ENVIRONMENTAL CORRELATES OF DIURNAL AND NOCTURNAL FORAGING PATTERNS OF NONBREEDING SHOREBIRDS

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ABSTRACT.—Knowledge of abiotic factors influencing the foraging ecology of nonbreeding shorebirds (Charadriiformes: Charadrii) is based on research conducted almost exclusively during the day. Consequently, we examined the relative contributions of environmental variables to diurnal and nocturnal foraging patterns (presence/absence) of nonbreeding shorebirds at Humboldt Bay, California, USA from January 1992 to January 1993. The influence of environmental variables on foraging patterns differed between day and night. Most notably, the diurnal presence of birds increased with: (1) shorter daylength [Black-bellied Plover (*Pluvialis squatarola*), dowitchers (*Limnodromus* spp.), and small sandpipers (*Calidris mauri* and *C. minutilla*)]; and (2) shorter durations of mud flat exposure [American Avocet (*Recurvirostra americana*), Marbled Godwit (*Limosa fedoa*), and Dunlin (*Calidris alpina*)]. By contrast, the nocturnal presence of most species increased during the fall [Marbled Godwit, dowitchers, Black-bellied Plover, Semipalmated Plover (*Charadrius semipalmatus*), and Dunlin] and on nights with a visible moon [Marbled Godwit, Willet (*Catoptrophorus semipalmatus*), dowitchers, Semipalmated Plover, and Dunlin]. Our results suggest that interspecific variation in diurnal and nocturnal feeding patterns of shorebirds is associated mostly with variation in tidal, seasonal, and moonlight conditions. Furthermore, our findings suggest that nocturnal foraging by most shorebird species at a northern temperate, intertidal site did not increase during periods of short daylength. *Received 28 July 1997, accepted 13 Jan. 1998.*

Nonbreeding distributions of shorebirds in coastal habitats are influenced by numerous environmental factors, especially tides and weather (see Burger 1984), which influence the availability of food resources. Tides predictably alter the amount of available foraging habitat, and variation in temperature, wind, and daylength further influence the availability of intertidal prey (Evans 1976). These generalizations, however, are based largely on research conducted during the day despite the growing body of literature (e.g., McNeil 1991, Dodd and Colwell 1996, McNeil and Rodríguez S. 1996) documenting nocturnal foraging by shorebirds. Consequently, the environmental correlates of nocturnal foraging by shorebirds remain poorly understood.

Only one study (Robert et al. 1989) has quantified environmental influences of both diurnal and nocturnal distributions of shorebirds. Most studies (e.g., Heppleston 1971, Zwarts et al. 1990, Evans and Harris 1994, Thibault and McNeil 1994) have evaluated the contributions of one environmental factor

(moonlight) to nocturnal foraging by shorebirds. Furthermore, with the exception of Robert and coworkers (1989) and Zwarts and coworkers (1990), most researchers have focused on a single species. Findings from these studies suggest that the nocturnal foraging ecology of shorebirds is influenced by variation in tides (Robert et al. 1989), moonlight (Heppleston 1971, Robert et al. 1989, Zwarts et al. 1990, Evans and Harris 1994, Thibault and McNeil 1994), and season (Rompré and McNeil 1994, Dodd and Colwell 1996).

In this paper, we examine the relative contributions of environmental variables to diurnal and nocturnal foraging by eight shorebird species at Humboldt Bay, California, USA, an important Pacific Coast estuary for nonbreeding shorebirds (Colwell 1994). Elsewhere (Dodd and Colwell 1996), we showed that shorebirds at North Humboldt Bay foraged principally during the day, although diurnal and nocturnal distributions varied both among seasons and species.

STUDY AREA AND METHODS

We studied shorebirds (Charadriiformes: Charadrii) from 10 January 1992–10 January 1993 at the Arcata Marsh Project in North Humboldt Bay, Humboldt Co., California, USA. 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

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mixed semidiurnal. The climate is characterized by a wet (November–March) and a dry (April–October) season, although we conducted our study during mostly drought conditions when yearly rainfall was 19.5 cm below normal (National Weather Service, Eureka, CA). For further details concerning the study area see Gerstenberg (1979) and Barnhart and coworkers (1992).

Bird censuses.—We established four 20 × 50 m study plots (marked with four 5 × 5 cm wooden corner stakes) on a high elevation mud flat (Gerstenberg 1979) within 50 m of the shoreline in areas of high shorebird use. Each week, we censused each plot twice within a 24-hour period: once during daylight and once during darkness on successive rising tides. We censused during 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. We conducted each census for 45 minutes beginning when the edge of the rising tide crossed the corner stake of a plot. For further details concerning sampling see Dodd and Colwell (1996).

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 (3–5 seconds) illuminating plots with a 400,000 candlepower spotlight (Black Max Q-beam, Brinkmann Corp., Dallas, TX) covered with a red or amber snap-on filter [see Dodd and Colwell (1996) for further details]. We illuminated plots immediately after we had recorded data on species, abundance, and behavior of birds (not presented in this paper). Additionally, we illuminated plots whenever we (1) heard, but could not see, shorebird(s) or (2) had not detected shorebirds for 5–7 min. Finally, 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 to evaluate whether or not data from plots were representative of surrounding mud flats (Dodd 1995).

At night, we had difficulty identifying some closely related species. Consequently, we combined 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". Hereafter, we treat these groups as if they were species.

Environmental variables.—For each census, we recorded season, moonlight, tide, daylength, and weather variables.

We categorized (*a priori*) censuses by season based on migratory patterns of shorebirds in the Humboldt Bay area (Gerstenberg 1979, Harris 1991) as: (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 recorded the phase of the moon in tenths (from 0 = a new moon to 10 = a full moon) based on United States Naval Observatory data (Tidelogs 1992, 1993); we did not distinguish between waxing and waning moons. At night, we recorded whether or not the moon was visible during any portion of a census.

We recorded the following based on National Oceanic and Atmospheric Administration data (Tidelogs 1992, 1993): (1) height (m) of low tide preceding a census tide; and (2) time (minutes) from low tide to a census tide.

We used the amount of time (minutes) between sunrise and sunset of the 24 hour census period (Tidelogs 1992, 1993) to represent daylength. In addition, we used the amount of time (minutes) between sunrise and sunset of the 24 hour census period in which tides occurred below 1.2 m (Tidelogs 1992, 1993) as an index of the duration of mud flat exposure during daylight (hereafter, referred to as available daylength). At 1.2 m, high elevation mud flats of North Humboldt Bay are usually just inundated by an advancing tide (Dodd, pers. obs.). Our index, however, did not account for variations from predicted tides caused by weather conditions such as strong onshore winds or heavy rainfall.

We categorized precipitation that occurred during a census as: (1) absent, (2) fog, or (3) rain; and the degree of cloud cover that prevailed for most of a census as: (1) ≤ 10%, (2) 11–75%, and (3) > 75%. We used the following data from the National Weather Service's daily record of surface weather observations for Eureka, California as an index of conditions at the study area (5.8 air-km away): (1) wind speed (km/h); (2) wind direction (eight compass points); and (3) air temperature (° C).

Data summary and analysis.—We restricted analyses to the eight most common species, including only observations from fall, winter, and spring because few shorebirds occurred during summer (Dodd 1995). Additionally, we omitted from analyses July–September censuses (*n* = 51) for Dunlin *(Calidris alpina)* because this species is a late fall migrant and usually does not arrive at Humboldt Bay until late September (Dodd, pers. obs.). We analyzed plot data for all species, with the exception of American Avocet (*Recurvirostra americana*) for which we analyzed area data because data from plots did not represent the surrounding the mud flat (Dodd 1995).

We evaluated the relative contributions of environmental variables to day and night foraging patterns of shorebirds using stepwise forward logistic regression (Hintze 1992; see also Hosmer and Lemeshow 1989) with a χ^2 cutoff value of 2.7 (df = 1, $P < 0.10$; e.g., Johnson and Temple 1990). All analyses were performed on an IBM-compatible computer using NCSS, ver. 5.3 software (Hintze 1992). We used stepwise regression because it is effective for screening many covariates, especially when little is known about the response variable (i.e., nocturnal foraging; Hosmer and

Lemeshow 1989). For each species, we conducted separate day and night analyses using presence or absence of foraging birds as the response variable and environmental variables as independent variables.

We examined all covariates for multicollinearity (high intercorrelations among independent variables) by regressing each independent variable against all others and evaluating the coefficient of determination (R^2; Hamilton 1992). We concluded that the following variables exhibited high intercorrelations ($R^2 > 0.60$): (1) daylength (day = 0.68, night = 0.76); (2) available daylength (day = 0.73, night = 0.91); (3) tide height at low water (day = 0.78, night = 0.86); and (4) amount of time since low water (day = 0.68, night = 0.62). Indeed, when the stepwise procedure selected more than one of these variables, it produced extremely high estimated standard errors and/or a reversal of one or more beta coefficient's signs, both indications of multicollinearity (Hamilton 1992). Consequently, for models fitted with more than one intercorrelated variable (day: four of eight, night: three of eight), we excluded from analyses three of the four intercorrelated variables (Hamilton 1992). For each model, we kept the intercorrelated variable with the highest χ^2 value based on univariate logistic regression.

Finally, we encountered a numerical problem of complete separation (Hosmer and Lemeshow 1989) associated with the analysis of Marbled Godwit (*Limosa fedoa*). Because this species occurred on plots at night exclusively during fall, complete discrimination between fall and the other seasons occurred, resulting in no possible maximum likelihood estimate and correspondingly high standard errors (Hosmer and Lemeshow 1989). To remedy this, we randomly added to plot data 1 of 2 winter occurrences and 1 of 17 fall occurrences from nights when Marbled Godwit foraged on areas, but not on plots (Dodd 1995).

RESULTS

Season contributed significantly to nocturnal use of mud flats by shorebirds (Table 1). For five of eight species, presence at night increased during fall. Moreover, fall contributed most (i.e., lowest *P*-value; see Hosmer and Lemeshow 1989) to nocturnal foraging patterns of Marbled Godwit, Black-bellied Plover (*Pluvialis squatarola*), and Semipalmated Plover (*Charadrius semipalmatus*). By contrast, season correlated significantly with diurnal feeding patterns of only two species: the diurnal presence of Semipalmated Plover and Willet (*Catoptrophorus semipalmatus*) increased and decreased, respectively during fall.

Moon variables contributed significantly to both day and night use of mud flats, but in different ways. At night, the presence of five of eight species increased on nights with a visible moon. In addition, moonlight contributed most to nocturnal foraging patterns of Willet, Dunlin, and dowitchers. During the day, we did not record the visibility of the moon; however, the phase of the moon correlated significantly with diurnal use of mud flats. The presence of dowitchers, Dunlin, and small sandpipers increased on days closest to a new moon.

Tidal variables contributed significantly to foraging patterns of a few species, but correlations differed between day and night. During the day, the presence of Dunlin increased when higher, low tides preceded censuses and the presence of American Avocet and Marbled Godwit increased when less time had elapsed since low tide. By contrast, the nocturnal presence of dowitchers and Dunlin increased when lower low tides preceded censuses. Overall, tidal factors influenced diurnal use more than nocturnal use. Shorter durations of exposed mud flat contributed most to diurnal foraging patterns of American Avocet, Marbled Godwit, and Dunlin.

During both the day (Black-bellied Plover, dowitchers, and small sandpipers) and night (American Avocet and small sandpipers), the presence of birds increased with shorter daylength or available daylength. However, the nocturnal presence of Willet increased with longer daylength. Short daylength or available daylength contributed most to diurnal use of mud flats by Black-bellied Plover, dowitchers, and small sandpipers, and nocturnal use by American Avocet.

Weather variables influenced day and/or night foraging patterns of most species. Correlations of temperature and windspeed differed between day and night. During the day, presence of birds increased at lower temperatures (Marbled Godwit) and windspeeds (dowitchers and Dunlin), whereas at night, presence of birds increased at higher temperatures (Dunlin) and windspeeds (Marbled Godwit). However, the presence of birds both during the day (Marbled Godwit and Willet) and night (dowitchers, Dunlin, and small sandpipers) increased with precipitation. Moreover, rain contributed most to the nocturnal foraging presence of small sandpipers. Wind direction correlated with diurnal (American Avocet and Willet) and nocturnal (Marbled Godwit, Willet, and dowitchers) use of

TABLE 1. Results of stepwise forward logistic regression examining the relationship between diurnal and nocturnal foraging patterns (presence/absence) of eight shorebird species and environmental variables.

Species	Day/ night	Variables selected	Beta coefficient	Standard error	χ^2	P	% Corr. class[a]	% Present[b]
American Avocet[c]	Day	Time since low tide[e]	−0.02	0.004	28.51	<0.001	80.4	76.7
		Southeast wind	−1.35	0.67	4.02	0.04		
	Night	Available daylength[e]	−0.007	0.001	27.71	<0.001	74.1	56.2
Black-bellied Plover	Day	Daylength	−0.007	0.003	4.04	0.04	91.5	08.5
	Night	Season: fall	3.24	1.04	9.77	0.002	86.6	13.4
Semipalmated Plover	Day	Season: fall	2.22	1.07	4.35	0.04	93.9	06.1
	Night	Season: fall	1.62	0.66	5.99	0.01	89.6	10.4
		Moon visible	0.92	0.53	2.95	0.09		
Marbled Godwit	Day	Time since low tide[e]	−0.009	0.002	13.75	<0.001	72.6	61.0
		Temperature	−0.15	0.05	8.23	0.004		
		Fog	1.55	0.83	3.45	0.06		
	Night	Season: fall	3.74	1.32	8.02	0.005	92.7	07.9
		Moon visible	1.39	0.66	4.42	0.03		
		Windspeed	0.15	0.07	3.97	0.046		
		Southeast wind	1.52	0.76	4.02	0.045		
Willet	Day	Season: fall	−1.67	0.37	20.36	<0.001	70.7	38.4
		Fog	1.58	0.62	6.55	0.01		
		North wind	−1.08	0.58	3.48	0.06		
	Night	Moon visible	2.92	1.23	5.63	0.02	97.6	03.1
		Daylength[e]	0.01	0.006	4.51	0.03		
		East wind	2.16	1.13	3.67	0.055		
Dowitchers	Day	Daylength	−0.01	0.002	20.17	<0.001	76.8	34.7
		Moonphase	−0.14	0.06	4.91	0.03		
		Windspeed	−0.05	0.03	3.92	0.048		
	Night	Season: fall	4.42	1.31	11.33	<0.001	90.2	12.2
		Moon visible	2.88	0.74	15.04	<0.001		
		Fog	2.08	0.79	6.86	0.009		
		Northeast wind	4.86	2.19	4.92	0.03		
		Tide height at low water	−1.99	1.04	3.67	0.055		
Dunlin[d]	Day	Tide height at low water[e]	1.77	0.61	8.55	0.003	69.9	54.9
		Moonphase	−0.19	0.07	6.80	0.009		
		Windspeed	−0.06	0.03	3.65	0.056		
	Night	Moon visible	3.57	0.98	13.11	<0.001	86.7	15.9
		Rain	3.23	1.13	8.21	0.004		
		Season: fall	1.79	0.84	4.49	0.03		
		Partly cloudy	−1.75	1.04	2.84	0.09		
		Tide height at low water[e]	−2.33	1.23	3.60	0.06		
		Temperature	0.20	0.12	2.75	0.097		
Small sandpipers	Day	Available daylength[e]	−0.005	0.001	18.16	<0.001	67.7	48.8
		Moonphase	−0.09	0.05	2.85	0.09		
	Night	Rain	1.74	0.53	10.91	0.001	82.9	19.5
		Available daylength	−0.004	0.001	5.73	0.02		

[a] Percent of the total number of observations that were correctly classified using a classification midpoint of 0.5 (i.e., a species was predicted as absent (<0.5) when actually absent and present (>0.5) when actually present).
[b] Percent of censuses ($n = 164$) in which we observed a species foraging on a plot.
[c] Area data used instead of plot data; $n = 163$ (day), $n = 162$ (night) censuses.
[d] Early fall censuses ($n = 51$) excluded, leaving $n = 113$.
[e] Indicates one of four intercorrelated variables kept in analysis.

mud flats, but no generalities of wind direction resulted.

DISCUSSION

Our findings suggest that the presence of foraging shorebirds on intertidal mud flats of Humboldt Bay is influenced by a variety of environmental factors, and that these correlates vary among species (Table 1). During the day, tides and daylength contributed most to foraging patterns of shorebirds; bird use increased with shorter daylength (three species) and shorter periods of exposed mud flats (three species). By contrast, nocturnal foraging patterns correlated strongly with moonlight and seasonal variables; mud flat use by most species (five of eight) increased during fall and/or on nights with a visible moon.

We are aware of only one other study (Robert et al. 1989) that quantified environmental correlates (wind velocity, percent cloud cover, moonphase, and tide level) of both diurnal and nocturnal distributions of nonbreeding shorebirds. Robert and coworkers (1989) found that tide level best explained variation in both day and night abundance of foraging birds; abundance increased at low and intermediate tide levels for most species. Robert and coworkers conducted their study during winter, so they could not evaluate season or daylength variables.

Here and elsewhere (Dodd and Colwell 1996), we showed that nocturnal foraging by shorebirds of most species predominated during fall at Humboldt Bay. This pattern may be related to the biology of a species and environmental conditions that vary seasonally (Dodd and Colwell 1996) including: (1) high energy demands associated with migration and the pre-basic molt; (2) large numbers of immature birds, which may be inefficient foragers; (3) less available alternate foraging habitat (i.e., coastal pastures; Colwell and Dodd 1995); and (4) lower low fall tides occurring at night.

In addition to season, visibility of the moon correlated strongly with nocturnal foraging patterns. But interestingly, variation in moonphase did not correlate with nocturnal patterns of any species. Phase of the moon may not have been an important factor in our study because we conducted almost half (48%) of our night censuses when the moon was below the horizon. Excluding nights when the moon was below the horizon, shorebirds foraged on more (61.4%, n = 57) nights when the moon was more than half full than nights (39.3%, n = 28) when the moon was half full or less. We suggest that future studies quantify ambient moonlight as well as phase of the moon to evaluate the influence of moonlight on nocturnal foraging patterns.

Many researchers have reported a relationship between variation in moonlight and variation in nocturnal foraging by shorebirds. For example, Robert and coworkers (1989) showed that Wilson's (Charadrius wilsonia) and Semipalmated plovers foraged more on nights with a full moon than moonless nights, a pattern duplicated for territorial Whimbrel (Numenius phaeopus) and Willet (McNeil and Rompré 1995) foraging on moonlit versus moonless nights. Additionally, Eurasian Oystercatcher (Haematopus ostralegus; Heppleston 1971) and American Avocet (Evans and Harris 1994) occurred in higher numbers on moonlit nights than on dark nights. However, not all species conform to this pattern. Nocturnal distributions of Semipalmated Sandpiper (Calidris pusilla) varied independently of moonlight (Manseau and Ferron 1991), and densities of Little Stint (Calidris minuta) on dark nights exceeded densities on full moon nights (Zwarts et al. 1990). None of these studies evaluated both the phase and visibility of the moon.

The relationship between moonlight and nocturnal foraging by shorebirds has been argued to be associated with a species' foraging behavior (e.g., McNeil and Robert 1988, Robert et al. 1989). Presumably, birds that search for prey visually should be more influenced by variation in moonlight than birds that use tactile maneuvers to locate prey. However, in our study, this was not always the case. Nocturnal use of mud flats by typically visual foragers, such as plovers (Pienkowski 1981, 1983a, 1983b; McNeil and Robert 1988; Robert and McNeil 1989), either increased (Semipalmated Plover) or was not influenced (Black-bellied Plover) by a visible moon. Most Scolopacid species, both visual and tactile feeders (Pienkowski 1981, McNeil and Robert 1988, Robert and McNeil 1989), increased their use of mud flats on moonlit nights. By contrast, nocturnal distributions of

a predominately tactile feeder, American Avocet (Evans and Harris 1994), varied independently of moonlight. Elsewhere (Dodd and Colwell 1996), we showed that diurnal abundance exceeded nocturnal abundance for Scolopacids, whereas abundance of American Avocet and plovers did not differ between day and night. It is noteworthy that Scolopacids predominated during day censuses and tended to feed on moonlit nights. However, nocturnal distributions of small sandpipers varied independently of moonlight, as was found elsewhere (Manseau and Ferron 1991).

We did not evaluate the influence of moon visbility on diurnal foraging patterns. However, diurnal use of mud flats by dowitchers, Dunlin, and small sandpipers increased on days closest to a new moon. Milsom (1984) reported that a greater proportion of Northern Lapwings (*Vanellus vanellus*) foraged during the day when more time elapsed to the next full moon. Several authors (Spencer 1953, Hale 1980, Milsom 1984, Barnard and Thompson 1985) have hypothesized that a negative relationship between diurnal feeding activity and moonphase indicates a preference by shorebirds to forage during nights with a full moon. However, Barnard and Thompson (1985) observed no foraging shorebirds on 11 nights with a full moon, despite the significant negative relationship they obtained between moonphase and the number of pastures used by lapwings during the day. The foraging ecology of shorebirds may be influenced by a lunar periodicity in invertebrate prey activity (e.g., Hale 1980, McNeil 1991, Thibault and McNeil 1994). Many marine invertebrates are known to be more active during full moons (Hale 1980, Ydenberg et al. 1984), although this is not the case for all invertebrates (e.g., Geppetii and Tongiorgi 1967, Zwarts 1990).

In marine habitats, tidal variation is considered the most important environmental factor influencing the abundance, distribution, and behavior of nonbreeding shorebirds (for review, see Burger 1984). In this study, we controlled most tidal variation by beginning censuses at the same tide height on rising tides. Despite this, tidal variation correlated with foraging patterns of some species and tidal influences seemed greater during the day than at night. Interestingly, the diurnal presence of birds increased with shorter durations of exposed mud flat, whereas the nocturnal presence of birds increased with longer durations of exposed mud flat. This difference may be attributed to diurnal and nocturnal variation in tides. At Humboldt Bay, diurnal and nocturnal tides typically are unequal in height, so that the lower low tide occurs during either daylight or darkness, depending on the season. For example, during fall, low tides averaged higher prior to day censuses than night censuses. Thus, birds foraging during the day tended to encounter relatively higher low tides than birds feeding at night, which may explain differences in day and night correlations of tide. Alternatively, differences would be explained if birds left mud flats earlier on rising diurnal tides than nocturnal tides. By contrast, other studies (Evans 1976, Hockey 1984, Manseau and Ferron 1991) have reported that shorebirds foraged for a shorter duration of the nocturnal tide cycle than diurnal tide cycle, with the exception of Turpie and Hockey (1993) who showed that shorebirds fed throughout the diurnal and nocturnal low tide period.

Numerous studies have shown that shorebirds spend more time foraging during the day in winter when foraging habitat is exposed for short durations of daylight (Goss-Custard 1969, Goss-Custard et al. 1977, Puttick 1979, Baker 1981, Pienkowski 1982, Maron and Myers 1985). At other northern temperate sites, nocturnal foraging by shorebirds is largely confined to winter (e.g., Goss-Custard 1969, Heppleston 1971, Pienkowski 1982). Other authors (Goss-Custard 1969, Goss-Custard et al. 1977, Evans 1988) have hypothesized that shorebirds at temperate latitudes are forced to feed at night in winter because high energetic requirements cannot be met during periods of short daylength. However, at Humboldt Bay, the nocturnal presence of only two species (American Avocet and small sandpipers) increased with shorter daylength, and the presence at night of Willet increased with longer daylength. Our findings suggest that most shorebird species at North Humboldt Bay do not have to forage at night when daylength is short.

Overall, weather variables were relatively unimportant correlates of both day and night foraging patterns. This may be due to the large-scale of both the response variable (i.e.,

presence/absence) and weather variables (i.e., we ignored microclimate). However, the presence of a few species increased with precipitation both during the day and night. Moreover, rain best explained the variation in nocturnal use of mud flats by small sandpipers. These results contradict findings from other studies (Goss-Custard 1970, Pienkowski 1981) which suggest that rain decreases the availability of invertebrate prey during the day.

Conclusions.—Our year-long study of shorebirds foraging on mud flats of North Humboldt Bay shows that environmental conditions associated with species' foraging patterns differed between day and night. Most notably, diurnal use of mud flats increased when intertidal habitats were exposed for shorter durations and daylength was short. By contrast, nocturnal use increased during fall, especially on nights with a visible moon. Finally and in contrast to other studies conducted at northern temperate sites, nocturnal foraging by most species did not increase during periods of short daylength. This finding suggests that most shorebirds wintering at Humboldt Bay are able to meet their energetic requirements during daylight.

We suggest that despite recent advances in our knowledge of nocturnal foraging by shorebirds, we do not understand the causes of the variation that occurs latitudinally, seasonally, and among species. Furthermore, we suggest that future studies examine influences of tidal, seasonal, and moonlight factors on diurnal/nocturnal patterns of shorebirds across a range of latitudes and taxa. Finally, findings from this study and Dodd and Colwell (1996) have important implications for how biologists determine the value of a particular site for nonbreeding shorebirds. In most cases, decisions on whether or not to protect an area are based on diurnal surveys. We urge researchers to evaluate both nocturnal and diurnal use of foraging habitats, especially during different seasons.

ACKNOWLEDGMENTS

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