.5	0.6
Black-bellied Plover	0.7	0.8
Family Recurvirostridae:		
American Avocet ^c	0.9	1.4
Family Scolopacidae:		
Dunlin	5.1	3.5
Dowitchers	9.7	2.9
Small sandpipers	12.0	2.5
Marbled Godwit	75.1	9.1
Willet	138.7	13.2

^a Calculated from monthly-interval means presented in Table 4.

^b Calculated from frequency of occurrence data presented in Table 2.

^c Area data used instead of plot data.

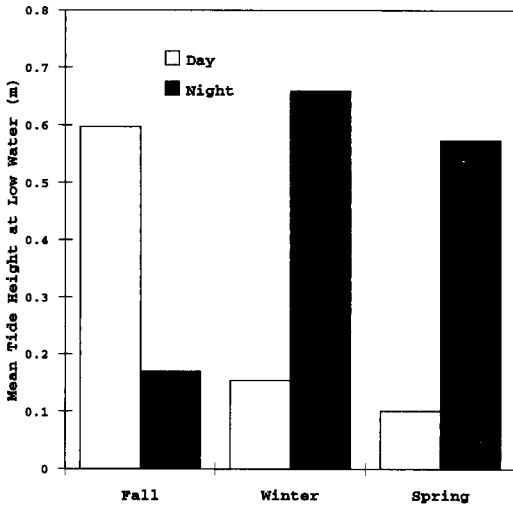


FIGURE 3. Seasonal and day/night variation in mean tide height (m) at low water from 10 Jan 1992–10 Jan 1993 (Tidelogs 1992, 1993). Fall, winter, and spring low tides greater than one half in daylight ($n = 260$) and darkness ($n = 245$) were included.

grants replace only body feathers (Hale 1980, Prater 1981, Evans and Pienkowski 1984). The pre-basic molt (fall) is energetically more costly than the pre-alternate molt (spring) (Hale 1980). Fall-molting birds may forage at night more than spring-molting birds to meet higher energy requirements associated with the pre-basic molt (sensu Evans and Pienkowski 1984, McNeil 1991). Alternatively, a temporal expansion of foraging by fall-molting birds may result from reduced mobility (sensu Hale 1980, Evans and Pienkowski 1984).

Second, flocks of fall-migrating shorebirds at Humboldt Bay are composed of both juveniles and adults (Gerstenberg 1972). Immature birds are relatively inefficient foragers compared to adults (Puttick 1979, 1984; Pienkowski and Evans 1984) and juveniles may need to forage at night in the fall to supplement diurnal intake of food.

Finally, seasonal variation in environmental conditions contribute to variation in day/night patterns of shorebirds at North Humboldt Bay (Dodd and Colwell, unpubl.). Fall tides tend to be lowest at night, whereas, spring and winter tides tend to be lowest in the day (Fig. 3). Fall migrants may use mud flats at night because the duration of mud flat exposure during the day is relatively short, or alternatively, because lower low nocturnal tides offer profitable foraging op-

portunities (Townshend et al. 1984). Shorebird use of coastal pastures adjacent to North Humboldt Bay increases in winter and spring when precipitation increases availability of earthworms (*Lumbricidae*) (Colwell and Dodd 1995). Consequently, the foraging success of fall migrants may depend more on intertidal habitat availability than wintering or spring-migrating birds, increasing the likelihood of fall migrants using exposed mud flats at night.

Energy requirements associated with spring migration and molt are also high (Kersten and Piersma 1987, P. R. Evans 1988, Zwarts et al. 1990), so why did spring migrants of most species forage at night on Humboldt Bay mud flats relatively infrequently and in relatively lower numbers than fall? We suspect that spring migrants obtained their energetic requirements without feeding much at night because: 1) lower low tides occurred frequently in daylight; 2) day length was long, and consequently, intertidal areas remained exposed for long daylight periods; and 3) when mud flats were inundated during the day, coastal pastures offered alternative foraging opportunities.

Alternatively, shorebirds may respond to seasonal changes associated with nocturnal invertebrate prey availability (Pienkowski et al. 1984, Townshend et al. 1984). On mud flats of northwestern Humboldt Bay, Carrin (1973) observed little vertical movement of invertebrates between day and night samples taken during two fall (July, August) tidal cycles. Carrin (1973) did not sample at night during other seasons. However, he reported that diurnal invertebrates exhibited lowest densities in winter and lowest biomass in spring; invertebrates exhibited moderate to high biomass and densities in fall. These findings suggest that nocturnal foraging by shorebirds occurred more frequently when diurnal invertebrate prey were equal to or more available than other seasons. This observation contradicts findings from other studies conducted at northern latitudes which suggest shorebirds forage more frequently at night in winter (Goss-Custard 1969) when diurnal invertebrate prey availability is low (Evans and Dugan 1984).

INTERSPECIFIC VARIATION

Day/night patterns of abundance and occurrence of shorebirds varied considerably among taxa (Table 5). Members of the family Charadriidae and Recurvirostridae were relatively more nocturnal than members of the family Scolopacidae.

Robert et al. (1989) also found interspecific variation associated with day/night patterns of waterbirds, but with different results from our study. For example, they reported that Black-bellied Plover foraged primarily during daylight, whereas small sandpipers, small plovers, and medium-sized shorebirds foraged mainly at night.

Different foraging maneuvers are typically used by different shorebird taxa. For example, plovers search for prey visually (Pienkowski 1981, 1983a, 1983b; McNeil and Robert 1988; Robert and McNeil 1989), whereas sandpipers locate prey using visual and tactile maneuvers (Pienkowski 1981, McNeil and Robert 1988, Robert and McNeil 1989). American Avocet use mainly tactile maneuvers (Evans and Harris 1994). Presumably, visual foragers should be more affected by darkness than tactile foragers (Dugan 1981, Robert et al. 1989, Zwartz et al. 1990, Martin 1991). But at Humboldt Bay, plovers were the most nocturnal taxa (Table 5).

According to Pienkowski (1983a), most plovers evolved at southern latitudes under arid conditions where invertebrate prey are active predominately at night. Interestingly, a comparison of rod/cone ratios from a Black-bellied Plover, a Short-billed Dowitcher, and a Greater Yellowlegs revealed that the plover had the greatest rod/cone ratio and the highest density of rods (Rojas de Azuaje et al. 1993). This suggests that the Black-bellied Plover may be better adapted for nocturnal vision than either of the Scolopacids. Additionally, plovers have comparatively greater olfactory bulb development than diurnal members of Charadriida (Healy and Guilford 1990). By contrast, Scolopacids have relatively smaller olfactory-bulb sizes than exclusively diurnal members of Scolopacida (Healy and Guilford 1990). We are not aware of any literature that documents the role of olfaction in foraging shorebirds, but other bird taxa are known to use olfaction for locating prey (see review by Martin 1991). Several authors have suggested that plovers sometimes locate prey using acoustic cues (Pienkowski 1983a, Martin 1991), but most evidence suggests that plovers continue to forage visually at night (Pienkowski 1983a, McNeil and Robert 1988, Robert and McNeil 1989).

Finally, among Scolopacids, smaller-bodied species were relatively more nocturnal than larger-bodied species (Table 5). Zwartz et al. (1990) reported a similar pattern among Charadriidae, Scolopacidae, and Haematopodidae taxa. Large shorebirds may be less active at night than small

shorebirds because they forage on relatively larger prey or because relative intake rate is high (Zwartz et al. 1990).

CONCLUSIONS

At North Humboldt Bay, the occurrence and abundance of nonbreeding shorebirds varied considerably between day and night. Moreover, day/night patterns varied greatly among seasons and across shorebird taxa. Shorebirds of most common species foraged primarily in the day, although plovers and American Avocet foraged as often at night as in the day. Nocturnal foraging by most species predominated during fall migration. Thus, the choice of a researcher's temporal scale or taxa may influence results considerably. Elsewhere, (Dodd and Colwell, unpubl.), we show that variation in environmental conditions such as moonlight also influence day/night patterns of shorebirds. Explanations for seasonal variation in day/night patterns of shorebirds at North Humboldt Bay require further research. Studies examining energetics of shorebirds and variation in availability of their invertebrate prey would best evaluate seasonal variation hypotheses.

ACKNOWLEDGMENTS

We thank M. Dodd for field assistance; L. George for advice on nonparametric ANOVA; and A. Dambmann for graphically portraying the study figure. This study benefitted from discussions with W. Kristan, D. Kristan, L. Shannon, and O. Williams; and reviews by R. Golightly and D. Kitchen. We thank the City of Arcata for allowing access to public works property. A Frank M. Chapman Memorial Grant partially funded this study.

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