

NOCTURNAL FORAGING BEHAVIOR OF BREEDING PIPING PLOVERS (*CHARADRIUS MELODUS*) IN NEW JERSEY

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ABSTRACT.—The nocturnal foraging behavior of breeding Piping Plovers (*Charadrius melodus*) was studied in New Jersey using a focal-animal approach in 1989 and 1990. More than 30% of the variation in the number of plovers foraging at night was explained by stage of the breeding cycle, tidal stage, and year. The greatest numbers of adult plovers fed in the intertidal zone during the prenesting and fledgling stages of the breeding cycle. Piping Plovers were more likely to be observed feeding during late ebb and early flood tides, than other times. Time devoted to feeding per 2-min sample was similar at each study site but differed significantly during the tidal stages. Pecking rate was higher during late ebb and early flood tides than late flood and early ebb tides. Time devoted to being alert varied depending on stage of the breeding cycle. Prenesting plovers and individuals with fledglings fed longer and were alert less per 2-min sample than plovers engaged in incubation or brood rearing. The nocturnal peck rate of Piping Plovers was considerably lower than daytime levels. Plovers foraging at night had significantly lower peck rates when disturbed. Abundance of intertidal polychaetes varied according to tidal stage and, where present, they constituted the main food of the plovers. We suggest that nocturnal foraging is a natural behavior pattern in Piping Plovers although it may vary in intensity. Future management should include the assessment of nighttime recreational use of beaches where Piping Plovers breed. Received 31 July 1992, accepted 25 November 1992.

ALTHOUGH SOME BIRDS, such as many species of owls, are nocturnal, most are diurnal and perform all their activities during the day. Recently, several researchers have examined the behavior of shorebirds both during the day and at night. Night feeding has been documented in six plover species, including Grey Plovers (*Pluvialis squatarola*; Dugan 1981, Pienkowski 1982), Ringed Plovers (*Charadrius hiaticula*; Pienkowski 1982), Piping Plovers (*C. melodus*; Burger 1984), Dotterels (*C. morinellus*; Kalas 1986), Wilson's Plovers (*C. wilsonia*; Robert and McNeil 1989), and Semipalmated Plovers (*C. semipalmatus*; Robert and McNeil 1989), as well as several other shorebird species (Burger 1984, Goss-Custard 1984, Robert et al. 1989). However, these data, with the exception of those in Kalas (1986), were obtained either during migration or on the wintering grounds, and there are no quantitative studies during the breeding season of nocturnal behavior of shorebirds. Furthermore, Cairns (1977) stated that, as darkness falls during the breeding season, adult Piping Plovers (*C. melodus*) escort chicks to cover or to their former nesting territories.

Feeding occurs at night during both migration and winter because energy requirements are high due to long-distance travel and adverse weather conditions, and because it is assumed

that shorebirds cannot obtain enough calories during the short days at these times (Goss-Custard 1969, 1976, Heppleston 1971, Pienkowski 1981, 1982, Myers and McCaffery 1984, Puttick 1984, Johnson and Baldassarre 1988). This suggests that the long and warm days of spring and summer afford shorebirds ample time to attend to all energy needs without feeding at night. Robert and McNeil (1989), however, showed that some shorebirds species wintering, or residing year-round in tropical environments, which are warmer and therefore less energy demanding environments, fed at night as well. They suggested that the lack of data on night foraging in shorebirds was likely due to technological difficulties associated with night observation and that night feeding may occur all year. They suggested, as did Dugan (1981), Pienkowski (1982) and Townshend et al. (1984), that increased availability of invertebrate prey at night may make it advantageous for shorebirds to forage then. Feeding activity of several shorebird species is partly a function of tidal stage (Burger 1984, Burger et al. 1977, Goss-Custard 1984). The diurnal feeding-activity rhythms of Piping Plovers during the breeding season have been linked to tidal factors and human disturbance (Burger unpubl. data).

Piping Plovers breed in the interior of North

America, in the Great Lakes region, and along the Atlantic Coast (AOU 1983, Haig 1985, U.S. Fish and Wildlife Service 1988). Piping Plovers typically nest on sparsely vegetated beaches or inland lake shores (Wilcox 1959, Cairns 1982, Haig and Oring 1985). Piping Plovers are listed as threatened and endangered both in the United States and Canada (Sidle 1985, Haig 1985).

Major reasons for the decline of the Atlantic Coast Piping Plover populations include loss of habitat, increased predation, and human disturbance (U.S. Fish and Wildlife Service 1988). Of these factors, the effect of human disturbance has received the greatest attention (Flemming et al. 1988, Burger and Gochfeld 1991, Burger unpubl. data, Goldin pers. comm., Griffin and Melvin pers. comm.). However, all of these studies were conducted during the day and focused primarily on adult and chick foraging behavior. Since no one has previously studied Piping Plovers at night, the lack of nighttime human disturbance data on the birds is not surprising. Recreationists do not congregate en masse on beaches at night, but they are nonetheless present. Their activities range from fishing and camping, to walking, jogging, and driving off-road vehicles (Strauss 1990).

We report on nighttime observations of Piping Plovers in New Jersey during the 1989 and 1990 breeding seasons. Our main objectives were to determine: (1) foraging behavior of Piping Plovers; (2) effect of tide, study site, and breeding stage on foraging behavior; (3) effect of nighttime human disturbance on foraging behavior; and (4) day and night prey availability.

METHODS

We studied Piping Plovers from 1 April to 15 August in 1989 and 1990 at three New Jersey locations: Brigantine Beach (39°22'30"N, 72°24'30"W), North Corson's (39°12'30"N, 74°38'30"W), and Whale Beach (39°10'30"N, 74°40'W). A fourth study site, Mantoloking (40°03'N, 72°40'W), was examined in 1990 only. All sites were located on barrier beach islands.

Brigantine Beach is 1.0 km north of the center of Atlantic City. The amount of artificial light emitted from Atlantic City and the surrounding residences creates an almost perpetual full-moon effect on the beach. The major nesting area is on the southernmost 2 km of outer beach (i.e. beach facing ocean), and 1 km of inlet beach (i.e. perpendicular to oceanfront and facing inlet waters). The width of the beach between the dunes and the waterline varies between 35 and 120 m depending on the tidal stage. The area

receives heavy recreational use throughout the summer. The southernmost 300 m of outer beach is used by off-road vehicles during the day and night. In 1989 there were 13 nesting pairs of Piping Plovers. In 1990 there were 12 pairs.

North Corson's is a state park located at the southern tip of Ocean City. The nesting area (the southernmost 2 km of outer beach and 750 m of inlet beach) receives only minimal artificial light because it is located more than 1.5 km from the nearest residential lighting and over 5.5 km away from concentrated light sources. The width of the beach between the dunes and waterline varies between 20 and 200 m depending on tidal stage. The area receives similar levels of recreational use as Brigantine Beach, but much less vehicular use (only park rangers and staff during the day). In 1989 there were seven nesting pairs and in 1990 there were six.

Whale Beach is approximately 1.6 km south of North Corson's. The nesting area is located entirely on the outer beach as there is no inlet. The width of the beach, depending on tidal stage, varies between 30 and 100 m. It receives much less light from artificial sources than either Brigantine or North Corson's and recreational use is also lower. There is no vehicular use. In 1989 there were 12 nesting pairs and in 1990 there were 9.

The three beaches mentioned above have similar sloping intertidal zones and similar vegetation. Further descriptions can be found in Burger (1991).

Mantoloking is a beach on New Jersey's northernmost barrier island. The nesting area is comprised of 2.4 km of outer beach. It receives minimal artificial light and recreational use. There are no vehicles permitted except those of the beach patrol. The width of the beach, 10 to 50 m depending on tidal stage, is much less than any other study site. The slope of the intertidal zone is greater than 20° which is markedly different from the other three study sites. There were seven nesting pairs in 1990.

Each study site was divided into five oceanfront transects (250 m × 50 m). These transects were established prior to the nesting season. Piping Plovers were observed between 2000 and 0500 EST, three to four nights a week using a Lenzar light-image intensifier.

The night scope allowed us to observe individual Piping Plovers from 100 to 120 m away depending on the amount of artificial and natural light (moonlight) present. All behaviors normally observed in full daylight (e.g. feeding, preening, brooding, distraction displays) could be detected and distinguished from each other. The night scope also made it possible to distinguish individual Piping Plovers from other shorebirds of similar shape and size (e.g. Semipalmated Plovers *C. semipalmatus*; Sanderlings, *Calidris alba*) from over 100 m.

During each night of observation we gathered two types of data: (1) abundance and activity; and (2) foraging behavior. Abundance and activity data were

used to determine the number of individuals involved in a particular activity over the course of a night (equivalent to 3 h of observations). We spent 1 h censusing a single transect and three transects were censused each night. Over the duration of the study 276 h (92 nights) of censuses were conducted.

We also collected data on foraging behavior using a focal-animal approach (Altmann 1974, Burger unpubl. data). Once a plover was spotted feeding, its behavior during a 2-min time trial was recorded onto a minicassette audio tape. Behaviors recorded for each 2-min trial included: the time spent feeding, alert, running or flying undisturbed, running or flying with people or vehicles within 50 m, engaged in conspecific aggression, or engaged in other activities (e.g. maintenance, loafing); and the number of pecks made at the substrate. Prior to each sample we recorded the date, time, temperature, percent cloud cover, moonphase, age (adult or chick), and stage of the breeding cycle.

All data were transcribed onto data sheets. During the study, 622 2-min foraging trials were conducted on at least 66 individual Piping Plovers. We distinguished four tidal stages: (1) early flood tide (the 3 h following slack low tide); (2) late flood tide (the 3 h before slack high tide); (3) early ebb tide (the 3 h after slack high tide); (4) late ebb tide (the 3 h before slack low tide).

The general temporal stages of the breeding cycle of Piping Plovers in New Jersey are as follows: prenesting (late March and April); incubation (late April to early June); with chicks and brood rearing (late May to early July); with fledgling and postfledgling (early July to the middle of August; (Wilcox 1959, U.S. Fish and Wildlife Service 1988). This chronology does not take renests into account.

Determinations of the stage of the breeding cycle were made by knowing the approximate locations of the territories of the pairs in each transect. All nests were monitored daily or weekly. Thus, we knew the total number of nests, adults, chicks, and fledglings over the course of each season at each study site. We assumed that plovers' nesting territories were continuous (Cairns 1977, Whyte 1985). We also assumed that territory size remained unchanged at night, an assumption supported by a study of wintering birds in a related species, the Grey Plover (Wood 1986). Piping Plovers in our study were not banded for two reasons. First, because they are designated federally as endangered, a banding moratorium is in effect until further notice. Second, the light-image intensifier was not sensitive enough, at the distances it was used, to distinguish band-color combinations.

Prey abundance was determined using 4.0-cm-deep and 12.5-cm-wide core samples. All samples were obtained from wet or recently wetted intertidal sand. Cores were taken during May, June, and July of 1990. On each sampling day, a single tidal stage was sampled from one study site during the day and at night

(e.g. early ebb tide at Brigantine Beach was sampled at 1100 and again at 2200). Once all four tidal stages were sampled from each study site a second set of core samples were obtained in the same manner. This resulted in 16 cores from each study site, one-half of which were taken during the day and half at night. Furthermore, during each sampling day, one of the two samples obtained was random and the other was taken in a nonrandom manner (i.e. from sand directly beneath where a Piping Plover had been feeding only moments before). Sampling points were randomized with respect to study site and transect location.

All samples were sieved through 2.0-mm and later through 0.6-mm meshes. Invertebrates were counted, grouped into phyla, and preserved in 70% formaldehyde. Organisms were identified to family or order using a dissecting microscope and field guides (Gosner 1971, 1978).

We calculated means and standard errors for all variables. Significant differences were determined using chi-square tests at the 0.05 probability level. Kruskal-Wallis tests (yielding an *H*-value; Sokal and Rohlf 1981) were used to determine significant differences between groups (e.g. tidal stages, study sites). A multiple-regression analysis (GLM; SAS Institute 1985) was performed. All independent variables (e.g. moonphase, percent cloud cover, tidal stage) were run singly and as combinations in our attempt to determine the best model explaining variation in the number of plovers foraging on a given night. The dependent variable was the number of Piping Plovers actively foraging during each night.

RESULTS

Abundance and activity censuses.—Overall, 31% of the variability in the number of plovers feeding on a given night was explained by tidal stage, stage of the breeding cycle, and year (Table 1). These variables in combination also explain the most variation when each study site is examined separately (Table 1). At Mantoloking, however, the number of plovers feeding at night is associated with breeding stage and not with tidal stage. On the remaining sites during both years, there was a greater probability of observing foraging plovers during early flood and late ebb tides than during late flood and early ebb tides (Fig. 1). Although feeding on the intertidal zone did occur during late flood and early ebb tides, most of the plovers observed during these tidal stages were engaged in maintenance activities (preening).

We also examined the number of adult plovers feeding per night as a function of stage of the breeding cycle. In each year and over the

TABLE 1. Factors contributing to variation in number of adult Piping Plovers feeding at night at each study site and over entire study.^a

	Brigantine	Mantoloking	North Corson's	Whale Beach	All Sites
	Model				
F	21.30***	7.80*	15.80***	23.90***	29.10***
R ²	0.38	0.08	0.16	0.31	0.31
	Variables entered				
Year	ns	— ^b	ns	6.7*	8.1*
Breeding stage	14.5***	6.1***	10.2***	17.6***	57.7***
Tidal stage	27.1***	ns	9.9**	26.7***	26.7***

^a ns, $P > 0.05$; *, $P < 0.05$; **, $P > 0.01$; ***, $P < 0.001$.

^b Not applicable. Data only collected for one year.

course of the study, more plovers were observed feeding during the early (prenesting) and late (with fledglings) stages of the breeding cycle (Table 2).

We found 66 breeding pairs over the course of this study (32 in 1989 and 34 in 1990) that had feeding territories extending into the transect areas. We recorded 2-min foraging trials for at least one member of every pair during each season.

Feeding behavior.—Piping Plover foraging trials during the 2-min focal observations were divided into two categories: foraging trials free of human-related disturbances; and trials when birds were disturbed.

At the four study sites for both years combined, adult plovers foraging without disturbance spent almost identical amounts of the 2-min trials feeding. Although the proportion of time spent feeding was not significantly different across the study sites, the peck rate was different ($H = 17.5$, $P < 0.0006$). Plovers on Brigantine and Whale Beach had pecking rates

approximately 22% and 33% higher than plovers on North Corson's and Mantoloking. No other behaviors differed significantly between study sites.

Piping Plovers devoted significantly different proportions of time to foraging depending on tidal stage ($H = 24.0$, $P < 0.0001$; Table 3). The number of pecks per 2-min trial was also significantly different during these times ($H = 61.5$, $P < 0.0001$). Plovers made 31% more pecks during early flood and late ebb tides than during early ebb and late flood tides. No other behaviors differed significantly during tidal stages.

Plovers also exhibited variation in their foraging behavior over the course of the breeding cycle (Table 4). Plovers fed for significantly greater proportions of the 2-min trials during the prenesting and fledgling stages of the cycle than during incubation or brood rearing ($H = 9.8$, $P < 0.02$). Peck rates also were significantly greater during the prenesting and fledgling stages (Table 4). Plovers were significantly more alert during the incubation and brood rearing stages than during the prenesting or fledgling stages. No other behaviors were significantly different over the course of the breeding cycle.

Feeding cycle and human disturbance.—For both years combined, foraging behavior per 2-min trial was significantly different for disturbed plovers than for those not disturbed (Table 5). Overall, plovers fed longer ($H = 89.6$, $P < 0.001$) and made more pecks ($H = 26.5$, $P < 0.0001$) per 2-min trial when foraging undisturbed. Plovers disturbed while foraging spent significantly less time in conspecific aggression than when foraging undisturbed ($H = 4.1$, $P < 0.04$). Disturbed plovers also spent 25% of the 2-min foraging trial running or flying from human related disturbance. This represents a 30-fold

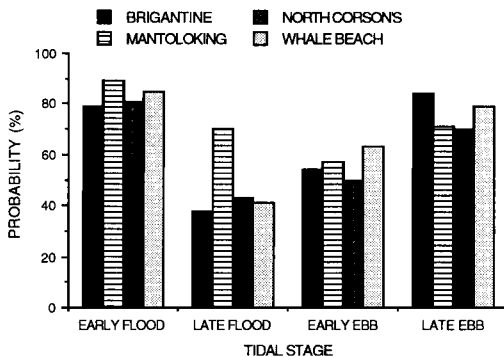


Fig. 1. Probability of observing at least one adult Piping Plover feeding per hour at night as function of tidal stage.

TABLE 2. Average number of adult Piping Plovers (\pm SE with n in parentheses) in intertidal zone as function of stage of breeding cycle.

Breeding stage	1989	1990	Total
Prenesting	3.40 \pm 0.31 (18)	3.10 \pm 0.32 (24)	3.22 \pm 0.22 (42)
Incubation	1.85 \pm 0.33 (18)	1.73 \pm 0.20 (24)	1.78 \pm 0.18 (42)
Brood rearing	2.13 \pm 0.16 (48)	2.37 \pm 0.09 (48)	2.25 \pm 0.08 (96)
Fledgling	5.00 \pm 0.33 (48)	4.10 \pm 0.22 (48)	4.55 \pm 0.24 (96)

increase from undisturbed plovers that were not forced to run or fly from disturbances at all (Table 5).

Prey abundance.—Most of the prey species collected and identified from core samples were from a single family of bivalve (Donacidae), polychaete (Spionidae), or crustacean (Hippidae). Several families of gammarid amphipods also were represented. Although the abundance of these organisms varied with respect to tide, and there were some differences between daytime and nighttime samples, the only regular pattern of variation occurred in the polychaetes (Table 6). Their abundance was higher during early flood and late ebb tides compared to the other tidal stages, both during the day and at night. Also, nonrandom samples contained significantly greater numbers of polychaetes than did the random samples regardless of tidal stage (i.e. there were more polychaetes where plovers were foraging than where they were not).

DISCUSSION

Since breeding stage and tidal stage were important in statistically explaining variations in both abundance and frequency of night foraging, we discuss each factor separately. Each breeding stage is discussed within the context of the breeding cycle as a whole.

Breeding cycle.—The number of Piping Plovers observed and the behavior of Piping Plovers foraging at night were strongly associated with particular stages of the breeding cycle. Foraging Piping Plovers were more numerous at night on the intertidal zone during the prenesting and fledgling stages of their breeding cycle than during either of the other two stages (incubation and brood rearing). Also, the proportion of each 2-min trial devoted to feeding, and the peck rate were significantly greater during these stages while the time spent alert was significantly less (Table 4). This general pattern was observed on all study sites except Mantoloking. Walters (1984) found similar results, with respect to time feeding during the day throughout the breeding season, in four species of lapwings (*Vanellus*). This seasonal pattern appears to be driven by parental constraints imposed by certain stages of the breeding cycle (Walters 1984, this study).

During the prenesting stage Piping Plovers, and shorebirds in general, devote time to establishing territories and mating. Consequently, individuals do not spend long hours at the nest site and are free to spend more time feeding and less time being alert. Furthermore, during the prenesting phase, females must obtain enough energy reserves to produce a clutch of four eggs (Welty and Baptista 1988). Although

TABLE 3. Comparison of nocturnally foraging adult Piping Plovers during each tidal stage. Each sample was 2-min focal observation ($\bar{x} \pm$ SE).

	Tidal stage				H^a
	Early flood	Late flood	Early ebb	Late ebb	
No. samples	139	62	114	220	
Time spent (s)					
Feeding	90.5 \pm 215	80.3 \pm 3.82	78.2 \pm 2.86	92.5 \pm 0.83	24.0***
Alert	7.1 \pm 1.31	7.8 \pm 1.65	10.7 \pm 1.59	5.9 \pm 0.89	ns
No. pecks	20.1 \pm 0.96	13.2 \pm 1.07	14.7 \pm 0.85	20.6 \pm 9.03	61.5***

^a ns, $P > 0.05$; ***, $P < 0.001$. Kruskal-Wallis H -test for differences in proportion of time.

TABLE 4. Comparison of nocturnally foraging adult Piping Plovers during each stage of breeding cycle ($\bar{x} \pm SE$).

	Stage of breeding cycle				H^a
	Prenesting	Incubation	Brood rearing	Fledgling	
No. samples	45	130	141	100	
Time spent (s)					
Feeding	91.6 \pm 2.60	83.8 \pm 2.59	82.8 \pm 2.48	92.7 \pm 3.01	9.8*
Alert	5.0 \pm 1.56	9.9 \pm 1.33	13.5 \pm 1.75	2.3 \pm 1.08	31.1***
No. pecks	18.7 \pm 1.03	16.5 \pm 0.86	15.9 \pm 0.74	21.2 \pm 0.93	51.5***

* *, $P < 0.05$; ***, $P < 0.001$. Kruskal-Wallis H -test for differences in proportion of time.

not verified, this increased requirement for food may have resulted in an increased number of females foraging at night.

The onset of egg laying brings increased parental care in the form of incubation duties, and it appears to decrease the abundance of Piping Plovers feeding nocturnally in the intertidal zone. This follows, since only one bird per pair is free to be foraging at any one time, since the other is incubating. We found a 46% decline in the number of plovers feeding at night during the incubation stage compared to the prenesting stage of the cycle. With respect to the plovers' foraging behavior during the incubation stage, individuals on average spent 9% less time feeding and 50% more time being alert than in the prenesting stage.

After the hatching of young, the time plovers spent being alert during each 2-min foraging trial increased by 33% over that exhibited during incubation. Since we perceived no increase in either the number of humans or predators during this stage of the breeding cycle compared to the other stages, we assumed that the nonbrooding member of a pair is contributing

to the parental care effort from a distance. Burger (1991) suggested that, during the day, Piping Plover pairs exhibit a pattern of alertness and vigilance during their breeding cycle. Both members of a pair monitor each other's behavior, even though they seemingly are incubating or feeding (Walter 1984, Burger 1991, this study). Being more alert at certain times during the cycle, especially during incubation and brooding, may allow for a quicker response when mates need assistance.

During the final stage, when pairs have fledglings and postfledglings, the number of adult plovers feeding at night more than doubled from that of the preceding two stages and reached a level slightly above that observed during the prenesting stage. Furthermore, time spent feeding per 2-min trial increased by 11% and the time alert decreased by 60% over that observed during the brood rearing stage. We link this change in behavior to the reduction of parental care that is associated with the fledgling and postfledgling stages of the breeding cycle, as well as to staging-up for the coming migration.

Tidal factors and prey abundance.—Many abi-

TABLE 5. Comparison of nocturnally foraging adult Piping Plovers when foraging undisturbed, and disturbed by human-related activities ($\bar{x} \pm SE$).

	Undisturbed	Disturbed	H^a
No. samples	534	88	
Time spent (s)			
Feeding	88.1 \pm 1.19	56.3 \pm 1.04	89.6***
Alert	7.5 \pm 0.08	9.4 \pm 0.47	ns
Running undisturbed	13.1 \pm 0.24	16.5 \pm 0.88	ns
Running disturbed	0.0 \pm 0.0	30.1 \pm 2.16	— ^b
Conspecific aggression	6.3 \pm 0.17	3.2 \pm 0.74	4.1*
Other activities	3.8 \pm 0.12	3.6 \pm 0.31	ns
No. pecks	18.6 \pm 1.47	13.5 \pm 0.96	26.5***

^a ns, $P > 0.05$; *, $P < 0.05$; ***, $P < 0.001$. Kruskal-Wallis H -test for differences in proportion of time.

^b Not applicable. Zero data cannot be used for statistical comparison.

TABLE 6. Comparison of invertebrate abundance (individuals per core sample) during each tidal stage ($\bar{x} \pm$ SE).

	Tidal stage			
	Early flood	Late flood	Early ebb	Late ebb
	Night			
Bivalves	13.1 \pm 10.9	44.0 \pm 35.2	10.0 \pm 8.25	34.4 \pm 27.7
Polychaetes	22.3 \pm 13.4	4.5 \pm 6.6	3.4 \pm 5.2	44.6 \pm 32.8
Amphipods and mole crabs	49.4 \pm 9.6	32.6 \pm 11.0	51.3 \pm 30.4	49.8 \pm 21.6
	Day			
Bivalves	26.6 \pm 13.9	16.4 \pm 10.4	17.0 \pm 7.8	21.8 \pm 16.5
Polychaetes	33.3 \pm 22.1	2.8 \pm 3.5	6.5 \pm 7.1	42.6 \pm 29.9
Amphipods and mole crabs	66.1 \pm 38.4	35.8 \pm 12.1	53.1 \pm 28.9	48.6 \pm 22.7

otic factors affect shorebird nocturnal behavior including shortened daylength (Goss-Custard 1969, Heppleston 1971, Pienkowski 1981, Puttick 1984), moonphase (Ralph 1956, Hale 1980, Milsom 1984), bioluminescence (Robert et al. 1989), tidal cycle (Dugan 1981, Robert et al. 1989), and human disturbance (Burger and Gochfeld 1991). These factors have emerged from studies of migrating or wintering shorebirds and only Robert et al. (1989), Burger and Gochfeld (1991), and Morrier and McNeil (1991) used night-vision equipment to observe and quantify shorebird behavior.

Our results suggest that during the breeding season the behavior of Piping Plovers, and possibly many other shorebirds, is strongly influenced by tide, regardless of the time of day. Furthermore, in light of this study and others (Burger 1984, Johnson and Baldassarre 1988) it is becoming increasingly apparent that the behavior of Piping Plovers is strongly influenced by tidal factors during all stages of their annual cycle. We observed that adult plovers spent significantly different proportions of each 2-min trial feeding depending on tidal stage. They spent the longest proportions of time feeding and exhibited the highest peck rates during early flood and late ebb tides (Table 3). This peck rate pattern is similar to the pattern of success rate observed in the Common Redshank (*Tringa totanus*); Goss-Custard 1976). The pattern of abundance (Fig. 1) was similar to that observed by Burger et al. (1977) for migrating shorebirds feeding on mudflats, but not on outer beaches. This habitat difference may be in response to many factors including temporal factors, prey abundance, prey preference, or prey availability at different times of the annual cycle.

The majority of information about the prey

items of Piping Plovers is observational. In general Piping Plovers eat marine worms (polychaetes), insects, crustaceans, and mollusks (Bent 1929, Palmer 1967, Cairns 1977, Whyte 1985). What Piping Plovers actually eat or prefer to eat, however, has not been determined and undoubtedly depends upon where the bird is feeding (locally throughout its range). The prey sampling results from our 1990 season indicate that the prey base of Piping Plovers is limited to members of a few marine invertebrate families (Table 6). Furthermore, there were no significant differences in overall prey abundance as a function of day or night. These results contradict reports that many shorebirds feed at night because of greater prey abundance or greater biomass of certain invertebrates, especially polychaetes (Dugan 1981). However, in our study we did not determine the biomass of invertebrates.

Polychaetes were the only prey to exhibit a distinct pattern with respect to their abundance and stage of the tidal cycle. Polychaete abundance was highest in samples taken during early flood and late ebb tides compared to the other tidal stages (Table 6). Moreover, polychaete abundance from the nonrandom samples was higher than that obtained from the random ones, regardless of tidal stage. This indicates that polychaete abundance is highest where plovers are feeding. These results suggest that, during the breeding season on outer beaches where intertidal polychaetes are present, polychaetes are the plovers' major food source. We make this suggestion because polychaetes are not ubiquitous (Gosner 1971, 1978). This was apparent from sampling the intertidal at Mantoloking where we collected only 12 individual polychaetes from 16 core samples. Bivalve

abundance was similarly low. Gammarid amphipod and mole crab (*Emerita talpoida*) individuals dominated these samples and, thus, seem to be the major food item at that site.

Comparisons to a daytime foraging study.—We compared the results of this foraging study with those of a daytime study conducted on Piping Plovers at the same sites (Burger unpubl. data). In general, plovers spent equivalent proportions of time feeding per 2-min trial (day, 71%; night, 73%). However, as expected for a species foraging visually, the peck rate dropped considerably at night (Pienkowski 1982). Indeed, it was almost halved (day, 34.1 pecks/2 min; night 18.6 pecks/2 min). There was a similar pattern at night (this study) and during the day (Burger unpubl. data) in the time plovers devoted to feeding as a function of stage of the breeding cycle. In both studies plovers spent more time per 2-min trial feeding during the prenesting and fledgling stages than during incubation and brood rearing periods of the cycle.

Human disturbance.—The effect of human disturbance on foraging behavior has been the focus of several recent Piping Plover studies (Flemming et al. 1988, MacIvor et al. 1990, Burger and Gochfeld 1991, Griffin and Melvin pers. comm.). Data from our study shows that the foraging behavior of Piping Plovers when disturbed was significantly different than when foraging undisturbed at night (Table 5).

People on the beach pose both direct and indirect threats to breeding Piping Plovers (U.S. Fish and Wildlife Service 1988). The disturbances observed in this study were indirect (i.e. walking, jogging). There was a 36% decrease in the time devoted to feeding and a greater than 27% decline in the peck rate as a result of these human activities. Such a decline over the course of the breeding season could be a negative factor affecting individual health and subsequent success of plover pairs and their offspring. Human activities on many beaches during the day impose strong negative impacts on Piping Plovers foraging behavior (Burger 1991, Goldin pers. comm.). Because beaches and, therefore, foraging areas preferred by plovers (intertidal zone, wrackline) often receive heavy recreational use during the day, feeding at night may be a feasible alternative for plovers to exploit these preferred habitats.

Although undisturbed plovers in this study showed almost a 45% reduction in their peck rate from that observed during the day, it is possible that this is better-quality foraging time.

That is, in the absence of large numbers of beachgoers at night, foraging plovers may engage in very long bouts of uninterrupted feeding. However, disturbance at night reduces the peck rate by more than 61% of the daytime level. In this regard, any disturbance at night may be too much.

Conclusions.—Piping Plovers foraged nocturnally at all four study sites suggesting that it is a usual occurrence. The data also support suggestions by Robert and McNeil (1989) and Morrier and McNeil (1991) that nocturnal foraging in shorebirds is a natural habit. We suggest that nocturnal foraging in Piping Plovers is an integral part of their foraging strategy. Future management of this species should include the assessment of nighttime recreational use on beaches where it breeds.

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LITERATURE CITED

- ALTMANN, J. 1974. Observational study of behavior: Sampling methods. *Behaviour* 49:222-265.
- AMERICAN ORNITHOLOGISTS UNION. 1983. Check-list of North American birds, 6th ed. Am. Ornithol. Union, Washington, D.C.
- BENT, A. C. 1929. Life histories of North American shorebirds. U.S. Natl. Mus. Bull. 146.
- BURGER, J. 1984. Abiotic factors affecting migrant shorebirds. Pages 1-72 in *Behavior of marine animals*. Vol. 6, Shorebirds: Migration and foraging behavior (J. Burger and B. L. Olla, Eds.). Plenum Press, New York.
- BURGER, J. 1991. Foraging behavior and the effect of human disturbance on the Piping Plover *Charadrius melodus*. J. Coastal Res. 7:39-52.
- BURGER, J., AND M. GOCHFELD. 1991. Human activity influence and diurnal and nocturnal foraging of Sanderlings *Caliidris alba*. *Condor* 93:259-266.
- BURGER, J., M. A. HOWE, D. C. HAHN, AND J. CHASE. 1977. Effects of tide cycles on habitat selection and habitat partitioning by migrating shorebirds. *Auk* 94:743-758.
- CAIRNS, W. E. 1977. Breeding biology and behavior of the Piping Plover *Charadrius melodus* in southern Nova Scotia. M.Sc. thesis, Dalhousie Univ., Halifax, Nova Scotia.

- CAIRNS, W. E. 1982. Biology and behavior of breeding Piping Plovers. *Wilson Bull.* 94:531-545.
- DUGAN, P. J. 1981. The importance of nocturnal foraging in shorebirds: A consequence of invertebrate activity. Pages 251-260 in *Feeding strategies of marine organisms* (N. V. Jones and W. J. Wolff, Eds.). Plenum Press, London.
- FLEMMING, S. P., R. D. CHIASSON, P. C. SMITH, P. J. AUSTIN-SMITH, AND R. P. BANCROFT. 1988. Piping Plover status in Nova Scotia related to its reproductive and behavioral responses to human disturbance. *J. Field Ornithol.* 59:321-330.
- GOSNER, K. L. 1971. Guide to identification of marine and estuarine invertebrates. Wiley-Interscience, New York.
- GOSNER, K. L. 1978. A field guide to the Atlantic seashore. Houghton Mifflin, Boston.
- GOSS-CUSTARD, J. D. 1969. The winter feeding ecology of the Redshank. *Ibis* 111:338-345.
- GOSS-CUSTARD, J. D. 1976. Variations in the dispersion of Redshanks on their wintering grounds. *Ibis* 118:257-263.
- GOSS-CUSTARD, J. D. 1984. Intake rates and food supply in migrating and wintering shorebirds. Pages 233-270 in *Behavior of marine animals. Vol. 6, Shorebirds: Migration and foraging behavior* (J. Burger and B. L. Olla, Eds.). Plenum Press, New York.
- HAIG, S. M. 1985. Status report on the Piping Plover in Canada. National Museum of Canada, Ottawa.
- HAIG, S. M., AND L. W. ORING. 1985. The distribution and status of the Piping Plover throughout the annual cycle. *J. Field Ornithol.* 56:334-345.
- HALE, W. G. 1980. *Waders*. Collins, London.
- HEPPLESTON, P. B. 1971. The feeding ecology of Oystercatchers (*Haematopus ostralegus* L.) in winter in Northern Scotland. *J. Anim. Ecol.* 41:651-672.
- JOHNSON, C. M., AND G. A. BALDASSARRE. 1988. Aspects of the wintering ecology of Piping Plovers in coastal Alabama. *Wilson Bull.* 100:214-223.
- KALAS, J. A. 1986. Incubation schedules in different parental care systems in the Dotterel *Charadrius morinellus*. *Ardea* 74:185-190.
- MACIVOR, L. H., S. M. MELVIN, AND C. R. GRIFFIN. 1990. Effects of research activity on Piping Plover nest predation. *J. Wildl. Manage.* 54:443-447.
- MILSOM, T. D. 1984. Diurnal behavior of lapwings in relation to moonphase during the winter. *Bird Study* 31:117-120.
- MORRIER, A., AND R. MCNEIL. 1991. Time activity budget of Wilson's and Semipalmated plovers in a tropical environment. *Wilson Bull.* 103:598-620.
- MYERS, J. P., AND B. J. MCCAFFERY. 1984. Paracas revisited: Do shorebirds compete on their wintering grounds? *Auk* 101:197-199.
- PALMER, R. S. 1967. Piping Plover. Page 270 in *The shorebirds of North America* (G. D. Stout, Ed.). Viking Press, New York.
- PIENKOWSKI, M. W. 1981. How foraging plovers cope with environmental effects on invertebrate behavior and availability. Pages 179-192 in *Strategies of estuarine organisms* (N. V. Jones and W. J. Wolff, Eds.). Plenum Press, London.
- PIENKOWSKI, M. W. 1982. Diet and energy intake of Grey and Ringed plovers, *Pluvialis squatarola* and *Charadrius hiaticula*. *J. Zool. (Lond.)* 197:511-549.
- PUTTICK, G. M. 1984. Foraging and activity patterns in wintering shorebirds. Pages 203-231 in *Behavior of marine animals. Vol. 6, Shorebirds: Migration and foraging behavior* (J. Burger and B. L. Olla, Eds.). Plenum Press, New York.
- RALPH, C. L. 1956. Present rhythms of activity and energy consumption in the earthworm. *Physiol. Zool.* 30:41-55.
- ROBERT, M., AND R. MCNEIL. 1989. Comparative day and night feeding strategies of shorebird species in a tropical environment. *Ibis* 131:69-79.
- ROBERT, M., R. MCNEIL, AND A. LEDUC. 1989. Conditions and significance of night feeding in shorebirds and other waterbirds in a tropical lagoon. *Auk* 106:94-101.
- SAS INSTITUTE. 1985. SAS/STAT guide for personal computers, version 6 ed. SAS Institute, Inc., Cary, North Carolina.
- SIDLE, J. 1985. Determination of endangered and threatened status for the Piping Plover. Federal Register 50 (238):50720-50734.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*, 2nd ed. W. H. Freeman, New York.
- STRAUSS, E. 1990. Reproductive success, life history patterns and behavioral variation in a population of Piping Plover subjected to human disturbance (1982-1989). Ph.D. dissertation, Tufts Univ., Medford, Massachusetts.
- TOWNSHEND, D. J., P. J. DUGAN, AND M. W. PIENKOWSKI. 1984. The unsociable plover. Use of intertidal areas by Grey Plovers. Page 140 in *Coastal waders and wildfowl in winter* (P. R. Evans, J. D. Goss-Custard, and W. G. Hale, Eds.). Cambridge Univ. Press, Cambridge.
- U.S. FISH AND WILDLIFE SERVICE. 1988. Atlantic coast Piping Plover recovery plan. U.S. Fish and Wildlife Service. Newton Corner, Massachusetts.
- WALTERS, J. R. 1984. The evolution of parental behavior and clutch size in shorebirds. Pages 243-287 in *Behavior of marine animals. Vol. 5, Breeding behavior and populations* (J. Burger and B. L. Olla, Eds.). Plenum Press, New York.
- WELTY, J. C., AND L. BAPTISTA. 1988. *The life of birds*. Plenum Press, New York.
- WHYTE, A. J. 1985. Breeding ecology of the Piping Plover *Charadrius melodius* in central Saskatchewan. M.Sc. thesis, Univ. Saskatchewan, Saskatoon.
- WILCOX, L. 1959. A twenty year banding study of the Piping Plover. *Auk* 76:129-152.
- WOOD, A. G. 1986. Diurnal and nocturnal territories in the Grey Plover at Teesmouth, as revealed by radio telemetry. *J. Field Ornithol.* 57:213-221.