Journal of Coastal Research	23	5	1159–1166	West Palm Beach, Florida	September 2007

Habitat Choice, Disturbance, and Management of Foraging Shorebirds and Gulls at a Migratory Stopover

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ABSTRACT

BURGER, D; CARLUCCI, S.A.; JEITNER, C.W., and NILES, L., 2007. Habitat choice, disturbance, and management of foraging shorebirds and gulls at a migratory stopover. *Journal of Coastal Research,* 23(5), 1159–1166. West Palm Beach (Florida), ISSN 0749-0208.

Habitat choice and interactions of foraging shorebirds and gulls were studied at a migratory stopover in Delaware Bay, New Jersey. Foraging, vigilance, aggressive behavior, and habitat choice of shorebirds were affected by the presence of gulls. There were significant differences in the time each species devoted to actively feeding; knots spent significantly less time foraging than did the other species. Birds congregated in the habitats where their foraging rates were the highest. When turnstones and laughing gulls fed in larger conspecific flocks, they had higher foraging times. Red knots were most aggressive toward laughing gulls, turnstones were most aggressive toward herring gulls, sanderlings were most aggressive toward turnstones, and semipalmated sandpipers were most aggressive toward knots.

There were significant differences in habitat use: 1) Gulls and turnstones were more abundant along the tide line, 2) turnstones were more abundant on the upper beach, 3) semipalmated sandpipers and turnstones were more abundant on sandbars, 4) only gulls fed on the beach mud, and 5) laughing gulls and semipalmated sandpipers were more common along creeks than were the other species.

Within 5 minutes of a human disturbance, gulls returned to predisturbance levels, while the shorebirds did not. Shorebirds responded most strongly to the presence of dogs than to other disturbances and did not return to beaches following a disturbance by a dog. These observations suggest that there may be some competition for foraging space among foraging species, especially between the shorebirds and the larger gulls, that human disturbance affects shorebirds more strongly than gulls, and that shorebirds and gulls use the habitats differently. The data can be used to manage human disturbance and to protect habitats where the shorebirds have the highest foraging rates, but the least exposure to gulls.

ADDITIONAL INDEX WORDS: *Foraging, vigilance, aggression, competition for space, habitat, shorebirds.*

INTRODUCTION

Foraging birds often form groups to reduce their risk of predation while decreasing the costs of vigilance (BEDNEKOFF and LIMA, 1998; HAMILTON, 1971). As group size increases, scanning rates or vigilance decreases (ELGAR, 1989; ROBERTS, 1996). However, some species form groups because of resource location; they forage together because the food is clumped or prey densities are higher in some places than others. When large groups of birds forage in the same place, competition can result, either for the prey itself or for access to the prey (STILLMAN, 2000). Competition occurs when feeding rate is negatively related to competitor density and when the presence of an individual impedes the access of another individual to a resource (CRESSWELL, 2001; SCHOENER, 1983; TRIPLET, STILLMAN, and GOSS-CUSTARD, 1999). Although feeding rate may decline, aggressive interactions may be relatively rare (YATES, STILLMAN, and GOSS-CUSTARD, 2000). Aggression should occur only when individuals can increase their share of resources that are concentrated by being aggressive (BEAUCHAMP, 1998). Increasing spatial clumping of resources, such as prey, can lead to increased competition (SCHMIDT *et al.,* 1998).

Migrating shorebirds provide an opportunity to study behavioral interactions among species for both prey and foraging space because they often forage in dense flocks, concentrating along relatively narrow tide lines (BOER and LONGAMANE, 1996). Further, because they often forage in mixed species flocks, behavioral interactions among species can be examined in relation to habitat selection. This paper focuses on foraging behavior of four shorebird species and two gull species at a shorebird migratory stopover site in Delaware Bay, New Jersey, U.S.A. All species were preying on the eggs of horseshoe crabs. One key question is whether interactions between the shorebirds and gulls have an adverse effect on the time that shorebirds can devote to foraging. Another factor that could play an important role in habitat use is the

DOI:10.2112/04-0393.1 received 10 October 2005; accepted in revision 23 June 2005.

Partial support for this project came from the New Jersey Nongame and Endangered Species Program and the Department of Environmental Protection.

Figure 1. Map of Delaware Bay showing the study sites.

effect of human disturbance on the shorebird–gull interactions. Our main interest was in determining whether there were species differences in habitat use or exclusion that might aid managers in protecting declining shorebird numbers, especially in the face of increasing gull populations.

We examined three questions to determine if there are adverse behavioral interactions among the species. The questions were designed to determine whether there was competition for foraging space or habitats among these species. Interactions with the gulls are of particular interest because they are several times larger than the shorebirds, giving them a distinct advantage.

1. Does the time devoted to foraging differ among the species and does it vary in different habitats?
2. Does each species spend equivalent amounts of time in the different foraging microhabitats, and does the time devoted to foraging (vigilance, and aggression) differ among the microhabitats for each species?
3. Does the time required to return to foraging after a human disturbance vary among species or as a function of the type of disturbance.

One of the largest spring concentrations of migrating shorebirds in the continental United States occurs in Delaware Bay each spring, when over a million shorebirds use the bay during a 3-week period in late May and early June (Figure 1, Burger, Niles, and Clark, 1997; Clark, Niles, and Burger, 1993). The shorebirds are drawn to the bay because of the superabundance of horseshoe crab eggs; Delaware Bay is the center of horseshoe crab breeding (Botton, Loveland, and Jacobsen, 1994). Delaware Bay is critical for these migrating shorebirds because of the abundance of eggs, high energy content of the eggs, and absence of other sufficient resources en route (Piersma and Baker, 2000). Because the eggs do not move, as do some other prey (Backwell, O'Hara, and Christy, 1998), they are not difficult to capture, providing an opportunity to examine species interactions without considering prey behavior.

Foraging shorebirds are exposed to a decline in availability of their primary prey (horseshoe crab eggs) in Delaware Bay. With declining prey availability (Botton and Loveland, 2000), it is critical to know whether the shorebirds are being displaced from their preferred foraging habitat by the much larger gulls and whether there are interspecific differences in the effects of human disturbance.

With this information, managers could impose additional measures to reduce the effects of human disturbance and consider measures to limit interactions between the shorebirds and gulls. The latter might take the form of increased protection of habitats where shorebirds can feed and where there are few gulls. Understanding the stresses birds face when migrating between breeding and wintering grounds, such as competition for foraging space, habitat use, predation, and human disturbance, is essential for sound management of migratory stopovers. As foraging habitats dwindle in many migratory stopovers, managers must focus on protecting the habitats and microhabitats that are most critical for species whose numbers are declining. Such protection requires a clear understanding of the factors that contribute to lowered foraging success.

STUDY AREA AND METHODS

In 2002 observations were made at several beaches at Villas, Reeds Beach, Moores Beach, Thompson Beach, and Fortescue on the New Jersey side of Delaware Bay (Figure 1). On the Cape May peninsula, shorebirds use a range of habitats including the Atlantic Ocean beaches, marshes, tidal mudflats, or back beaches (Burger, Niles, and Clark, 1997). The Delaware Bay is separated from the Atlantic Ocean by 10 km of upland habitat. The habitat on Delaware Bay includes sandy beaches, sod banks, and creek and river inlets, backed by tidally flooded salt marshes (*Spartina alterniflora*). The prime foraging sites are along a relatively narrow belt at the high tide line (Clark, Niles, and Burger, 1993), creating the potential for competition for both food and space to forage. Further, although the greatest number of eggs is consistently available at the tide line, there are other habitats where eggs concentrate, such as sandbars, jetties, and creeks. Thus, within the "beach habitat" there are microhabitats. Because of concern for declining shorebird numbers, many of the beaches are closed to human activity during the migratory season, but enforcement is not complete.

The overall study included three types of data collection: 1) observations on focal animals that were actively foraging, 2) censuses of the composition of foraging birds in 10-m sections of the habitat, and 3) observations of disturbances. Observations required three observers and were made every day from May 19, 2002, to June 6, 2002, which is the peak of the shorebird migration.

1. Time devoted to foraging. The foraging behavior of focal shorebirds was observed following a similar protocol used

for foraging piping plover (*Charadrium melodus,* BURGER, 1994), sanderlings (*Calidris alba,* BURGER and GOCHFELD, 1991b), and laughing gulls (BURGER and GOCHFELD, 1991a). The daily protocol was to go to one of the designated beaches at first light, and begin collecting data on foraging shorebirds by selecting a focal bird on the edge of the flock; flocks were generally oriented horizontally along the tide line, and we selected a bird at the right or left end of the flock. Then another individual shorebird about 1 m from the initial bird was selected for observation, and this procedure was followed until the birds moved or were no longer individually observable. In general, birds were not disturbed during our observations, and we were able to sample the entire flock. The focal bird chosen was actively foraging, and if it left before the end of 30 seconds, it was eliminated from the study. Each focal bird was observed for 30 seconds. Before beginning to take data on a focal bird, the following data were recorded: observer, time of day, flood state, hours before low tide, habitat (sand bar, tide line, upper beach, creek, beach mud), and species of shorebird. Data taken on the focal bird during the 30 seconds included: seconds devoted to foraging, vigilance, and aggression; number of pecks at the sand for eggs; number of aggressive interactions; and who won. Vigilance was defined as the bird looking up or around, rather than at the water where it was foraging (by pecking).

2. Time in different foraging microhabitats. To examine the use of habitat by the mixed-species flocks of shorebirds and gulls, we recorded the number of each species present in randomly selected 10-m sections of the beach (653 censuses). A tide line transect included the upper beach. These data were taken every 15 minutes throughout the day. The habitat was divided into tide line (within 2 m of water line), upper beach (area 2 m above the tide line), sand bar (a sandy area separated from the main tide line by water), beach mud (a cul-de-sac near a jetty where mud and an abundance of horseshoe crab eggs were trapped), and creek (the interior sandy beaches along any creek leading into the bay).
3. Effect of disturbances. Observers were able to see whole stretches of beach and could observe approaching people, dogs, and vehicles. Although these disturbances were against the law, they occurred nonetheless. Whenever observers saw an approaching person (or dog or vehicle), they recorded the number of birds (by species) in the 30-m stretch where the person would intersect the beach. In all cases, all birds flew up when faced with a person, dog, or vehicle. Observers then recorded the number of birds by species returning to the beach 30 seconds, 1 minute, 2 minutes, 5 minutes, and 10 minutes after the disturbance had passed.

Statistics

Kruskal-Wallis nonparametric one way analysis of variance (SAS Proc NPAR1WAY—Wilcoxon option) was used to distinguish significant differences among species (SAS, 1995). We used Kendall tau correlations to determine relationships among behaviors (SAS 1995). In all cases we test the null hypothesis of no differences among species in foraging behavior or habitat use. We used a significance level of 0.05. Arithmetic means and standard errors are given in the text and tables.

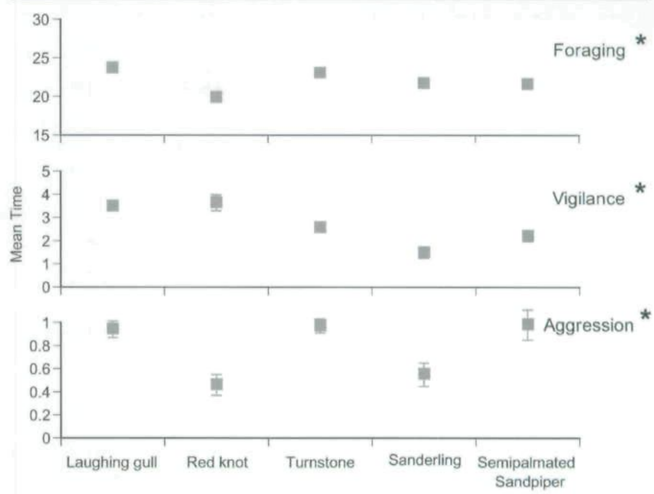

Figure 2. Time (mean ± standard error) devoted to foraging, vigilance, and aggression for laughing gulls and shorebirds foraging along Delaware Bay. An * indicates there are significant differences (χ^2 tests in text).

RESULTS

Foraging and Habitat Use

On the migratory stopover at Delaware Bay, shorebirds spent time foraging, roosting, or resting (preening and other activities). There were significant differences in the time each species devoted to actively feeding (Figure 2). Based on the 30 seconds foraging data of focal birds, knots spent significantly less time foraging than did the other species ($\chi^2 = 68.1$, $p < 0.0001$), largely because they devoted more time being vigilant, but less time to actual aggression.

Similarly, there were significant differences between species in time devoted to vigilance and aggression ($\chi^2 = 58.1$, $p < 0.001$; $\chi^2 = 43.7$, $p <$ than 0.001, Figure 2). There were also differences in time devoted to vigilance as a function of their nearest neighbor for all species except herring gulls and sanderlings (Table 1). Red knots were most aggressive toward laughing gulls, turnstones were most aggressive toward herring gulls, sanderlings were most aggressive toward turnstones, and semipalmated sandpipers were most aggressive toward knots (Table 1, χ^2 tests).

Within a species, there were significant differences in habitat use (Table 2): 1) Gulls and turnstones were more abundant along the tide line than other species, 2) turnstones were more abundant on the upper beach than other species, 3) laughing gulls and turnstones were more abundant on sandbars, 4) only gulls fed on the beach mud, and 5) semipalmated sandpipers were more common along creeks than were the other species. These numbers largely reflect abundance in the foraging flocks generally. Over half of the for-

Table 1. *Mean time spent aggressive for gulls and shorebirds feeding on Delaware Bay (2002). Observations were of focal birds during 30 s observation. Given are means followed by (n) and then the standard error.*

	Closest Species						
Focal Species	Herring Gull	Laughing Gull	Red Knot	Turnstone	Sanderling	Semipalmated Sandpiper	Kruskal-Wallis χ^2
Herring gull	2.17 (6) ± 1.64	1.86 (22) ± 0.84	0.00 (2) ± 0.00	0.40 (10) ± 0.40	0.00 (1)*	2.50 (2) ± 2.50	3.18 (ns)
Laughing gull	2.14 (7) ± 1.06	0.81 (978) ± 0.06	1.25 (8) ± 0.82	2.44 (82) ± 0.44	0.33 (9) ± 0.24	1.36 (11) ± 0.97	31.5 (0.0001)
Red knot	0.50 (2) ± 0.50	1.14 (44) ± 0.38	0.34 (87) ± 0.19	0.39 (133) ± 0.10	0.00 (17) ± 0.00	0.00 (8) ± 0.00	16.7 (0.005)
Turnstone	1.94 (16) ± 0.76	1.22 (313) ± 0.13	0.57 (14) ± 0.37	0.88 (828) ± 0.07	1.41 (37) ± 0.59	0.65 (34) ± 0.16	12.2 (0.059)
Sanderling	†	0.63 (16) ± 0.40	0.00 (5) ± 0.00	0.88 (60) ± 0.24	0.39 (132) ± 0.09	0.56 (32) ± 0.20	4.87 (ns)
Semipalmated sandpiper	0.00 (1)*	0.97 (37) ± 0.37	2.67 (3) ± 1.45	1.70 (54) ± 0.34	0.00 (13) ± 0.00	0.90 (294) ± 0.18	25.6 (0.0003)

* No standard error because $n = 1$.
† No aggressive interactions were observed between species.

aging herring gulls were feeding at holes dug up by turnstones (usually by driving them away) on the upper beach above the tide line and the upper reaches of creek areas.

There were significant differences in the time devoted to actively feeding in the different habitats (in the 30 seconds focal animal data set, Table 3). These differences were significant for laughing gulls, turnstones, sanderlings, and semipalmated sandpipers. Generally the birds congregated where their foraging rates were the highest. There was also a clear relationship for some species (turnstones, laughing gulls) between the number of conspecifics in flocks and their time devoted to foraging (Figure 3). When they fed in larger flocks with a higher percent of conspecifics, they had higher foraging times.

Responses to Disturbances

Although many beaches on Delaware Bay have human access restrictions imposed by the state, people, dogs, and vehicles (planes, cars, boats) sometimes disturbed the birds, causing the foraging flocks to fly from the beaches. Vehicles were not on the beaches themselves, but planes could fly low, boats could approach shore, and loud cars sometimes were near the beach. The responses of the gulls and shorebirds differed significantly. In general, within 5 minutes of a disturbance the number of gulls had returned to predisturbance levels, while the shorebirds did not return to these levels (Figure 4). The shorebirds responded most strongly to the presence of dogs and did not return to the beach following such a disturbance.

There were differences among the shorebirds, both in their response to different types of disturbance stimuli and in their recovery time (Table 4). Within 30 seconds of the cessation of a vehicular disturbance, some shorebirds returned to the beaches, although semipalmated sandpipers did not when the disturbance was a person. Within 5 minutes of the cessation, only half the turnstones had returned, but far fewer of the other species returned.

Shorebirds began returning to the beach within a minute of when a human intruder was on the beach; however, only about 20% of the sanderlings returned (Table 4). At 10 minutes after the disturbance ceased, knots had not yet returned, while some of the other species were returning. For all shorebirds combined, there were significant differences in the number of birds present before a disturbance, and 5 minutes after the disturbance (χ^2 tests, $p < 0.05$), but these differences were not significant for laughing gulls (Figure 4).

The most severe response of shorebirds was to the presence of dogs (Table 4, Figure 4). Although turnstone numbers began to recover after 2 minutes, by 10 minutes, numbers were still only a quarter of predisturbance numbers. Knots, semipalmated sandpipers, and sanderlings did not return within 10 minutes of the departure of a dog from the beach.

DISCUSSION

Foraging and Habitat Use

In this study, foraging success was related to both microhabitat and foraging associations. The birds concentrated in

Table 2. *Foraging habitats used by shorebirds at Reed's Beach, Delaware Bay (2002). Mean ± SE number foraging in 10 m beach counts (N = 653), of each species observed feeding in different habitats. Refer to Figure 2 for habitats.*

	Herring Gull	Laughing Gull	Red Knot	Turnstone	Sanderling	Semipalmated Sandpiper
N*	365	553	189	378	203	146
Feeding at tide line	3.4 ± 0.3	115.8 ± 9.6	22.6 ± 5.7	123.7 ± 15.0	21.3 ± 3.1	22.6 ± 3.4
Feeding at upper beach	6.3 ± 1.7	44.0 ± 5.7	17.3 ± 3.5	111.7 ± 13.7	34.4 ± 17.4	12.4 ± 2.3
Feeding at creek	2.6 ± 0.4	46.2 ± 11.3	13.1 ± 5.8	40.8 ± 11.9	41.1 ± 17.2	88.4 ± 18.8
Feeding at sandbar	15.4 ± 6.1	65.9 ± 32.4	14.7 ± 4.1	105.0 ± 29.0	14.2 ± 5.1	5.6 ± 2.0
Feeding at beach mud	†	123.8 ± 37.2	†	†	†	†
χ^2 (p)	5.9 (ns)	56.5 (<.0001)	0.5 (ns)	9.6 (0.02)	3.1 (ns)	37.0 (<.0001)

* Number of the 653 censuses that had each species.
† No birds fed there.

Table 3. *Mean time gulls and shorebirds on Delaware Bay spent foraging (2002). Data are for focal birds when feeding at tide line, upper beach, creek, sandbar, or beach mud. Given are means ± SE.*

	Herring Gull	Laughing Gull	Red Knot	Turnstone	Sanderling	Semipalmated Sandpiper
N	62	1111	298	12.89	245	440
Tide line	12.6 ± 2.26	24.0 ± 0.27	19.92 ± 0.87	22.3 ± 0.33	21.17 ± 0.78	22.0 ± 0.56
Upper beach	11.7 ± 2.39	22.0 ± 0.70	19.06 ± 0.77	23.73 ± 0.3	20.35 ± 0.98	22.9 ± 0.98
Creek	*	23.9 ± 1.61	22.09 ± 1.58	22.19 ± 1.46	25.44 ± 1.20	22.3 ± 1.02
Sandbar	17.5 ± 3.37	21.6 ± 0.89	22.17 ± 1.86	23.0 ± 1.4	23.91 ± 1.68	18.5 ± 1.04
Beach mud	*	26.7 ± 0.44	*	20.0†	*	*
χ^2 (p)	3.7 (ns)	15.28 (0.004)	4.0 (ns)	12.61 (0.01)	10.63 (0.01)	13.0 (0.005)

* No birds fed there.
† No standard error because $n = 1$.

different microhabitats: 1) Gulls and turnstones were more abundant along the tide line, 2) turnstones were abundant on the upper beach, 3) semipalmated sandpipers and turnstones were more abundant on sandbars, 4) only gulls fed on the beach mud, and 5) laughing gulls and semipalmated sandpipers were more common along creeks than were the other species. There were significant differences as a function of microhabitat for laughing gulls, turnstones, and semipalmated sandpipers. Generally the birds congregated where the birds spent the most time feeding.

These data have several implications for understanding their foraging behavior. Firstly, shorebirds seem to be integrating food, habitat, and interactions with other species. A given species can maximize its foraging success in certain habitats by feeding mainly with conspecifics, and where they are not in direct competition with larger species (especially gulls) for foraging space. A timid species, such as knots, that had relatively low aggression rates could increase its foraging rate by feeding in locations without the larger gulls (*i.e.,* sandbars). Second, some species can make use of the foraging ability of others. Herring gulls and sanderlings make use of the digging ability of turnstones to uncover clutches of eggs buried in the sand. The importance of habitat characteristics in influencing interference competition is a key feature requiring more extensive research (see CRESSWELL, SMITH, and RUXTON, 2001), particularly in shorebirds.

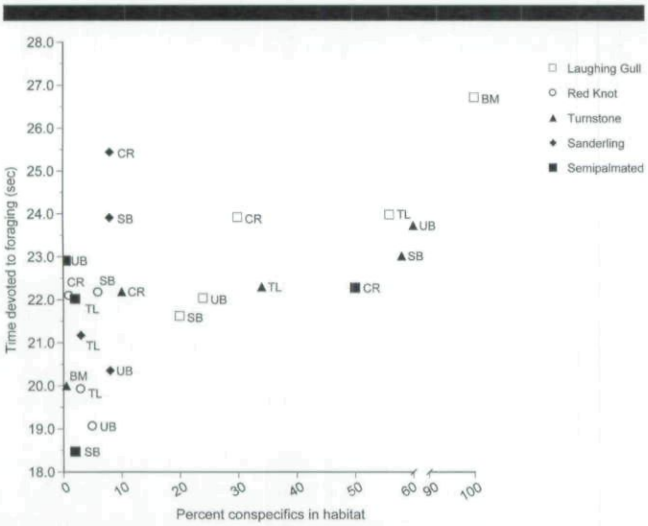

Figure 3. Relationship between the percent of conspecifics foraging in a given habitat and the time devoted to foraging along Delaware Bay. CR = creek, SB = sandbar, UB = upper beach, TL = tide line, and BM = beach mud.

Aggressive Interactions

While considerable attention has been devoted to aggression in monospecific foraging flocks for decades (CONNORS *et al.,* 1981; HAMILTON, 1959), less attention has been devoted to aggression in mixed-species flocks (BURGER *et al.,* 1979; NORRIS and JOHNSTONE, 1998), partly because of the difficulty of tracking individuals and species in such dense groups. Further, in most foraging situations, shorebirds are feeding on prey that are distributed over a relatively large

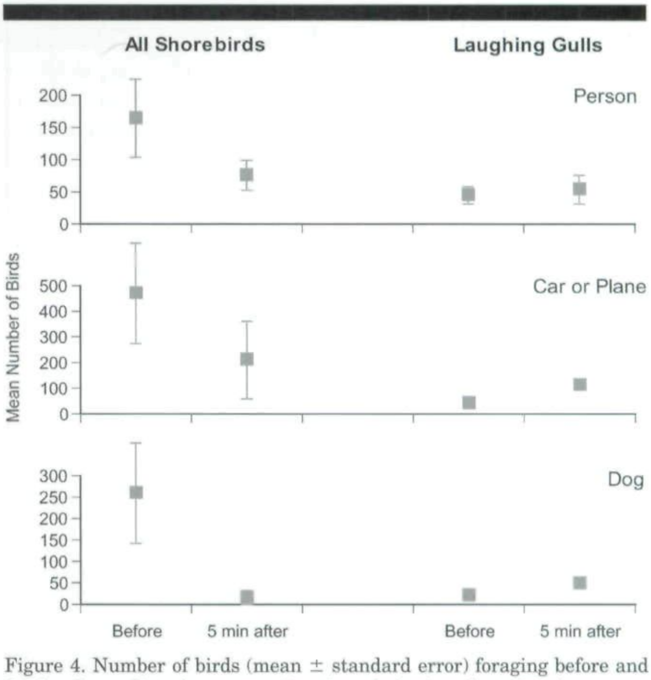

Figure 4. Number of birds (mean ± standard error) foraging before and 5 min after a disturbance as a function of whether that disturbance was caused by a person walking, or a car, plane, boat, or dog (with or without a person). Following the disturbance of a dog, no shorebirds came back after 5 minutes.

Table 4. *Effects of disturbance on foraging gulls and shorebirds in Delaware Bay (2002). Shown are the number of birds present on beach before and after disturbances (N = 25) on Delaware Bay. Given are means ± SE.*

		Time after Disturbance				
	Before Disturbance	≤30 s	1 min	2 min	5 min	Over 10 min
Disturbance = Car or Plane						
Herring gull	0.4 ± 0.4	0.1 ± 0.1	0.4 ± 0.2	1.7 ± 1.7	1.7 ± 1.7	
Laughing gull	41.2 ± 21.4	35.6 ± 14.2	96.0 ± 15.7	145.0 ± 52.7	111.7 ± 19.7	
Total shorebirds	478.4 ± 190.4	88.9 ± 88.9	80.2 ± 58.5	0.0 ± 0.0	225.0 ± 141.9	
Red knot	25.2 ± 19.3	11.1 ± 11.1	0.2 ± 0.2	0.0 ± 0.0	1.7 ± 1.7	
Turnstone	433.0 ± 173.1	66.7 ± 66.7	80.0 ± 58.3	0.0 ± 0.0	223.3 ± 140.3	
Sanderling	20.2 ± 20.0	11.1 ± 11.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	
Semipalmated sandpiper	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	
Disturbance = Person						
Herring gull	6.4 ± 3.0	55. ± 2.7	8.3 ± 3.8	12.0 ± 5.0	13.7 ± 4.7	16.3 ± 17.5
Laughing gull	44.6 ± 13.4	117.9 ± 32.8	74.2 ± 30.6	64.6 ± 21.3	52.9 ± 19.7	86.3 ± 37.5
Total shorebirds	162.5 ± 60.6	0.0 ± 0.0	7.7 ± 6.8	8.9 ± 6.2	66.7 ± 22.2	95.0 ± 95.0
Red knot	3.6 ± 1.7	0.0 ± 0.0	0.5 ± 0.5	0.0 ± 0.0	0.0 ± 0.0	1.7 ± 1.7
Turnstone	137.3 ± 53.6	0.0 ± 0.0	3.2 ± 3.2	8.3 ± 6.2	58.3 ± 23.3	83.3 ± 83.3
Sanderling	7.5 ± 6.2	0.0 ± 0.0	0.9 ± 0.9	0.0 ± 0.0	0.0 ± 0.0	6.7 ± 6.7
Semipalmated sandpiper	14.1 ± 9.4	0.0 ± 0.0	3.2 ± 2.4	0.6 ± 0.6	8.3 ± 4.1	3.3 ± 3.3
Disturbance = Dog						
Herring gull	6.0 ± 3.1	0.0 ± 0.0	0.7 ± 0.7	1.3 ± 1.3	1.7 ± 1.2	6.5 ± 3.4
Laughing gull	20.3 ± 7.9	9.0 ± 9.0	33.7 ± 13.3	45.7 ± 15.1	48.3 ± 6.7	43.7 ± 4.3
Total shorebirds	259.0 ± 116.9	0.0 ± 0.0	0.0 ± 0.0	2.3 ± 2.3	16.0 ± 16.0	87.5 ± 87.5
Red knot	4.0 ± 3.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Turnstone	235.0 ± 110.9	0.0 ± 0.0	0.0 ± 0.0	2.3 ± 2.3	16.0 ± 16.0	87.5 ± 87.5
Sanderling	10.0 ± 5.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Semipalmated sandpiper	10.0 ± 5.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

area of mudflat, although they may be compressed during high tide.

In contrast, the shorebirds feeding on horseshoe crab eggs are concentrated exactly at the tidal line, often on relatively steep beaches that do not provide a wide foraging belt along the tide. On Delaware Bay, the bulk of crab eggs are available in the boiling surf, although some shorebirds (turnstones and their kleptoparasites) have access to the eggs buried in the sand. In this case, because of the small size of the eggs, kleptoparasitism is on the nests with the eggs rather than on shorebirds holding the food (*i.e.,* eggs, see LEEMAN *et al.,* 2001).

The aggressive behavior of shorebirds seemed to us to be a function of their foraging methods and habitat choices. Red knots were most aggressive toward laughing gulls when they foraged together along the tide line. Turnstones were most aggressive toward herring gulls, mainly when the gulls tried to take egg masses that the turnstones had dug up on the upper beach. Sanderlings were most aggressive toward turnstones, mainly on the upper beach, because they were attempting to steal the eggs masses the turnstones had dug up. Semipalmated sandpipers were most aggressive toward knots that were trying to displace them from sandbars, where they both congregated in foraging flocks.

The behavior observed in the foraging flocks along Delaware Bay suggest that aggression rates are dependent upon not only prey, but on competition for space, species composition, and habitat availability. The availability of different microhabitats with sufficient horseshoe crab eggs provides the shorebirds with options where they can minimize competition for space and aggressive interactions with other (perhaps larger) species, while making use of their foraging skills.

Behavioral Responses to Disturbances

Gulls and shorebirds responded differently to the presence of vehicles, people, and dogs. Once the disturbing stimulus had departed, gulls returned within 30 seconds, while shorebirds did not fully return to the beaches even within 10 minutes. These differences may be partly due to species differences in vulnerability (the gulls are larger), but in reality both people and dogs could take either gulls or shorebirds. The propensity of gulls to return immediately, however, has consequences in terms of interference competition. In many cases, there were more gulls within 5 minutes of a disturbance than there had been before, indicating that there was some recruitment from flocks resting on nearby sandbars and upper beaches. The increase in the number of gulls would make it more difficult for the smaller shorebirds to enter the foraging flock. Repeated disturbances then might have the effect of increasing interference competition for foraging space, resulting in even fewer shorebirds having access to the best foraging sites.

These data further suggest that it is imperative to keep people and dogs off the Delaware beaches when shorebirds are foraging. Increased disturbances may have the effect of giving the competitive advantage to gulls because they return more quickly, filling up the prime habitat where the horseshoe eggs are most abundant. While previous studies on Delaware Bay have indicated that dogs can be an important dis-

turbance (BURGER, 1986, BURGER, GOCHFELD, and NILES, 1995), the present study indicates that they are currently the prime and most important factor disturbing the shorebirds at protected beaches. This is partly a function of the protection afforded the beaches by the Endangered and Nongame Species Program of the New Jersey Department of Environmental Protection. Whereas they have been successful in lowering the number of disturbances due to photographers, birdwatchers, and walkers, dogs have been harder to control.

Management and Conservation Implications

Understanding foraging behavior of the mixed species flocks of shorebirds and the effect of negative interactions between shorebirds and gulls is critical because the spring concentration of shorebirds on Delaware Bay is the largest in the continental United States, and the supply of horseshoe crab eggs may be dwindling (BAKER *et al.,* 1999; BURGER, NILES, and CLARK, 1997; TSIPOURA and BURGER, 1999). The shorebirds do not feed on viable eggs, but rather on excess horseshoe crab eggs that have risen to the surface because of the spawning activity of other female crabs. Thus, the number of spawning horseshoe crabs that is necessary to ensure healthy populations of horseshoe crabs may be insufficient to provide enough excess eggs for foraging shorebirds.

An increase in the harvest of spawning horseshoe crabs in recent years has led conservationists to be concerned that there is an insufficient number of breeding horseshoe crabs to produce the excess of eggs necessary to feed the migrating shorebirds (BAKER *et al.,* 1999; TSIPOURA and BURGER, 1999). The availability of eggs in the surface sands has fallen from a high of over 100,000 eggs/m^2 in 1990 to 10,000 eggs/m^2 in 2000 (BOTTON and LOVELAND, 2000). The shorebirds and gulls forage where the eggs are most abundant (BOTTON, LOVELAND, and JACOBSEN, 1994; BURGER and GOCHFELD, 1991a). There is little niche differentiation in prey selection, as occurs in most shorebirds at stopover sites (DAVIS and SMITH, 2001), because the horseshoe crab eggs are nearly all the same size. The small size of prey means that there are no handling time differences (JOHNSON, GIRALDEAU, and GRANT, 2001).

Although nearly 15 species of shorebirds feed on horseshoe crab eggs in the spring (CLARK NILES, and BURGER, 1993), three species of shorebirds depend more heavily on them, including red knot (*Calidris canutus*), ruddy turnstone (*Arenaria interpres*), and sanderling (*Calidris alba*; CASTRO and MYERS, 1989; MYERS *et al.,* 1987; TSIPOURA and BURGER, 1999). The semipalmated sandpiper (*Calidris pusilla*) is of interest because they are also declining (BURGER, NILES, and CLARK, 1997). All the shorebirds that migrate through Delaware Bay have generally shown a decline (MORRISON *et al.,* 2001), but knots and turnstones are especially vulnerable because their foraging is more limited to Delaware Bay beaches than is the foraging of the other species (BURGER, NILES, and CLARK, 1997).

In this study, foraging success varied among species and among habitats. Foraging rates were not independent of species composition and density of the flocks, nor of habitats. Species selected those habitats where aggression was minimized and foraging rates were highest. The management implications of the data on foraging success, habitat use, and human disturbance are clear—state officials should protect large stretches of the Delaware Bay beaches that have a maximum of different types of microhabitats. This includes not only tide line, but all the places where abundant excess horseshoe eggs can be found, including creeks, mudflats, and sandbars. Further, because the foraging shorebirds are disturbed by people and dogs (see the following paragraph), the diversity of habitats should be protected, not just the tide line. That is, beach mud, creek, and upper beach habitats should be equally protected from the effects of disturbance because they serve as a buffer to the tide line foraging, and because they are used for foraging by some shorebirds.

Moreover, the competition among gulls and shorebirds for foraging space and the different response to disruptions suggests that considerable management attention should be given to the gull–shorebird interactions. These data showed that gulls return following a disturbance, and most shorebirds do not. Thus the shorebirds are displaced from their foraging beaches by disturbances. These data suggest that regulatory agencies should eliminate all disturbances, particularly those of dogs. This may require additional law enforcement to severely fine dog owners, thereby deterring others from allowing their dogs to wander the beaches. It may also require limiting the effects of scientists by requiring all people to maintain a buffer distance from foraging shorebirds.

ACKNOWLEDGMENTS

We thank K. Clark and M. Gochfeld for help and advice throughout the study, and R. Ramos for graphics.

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