The Condor 93:259–265

HUMAN ACTIVITY INFLUENCE AND DIURNAL AND NOCTURNAL FORAGING OF SANDERLINGS (*CALIDRIS ALBA*)[1]

JOANNA BURGER
Department of Biological Sciences, Rutgers University, Piscataway, NJ 08855

MICHAEL GOCHFELD
Environmental and Community Medicine, UMDNJ-Robert Wood Johnson Medical School, Piscataway, NJ 08854

Abstract. We studied the foraging behavior of Sanderlings (*Calidris alba*) in the winter of 1986, 1988 and 1990 in Florida to determine whether the presence of people influenced foraging behavior, and whether foraging behavior varied as a function of time of day. We used a focal animal sampling approach. For all three years, the models explaining the greatest variation in seconds per minute devoted to feeding included the number of people within 100 m of foraging Sanderlings. Although the number of people within 10 m of foraging Sanderlings during the day did not increase from 1986 to 1990, the number of people within 100 m rose dramatically, and foraging time per minute decreased. Sanderlings continued to feed through dusk into night and the time devoted to foraging and to aggression was greater at night, while the time devoted to avoiding people was less at night than during daylight or dusk.

Key words: *Sanderling;* Calidris alba; *shorebird; nocturnal foraging; human disturbance.*

INTRODUCTION

Much of the work on migrant and wintering shorebirds has concentrated on foraging behavior on extensive mudflats where human disturbance is minimal (Burger 1984, Goss-Custard 1984). Investigators working with shorebird foraging have examined the effects of temporal (McLachlan et al. 1980), tidal (Recher 1966, Wolff 1969, Puttick 1979, Johnson and Baldassarre 1988), salinity (Prater 1981), weather-related (Evans 1981), and habitat (Duffy et al. 1981) factors on foraging behavior and success. Studies on prey abundance and prey availability (see review in Myers et al. 1979a, 1979b; Goss-Custard 1984), and on prey detection (Metcalfe 1985) have provided models for understanding shorebird habitat use and foraging behavior.

It has been possible to examine the foraging behavior in the absence of human disturbance because people generally avoid mudflats, since they provide a formidable barrier between the land and the sea, and offer no suitable swimming or sunning spots. Some shorebird species spend a considerable portion of their time foraging on the beach front where there are varying degrees of human presence. The effects of people on foraging shorebirds may be amplified because beach habitats are often narrow with a steep tidal gradient. As human use of beaches increases, shorebirds may encounter increased difficulties in foraging undisturbed. Shorebirds may habituate to humans and tolerate close approach, but they must move to stay out of the path of strollers, joggers and vehicles and may take flight when frightened.

In this paper we examine the foraging behavior of Sanderlings (*Calidris alba*) in the winter of 1986, 1988 and 1990 at Delray Beach, Florida. We examined: 1) the temporal differences in the presence of people, 2) the daily and temporal differences in the foraging behavior of Sanderlings, 3) the effect of people on foraging behavior of Sanderlings. We were particularly interested in whether Sanderlings fed at night since this might be one mechanism of avoiding people.

The foraging behavior of Sanderlings has been extensively studied with respect to their defense of territories (Myers et al. 1979a), response to prey abundance (Myers et al. 1979b), habitat use (Burger et al. 1977), and response to abiotic factors (McLachlan et al. 1980). Sanderlings feed all day, but a maximum number are often present in the early morning and late afternoon (McLachlan et al. 1980), although they will feed at night (Burger 1984). Several species of shorebirds have been reported incidentally feeding at night

[1] Received 30 April 1990. Final acceptance 14 January 1991.

TABLE 1. Factors entering the regression models explaining variations in the seconds alert and seconds feeding for Sanderlings foraging during daylight in Florida.

	1986		1988		1990	
	Alert	Feed	Alert	Feed	Alert	Feed
Model						
F	ns	3.12	22.0	21.89	11.58	7.35
P		0.05	0.0001	0.0001	0.0001	0.0001
R^2		0.54	0.61	0.60	0.36	0.26
Factors entering model						
Time of day		ns	24.9 (0.0001)	32.2 (0.0001)	25.0 (0.0001)	12.7 (0.0005)
Nearest neighbor distance		ns	ns	ns	ns	7.41 (0.007)
Group size		4.91 (0.04)	ns	ns	ns	ns
Number of people within 100 m		4.58 (0.05)	4.48 (0.03)	6.99 (0.01)	48.7 (0.0001)	30.6 (0.0001)
Number of people within 10 m		ns	79.6 (0.0001)	37.4 (0.0001)	3.25 (0.07)	ns

(see review in Burger 1984), and the importance of night foraging has been clearly acknowledged (Dugan 1981), although infrequently studied. Recently night foraging has been reported for several species of shorebirds during the winter in the tropics (Venezuela) without the influence of people (McNeil and Robert 1988, Robert and McNeil 1989a, Robert et al. 1989).

STUDY AREA AND METHODS

We studied Sanderlings foraging along a tidal beach at Delray Beach, Florida during the last week in December and the first two weeks of January of 1985–1986, 1987–1988 and 1989–1990 (hereafter referred to as 1986, 1988 and 1990). Delray Beach is a municipal beach, bordered by extensive residential tourist and commercial tourism properties. The beach itself is narrow (20–50 m wide at low tide), and is bordered by a narrow band of sea grape bushes, *Coccolobo uvifera.* Except in heavy rains, the beach always has some people swimming, sunning, jogging, or otherwise engaged in recreational activities. The beach area we examined was about 5 km long, and Sanderlings fed along the entire stretch at some time during our study.

Observations were conducted from 09:00 to 17:00 in 1986, from 15:00 to 17:00 (dusk) in 1988, and from 15:00 to 23:00 in 1990. All observations were made within 3 hr of low tide to reduce tidal variables, and to provide maximum foraging habitat. Few observations could be made on hot, sunny afternoons when the most beach goers were present because foraging birds were usually difficult to find. We regularly walked the beach, and recorded foraging data on each Sanderling encountered. Only one transect was conducted each day to minimize the likelihood of sampling the same individual. We walked at about 7–10 m from the surf to eliminate any effect of our presence, and we used binoculars to observe their behavior. At night we used a 4× Smith and Wesson Image Intensifying Night Telescope to observe foraging behavior.

When a foraging Sanderling was encountered, we recorded the following data before the start of the one-minute foraging sample: date, time, number of birds in the flock, nearest neighbor distance, species of nearest neighbor, number of people within 10 m and 100 m of the bird, and distance the Sanderling was from the water. If the Sanderling flew out of sight during the minute it was eliminated from our sample. We then observed each Sanderling in the flock for one minute, using two stopwatches to record the total time the bird fed, was alert, aggressive or ran or flew from people or while feeding. When the focal Sanderling ran or flew from people we recorded the distance moved, the number of people causing the movement, and the number of movements per minute. In all three years we used the same methods, recording the data on similar data sheets.

Means and standard deviations were obtained for variables, and significant differences among groups were determined with Kruskal-Wallis tests yielding a χ^2 statistic. A multiple regression model procedure (SAS, Proc GLM, SAS 1985) was

TABLE 2. Comparison of daytime foraging behavior of Sanderlings in 1986, 1988, and 1990. All times are in Eastern Standard.

	1986		1988	1990
	All data	Only 15:00 to 17:00 hr	Only 15:00 to 17:00 hr	Only 15:00 to 17:00 hr
Number	117	34	76	155
Mean time of day	11:45 ± 30.0	16:49 ± 7.3	16:54 ± 12.8	16:53 ± 7.5
Group size	9.0 ± 1.1	9.2 ± 1.0	8.1 ± 1.2	8.1 ± 0.5
Nearest neighbor distance (m)	11.8 ± 1.3	7.3 ± 2.6	3.8 ± 3.2	1.8 ± 0.2
Time allocation (sec)				
Feeding	50.5 ± 2.5	53.4 ± 1.9	52.2 ± 1.4	41.9 ± 1.4
Alert	3.5 ± 0.8	0.6 ± 0.3	2.0 ± 1.4	9.1 ± 0.9
Agression	0.05 ± 0.02	0 ± 0	0 ± 0	0 ± 0
Run (undisturbed)	3.0 ± 0.7	4.1 ± 1.7	2.9 ± 0.8	4.9 ± 0.9
Fly (undisturbed)	1.2 ± 0.7	0.8 ± 0.0	1.9 ± 0.6	0.8 ± 0.3
Run (from people)	3.1 ± 0.01	0.6 ± 2	1.5 ± 0.2	6.2 ± 0.7
Fly (from people)	2.3 ± 0.09	0.4 ± 3	0.6 ± 0.2	2.3 ± 0.4
Number of pecks	25.2 ± 1.8	30.1 ± 2.2	15.8 ± 1.8	18.9 ± 1.0
People within 10 m	1.85 ± 0.1	0.9 ± 0.2	0.6 ± 0.1	1.2 ± 1.8
People within 100 m	3.92 ± 0.2	1.3 ± 0.3	1.6 ± 0.1	17.2 ± 1.8

performed on the data to determine the best models explaining variations in time devoted to feeding and vigilance (time alert) as a function of independent variables (date, time of day, nearest neighbor distance, group size, distance from water, and number of people within 10 and 100 m of the foraging bird). We selected variables for the model using a stepwise regression procedure which selects the factor that contributes the most to the R^2, and then selects the second variable that increases the R^2 the most, etc. (SAS 1985). Thus, variables that vary colinearly are not entered in the model.

RESULTS

FORAGING MODELS

In all three years the best model explaining variations in time devoted to foraging accounted for 26 to 60% of the variation (Table 1), and included the number of people within 100 m (all three years) or within 10 m (1988 only), time of day (1988 and 1990), nearest neighbor distance (1990), and group size (1986). Thus in all years the number of people within 100 m of the foraging Sanderling was an important contributor to variation in time feeding.

In 1988 and 1990 the best model explaining variation in time alert (sec/min) accounted for 61 and 36% of the variability by time of day, and the number of people within 10 and 100 m (Table 1). No alert model was significant in 1986.

YEARLY VARIATIONS IN FORAGING

For all three years we had adequate foraging samples for the 15:00 to 17:00 time period, allowing comparisons across years (Table 2). Group size did not vary markedly during the study, and average group size was 8–9. However, as nearest neighbor distance decreased, flocks foraged closer together. From 1986 to 1990 time devoted to foraging decreased and time devoted to alertness increased.

Although there were no clear trends in the time birds spent running or flying while foraging, the time spent avoiding people increased from 1986 to 1990. The number of people within 10 m of the foraging Sanderlings did not differ dramatically from 1986 to 1990, but the average number of people within 100 m increased dramatically from about 2 in 1986 and 1988, to 17 in 1990. These two observations suggest that the overall beach is becoming more crowded, but the Sanderlings attempt to feed in areas with fewer people.

DAILY VARIATIONS IN FORAGING

In 1990 we had the opportunity to use a night scope, allowing us to observe Sanderlings not only in the daylight and dusk, but at night (Table 3). This allowed us to observe the transition from diurnal to nocturnal foraging.

Group size during the day averaged eight, but as light levels decreased the Sanderlings coalesced into larger groups of 10 to 35 birds, and

TABLE 3. Comparison of foraging behavior of Sanderlings by time of day for 1990.

	Daylight	Dusk	Evening	Kruskal-Wallis χ^2
Number	155	182	191	
Mean time of day	16:53 ± 7.5	17:49 ± 8.9	20:20 ± 3.1	—
Range in time of day (E.S.T.)	15:00–17:00	17:00–19:00	19:00–23:00	
Group size	8.1 ± 0.5	17.3 ± 1.2	5.7 ± 0.5	93.5 (0.0001)
Nearest neighbor distance (m)	1.8 ± 0.2	1.3 ± 0.1	2.7 ± 0.2	26.4 (0.0001)
Time allocation (sec)				
Feeding	41.9 ± 1.4	46.4 ± 0.9	51.2 ± 0.8	37.8 (0.0001)
Alert	9.1 ± 0.9	4.0 ± 0.3	0.4 ± 0.1	164.4 (0.0001)
Aggression	0 ± 0	0.7 ± 0.2	5.9 ± 0.7	124.5 (0.0001)
Crouch	0 ± 0	0.02 ± 0.02	0.02 ± 0.02	ns
Run	4.9 ± 0.9	1.9 ± 0.3	1.8 ± 0.5	21.4 (0.0001)
Fly	0.8 ± 0.3	0.4 ± 0.1	0 ± 0	25.4 (0.0001)
Run (people)	6.2 ± 0.7	5.9 ± 0.7	1.5 ± 0.4	56.2 (0.0001)
Fly (people)	2.3 ± 0.4	4.3 ± 0.2	0.2 ± 0.08	56.0 (0.0001)
Number of pecks	18.9 ± 1.0	19.5 ± 0.7	16.8 ± 0.8	10.5 (0.005)
Disruptions (number)				
Run from people	0.04 ± 0.01	0.02 ± 0.01	0.01 ± 0	ns
Run from birds	0.6 ± 0.06	0.3 ± 0.03	0.2 ± 0.02	51.6 (0.0001)
Fly from people	0.4 ± 0.01	0.03 ± 0.03	0 ± 0	6.8 (0.03)
Fly from birds	0.3 ± 0.04	0.2 ± 0.03	0.02 ± 0.01	38.0 (0.0001)
Distance flush (people)	5.0 ± 0.5	8.3 ± 0.8	6.3 ± 0.8	17.4 (0.0002)
Number of people within 10 m	1.2 ± 1.8	1.1 ± 0.1	0.2 ± 0.03	78.1 (0.0001)
Number of people within 100 m	17.2 ± 1.8	4.3 ± 0.1	0.2 ± 0.03	251.8 (0.0001)
Distance from water (m)	2.4 ± 0.2	1.3 ± 0.1	2.6 ± 0.4	73.6 (0.0001)

these did not break up until it was fully dark (Table 3). Correspondingly, nearest neighbor distances decreased in these large flocks, and increased after darkness.

The time devoted to foraging increased from daylight to total darkness, with a corresponding decrease in alertness and increase in aggression (Table 3). Birds ran and flew less at night, both while feeding undisturbed and when disturbed by people. There were fewer people on the beach

TABLE 4. Correlation of group size and foraging behavior of Sanderlings, with number of people on Florida beaches (1989–1990). Correlation coefficient above diagonal, probability below diagonal.

	Nearest neighbor distance	Group size	Feed (sec)	Alert (sec)	Aggression	Run	Fly
Time	ns	−0.11	0.17	−0.40	0.39	−0.16	−0.13
Nearest neighbor distance	—	−0.25	ns	0.07	0.10	0.07	−0.10
Group size	0.0001	—	−0.14	0.18	ns	ns	0.12
Feed (sec)	ns	0.0001	—	−0.44	−0.16	ns	0.07
Alert (sec)	0.04	0.0001	0.0001	—	−0.25	ns	0.08
Aggression (sec)	0.005	ns	0.0001	0.0001	—	−0.12	ns
Interruptions							
Run (sec)	0.07	ns	ns	ns	0.003	—	ns
Fly (sec)	0.01	0.001	0.04	0.04	ns	ns	—
Run (people)	0.01	0.0001	0.0001	0.0001	0.0001	0.03	ns
Fly (people)	ns	ns	0.0001	0.0001	0.0007	ns	ns
People within 10 m	0.0001	0.0001	0.0001	0.0001	0.0001	0.01	ns
People within 100 m	0.006	0.0001	0.0001	0.0001	0.0001	0.02	0.03

at night than during the day or at dusk, but Delray Beach has many people who walk or jog on the beach at night, so Sanderlings suffered some disturbances even at night. Nonetheless, the number of disturbances decreased from daylight to dark. Sanderlings flushed at significantly further distances during twilight compared to daylight or evening (Table 3).

EFFECT OF GROUP SIZE ON FORAGING

Nearest neighbor distance decreased as group size increased (Table 4). In less dense flocks there was a slight but significant increase in time spent alert or aggressive. As nearest neighbor distance decreased, the time Sanderlings ran from people increased. As group size increased the time devoted to foraging decreased, and unexpectedly alertness increased.

EFFECT OF PEOPLE ON SANDERLINGS

The regression models clearly indicated that the number of people within 100 m of foraging Sanderlings was a significant contributor to variations in time devoted to foraging (Table 1). We examined the effects of people for the daytime samples when more people were present (Table 5). In all three years there were significant negative correlations between time devoted to feeding and the time Sanderlings flew or ran because of people and the number of people within 10 and 100 m of the feeding Sanderlings (Table 5). On the contrary, there was no significant correlation between time devoted to feeding and the seconds they ran or flew while foraging undisturbed.

TABLE 4. Extended.

Run (people)	Fly (people)	People (10 m)	People (100 m)
−0.24	−0.21	−0.31	−0.54
−0.09	ns	−0.14	−0.09
0.15	ns	0.13	0.17
−0.48	−0.33	−0.43	−0.45
0.27	0.25	0.27	0.55
−0.21	−0.14	−0.25	−0.35
−0.09	ns	−0.10	−0.08
ns	ns	ns	0.08
—	0.23	0.58	0.45
0.0001	—	0.41	0.39
0.0001	0.0001	—	0.59
0.0001	0.0001	0.0001	—

DISCUSSION

TEMPORAL CHANGES IN FORAGING AND HUMAN USE

Our regression models clearly indicated that in all years of the study the number of people on the beach contributed significantly to explaining variations in the time Sanderlings devoted to feeding. Further, the time devoted to active feeding decreased from 1986 to 1990.

Human populations in Florida have continued to grow in the last six years, and the Delray Beach area has experienced increased residential development which appears to be reflected in increased numbers of observed people on the beach from 1986 to 1990, although our sampling periods were not completely comparable. During the daylight hours, in 1990, it was difficult to find a stretch of 200 m of beach without any people, whereas this was possible in 1986 and 1988.

Nonetheless the Sanderlings foraging during the day managed to feed in 20 m stretches of beach with an average of only two people. The Sanderlings seemed to concentrate where there were the fewest people, and to run or fly to new spots when people moved rapidly toward them or when there were large groups moving along the beach (however slowly the group moved).

The increase in the number of people is associated with the Sanderlings spending more time directly running or flying from human intruders. Such intruders were usually walking or running directly toward them, because both Sanderlings and people prefer the surf zone. In 1990, some Sanderlings ran or flew from people up to five times a minute, even though they continued to try to forage. In previous years Sanderlings ran or flew no more than three times a minute. One possible mechanism for avoiding people is to feed at night, and the Sanderlings in Florida did so in this study.

GROUP SIZE AND ALERTNESS

There is substantial literature showing that birds tend to spend less time alert as group size increases. The converse was true for the Sanderlings in this study. The relationship is confounded in this study by the fact that birds assembled in larger groups at the time when they were more responsive and when the pattern of human disturbance changed (see below). Moreover, intraspecific aggression increased and contributed to alertness.

TABLE 5. Correlation of Sanderling feeding with the number of people and with the number of disruptions for daytime observations.

	1986	1988	1990
Number of Sanderlings	117	76	155
Correlation of seconds feeding with			
Nearest neighbor distance	ns	ns	ns
Group size	0.48 (0.003)	0.32 (0.0001)	15 (0.01)
Fly because of people	−0.33 (0.0001)	−50 (0.0001)	−0.36 (0.0001)
Run because of people	−0.54 (0.0001)	−53 (0.0001)	−0.53 (0.0001)
Number of people within 10 m	−58 (0.0001)	−0.50 (0.0001)	−0.49 (0.0001)
Number of people within 100 m	−50 (0.0001)	−0.33 (0.0008)	−0.52 (0.0001)
Fly while feeding	ns	ns	ns
Run while feeding	ns	ns	ns

NIGHT FORAGING

Initially investigators that primarily studied diurnal foraging reported that some shorebirds fed at night (see review in Burger 1984). In the last ten years, however, the number of shorebirds known to forage at night has increased dramatically. Night foraging seems to be prevalent during the winter to counter low temperatures and decreased hours of daylight (Goss-Custard 1979, Puttick 1979). Presumably, birds feed at night because they cannot obtain enough food during the day (Heppleston 1971). Even visual foragers are able to feed at night by using low intensity light or detecting their prey by touch or sound (Pienkowski 1981). Nonetheless, the pecking rate of visual foragers might decrease more than that of tactile foragers at night (Pienkowski 1982). Dugan (1981) recently discussed the importance of nocturnal foraging in shorebirds, noting that some prey organisms are more active at night.

Robert et al. (1989) reported that in a tropical habitat without human disturbance a wide variety of shorebirds fed at night during the winter, and some species fed with comparable frequency to daytime rates. Tide level was the most important variable, which may be the causal factor for night foraging. Species that fed visually during the day either continued to feed visually at night, fed visually at night with reduced frequency, or did not feed visually at night (McNeil and Robert 1988, Robert and McNeil 1989a). In their study prey abundance was higher at night than during the day. Wood (1986), using radio telemetry, showed that Black-bellied Plover *Pluvialis squatarola* maintain and defend territories during the day and at night during the non-breeding season, particularly at low tide. Thus some species may feed equally often during the day and at night. Other species specifically examined, such as Brown Pelican (*Pelecanus occidentalis*), feed very infrequently at night (Robert and McNeil 1989b).

In our study of Sanderlings on the wintering grounds in Florida we concluded that 1) with decreasing light Sanderlings coalesced into tighter and larger foraging flocks, 2) some Sanderlings continued to forage through dusk into darkness, 3) Sanderlings were most easily flushed at dusk when light levels were low, 4) the amount of time they devoted to actively feeding increased at night even though the number of pecks decreased slightly (but significantly), and 5) there was an increase in aggression at night.

It was our impression that as light levels decreased Sanderlings feeding solitarily or in small groups flew to join larger groups. These groups sometimes continued to feed as light levels decreased. At other times these groups fed until it was very dark, and then they roosted on the beach in a dense flock for 20–40 minutes. Thereafter, the group began to break up as individuals walked off and resumed foraging.

During dusk, Sanderlings flushed when human intruders were farther away than at other times. We feel this difference was partly due to differences in human behavior. Throughout the day people engage in a variety of relatively stationary activities (sunning, talking, swimming) and a few mobile ones (Frisbee, active swimming, walking). As light levels decreased people who were relatively inactive began to pick up their belongings and depart (in unpredictable directions). Further, as the afternoon temperature decreased the number of joggers increased, and shorebirds were more

responsive to the rapid movements of joggers than to slow walkers (see Burger 1981).

In the complete darkness, Sanderlings again allowed people to approach more closely before flushing. Whether this is due to decreased perception or to decreased fear is unclear. On most nights it became sufficiently dark that we were unable to see either the Sanderlings or the approaching people at 10 m without the night scope. In some cases we could hear people approaching (because they were talking), and presumably the Sanderlings responded accordingly.

Even though there were some disturbances from people at night, there were far fewer compared to during the day. Thus, Sanderlings that forage primarily during low tide can both increase the amount of time they feed at low tide and decrease human disturbance by feeding at night.

ACKNOWLEDGMENTS

We gratefully acknowledge D. J. Gochfeld and D. A. Gochfeld for field and computer assistance and stimulating discussions; and Anne and Alex Gochfeld for logistical support. We thank K. Stain for discussions and computer assistance.

LITERATURE CITED

BURGER, J. 1981. The effect of human activity on birds at a coastal bay. Biol. Conserv. 21:231–241.

BURGER, J. 1984. Abiotic factors affecting migrant shorebirds, p. 1–73. *In* J. Burger and B. L. Olla [eds.], Shorebirds: migration and foraging behavior. Plenum Press, New York.

BURGER, J., M. A. HOWE, D. C. HAHN, AND J. CHASE. 1977. Effects of tide cycles on habitat selection and habitat partitioning by migrant shorebirds. Auk 94:743–758.

DUFFY, D. C., N. ATKINS, AND D. C. SCHNEIDER. 1981. Do shorebirds compete on their wintering grounds? Auk 98:215–229.

DUGAN, P. J. 1981. The importance of nocturnal foraging in shorebirds, p. 251–260. *In* N. V. Jones and W. J. Wolff [eds.], Feeding and survival strategies of estuarine organisms. Plenum Press, New York.

EVANS, P. R. 1981. Migration and dispersal of shorebirds as a survival strategy, p. 275–290. *In* N. V. Jones and W. J. Wolff [eds.], Feeding and survival strategies of estuarine organisms. Plenum Press, New York.

GOSS-CUSTARD, J. D. 1979. The winter feeding ecology of the Redshank, *Tringa totanus*. Ibis 111: 338–356.

GOSS-CUSTARD, J. D. 1984. Intake rates and food supply in migrating and wintering shorebirds, p. 233–270. *In* J. Burger and B. L. Olla [eds.], Shorebirds: migration and foraging behavior. Plenum Press, New York.

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 Plover in coastal Alabama. Wilson Bull. 100:214–223.

METCALFE, N. B. 1985. Prey detection by intertidally feeding Lapwing. Zeits. Tierpsychologie 64:45–57.

MCLACHLAN, G. R., T. WOOLDRIDGE, M. SCHRAMM, AND M. KUHN. 1980. Seasonal abundance, biomass and feeding of shorebirds on sandy beaches in the Eastern Cape, South Africa. Ostrich 51:44–52.

MCNEIL, R., AND M. ROBERT. 1988. Nocturnal feeding strategies of some shorebird species in a tropical environment. Acta 19 Int. Ornithol. Congr. 2328–2336.

MYERS, J. P., P. G. CONNORS, AND F. A. PITELKA. 1979a. Territory in nonbreeding shorebirds, p. 231–246. *In* F. A. Pitelka [ed.], Studies in avian biology No. 2. Allen Press, Lawrence, KS.

MYERS, J. P., P. G. CONNORS, AND F. A. PITELKA. 1979b. Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. Auk 96:551–561.

PIENKOWSKI, M. W. 1981. How foraging plovers cope with environmental effects on invertebrate behavior and availability, p. 179–192. *In* N. V. Jones and W. J. Wolff [eds.], Feeding and survival strategies of estuarine organisms. Plenum Press, New York.

PIENKOWSKI, M. W. 1982. Diet and energy intake of Grey and Ringed Plovers *Pluvialis squatarola* and *Charadrius hiaticula*, in the non-breeding season. J. Zool. 197:511–549.

PRATER, A. J. 1981. Estuary birds of Britain and Ireland. Poyser, Calton, England.

PUTTICK, G. M. Foraging behaviour and activity budgets of Curlew Sandpipers. Ardea 67:111–122.

RECHER, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47:393–407.

ROBERT, M., AND R. MCNEIL. 1989a. Comparative day and night feeding strategies of shorebird species in a tropical environment. Ibis 131:69–79.

ROBERT, M., AND R. MCNEIL. 1989b. Night activity in the Brown Pelican. Colonial Waterbirds 12:118–119.

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. 1985. SAS user's guide: statistics. SAS Institute, Cary, NC.

WOLFF, W. J. 1969. Distribution of non-breeding waders in an estuarine area in relation to the distribution of their organisms. Ardea 57:1–25.

WOOD, A. G. 1986. Diurnal and nocturnal territoriality in the Grey Plover at Teesmouth, as revealed by radio telemetry. J. Field Ornithol. 57: 213–221.