Journal of Coastal Research	7	1	39-52	Fort Lauderdale, Florida	Winter 1991

Foraging Behavior and the Effect of Human Disturbance on the Piping Plover (*Charadrius melodus*)

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ABSTRACT

BURGER, J. 1990. Foraging behavior and the effect of human disturbance on the piping plover *Charadrius melodus*. *Journal of Coastal Research*, 7(1), 39-52. Fort Lauderdale (Florida), ISSN 0749-0208.

Foraging behavior of Piping Plover (*Charadrius melodus*) was studied using a focal animal approach from 1985-1986. Time devoted to foraging decreased as vigilance (time devoted to being alert) increased. Variations in vigilance were explained by beach, reproductive stage, brood size, time of day, and number of people nearby. Overall, Piping Plovers foraged from 46-79 sec., were alert for 14-57 sec., and displayed or ran from people for 1-8 sec. in the 2 min. samples. Plovers at sites less disturbed by people (Little Beach, Holgate) generally devoted more time to foraging and less time to vigilance than birds at the other sites. Time devoted to foraging was generally higher in May, lower in June, and increased again in July. Plovers that were incubating or caring for chicks spent less time foraging than those that had lost their chicks. Chicks spent less time foraging and more time being alert, running, and crouching than did their parents foraging during the same time periods. With increasing brood size, chicks spent less time foraging and more time running or crouching although the number of people nearby did not vary. Behavior was correlated within members of a pair: birds spent less time foraging as their mates increased time devoted to alertness, being off the nest, or displaying. When brooding birds increased alert time, their mates increased their alertness and displaying, and decreased foraging time. As the number of people near foraging plovers increased, time devoted to running and crouching increased and time devoted to feeding decreased. It appears that the presence of people is stressful for breeding adults and chicks, forcing them to spend significantly less time foraging, perhaps accounting for decreased overall reproductive success.

ADDITIONAL INDEX WORDS: *Shorebirds, habitat destruction, defense, coastal birds, coastal nesting species, barrier beaches, endangered species.*

INTRODUCTION

Bird species that nest along temperate coasts are constrained by habitat destruction, increased development and disturbance. Available habitat may be unsuitable because physical features have changed or predator numbers have increased. Increased human activity affects coastal nesting species directly by disturbing incubating and brooding birds. Although these features have been the focus of studies on beach nesting colonial species such as Least Terns (*Sterna antillarum*, NISBET, 1973; ERWIN *et al.*, 1981; FAANES, 1983; BURGER, 1984a, 1984b), less attention has been directed toward solitary nesting species. Although we frequently examine the direct effects of habitat loss and death, we seldom examine the indirect impacts on the behavior, ecology, and fitness of animals.

89045 received 17 August 1989; accepted in revision 10 March 1990.

In this paper I examine foraging behavior of Piping Plover to determine factors that affect the time plovers devote to foraging. Objectives of the study were to determine: (1) where Piping Plovers foraged, (2) time devoted to foraging as a function of nesting beach, reproductive stage and brood size, and (3) the effect of human activities on foraging time. Piping Plovers are ideal for such an examination because they nest solitarily on barrier beach islands that have suffered from increased human development and recreational activities. I examined foraging behavior because clutch size, and nest sites do not seem to be causing population declines (see BURGER, 1987). Thus I wanted to determine whether Piping Plover experienced difficulties foraging because of people. Reproductive success is lower in areas with high human disturbance (BURGER, 1987).

Piping Plovers nest on wide, sparsely-vegetated beaches or on inland lake shores (WIL-

COX, 1959; RENAUD, 1979; CAIRNS, 1982; HAIG and ORING, 1985). They generally forage on the intertidal ocean beach on the East and Gulf Coasts (TULL, 1984; JOHNSON and BALDASSARRE, 1988). Piping Plovers were recently listed on the United States list and on the Canadian list as endangered (DYER *et al.*, 1987; HAIG and ORING, 1988).

STUDY AREAS AND METHODS

Observations on foraging plovers were made at North and South Corson's Inlet in 1985 and 1986, and at Brigantine, Whale Beach, Little Beach, and Holgate in 1986. Observations were conducted from 0700-1700 five days a week at each site except the latter two, requiring several field assistants. All study sites are located on barrier beach islands. Brigantine Beach, opposite Atlantic City, is a flat beach 2 km long and 200 m wide, with a belt of dunes on the landward side as a buffer from homes. On the back side of the beach is a bay not exposed to direct tidal waves.

North Corson's Inlet is a state park at the end of a barrier island at Corson's Inlet. The beach is less flat, and has higher, less stable dunes than Brigantine. A Least Tern colony here is delineated by string and signs. South Corson's Inlet has a similar physiognomy to North Corson's Inlet, but has fewer Least Terns nesting. Whale Beach, adjacent to South Corson's Inlet, is similar in physiognomy, although narrower.

Little Beach and Holgate, part of Edwin B. Forsythe National Wildlife Refuge (formerly Brigantine NWR), are the southern and northern barrier spits bordering Little Egg Inlet. Both are wide expanses of beach with stable dunes and a back tidal bay protected from the surf. Little Beach is a wilderness area, and so has almost no human disturbance.

Foraging behavior was examined by observing individual Piping Plovers for two minute samples. I used two minutes sample periods because birds could be easily followed for that time period, were not always interrupted, and preliminary observations indicated 2 min. was long enough to include usual foraging behaviors such as pecking, vigilance, running and watching chicks.

Observers walked a regular transect down the beach, through the dunes, back along the bay, and over to the beach. Although the amount of bay, ocean and dunes differed at each study site, we defined study plots in each habitat so they were equal in size. Whenever observers saw any feeding Piping Plovers they immediately took data on those individuals. Observers remained back from the areas where the birds fed, used binoculars, and the plovers did not alter their behavior. If such differences were noted, the plover was not included in the example.

In 1985 observations were made at North and South Corson's Inlet. Since all nests were marked in 1985, adults could be assigned to nest, and in most pairs, sex could be determined. Males have a darker, more distinct neck band than females (CAIRNS, 1982), and when the pair remain together they can be distinguished. Questionable birds were not assigned to a nest or sex.

In 1986 foraging behavior was examined at several beaches (Brigantine, North and South Corson's, Whale Beach, Little Beach and Holgate) with varying amounts of human disturbance. Because marked individuals were not followed in 1986, the foraging behavior data are divided into temporal periods corresponding to normal breeding activities at those times (preincubation, incubation, chick phase).

In both years and at all sites, data were collected in a similar manner using the same data sheets. Each day the observer walked the beaches looking for Piping Plovers. Data recorded before the start of each two minute foraging sample included: date, time, nest number, stage (incubation, chick phase, eggs or chicks lost), age in 1985 (days in incubation or age of chicks), number of chicks, age (adult, chick), sex (male, female, unknown adult, and unknown chick), and interbird distance (estimated using body lengths). Stopwatches were used to record the time spent foraging, alert, running or flying from people, running or flying while feeding, and crouching or displaying. An alert bird was one that looked up and about, rather than looking at the sand. Since Piping Plover sometimes search for prey visually, such searching was not included as alert behavior. Parents display or crouch in defense of their eggs or chicks, and all adults devote time to being alert or running from disturbances (GOCHFELD, 1984). During the two minute samples the number of times plovers ran from people, the number of pecks at food items, and

the number of people within 10 and within 50 m of the foraging bird were also recorded.

Preliminary observations were made on 20 Piping Plover feeding on Ohio Key, Florida, in early January 1988. The same protocol was followed as performed on Piping Plover during the breeding season.

Means and standard deviations were obtained for variables, and significant differences among groups were determined by Kruskal-Wallis tests yielding a X^2 statistic (abbreviated as X^2 throughout the text). A multiple regression model procedure (SAS, PROC GLM) was performed on log-transformed data to determine the best models explaining variations in the dependent variables as a function of the independent variables. My initial design was unbalanced since the number of breeding pairs at each site differed. The procedure selects the factor that contributes the most to the R^2, and then selects the second variable that increases the R^2 the most (SAS, 1985). Thus variables that vary colinearly are not entered in the model.

RESULTS

Foraging Models

While foraging, plovers either actively foraged, were alert or were engaged in antipredator behavior. In both 1985 and 1986 reproductive stage, time of day, and the presence of people affected the amount of time foraging plovers were alert (Table 1). In 1985 brood size, and in 1986, location (*i.e.*, beach studied) also entered the models. Each of the significant variables will be discussed below.

Location Differences

The time devoted to foraging varied from 46 to 80 seconds (of the 120 sec. samples) on the different beaches (Table 2). Similarly, the time devoted to being alert, running, flying or displaying to people also varied among locations. The number of people present also varied (Table 2), with more people present at Brigantine and Corson's Inlet than at Little Beach or Holgate.

Reproductive Stage

In both years reproductive stage (or temporal differences) contributed significantly to explaining the variation in time devoted to being alert (and thus to foraging). Overall, adults devoted more time to foraging (and less to being alert) in the pre-incubation and incubation phases, and less to foraging when they had chicks (Tables 3 and 4, t tests for pair-wise comparison). However, the pattern varied slightly among beaches. At Brigantine, birds spent more time alert during early incubation and after June (when most pairs had chicks); at North and South Corson's and Whale Beach plover spent more time alert during June (when most pairs had chicks there), and were less alert in May when they were courting or incubating (Table 3).

Data in 1985 could be ascribed to particular

Table 1. *Models explaining variations in time devoted to alert behavior of foraging Piping Plover adults, based on two-minute samples of foraging plover.*

	1985 (Corson's Inlet)	1986 (All beaches)
Model		
F	8.06	56.50
R^2	.87	.89
df	(4,224)	(5,745)
P	0.01	0.0001
Factors Entering Model[a]		
Location	NA	212.0(0.0001)
Reproductive stage	4.65(0.08)	27.2(.001)
Brood size	7.21(.04)	NA
Number of runs from people	NS	2.81(0.09)
Time of day	14.05(0.01)	5.46(0.02)
People within 50m	12.62(0.02)	6.44(0.01)

[a]Given are F values (levels of significance). Individual did not enter any model as a significant variable.
NS = Not significant. NA = Not applicable to that year.

Table 2. *Feeding behavior of adult Piping Plovers at different locations based on two minute samples. Given are means ± standard errors.*

	Corson's Inlet[a] 1985	Brigantine 1986	North Corson's 1986	South Corson's 1986	Whale Beach 1986	Holgate 1986	Little Beach 1986
Number of birds	48	24	18	24	10	16	10
Number of Samples	228	226	129	192	135	43	25
Seconds Feeding[b]	51.0 ± 6	72.9 ± 2	57.01	53.0 ± 1	46.1 ± 12	73 ± 7.1	79.6 ± 2.7
Alert[c]	39.2 ± 5	35.7 ± 2	41.2 ± 1	47.0 ± 2	57.4 ± 12	14.9 ± 5.2	33.0 ± 2.2
Display, Run or fly from people	8.1 ± 3	4.7 ± 1	0.9 ± 0.2	1.6 ± 0.2	2.2 ± 0.4	4.8 ± 2.8	0
Run or fly while feeding	13.9 ±	4.1 ± 2	19.6 ± 1	17.6 ± 1	11.7 ± 0.6	10.7 ± 2.3	7.3 ± 1.1
Crouch	6.8 ± 1	0.6 ± 0.5	0.4 ± 0.1	0.8 ± 0.2	0.9 ± 0.2	0.8 ± 0.8	0
Number of pecks[d]	26.2 ± 4	37.2 ± 1	30.6 ± 1	30.1 ± 1	31.1 ± 1	6	80.0 ± 2.7
Number of people within 10 m	1.7 ± .5	0.4 ± 0.05	0.1 ± 0.04	0.2 ± 0.02	0.1 ± 0.04	0.04 ± 0.2	0
Number of people within 50 m	4.4 ± 1	2.2 ± 0.2	1.6 ± 0.9	1.5 ± 0.07	1.6 ± 0.08	0.7 ± 0.2	0

[a]Both North and South combined
[b]$X^2 = 144.3$, $P < 0.0001$
[c]$X^2 = 18.3$, $P < 0.006$
[d]$X^2 = 14.4$, $P < .005$

known adults, thus it was possible to compare feeding behavior in more detail (Table 4). Adults spent significantly more time foraging after they lost chicks, than when they were incubating or brooding chicks. Adults that had lost their chicks neither crouched nor displayed, they simply flew away if disturbed, whereas parents remained to crouch or display. The number of people and the number of disturbances (times plover ran from people) were lower during incubation than when parents had chicks (sunbathers come to the beach more in late June than in late May, unpublished data).

During the chick phase there were significant differences in the foraging behavior of parents and their chicks (Table 4). Although parents spent 48 seconds foraging, chicks spent only 27 seconds; the difference was largely accounted for by the time chicks ran from people (47 sec.) compared to their parents (8 sec.). Similarly, chicks spent more time crouching than their parents. Because the observations were taken simultaneously, there were no differences in the number of people or the number of disturbances (Table 4). Thus, foraging behavior differences between parents and their chicks were due to response differences.

Preliminary observations were made on 20 Piping Plovers wintering on Ohio Key, Florida, in early January 1988 to determine time normally devoted to foraging during the non-breeding season, without the presence of people. The plovers fed on a mudflat surrounded by vegetation, 100 m from the ocean. For the two minute sample periods, plovers fed for an average of 108 ± 4 sec., were alert for 3.7 ± 1.4 sec., and spent the rest of the time running while feeding. Mean interbird distance was 3.1 ± .6 m.

Sexual and Parental Differences

When males and females were feeding alone (not guarding nests or chicks) there were no significant sexual differences in time devoted to feeding, being alert or displaying. However, females ran less than males ($X^2 = 5.27$, $P < .02$) and crouched more than males ($X^2 = 4.52$, $P < .03$). There were no differences among sexes in the number of people within 10 or 50 m of foraging plovers ($X^2 = 0.02$).

Plovers often feed in sight of the nest or brood, and both members of pairs engage in defense and display behavior. In this discussion, I refer to the bird incubating or watching the nest or chicks as the attending bird, and the other member of the pair as the mate. During incubation, when both members of the pair were visible on their territory, the mate spent significantly more time displaying to human intruders than did the incubating bird, and less time alert and resting (Table 5). On average,

Table 3. *Piping Plover foraging behavior in 1986 as a function of season. Given are means ± SE.*

	Brigantine	North Corson's	South Corson's	Whale Beach	Little Beach	Holgate
Before 15 May						
N	25	26	26			
Seconds Feed	18 ± 8	62 ± 1	57 ± 7	—	—	—
Seconds Alert	96 ± 10	32 ± 1	33 ± 2	—	—	—
People 50 m	0.00	0.13 ± 0.03	0.06 ± 0.03	—	—	—
Times Fly from people	0	0.3 ± 0.1	0.8 ± 0.5			
Times Run from people	0	0.04 ± 0.02	0.05 ± 0.03			
Total Aggression	0.61 ± 0.06	0.51 ± 0.23	1.0 ± 0.3			
May 16–31 May						
N55 29 40						
Seconds Feed	73 ± 3	57 ± 5	60 ± 2	—	—	—
Seconds Alert	34 ± 3	43 ± 6	41 ± 3			
People 50 m	2.4 ± 0.5	0.3 ± 0.2	0.3 ± 0.2			
Times Fly from people	0	0	0	—	—	—
Times Run from people	0.2 ± 0.05	0	0.05 ± 0.05			
Total Aggression	0.4 ± 0.2	0.5 ± 0.5	0			
1–15 June						
N	53	26	49	62		
Seconds Feed	84 ± 3	44 ± 5	48 ± 2	35 ± 4		
Seconds Alert	24 ± 2	58 ± 4	56 ± 2	67 ± 3		
People 50 m	1.2 ± 0.2	1.3 ± 0.3	0.9 ± 0.2	0.5 ± 0.2	—	
Times Fly from people	0.3 ± 0.1	0	0.06 ± 0.06	0	—	
Times Run from people	0.4 ± 0.07	0.3 ± 0.2	0.2 ± 0.6	0.5 ± 0.3	—	
Total Aggression	0	0.2 ± 1.2	0.2 ± 0.1	0.5 ± 0.5	—	
16–30 June						
N	61	23	33	41	25	23
Seconds Feed	83 ± 4	42 ± 6	39 ± 8	32 ± 3	82 ± 3	65 ± 11
Seconds Alert	26 ± 3	65 ± 6	67 ± 7	68 ± 4	31 ± 2	26 ± 11
People 50 m	3.5 ± 0.6	1.8 ± 0.4	1.0 ± 0.3	0.3 ± 0.1	0	1.7 ± 0.4
Times Fly from people	1.1 ± 0.6	0	0	0	0	5.1 ± 3.8
Times Run from people	0.3 ± 0.07	0.4 ± 0.2	0.6 ± 0.2	0.2 ± 0.1	0	0.4 ± 0.1
Total Aggression	0.3 ± 0.2	0	0	0	0	0
After 30 June						
N	32	25	44	32	20	
Seconds Feed	56 ± 4	55 ± 3	54 ± 3	51 ± 2	—	79 ± 8
Seconds Alert	56 ± 3	52 ± 3	53 ± 3	53 ± 2	—	7 ± 3
People 50 m	2.6 ± 0.7	1.0 ± 0.3	0.5 ± 0.2	0.7 ± 0.1	—	1.5 ± 3
Times Fly from people	—	0.2 ± 0.2	0.8 ± 0.06	0.2 ± 0.09	—	4.6 ± 4.0
Times Run from people	0.1 ± 0.07	0.1 ± 6.00	0.09 ± 0.04	0.2 − 0.03	—	.2 ± .1
Total Aggression	1.3 ± 0.6	1.4 ± 0.3	1.3 ± 0.5	1.7 ± 0.6	—	4.2 ± 3.2

visible mates were about 38 m from their nests. During the chick phase the attending bird spent more time resting with the brood, but equal amounts of time being alert and displaying as it mate (Table 5). In comparing the two phases, there were nearly twice as many people nearby during the chick phase compared to incubation.

To examine the possibility that the behavior of one member of a pair related to that of its mate, I examined the correlation of behavior between them (Table 6). As the distance between the mate and the next increased during the incubation phase, the time the incubating bird was alert decreased (Figure 1). Furthermore, as the time the mate spent displaying increased, the time the incubating bird spent displaying also increased (Figure 2). Thus the mate spent less time foraging when the incubating bird was alert (Figure 3). The correlations between the time the attending bird was alert and when its mate was feeding showed a threshold in that when the attending bird spent more time alert, its mate spent less time feeding.

During the chick phase the amount of time the brooding or attending adult spent alert was positively correlated with the time its mate was alert or displaying, and negatively correlated with the time its mate spent foraging (Table 6, Figure 4). This was even more obvious when the

Table 4. *Feeding behavior of Piping Plover adults as a function of stage in cycle. Given are means ± one standard deviation (1985).*

	Adults						Comparison of chicks and adults[e]	
	Incubation	Chick phase	Lost chick phase	X^2	P	Chicks	X^2	*P*
Number of samples	66	136	26			89		
Behavior								
Seconds Feeding[a]	54 ± 11	48 ± 25	62 ± 11	7.46[d]	0.02	27 ± 28	4.73[d]	0.03
Seconds run or fly while feeding	8.1 ± 2	10.2 ± 4	6.1 ± 3	2.62	NS			
Seconds alert[b]	41 ± 27	39 ± 21	41 ± 17	2.34	NS	32 ± 21	4.73	0.03
Seconds run or fly from people	6.6 ± 8	8.1 ± 2	5 ± 2	2.76	NS	47 ± 24	14.95	0.0001
Seconds displaying	4 ± 13	5 ± 13	0	2.97	NS	0	15.04	0.0001
Seconds crouched	6 ± 13	8 ± 21	0	4.03	NS	12 ± 14	14.25	0.0002
Number of runs	0.8 ± 0.8	1.6 ± 0.6	0.2 ± 0.1	5.72	0.05	1.4 ± 1.2	4.43	0.04
Pecks at food	28 ± 19	25 ± 18	32 ± 11	2.95	NS	18 ± 14	9.10	0.002
Presence of people								
Number of disturbances[c]	1.0 ± 1.2	2.1 ± 1.8	1.8 ± 1.5	20.34	0.0001	1.9 ± 1.5	0.30	NS
People within 10m	0.4 ± 0.9	0.8 ± 1.4	0.4 ± 0.5	2.01	NS	0.4 ± 0.9	2.99	NS
People within 50m	2.1 ± 1.2	5.6 ± 7.5	4.8 ± 1.5	43.10	0.0001	4.7 ± 2.6	0.41	NS

[a] Per 2 min sample period.
[b] Plovers not displaying.
[c] Number of people that walked close enough for plover to display or depart.
[d] Using Kruskal-Wallis X^2
[e] Compares only adults feeding during the chick stage with chicks.
[f] One chick per brood in each observation period.

Table 5. *comparison of behavior of members of Piping Plover pairs engaged in incubation and chick care (Corson's Inlet 1985). Attending bird = bird incubating, by nest, or brooding chicks. Given are means (± standard errors) for 2 min samples for data where both adults were present together.*

	Attending Bird (sec)		Mate (sec)	X^2 (*P*)[a]
Incubation				
Sample	27		27	
Time alert on nest	9 ± 2		—	
Time displaying	17 ± 1		32 ± 2	9.61(0.002)
Time alert off nest	26 ± 3		22 ± 2	8.31(0.004)
Time resting	68 ± 3		7 ± 2	13.57(0.001)
Time feeding	—		49 ± 11	
Distance from nest (m)	0		38 ± 30	
People within 15m of nest		1.7 ± 1.4		
People within 50m of nest		3.7 ± 2.4		
People within 35m of beach front where mate was feeding		2.4 ± 2.9		
Chick Phase				
Sample	52		52	
Time alert	19 ± 3		14 ± 2	1.63(NS)
Time displaying	30 ± 2		33 + 2	2.05(NS)
Time resting	61 ± 4		15 ± 1	11.21(0.001)
Time feeding	—		38 ± 2	—
Distance from nest (m)	25 ± 20		42 ± 23	1.20(NS)
People within 15m of nest site		3.9 ± 3.9		
People within 50m of brood		7.1 ± 5.7		
People within 50m of beach front where birds were feeding		3.8 ± 3.4		

[a] Kruskal-Wallis X^2

Table 6. *Correlation of defense behavior within Piping Plover pairs (Corson's Inlet 1985). Kendall coefficient with probability in parentheses.*

	Alert	Off nest	Displaying
		Incubating Bird	
Mate			
Distance away	− 0.26(0.05)	− 0.29(0.04)	− 0.39(0.04)
Alert	0	NS	NS
Display	NS	0.25(0.05)	0.34(0.04)
Feed	− 0.34(0.01)	− 0.31(0.05)	− 0.51(0.008)
		Brooding Bird	
Mate			
Distance away	NS		NS
Alert	0.45(0.0001)		NS
Display	0.22(0.003)		NS
Feed	− 0.26(0.002)		− 0.46(0.001)

N = 24 pairs for all comparisons.

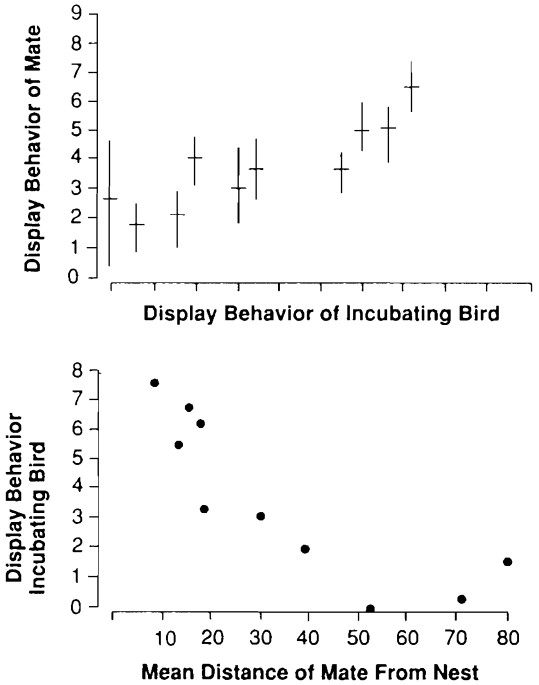

Figure 1. Relationships of display behavior of incubating bird to its mate for all 24 Piping Plover (top, mean ± standard deviation) and display behavior of incubating bird as a function its mate is from the nest (bottom).

mean values for each pair were considered (Figure 5). That is, pairs in which the mate had a high level of alertness for both the incubation and brood phase, the attending bird also had a high level of alertness. This was not due to differences in the number of people present (X^2 values not significant), but to their response to people. Taken altogether, my results suggest that the behavior of members of a pair is correlated, indicating that they are both aware of the vigilance and display behavior of each other, and each is monitoring the presence of people and their mate's behavior.

Foraging behavior also was influenced by brood size (Figure 6). With increased brood size, chicks spent more time running and crouching and less time foraging. Chicks in broods of one spent over 30 seconds of every 2 minutes for-

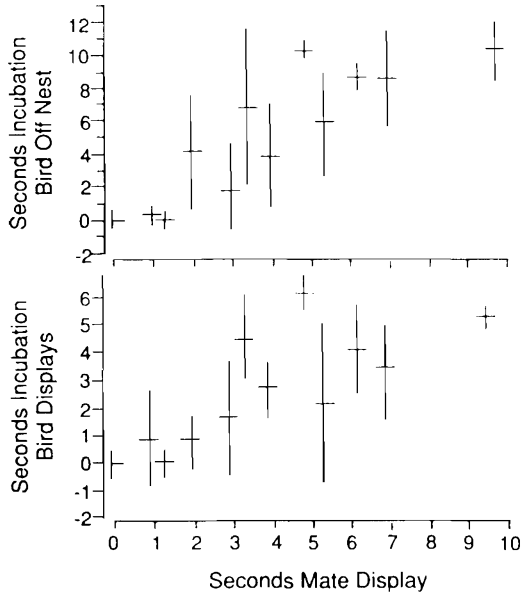

Figure 2. Time devoted to displaying by mates as a function of the time incubating birds were off the nest and displaying. Shown are mean ± standard deviation for 24 pairs.

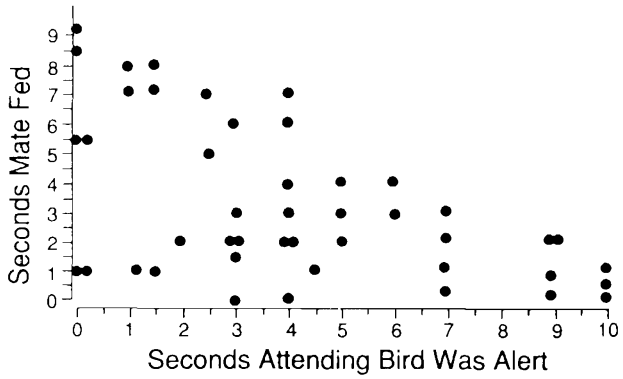

Figure 3. Relationship between time devoted to feeding by mate and seconds attending bird was alert for 24 pairs.

aging whereas those in broods of four spent less than 10 seconds foraging. Crouching showed a different pattern in that chicks in broods of two or three crouched whereas those in broods of four crouched less (due to their investment in running, Figure 6). The number of people within 10 and 50 m did not vary significantly among brood sizes (Figure 6).

Foraging and Human Disturbances

In general, most people at Brigantine were sunbathing, whereas at the other beaches most people were walking. For all sites and years there was a positive correlation between the number of people within 50 m and the seconds that foraging Piping Plovers ran and the number of times they ran (from people, rather than while feeding); and a negative correlation with

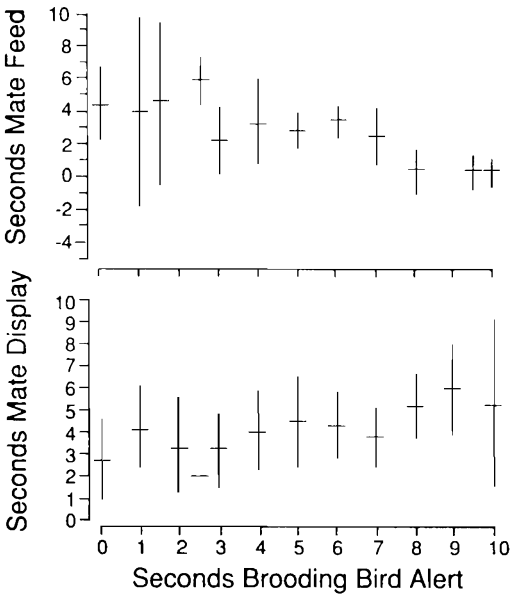

Figure 4. Relationships of attending bird (Brooding bird) to the feeding and display behavior of its mate during the chick phase for all Piping Plover observation periods. Shown are mean ± standard deviation for 24 pairs.

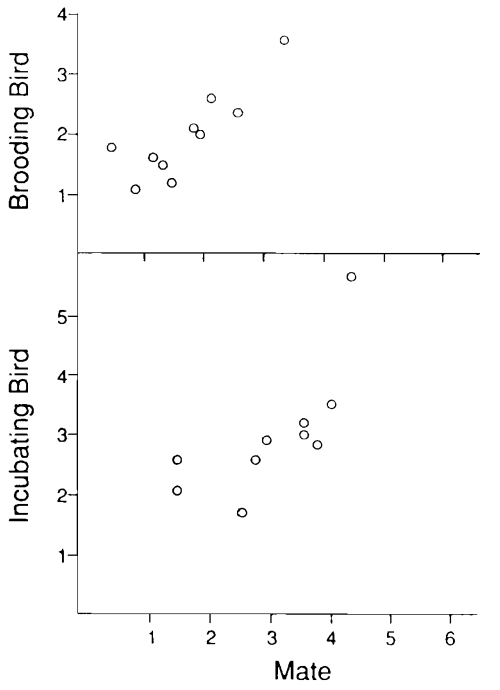

Figure 5. Relationships of mean time alert (in min.) for incubating and brooding mate members of 10 Piping Plover pairs observed frequently from egg-laying through fledging.

time devoted to foraging (except for Brigantine, Table 7). Overall, when more people were present, plovers spent more time running, flying and crouching (or displaying), and less time foraging.

DISCUSSION

Abiotic factors affect the distribution of all marine organisms, including shorebirds. Foraging behavior is particularly affected by temporal (seasonality, time of day and day length), tidal, and weather-related factors (wind, temperature, precipitation [BURGER, 1984c]). Length of daylight is critical because visual foragers have decreased foraging success at night, although tidal conditions may make night foraging necessary (PUTTICK, 1979, 1984; GOSS-CUSTARD, 1969, 1979; EVANS, 1976; HULSCHER, 1976; DUGAN, 1981; PIENKOWSKI, 1982). Weather-related variables affect foraging shorebirds most in the late fall and winter when excessively high winds or severe low temperatures affect not only foraging shorebirds but the distribution of prey (GOSS-CUSTARD 1969; SMITH, 1975; TOWNSHEND, 1981). However, breeding Piping Plovers are usually not subjected to these extreme conditions while foraging, except during severe storms and hurricanes.

Tidal factors are the major factors influencing foraging shorebird distribution (EVANS, 1979), as tide affects both the amount of foraging space and availability of prey (RECHER, 1966; EVANS, 1979). In general, shorebirds feed on exposed intertidal areas at low tide (see papers in PITELKA, 1979). Indeed JOHNSON and BALDASSARRE (1988) found that tides were the most important factor affecting foraging Piping Plover in the winter in Alabama. Many species of shorebirds move to upland fields or marshes (HEPPLESTON, 1971) or man-made habitats such as rice paddies, fish ponds and salt ponds (BURGER, 1984c) during high tide when mudflats are unavailable.

Breeding Piping Plovers, however, differ from the species investigated above in two fundamental aspects of their foraging: (1) they are usually restricted to the 100 m or so of coastal surf along their territory for foraging rather

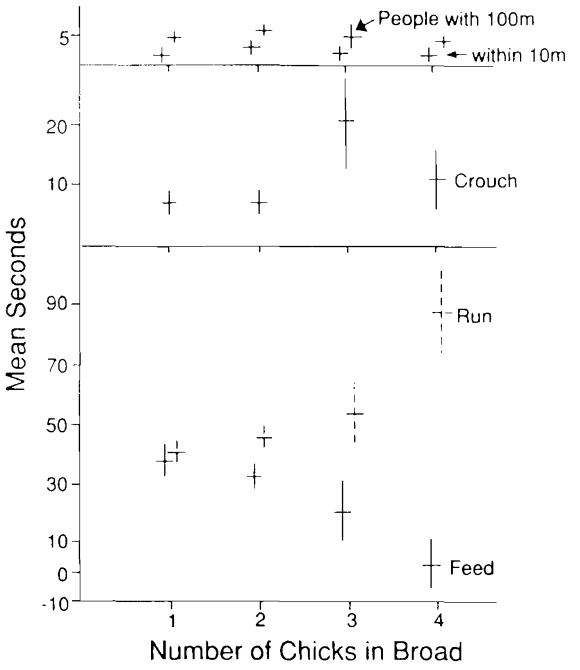

Figure 6. Time spent foraging and running (bottom), and crouching (middle) as a function of brood size for Piping Plover chicks. Top shows the number of people close to the plover at different brood sizes. Shown are mean ± standard deviation.

Table 7. *Correlation of number of people within 100m and Piping Plover behavior in response to people.*

	Corson's Inlet 1985	Brigantine 1986	North Corson's 1986	South Corson's 1986	Whale Beach 1986	Holgate 1986
Sample size	228	226	129	192	135	43
Seconds run	34***	.30***	.48***	.64***	.60***	.30*
Seconds crouch and display	25***	− .08	.28***	.17**	.25**	− .03
Number of times run	19**	.35***	.46***	.68***	.62***	.42**
Seconds fly	24**	.07	.14(0.9)	.10	.29***	.34**
Seconds feed	− 36*** 30**	.02	− .41***	− 30**	− 19**	—

than moving freely up and down the beach, and (2) they do not move to uplands, marshes or ponds to forage during high tide. Instead Piping Plover generally remain within their territory, and attempt to feed throughout the day and tide cycle as best they can. This may impose constraints on prey availability as well as foraging space, but has the advantage of allowing mates to be in contact and to participate in distraction behavior should predators threaten eggs or chicks. Where available (*e.g.*, Brigantine), adults may move into tidal back bays, away from joggers and sunbathers. However these areas are often used by fishermen.

In this study the behavior of parents in visual contact with each other was clearly correlated. Both parents participated in defense of nest and chicks, and in being vigilant. During incubation, when the incubating bird became more alert, left the nest, or displayed, its mate moved closer to the nest, and ceased foraging. Similarly, during the chick phase as the brooding bird was alert more and gave more displays, so did its mate. These behavior patterns suggest

that both members of a pair are monitoring each other's behavior, even though they seemingly are merely incubating or feeding. The coordination of display behavior further suggests that the presence of both parents may be essential for adequate defense of the nest or chicks. If adults are forced to leave their territories to forage on back bays where they no longer can observe their mate or chicks, their reproductive units (either eggs or chicks) may not receive the quality care they might if both parents are present. Nonetheless, the availability of back bay areas may be critical at high tide when the ocean front is unavailable, or when the ocean beach is crowded with people making foraging difficult.

People pose an additional threat to species such as Piping Plover that generally restrict their foraging activities to the limited space of their territory (CAIRNS, 1977). Plovers with sections of beach that are particularly popular with people run the risk of reduced foraging time and space. Further, the number of people using a beach increases dramatically from early April when plovers are establishing territories to June and July when plovers are guarding chicks (BURGER, 1987). In this study the number of pecks made by foraging Piping Plovers related to the time devoted to actually feeding, thus time required to look for or avoid people directly affects feeding ability. Foraging success (the number of pecks that result in food) varies by temporal, tidal, and weather-related factors, but in this study I was primarily interested in how people affect the foraging time of Piping Plovers.

The presence of people has several effects including: (1) causing shifts in habitat use from ocean front to back bays (in the case of adults), and from ocean front to dunes (in the case of chicks), (2) decreasing foraging time and increasing vigilance (time devoted to alertness), and (3) differentially affecting foraging time in broods of different sizes. Habitat shifts would be critical if foraging success is lower in the back bays and dunes, a factor requiring verification. Further, chicks in broods of three and four devoted less time to foraging, and more time to being alert and running than chicks in broods of one or two. This might have the effect of decreasing brood size; chicks starve or fall prey to predators because they are weaker or are too scattered for effective antipredator behavior by parents. Unlike Lapland Longspurs (*Calcarius lapponicus* [MCLAUGHLIN and MONTGOMERIE, 1985]), Piping Plover do not divide their brood, but try to keep the chicks together. Predators pose a problem to nesting shorebirds (PAGE *et al.*, 1985), and on my study sites crows (*Corvus brachyrhynchos*), gulls (*Larus*) and fox (*Vulpes vulpes*) ate Piping Plover eggs and chicks (BURGER, 1987). Further, antipredator behavior of shorebirds can be fatal to the birds themselves (BRUNTON, 1986; ENGLAND, 1986).

Vigilance behavior has been extensively studied for flocking and colonial species where vigilance of individuals decreases with flock or colony size (KRUUK, 1964; LEMMETYINEN, 1971; ANDERSSON, 1976; HOOGLAND and SHERMAN, 1976; BURGER, 1981; FLEISCHER, 1983). NUECHTERLEIN (1981) and BURGER (1984d) have shown that some colonial species that do not participate in mobbing often nest in colonies of species that do, to deriving added antipredator defense as well as early warning of predators. Piping Plovers regularly nest in Least Tern colonies, and clearly derive such benefits (FAANES, 1983; BURGER, 1987). Yet vigilance has not been examined as a direct effect of the number of predators or the number of people present. This study clearly indicates that vigilance (or time devoted to being alert) increases on beaches with more people.

Given the results of this study, I propose that increases in the number of people on beaches may depress foraging time sufficiently to have a negative effect on chick survival and adult maintenance (Figure 7). Normally, in the absence of people, foraging plovers devote time to feeding, vigilance, and defense of feeding territories. With the presence of people, plovers allocate additional time to scan for people, and this time increases as the number of people increases (Figure 7B). Although increased vigilance for predators may result in decreased predation, increased vigilance toward people does not because people generally do not directly harm the plover. Self defense may either remain constant, or as I suspect, increase because plovers are forced by people to move into the territories of other plovers. Once plovers have eggs or chicks, they allocate additional time to their defense, reducing foraging time still further. Presumably, such decreases

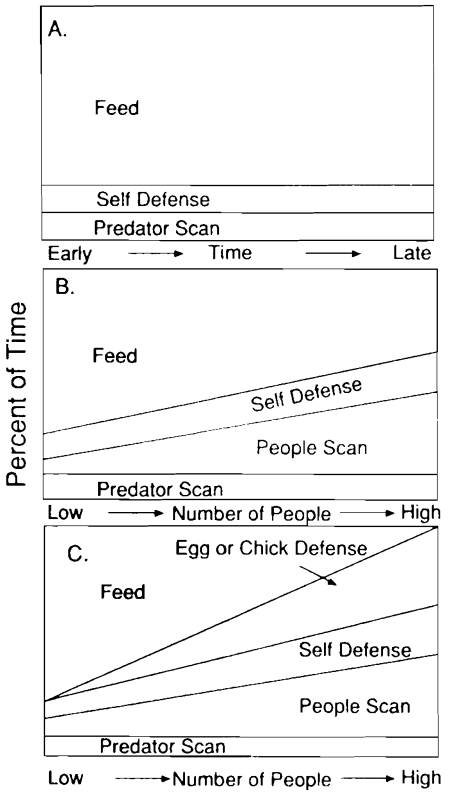

Figure 7. Theoretical models of time devoted to activities as a function of stage in year and presence of people causing disturbance.

in foraging time force parents to forage for more of the day (providing less care for chicks), to shift habitats, or to deplete fat reserves. If parents forage for longer, or shift habitats, the brood may spend more of the day without the protective behavior of both parents. I suggest that in addition to habitat loss and nest and chick destruction by people, the presence of people may be critically reducing foraging time for plovers, resulting in decreased fitness.

ACKNOWLEDGEMENTS

I especially thank M. Gochfeld for valuable discussions throughout the study; R. Steidl, and M. Caffrey for computer assistance; and V. Doig, D. J. Gochfeld, D. Jenkins, D. Grembowicz, and R. Steidl for field assistance. I thank D. L. Beall and H. Laskowski of Edwin B. Forsythe National Wildlife Refuge for permission and research assistance to work on the Holgate and Little Beach sites. This research was partially funded by the Endangered and Non-Game Species Project of the New Jersey Department of Fish, Game, and Wildlife, and I thank J. Frier-Murza, L. Nihls and D. Jenkins for their continued help and advice. Manuscript preparation was aided by funds from the Charles and Johanna Busch Fund.

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☐ RESUMEN ☐

Se ha estudiado el comportamiento alimentario del Piping Plover (Charadrius melodus) utilizando una aproximación animal focal en el período 1985–1986. El tiempo dedicado a la alimentación decrece a medida que las vigilancia (tiempo emepleado en estar alerta) crece. Las variaciones en el nivel de vigilancia se han explicado en función de la playa, etapa de la reproducción, tamaño de la nidada, hora del día y número de personas en las proximidades. En general, los Piping Plovers pastan durante 46 a 79 sg, están alerta unos 14 a 57 sg y se exponen o corren de las personas durante 1 a 8 sg en las muestras de 2 minutos. Los Plover situados en lugares menos perturbados por la gente (Little Beach, Holgate) emplean generalmente más tiempo en pastar y menos en la vigilancia que los paaajarps em otros puntos. El tiempo empleado para pastar fue generalmente mayor en Mayo, menor en Junio y se incrementó de nuevo en Julio. Los Plovers que estaban incubando o cuidando pollos emplearon menos tiempo pastando que aquéllos que habían perdido sus pollos. Los pollos emplearon menos tiempo pastando y más tiempo en estado de alerta, corriendo y agazapándose que el que emplearon sus padres en pastar en los mismos períodos de tiempo. Con el aumento del tamaño de la nidada, los pollos emplearon menos tiempo pastando y más tiempo corriendo o agazapándose, aunque el número de gente en las proximidades no varió. El comportamiento se correlacionó dentro de los miembros de la pareja: los pájaros emplearon menos tiempo pastando a medida que sus compañeros incrementaban el tiempo empleado en estar alerta, en el nido o exponiéndose.

Cuando los pájaros que incubaban incrementaron su tiempo de alerta, sus parejas lo aumentaron también y disminuyeron el tiempo dedicado a pastar. A medida que aumentaba el número de personas en las proximidades de los Plovers, el tiempo empleado en correr y agazaparse se incrementaba y disminuía el tiempo empleado en alimentarse. Parece ser que la presencia de gente genera stress en los adultos y pollos, obligándoles a dedicar menos tiempo en pastar, produciéndose quizás un descenso general del éxito reproductivo.—*Department of Water Sciences, University of Cantabria, Santander, Spain.*

☐ RÉSUMÉ ☐

On a étudié de 1985 à 1986 le comportement du vanneau siffleur *Charadrius melodus* durant le picorage. Le laps de temps dévolu au picorage décroît avec l'accroissement de la vigilance (temps durant lequel l'oiseau est en alerte). Le vanneau picore durant 46 à 79 s, est en alerte de 14 à 57 s, se disperse ou fuit l'homme pendant 1 à 8 s. Les échantillons sont de 2 minutes. Les vanneaux des sites moins perturbés par l'homme (Little Beach, Holgate) picorent plus longtemps et sont moins vigilants que les oiseaux des autres sites. Le picorage dure en général plus longtemps en mai, moins en juin, et réaugmente en juillet. Les vanneaux qui couvent ou ont des poussins passent moins de temps à picorer que ceux qui ont perdu leurs petits. Les poussins passent moins de temps à picorer et sont plus longtemps en alerte se dispersent ou se blotissent alors que leurs parents picorent durant le même laps de temps. Lorsque la taille de la couvée grandit, les poussins picorent moins, se dispersent et se blotissent davantage, même si le nombre d'humains ne varie pas. Le comportement a été correllé à l'intérieur des membres d'un couple: loin du nid ou dispersés, les males picorent moins longtemps alors que le temps de la vigilance est accru pour les femelles. Lorsque les males couvant accroissent leur temps de vigilance, la vigilance et la dispersion des femelles augmente, le temps consacré à courir et à se blottir augmente et le temps consacré à se nourrir diminue. Il semble que la présence humaine soit source de stress pour les adultes nourrissiers et les poussins, en les forçant à employer significativement moins de temps au picorage. Il se peut que cela compromette le succès de la couvée.—*Catherine Bressolier-Bousquet, Géomorphologie EPHE, Montrouge, France.*

☐ ZUSAMMENFASSUNG ☐

Das Verhalten des Strandläufers (*Charadrius melodus*) bei der Futtersuche wurde 1985–1986 untersucht. Die mit der Nahrungssuche verbrauchte Zeit nahm in dem Maße ab, in dem die Wachsamkeit (die Zeit in Alarmbereitschaft) zunahm. Veränderungen in der Wachsamkeit erklärten sich durch den Strand, die Reproduktionsphase, die Größe der Brut, die Tageszeit und die Anzahl der sich in der Nähe aufhaltenden Menschen. Innerhalb von jeweils zweiminütigen Sequenzen waren die Strandläufer 46–79 sec auf Nahrungssuche, 14–57 sec wachsam und 1–8 sec lang zeigten sie sich oder liefen vor den Menschen weg. An Orten, wo Strandläufer weniger von Menschen gestört werden (Little Beach, Holgate), widmeten sie im allgemeinen mehr Zeit der Nahrungssuche und weniger Zeit der Wachsamkeit als an den anderen Orten. Die Zeit für die Nahrungssuche war im Mai gewöhnlich länger, im Juni kürzer und stieg im Juli wieder an. Strandläufer, die brüteten oder sich um die Küken kümmerten, verbrachten weniger Zeit mit der Nahrungssuche als solche, die ihre Küken verloren hatten. Die Küken wandten weniger Zeit zur Nahrungssuche auf und mehr damit, wachsam zu sein, herumzulaufen oder sich zu ducken als ihre Eltern im gleichen Zeitraum für Nahrungssuche. Mit zunehmendem Wuchs wandten die Küken weniger Zeit zur Nahrungssuche auf und mehr Zeit damit, herumzulaufen oder sich zu ducken, obwohl die Anzahl der sich in der Nähe befindenden Menschen gleich blieb. Das Verhalten wurde paarweise korreliert: Die Vögel verbrachten weniger Zeit mit der Nahrungssuche, wenn ihre Partner die Zeit der Wachsamkeit erhöhten, während sie außerhalb des Nestes waren oder sich darstellten. Wenn brütende Vögel die Zeit der Wachsamkeit erhöhten, verwandten ihre Partner auch mehr Zeit zur Wachsamkeit oder zum sich zur Schau Stellen und die Zeit für ihre Nahrungssuche nahm ab. hagm die Anzahl der Menschen in der Nähe von sich auf Nahrungssuche befindenden Strandläufern zu, dann nahm auch deren Zeit für das Weglaufen und sich Ducken zu und die Zeit für das Füttern nahm ab. Es scheint so zu sein, daß die Anwesenheit von Menschen einen Streß für brütende erwachsene Vögel und für Jungvögel darstellt, der sie zwingt, signifikant weniger Zeit für die Nahrungssuche aufzuwenden. Vielleicht ist dies auch für eine generelle Abnahme der Reproduktionsrate verantwortlich.—*Helmut Brückner, Geographisches Institut, Universität Düsseldorf, F.R.G.*