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PHYSICAL AND SOCIAL DETERMINANTS OF NEST-SITE SELECTION IN PIPING PLOVER IN NEW JERSEY[1]

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Abstract. I examined nest-site selection and reproductive success in Piping Plover (*Charadrius melodus*) over a 4-year period on four nesting beaches in New Jersey. Nest site characteristics varied among the four nesting locations with respect to distance to dunes, water, nearest Least Tern (*Sterna antillarum*) nest, and percent shell cover. Compared with random points, Piping Plover nests were closer to dunes and vegetation, farther from water, closer to tern nests, farther from other Piping Plover nests, in spots with more shell cover. Reproductive success varied among colonies and years, but was generally higher at Brigantine than the other sites. Causes of nest failure included predation, human destruction, abandonment, and flooding. Plovers derived antipredator benefits from nesting near terns, and plover nesting in tern colonies often had higher success than those nesting outside of tern colonies.

Key words: Piping Plover; Charadrius melodus; *nest-site selection; shorebirds; nesting success; social facilitation; Least Terns.*

INTRODUCTION

Habitat selection involves the choice of a particular habitat from available habitats, resulting in the nonrandom distribution of animals in space. For most birds breeding habitat selection involves a series of choices: general habitat selection, territory selection, and nest-site selection (Gochfeld 1977, Burger 1985). These choices may not be made at the same time, or by the same member of the pair. All three choices influence reproductive success by affecting acquisition of resources such as food, shelter, mates, nest materials (Schoener 1974), and protection of eggs and young from predators and inclement weather.

Information on habitat selection, rather than habitat use, is generally lacking for many solitary-nesting shorebirds because nests are difficult to locate or are very sparse (e.g., Johnsgard 1981). Although selection has been examined for colonial species nesting on beaches (Nisbet 1973, Erwin et al. 1981, Burger 1984a), little is known of solitary, beach-nesting species (Pitelka 1979, Burger 1984b). In this paper I examine habitat and nest-site selection of Piping Plover (*Charadrius melodus*) nesting on four coastal beaches in New Jersey. I also present data on reproductive success and causes of nest failure.

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Piping Plover breed in the interior of North America from central Alberta and Manitoba south to Montana and South Dakota; in the Great Lakes region; and in Atlantic coastal areas from Newfoundland to Virginia (AOU 1983, Haig 1985). Piping Plover nest on wide, sparsely vegetated, deserted beaches although they often nest close to vegetation (Wilcox 1959, Renaud 1979, Faanes 1983). Piping Plover have just been listed on the United States Federal list as endangered in the Great Lakes region and threatened elsewhere; and on the Canadian list as endangered. One cause of population decreases is habitat loss, with Piping Plover nesting on suboptimal nest sites.

Although nest sites have been described in the interior (Weseloh and Weseloh 1983), little recent information is available from coastal nesting populations, and selection from available habitat has not been studied. Such data are critical to our understanding of the breeding biology and population dynamics of shorebirds, and for developing sound recovery plans for threatened or endangered species.

The objectives of this study were (1) to determine the factors Piping Plovers use to select nest sites, (2) to determine if plover nest-site characteristics changed during the study, (3) to provide data on nest sites that can be compared to sites selected by this species at other coastal locations, and (4) to examine reproductive success.

TABLE 1. Egg-laying dates of Piping Plover on four New Jersey beaches (Brigantine, North and South Corson's Inlets, Whale Beach).

	No. of pairs	Mean date (±SD)	Range
1983*	19	12 May ± 10 days	2 May–28 June
1984*	13	17 May ± 9 days	11 May–27 June
1985	40	14 May ± 13 days	29 April–3 July
1986	38	17 May ± 12 days	23 April–27 June

* Brigantine Beach only.

STUDY AREAS AND METHODS

Observations were made at Brigantine Beach from 15 May to 15 July 1983 to 1986, and at North and South Corson's Inlet, and Whale Beach from 15 May to 15 July 1985 to 1986. During this period observations were made from 07:00 to 17:00, 5 days a week at each site, and these procedures required a full-time field assistant at each site.

All four study sites are located on barrier beach islands. Brigantine Beach, opposite Atlantic City, is flat, 2 km long and 200 m wide with a belt of dunes on the landward side separating the tern colony from condominiums. The beach is open to the public with restricted access by pathways through the dunes. Except where a Least Tern (*Sterna antillarum*) colony is delineated by a string fence, the city regularly scrapes the beach using bulldozers to remove shells and other objects.

North Corson's Inlet beach is a state park at the end of a barrier island jutting into Corson's Inlet. The beach is less flat, and has higher, less stable dunes than Brigantine. It also has a Least Tern colony delineated by string. South Corson's Inlet is south of the inlet, and has a similar physiognomy to North Corson's Inlet. Least Terns nested on South Corson's Inlet only in 1985. Whale Beach is similar in physiognomy to South Corson's Inlet, but narrower.

The study sites all experience similar tidal regimes. Corson's Inlet and Whale Beach experience frequent winter washovers that change the beach physiognomy. Brigantine Beach is more stable than the other sites, and remained relatively unchanged during the study. Each beach has less than 1% cover of *Solidago* or *Ammophila,* although *Ammophila* grows profusely on adjacent dunes.

NEST-SITE SELECTION

Nest-site selection was examined by comparing nest-site characteristics with the same characteristics at random points on the same beaches (after Burger and Lesser 1980). Random points were selected by using a table of random numbers to generate x and y coordinates. Nest-site characteristics recorded at the time each nest was located included: distances to dune, high tide level, and vegetation; species of vegetation, percent shell cover within 1 m of the nest (but excluding the nest itself), slope, distance to nearest Least Tern

TABLE 2. Characteristics of Piping Plover nest sites and random points at two beach colonies. Given are $\bar{x} \pm 1$ SD.

	Brigantine Beach				
	Nest				Comparison among years
	1983	1984	1985	1986	
No. of nests	19	14	21	13	
Distance to (m):					
Dune	27 ± 20	22 ± 18	30 ± 18	*53 ± 31	6.69 (0.02)
Water	173 ± 23	179 ± 21	169 ± 24	145 ± 51	ns
Vegetation	9 ± 12	9 ± 20	10 ± 18	*40 ± 30	6.21 (0.01)
Nearest tern nest	15 ± 12	5 ± 13	17 ± 23	*36 ± 27	7.85 (0.001)
Nearest plover nest	86 ± 13	85 ± 59	93 ± 60	99 ± 50	ns
Percent shell cover	8 ± 13	13 ± 10	14 ± 22	1 ± 3	ns
Most frequent habitat	Flat	Flat	Flat	Flat	ns

* Using analysis of variance, the year is significantly different.

nest, and distance to nearest Piping Plover nest. Similar characteristics were recorded at each random point.

To evaluate the importance of Least Terns to nesting Piping Plovers I divided Brigantine Beach into 100-m long segments, and recorded the number of Piping Plover and Least Tern nests in each segment. To assess antipredator behavior of Least Terns at Brigantine Beach in 1985 and 1986 I recorded their defensive behavior over tern and Piping Plover nests within the tern colony. I recorded the distance the tern or plover left its nest when a person approached, the number of terns diving, and the total number of dives in a 2-min period.

REPRODUCTIVE SUCCESS

All nests were numbered with 2-cm tall wooden markers placed 2 to 3 m from the nest. Thereafter, nests were checked daily with the use of binoculars from 10 m away. If no adult was incubating, the nest was examined closely to determine if the eggs were present, abandoned, or preyed upon. Data recorded included: initial clutch size; eggs taken by predators, people, or floods; eggs abandoned; eggs missing; and number of eggs that hatched. Where possible broods were followed to obtain estimates of fledging success. Hatching rate was defined as the number of eggs hatched per active nest, and fledging success was defined as the number of young fledged (21 days) per active nest.

RESULTS

NEST SITE SELECTION

Breeding chronology in New Jersey was consistent from year to year with egg laying from late April until early July (Table 1). The peak of egg laying was generally mid-May.

Brigantine Beach. At Brigantine Beach Piping Plover generally nested close to dunes, and far from the high tide line, near vegetation, and on areas with 5 to 20% shell cover (Table 2). Piping Plover selected flat places, rather than slopes, peaks, or troughs. Generally, plover nests were 5 to 36 m from tern nests, and 85 to 99 m from other plover nests. At Brigantine Beach there were no differences among nest-site characteristics from 1983 to 1985 (Table 2). However, in 1986, the distance to dunes and vegetation was significantly greater than for the other years, and the nearest tern nest was significantly farther away than it had been previously.

The nest characteristics of Piping Plover at Brigantine differed significantly from the random points with respect to all factors except distance to high tide (Table 2). Generally Piping Plover nested closer to dunes and vegetation, farther from other Piping Plover, and on flatter spots with more shell cover than was present at the random points. Similarly, in 3 of 4 years, plovers nested significantly farther from water than the random points ($\chi^2 = 5.3$, $P < 0.001$). The distance to the nearest tern nest was significantly less in 1983 to 1985 than that of the random points. From 1983 to 1985 most plover nested in the tern colony, whereas in 1986 many nested outside the colony far from tern nests.

North Corson's Inlet. Plover at North Corson's Inlet nested on flat places very close to dunes and vegetation. Nearest tern nests were 5 to 40 m away, and nearest plover nests were usually over 50 m away. Nest-site characteristics varied between 1985 and 1986 only with respect to distance to vegetation (Table 3). Compared to ran-

TABLE 2. Extended.

Brigantine Beach		South Corson's Inlet[a]					
		Nests			Random points		
Random points	Comparison between nest and random points	1985		1986	1985 1986	Comparison of nests and random points
64		14		17	48	
48 ± 29	2.71 (0.09)	11 ± 6		23 ± 17	21 ± 18	ns
150 ± 28	ns	61 ± 38	*	130 ± 79	35 ± 19	9.7 (0.01)
38 ± 29	3.99 (0.05)	10 ± 26		4 ± 7	21 ± 13	ns
42 ± 9	9.92 (0.01)	25 ± 26		–		–
42 ± 37	16.36 (0.001)	99 ± 80	*	106 ± 62	36 ± 23	27.1 (0.001)
2 ± 2	12.12 (0.005)	9 ± 3	*	5 ± 8	2 ± 5	31.5 (0.001)
Slope	3.51 (0.06)	Flat		Flat	Flat	Slope

[a] Few terns nested at South Corson's Inlet.

TABLE 3. Characteristics of Piping Plover nests and random points at North Corson's Inlet and Whale Beach (1985 and 1986).

	North Corson's Inlet					Whale Beach nests
	Nests			Random points	Comparison of nests	
	1985		1986	1985/1986	and random points	1986
No. of nest	17		12	48		5
Distance to (m):						
Dune	9 ± 9		16 ± 15	38 ± 18	9.6 (0.01)	20.0 ± 20.5
Water[a]	54 ± 35		103 ± 71	37 ± 21	16.7 (0.0001)	53 ± 19.0
Vegetation[b]	13 ± 18	*	5 ± 12	19 ± 11	ns	21 ± 2.4
Nearest tern nest	17 ± 9		18 ± 14	32 ± 11	12.1 (0.001)	—
Nearest plover nest[c]	70 ± 60		153 ± 120	38 ± 26	27.1 (0.0001)	112 ± 71
Percent shell cover[d]	3 ± 3		5 ± 8	2 ± 5	ns	9 ± 3
Most frequent habitat	Flat		Flat	Flat	ns	Flat

[a] $\chi^2 = 9.49$, $P < 0.002$ for South Corson's Inlet comparing 1985 and 1986 nests.
[b] $\chi^2 = 15.2$, $P < 0.0001$ for North Corson's Inlet comparing 1985 and 1986 nests. * = significant differences.
[c] $\chi^2 = 3.9$, $P < 0.05$ for South Corson's Inlet comparing 1985 and 1986 nests.
[d] $\chi^2 = 5.3$, $P < 0.02$ for South Corson's Inlet comparing 1985 and 1986 nests.

dom points, plovers nested significantly closer to the dunes and to tern nests, and farther from the water and other Piping Plover nests (Table 3).

South Corson's Inlet. At South Corson's Inlet plover nested closer to dunes, farther from water, and in flatter areas with higher shell cover than random points (Table 2). Some plover nested near the tern colony in 1985, but no terns nested in 1986. Plover nested closer to the water, closer to other piping plover, and in areas with higher shell cover in 1985 compared to 1986.

Whale Beach. The Piping Plover pairs nested closer to the dunes than to the ocean, very near to vegetation on flat places. Internest distances averaged over 100 m (Table 2).

Comparison of Nest Sites Among Locations. The four study sites differed in structure. Whale Beach was the narrowest, Brigantine Beach the widest (200 m), and Corson's Inlet North and South were narrow at one end leading into a wide sandy beach at the inlet. Brigantine had a band of several lines of dunes, while South Corson's and Whale Beach had a single, narrow band of dunes.

Nest characteristics differed among the locations with respect to distance to dunes ($\chi^2 = 31.4$, $P < 0.001$), water ($\chi^2 = 9.7$, $P < 0.02$), vegetation ($\chi^2 = 8.1$, $P < 0.04$), and percent shell cover ($\chi^2 = 8.0$, $P < 0.05$). Piping Plover at Brigantine nested where there was more shell cover and they nested farther from water and dunes than at other colonies.

The relationship of nest placement with respect to dunes and high tide line varied among colonies and years. At Brigantine, when plovers increased their distance from dunes, they decreased their distance to water, reflecting a beach of uniform width. However, at Corson's Inlet the birds increased their distance from both the dunes and the high water line between 1985 and 1986. Thus, some plover shifted from the narrow part of the beach to the wider part nearer the inlet.

Social Factors Affecting Nest-Site Selection. Piping Plover generally nested closer to Least

TABLE 4. Defensive behavior of Least Terns over tern and Piping Plover nests at Brigantine Beach.

	Over Least Tern nest				Over Piping Plover nest	
	1985		1986		1986	
Defensive behavior	$\bar{x}$ ± SD	Range	$\bar{x}$ ± SD	Range	$\bar{x}$ ± SD	Range
Number of samples	26		113		39	
Distance tern or plover leaves nest[a]	27 ± 13	25–60	25 ± 10	13–53	21 ± 18	1–99
Mean number of terns diving[b]	4 ± 3	3–12	4 ± 2	1–12	3 ± 2	1–10
Total dives per 2 min[c]	21 ± 17	18–67	33 ± 14	1–71	24 ± 12	4–49

[a] Kruskal-Wallis χ^2 for 1986 = 1.02, not significant.
[b] Kruskal-Wallis χ^2 for 1986 = 0.04, not significant.
[c] Kruskal-Wallis χ^2 for 1986 = 12.9, $P < 0.003$.

TABLE 5. Piping Plover reproductive success (per active nest) at four New Jersey areas.

	No. of nests (pairs[a])	Clutch size ($\bar{x} \pm 1$ SD)	Hatching rate ($\bar{x} \pm 1$ SD)	Fledging rate ($\bar{x} \pm 1$ SD)
Brigantine Beach				
1983	19 (19)	3.44 ± 0.89	2.50 ± 1.71	1.26 ± 1.01
1984	14 (13)	3.45 ± 1.04	2.36 ± 1.91	1.07 ± 0.09
1985	21 (12)	3.50 ± 1.06	1.95 ± 1.90	0.85 ± 0.72
1986	13 (12)	3.85 ± 0.38	2.69 ± 1.65	1.00 ± 0.41
North Corson's Inlet				
1985	17 (12)	3.29 ± 0.88	1.53 ± 1.59	0.23 ± 0.81
1986	12 (9)	2.83 ± 1.19	1.58 ± 1.73	0.77 ± 0.62
South Corson's Inlet				
1985	14 (12)	3.71 ± 0.47	1.79 ± 1.58	0.57 ± 1.01
1986	17 (12)	3.27 ± 1.16	1.20 ± 1.61	0.33 ± 0.51
Whale Beach				
1986	8 (5)	3.66 ± 1.01	2.20 ± 1.25	1.40 ± 0.82

[a] Estimated from territory location.

Terns (internest distances of less than 25 m) and farther from Piping Plover (internest distances of over 70 m) than expected. To examine benefits Piping Plover derive from nesting near tern nests I examined the antipredator behavior of terns directed toward an approaching person at Brigantine (Table 4).

When predators approached, Least Terns flew over the predator and dive-bombed them, while Piping Plovers walked or flew away, performing distraction displays. Both plovers and terns left their nests at 20 to 30 m when the experimenter approached. Three to seven terns mobbed the person, making 15 to 40 dives in a 2-min period. There was no significant difference in the number of terns diving at the experimenter whether the experimenter stood next to a plover or tern nest, although the terns made somewhat fewer dives over the plover nest (Table 4).

Piping Plover nesting among tern nests had increased antipredator benefits as the maximum number of terns diving (Kendall's tau = 0.55, $P < 0.001$) and the number of dives per 2 min (tau = 0.35, $P < 0.009$) over Piping Plover nests were directly related to the number of tern nests within 10 m, and the number of tern nests within 5 m (tau = 0.93, $P < 0.0006$). The tern having the closest nest contributed the most dives to the antipredator effort (tau = 0.76, $P < 0.0001$).

REPRODUCTIVE SUCCESS

Mean clutch size varied from 2.83 at North Corson's Inlet (1986) to 3.85 eggs/nest at Brigantine Beach (1986, Table 5, $\chi^2 = 7.4$, $P < 0.06$). Hatching rate varied from 1.20 at South Corson's Inlet (1986) to 2.69 eggs hatched per nest at Brigantine (1986, $\chi^2 = 7.6$, $P < 0.05$). Fledging success ranged from 0.23 at North Corson's Inlet to 1.26 young fledged per nest at Brigantine. Generally reproductive success was higher at Brigantine Beach than at the other colonies.

Causes of egg loss included predation, destruction by people, abandonment, flooding, or unknown. Causes of egg loss varied among years and colonies (Fig. 1). Egg losses due to predation varied among years at Brigantine ($\chi^2 = 5.3$, $P < 0.02$) and North Corson's Inlet ($\chi^2 = 16.2$, $P < 0.001$); abandonment varied by year at Brigantine ($\chi^2 = 8.1$, $P < 0.0002$) and North Corson's ($\chi^2 = 16.2$, $P < 0.0001$); the number of missing eggs varied by year at Brigantine ($\chi^2 = 2.6$, $P < 0.06$) and North Corson's Inlet ($\chi^2 = 5.2$, $P < 0.02$), and the number flooded out varied by year at North ($\chi^2 = 16.2$, $P < 0.001$) and South Corson's Inlet ($\chi^2 = 21.0$, $P < 0.0001$).

In some Piping Plover nests all the eggs hatched, but in others only two or three eggs hatched because some eggs were taken by predators or were infertile. Hatching success within tern colonies related to the nesting density of the terns, with Piping Plover nests in areas with over 20 terns per 100 m² often hatching three or four eggs (Fig. 2). In most years hatching success was higher for plover nesting within tern colonies compared to those nesting outside tern colonies. At Brigantine Beach in 1983 and 1984 the six nests that were outside the tern colony failed; in 1985 eight of the 10 nests outside the tern colony failed, while

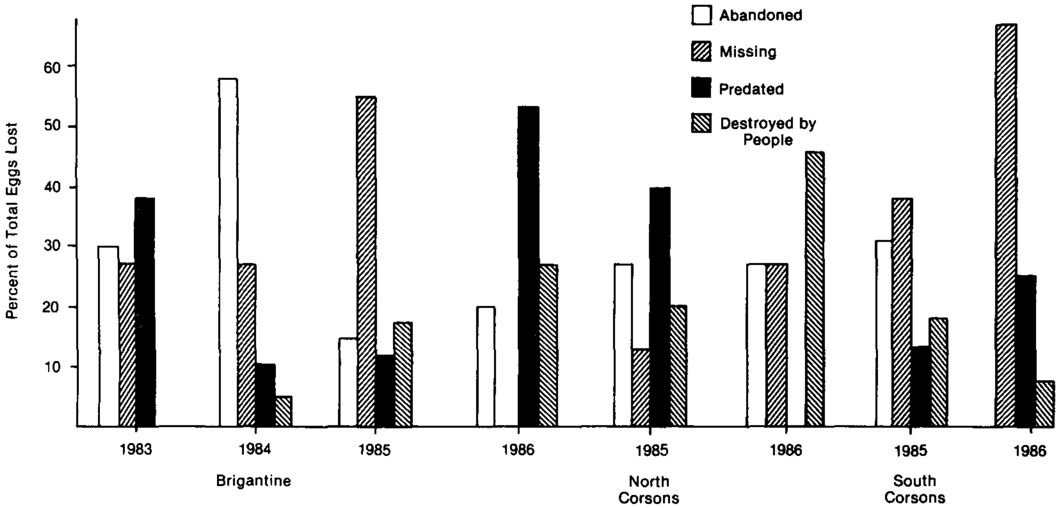

FIGURE 1. Causes of Piping Plover egg loss among colonies and years.

only two of 11 failed within the tern colony. In 1986 the hatching rate was similar inside and outside the Brigantine tern colony. Comparable data for Corson's Inlet are available only for 1986: 73% of the Piping Plover nests within tern colonies were successful compared to 45% success for those plover nesting outside of the tern colony.

DISCUSSION

NEST SITE SELECTION

Sandy ocean beaches are generally long, flat, devoid of vegetation except for occasional herbs,

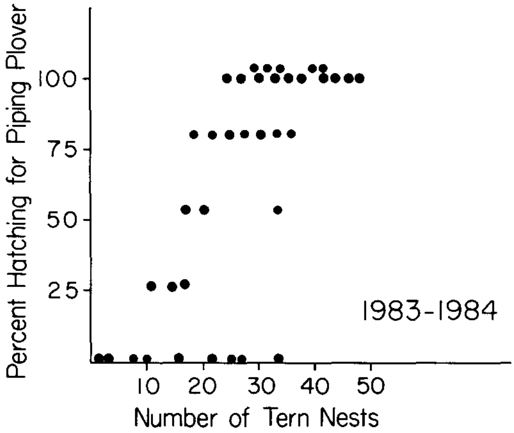

FIGURE 2. Hatching success of Piping Plover as a function of number of terns nesting in the 100-m^2 section around each plover nest.

and bounded by ocean water and sand dunes. Thus, birds nesting on beaches have few features to choose from, and must often rely on minor differences in elevation, vegetation, and placement (location relative to the dunes and water) to provide the necessary protection from predators, people, and inclement weather.

Sandy beaches are usually adjacent to dry land habitats, providing opportunities for mammalian predator access. Nearby, vegetated sand dunes also provide additional shelter for mammalian predators. Nesting near vegetation has the advantage of providing chicks with shelter from the hot sun, heavy rains or aerial predators, but has the disadvantage that predators can learn to search vegetation for eggs or chicks. I observed American Crows (*Corvus brachyrhynchos*), dogs (*Canis familiaris*), and fox (*Vulpes fulva*) moving from *Solidago* to *Solidago* along the beach in search of eggs or chicks. The cryptic coloration of chicks provided protection from predators and people.

Piping Plover in this study usually nested on flat places on the beach rather than on slopes or troughs. By nesting on flat places they maximized their ability to see approaching predators. Nesting in shallow troughs reduces their visibility of approaching predators or people, while nesting on relatively high places might make them more visible to predators and would expose them to excessive sandblasting during heavy winds. Spots with shells provide protection to chicks and incubating adults from wind, provide camouflage to eggs and chicks, or indicate places of higher elevations where recent flood tides have been unable to remove the shells.

Placement of Piping Plover nests between the dunes and the ocean provides an example of contrasting selection pressures. If they nest too close to the ocean they may be flooded out by high tides; if they nest too close to the dunes they risk mammalian predation. At Brigantine the birds shifted away from the dunes (and closer to the ocean) when fox predation increased in late 1985 and 1986. At Corson's Inlet, however, birds relocating nests farther up the spit were both farther from the dunes and farther from the ocean. This appeared to be a response to predators coming from the dunes, and to human disturbance coming from near the surf.

SOCIAL FACTORS

On all beaches Piping Plover nested closer to Least Terns, and farther from other plover than expected. In some years most plover nested in or near the tern colonies, in other years fewer did so. However, in all years Piping Plover spaced out from conspecifics along the beach. Despite differences in predation rates, flooding and human disturbance, the plover still maintained large, linear territories along the beach.

Piping Plover nesting in Least Tern colonies had higher productivity and apparently derived several benefits from them: (1) early warning from predators, (2) increased antipredator behavior, and (3) decreased vulnerability. Plover derived early warning because more birds watched for predators in colonies, and terns spent more time in the air where they could more easily see approaching mammalian predators. Early warning derived from nonconspecifics has been termed information parasitism by Nuechterlein (1981), and is used by grebes (*Rollandia rolland, Podiceps occipitalis, Aechmophorus occidentalis*) nesting in gull (*Larus*, Burger 1984c) and tern (*Sterna*, Nuechterlein 1981) colonies.

Least Terns harassed predators within their colonies, whether the predator was near a tern or a plover nest. Such antipredator behavior has a deterrent effect for some predators, and is successful in repelling most human intruders (Kruuk 1964, Lemmetyinen 1971, Andersson 1976, Wittenberger and Hunt 1985). Piping Plover rely on cryptic coloration of eggs and young as an antipredator strategy (Lack 1954, 1968) and give distraction displays when predators approach too closely (Gochfeld 1984). By nesting in tern colonies plovers make use of the antipredator behavior of the terns (Burger 1981, 1984c), and then give distraction displays when the tern defenses are unsuccessful.

Another advantage for plovers nesting in tern colonies is of a selfish-herd nature (Hamilton 1971, Nisbet 1975). A solitary plover nest may be the only food around, but a plover nest in a tern colony is only one of many nests. This advantage may be reduced if predators are recruited to the tern colony because it is so visible or if plovers nest much earlier than the terns.

Given the advantages of nesting in tern colonies, one may wonder why all plover don't nest there. Firstly, in some places plovers nest earlier than the resident terns. Secondly, in this study plovers defended a 70- to 100-m stretch of beach from other plovers, and this may prevent more pairs from nesting within a tern colony. Thirdly, when a particularly persistent mammalian predator systematically searches for prey in a tern colony, the plover nests are equally vulnerable. This happened at Brigantine in 1986, and later-nesting plovers nested outside of the tern colony. Lastly, when predation is severe, Least Terns desert the colony site leaving the plover nests as the only available food source.

On many New Jersey beaches Piping Plover may be forced to nest in Least Tern colonies because these are the only places protected from human use. Plover that nest early, and subsequently find they are outside of tern colonies, may lose their eggs to people. These pairs often renest in the tern colony when it is included in their territory. Further, it is difficult for tern wardens to protect one solitary Piping Plover nest, and easier to delineate and protect a Least Tern colony. By so doing, they help determine which Piping Plover reproduce successfully.

Generally early-nesting Piping Plover are more successful than late-nesting pairs because chicks fledge before human disturbance becomes severe, and early-fledged chicks may have more time to gain weight before migration than those of late-nesting pairs. Selection for early nesting and for nesting in tern colonies (of whatever species) act in opposing directions. Late-nesting (or renesting) pairs may choose to nest in tern colonies while early-nesting pairs may not have that opportunity.

REPRODUCTION SUCCESS

Fledging success of Piping Plover in this study ranged from 0.23 to 1.26 young fledged per active nest. This is similar to recent fledging rates reported for Maine (0.9 to 1.80, J. Arbuckle, pers. comm.), Rhode Island (0.6 to 1.36, C. Raithel and J. Myers, pers. comm.) and Nova Scotia (0.7 to 2.1, Cairns 1982). These rates are not always comparable since some are per pair, and others are per active nest. Although Wilcox (1959) reported a hatching rate of 3.52 young per nest for Long Island, he did not report fledging rates. However, since the Long Island hatching rate in the 1950s was considerably higher than the New Jersey rate, the Long Island fledging rate may also have been higher from 1937 to 1957.

The lower reproductive success of current studies may reflect decreases in optimal habitat, increases in human disturbance, and increases in predators on barrier islands. Increases in predators may also be attributable to people providing them with a more dependable food supply in the form of garbage.

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