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SOCIAL ATTRACTION IN NESTING LEAST TERNS: EFFECTS OF NUMBERS, SPACING, AND PAIR BONDS[1]

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Abstract. These experiments examined the role of colony numbers, spacing pattern, and mating status on the social attraction of Least Terns (*Sterna antillarum*). Decoys were used to simulate different social conditions. Least Terns were more attracted to larger rather than smaller groups of terns, to terns spaced out at 1.5 m intervals rather than at 0.5 m intervals, to solitary rather than paired terns, and to plots containing single birds together with paired terns rather than to either alone. Taken together, these experiments suggest that colony size, spacing patterns, and mating status contribute to the relative social attraction of conspecific Least Tern groups. The specific choice of larger groups, larger interbird distances, and pairs plus singles allows (1) males to establish territories within the center of a colony, (2) both sexes to court unmated birds, and (3) both sexes to obtain maximum vigilance and antipredatory benefits from being in a larger group.

Key words: Social attraction; Least Tern; Sterna antillarum; *colony formation; coloniality; nesting.*

INTRODUCTION

Many groups of wild birds form foraging or migratory flocks that may be transitory or maintained for several days or weeks. Some birds nest in dense breeding colonies where several hundred or thousand birds may breed in one small location (Lack 1954). One advantage of coloniality is increased vigilance and antipredator behavior (Tinbergen 1956, Hamilton 1971), with a decreased cost of that vigilance and antipredator behavior to each individual in the colony (Alexander 1974, Hoogland and Sherman 1976, Burger 1981, Kharitonov and Siegel-Causey 1988). The possible transfer of information about food resources among colony members may be an added advantage (Ward and Zahavi 1973, Krebs 1978). Selection of a colony and nest site affects individual fitness through reproductive success and is likely to be influenced by social attraction features (Coulson 1966).

Darling (1938) proposed that large groups of larids provide more social facilitation than smaller groups, leading to greater egg-laying synchrony and higher reproductive success for individuals nesting in large colonies (Southern 1974). Yet the relative attractiveness of different-sized groups to birds establishing territories in a colony has not been examined. Spacing may be influential in social attraction because the same number of birds may appear to be a larger group if birds are moderately separated rather than being tightly packed or very far apart. Given that birds prefer to be in the center of nesting aggregates (Coulson 1968, Ryder 1980), they may be more attracted to spatial groups when there is room for them to introduce themselves within the group.

In larids, males often establish a territory and then display to obtain a mate (Tinbergen 1960, Nisbet 1973). Males will sometimes try to court and copulate with an unguarded, mated female remaining alone on her territory (Burger and Gochfeld, unpubl. data). Females seeking mates land and display next to solitary males to determine interest. Thus both males and females should be attracted to groups containing some single birds, rather than only pairs, to increase their chances of finding a mate. Groups of only pairs provide no unmated birds, and those of only singles may mean birds are unmated or that birds are all incubating and so also have mates.

In this paper I examine the features of aggregates that may play a role in attracting individuals to nesting Least Tern (*Sterna antillarum*) colonies. Several features could be important, including number and spacing of individuals, and reproductive stage. Terns could either be attracted to conspecifics in direct relation to the number of conspecifics or the attraction could increase disproportionately to the increase in numbers of

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conspecifics. I designed several experiments using decoys to examine the role these features play in social attraction, and generated four predictions: (1) Terns should be more attracted to larger rather than smaller numbers of terns. (2) Terns should be more attracted to groups with unfilled spaces compared to densely packed groups. (3) Terns should be more attracted to groups of single birds compared to groups composed only of pairs of birds. (4) Terns should be more attracted to groups with singles and pairs compared to groups composed of only singles or only pairs.

STUDY AREAS, SPECIES AND METHODS

All observations and experiments were conducted at Least Tern colony sites in New Jersey at Brigantine Beach, Cedar Bonnet, and Mike's Island (Barnegat Bay) in 1983 and 1984. Brigantine is a barrier beach island. The Brigantine Beach site is a 200-m wide sandy strip bordered by dunes on one side and the Atlantic Ocean on the other. The sand is generally flat with less than 2% vegetation cover. The adjacent dunes are covered with *Ammophila* grass. Cedar Bonnet is a large dredge spoil island. The center of the island, often used by nesting terns, is a bare dredge sand area approximately 200 m^2 fringed with *Phragmites*. Mike's Island is a round dredge spoil island with an open sand dome (200 m^2 in diameter) fringed by 10 to 20 m of dense *Phragmites*. All three sites have been used for nesting by terns, although sections used for the experiments were not previously used by the terns.

Least Terns traditionally nest on the sandy sections of barrier islands adjacent to the surf (Wolk 1974). With increasing use of barrier beaches by people for homes, marinas, bathing beaches, and other recreational activities, Least Terns have been forced to use other habitats such as dredge spoil islands, beach dunes, and dredge spoil on barrier islands and the mainland (Massey 1974, Erwin 1980, Erwin et al. 1981, Burger 1984). Habitat loss and displacement have been followed by decreasing population levels throughout their range, and the Least Tern is federally listed as endangered (west coast, interior race, Massey 1974). New Jersey has a breeding population of up to 1,200 breeding pairs (Burger 1984), and breeding colonies usually range from three to 300 breeding pairs.

Least Terns are well-suited for an examination of social attraction because a stressed species might be especially prone to using the presence of conspecifics as an indication of safe nesting areas (safe from predators and human disturbance). The New Jersey State Endangered and Non-game Species Project authorized the present study to learn what configurations are most attractive to Least Terns so that terns could be drawn to new, suitable, predator-free sites that could be protected from human disturbance.

Observations were made from 20 May to 15 June 1983 and 1984 (prior to egg laying), three to four times a week at each of the three study sites, from 07:00 to 11:30 each day. During this period six experiments were conducted to determine the effect of spacing, numbers, and mating status on the attractiveness of a colony to prospecting terns. Two full-time field assistants and the author conducted the experiments. Each experimenter used the same protocol, set up the experiments in an identical manner, remained at the same distance from the decoys (for observation), and recorded the same behavioral measures.

In 1983 one experiment was conducted at each study site simultaneously. In 1984 four different experiments were conducted in an ordered pattern so that in each 2-day period each experiment was conducted for one 2-hr period. The order of experiments was shifted in each successive 2-day period so that each experiment was conducted from 07:00 to 09:00 in every 4-day period. Thus each experiment was conducted for 13 2-hr periods. From 12 to 15 June 1985 an assistant and I conducted a sixth experiment at Mike's Island to evaluate social status and spacing. The experimental design is shown in Table 1.

Since it was not possible to set up experiments with live terns I used tern decoys which were carved by a professional decoy maker and were sufficiently lifelike to attract terns (Kotliar and Burger 1984). Male terns courted and displayed to the decoys, and a few males even presented fish to them. In the experiments, I varied the number of decoys present (10, 15, 20), the spacing of decoys (0.5, 1.0, or 1.5 m apart, after Goodrich 1982), and mating status (pairs, singles, or a combination thereof) of the decoys in each plot (Table 1). A plot was defined as that space occupied by one experimental condition (see Table 1), and was 6 × 4 m. When the decoys used less space, they were placed in the center of the plot. To simulate a pair, I placed two decoys 5 cm apart, facing in the same direction. For each experiment there were two to four plots being

TABLE 1. Experimental design for examining effect of group size, spacing, and social status. One sample = one 15-min observation period.

Experiment	No. samples per colony	Plot	No. decoys	Decoy area[a] (m)	Status	Intersocial distance[b] (m)
1	40	A	20	4.0 × 3.0	Singles	1.0
	40	B	10	3.0 × 2.0	Singles	1.0
	40	C	10	3.0 × 2.0	Singles	1.0
2	104	A	20	2.0 × 1.5	Singles	0.5
	104	B	10	1.5 × 1.0	Singles	0.5
3	104	A	15	6.0 × 3.0	Singles	1.5
	104	B	15	2.0 × 1.0	Singles	0.5
4	104	A	20	1.5 × 1.0	Pairs	0.5
	104	B	10	1.5 × 1.0	Singles	0.5
5	104	A	20	3.0 × 2.0	Pairs	1.0
	104	B	10	3.0 × 2.0	Singles	1.0
6	48	A	16	1.5 × 1.5	Singles	0.5
	48	B	16	1.4 × 0.5	Pairs	0.5
	48	C	16[c]	4.5 × 3.0	Singles and pairs	1.5
	48	C	16[c]	1.5 × 1.0	Singles and pairs	0.5

[a] Area covered by decoys.
[b] Interbird distance = distance between decoys.
[c] For singles and pairs I used six pairs and four singles.

observed, with 2 m between each plot (Table 1). When four plots were being used, two people were necessary to record data. With different combinations of numbers, spacing, and mating status I could test the predictions outlined above.

All behaviors were recorded for the 2-hr duration of the experiment for each plot. Behavioral measures recorded during each experiment were: (1) number of terns flying over the plot; (2) solitary terns landing; (3) pairs landing; and (4) terns courting the decoys within the plots. For a bird flying over to be counted it had to be less than 5 m above the plot, and within the edge of the plot. We also recorded the number of times males presented fish to the decoys, but this was relatively rare. The observer was in a blind 8 m from the decoys, positioned in the center, so that the exact location of birds flying over could be assigned to the appropriate plot. Kruskal-Wallis χ^2 tests were used to distinguish means, and means ± one standard deviation are given in tables and the text.

RESULTS

In experiment 1, I tested whether terns were differentially attracted to groups of 10 or 20 decoys, where decoys were 1 m apart (Table 1). Data were pooled from all three colonies as there were no significant differences among colonies in this experiment. More terns landed near the group of 20 decoys than near either group of 10 decoys (Table 2). The results of this experiment suggest that terns are attracted to large groups.

Since attraction may vary as a function of interindividual distance, I examined the social attraction of small groups and large groups of decoys placed 0.5 m apart (Table 1, experiment 2). Unlike experiment 1, the responses of the

TABLE 2. Responses of Least Terns to the number of decoys in three experimental plots during experiment 1 in 1983.

	No. decoys			χ^2 (*P*)
	10	10	20	
Mean number of terns flying over per 15 min	4.3 ± 2.1	6.2 ± 3.1	13.2 ± 0.3	ns
Percent of terns that landed				
Single terns	10	5	46	285 (0.0001)[a]
Pairs	7	6	20	
Single terns displaying to decoys	0	0	6	

[a] Kruskal-Wallis χ^2 on raw data. Based on 120 15-min sample periods, $n = 312$ birds.

TABLE 3. Behavior of Least Terns in each experiment. Given are number of birds responding, χ^2 values, and probability levels.

	Birds flying over	Single birds landing	Pairs landing	Single birds displaying to decoys
Experiment 2				
Mike's Island				
10 decoys	189	54	22	50
20 decoys	399	111	49	37
χ^2 (*P*)	37.5 (0.001)	19.7 (0.001)	10.3 (0.01)	ns
Cedar Bonnet				
10 decoys	93	56	14	4
20 decoys	237	57	17	9
χ^2 (*P*)	62.8 (0.001)	ns	ns	ns
Brigantine Beach				
10 decoys	201	10	15	1
20 decoys	218	132	21	11
χ^2 (*P*)	ns	104.8 (0.001)	ns	8.2 (0.01)
Experiment 3				
Mike's Island				
0.5 m apart	562	90	12	13
1.5 m apart	701	300	25	28
χ^2 (*P*)	15.2 (0.001)	113.1 (0.001)	29.7 (0.001)	ns
Cedar Bonnet				
0.5 m apart	38	53	11	6
1.5 m apart	321	54	22	10
χ^2 (*P*)	223.1 (0.001)	ns	ns	ns
Brigantine Beach				
0.5 m apart	176	17	15	0
1.5 m apart	172	73	19	0
χ^2 (*P*)	ns	34.8 (0.001)	ns	–
Experiment 4 (0.5 m apart)				
Cedar Bonnet				
Singles	49	33	14	3
Pairs	62	10	9	1
χ^2 (*P*)	ns	12.3 (0.001)	ns	ns
Brigantine Beach				
Singles	112	46	26	0
Pairs	126	25	48	0
χ^2 (*P*)	ns	6.2 (0.02)	6.5 (0.02)	–
Experiment 5 (1 m apart)				
Cedar Bonnet				
Singles	49	24	9	0
Pairs	25	6	5	4
χ^2 (*P*)	8.7 (0.01)	10.8 (0.01)	ns	ns
Brigantine Beach				
Singles	118	32	9	0
Pairs	112	16	5	0
χ^2 (*P*)	ns	5.2 (0.05)	ns	–
Experiment 6				
Singles and pairs				
1.5 m apart	112	38	26	10
0.5 m apart	98	25	10	3
Singles—0.5 m apart	42	16	14	2
Pairs—0.5 m apart	27	14	3	2
χ^2 (*P*)	148.9 (0.001)	30.8 (0.001)	42.1 (0.001)	27.5 (0.001)

terns varied significantly by study site. The number of birds flying over the decoys varied significantly by number of decoys for Mike's Island and Cedar Bonnet, but not for Brigantine Beach (Table 3). However, with respect to the birds that landed there were significant differences only for Mike's Island and Brigantine Beach. Further a higher proportion of terns displayed to the decoys at Mike's Island compared to the other colonies. The results of this experiment indicate that terns generally landed more in areas with larger groups of decoys and confirmed prediction 1.

SPATIAL CONSIDERATIONS

The above experiments suggested that spacing as well as numbers of conspecifics may play a role in social attraction. Yet in experiment 2 these two factors could not be easily separated. Thus I designed experiment 3 to examine the social attraction of 15 solitary decoys with different interbird distances (0.5 and 1.5 m, Table 1).

The number of birds flying over the decoys was significantly different for Mike's Island and Cedar Bonnet, but not for Brigantine Beach (experiment 3, Table 3). However the landing behavior of the terns was not significantly different at Cedar Bonnet. In all cases more terns landed in the plots where the terns were spaced at 1.5-m intervals compared to 0.5 m, and this supports prediction 2.

In this experiment terns preferred to land where there were spaces between the birds rather than where birds were only 0.5 m apart. Furthermore, terns usually landed within the group of decoys rather than at the edge. Terns could have landed on the edge of either group of decoys. However in the spaced-out group they also had a choice of selecting a territory in the center and they did so. This corroborates Coulson's (1968) findings that larids prefer the center of a group rather than an edge.

MATING STATUS

Terns attracted to colonies must find both a suitable nesting site and a suitable mate (if they lack one). Finding a suitable nesting site may mean finding one with sufficient neighbors for adequate antipredator behavior, while finding a suitable mate may require finding a colony where not all birds are paired and where there are single unmated terns. Thus mating status of potential colony members might be an important feature of social attraction at the beginning of the nesting season when I performed these experiments. I simulated the single and mated state by placing decoys either singly or in pairs 0.5 m apart (experiment 4) or 1.0 m apart (experiment 5). These experiments were designed to test for the importance of social status in mating attraction.

When decoys were 0.5 m apart the number of birds flying over the decoy plots was not significantly different for either test colony (Table 3). Birds flew over the plots equally. However, at both colonies the number of single birds that landed was greater for the plot with single decoys (Table 3). Single terns were most attracted to the plots with solitary decoys. The number of pairs that landed differed at Brigantine, but not at Cedar Bonnet. At Brigantine more tern pairs landed in the plot with pairs of decoys.

When the decoys were 1 m apart the number of birds that flew over the decoys was similar at Brigantine, but differed at Cedar Bonnet where more birds flew over the single decoys (Table 3). More single birds landed in the plots with single decoys at both study sites (Table 3).

In these experiments, for the most part, more single terns were attracted to the plots with single decoys than to the plots with pairs even though there were more decoys in the "pair" plot. These results support prediction 3 that terns are more attracted to sections with apparently single birds.

MATING STATUS AND SPACING

In the above experiments terns could select plots with either singles or pairs. In nature, tern colonies usually have sections that contain singles and pairs, singles only, or pairs only. I designed experiment 6 to test the relative attractiveness of singles and pairs, singles only, or pairs only. I had predicted that singles and pairs should be most attractive because all pairs or all singles might indicate that the colony is at an early (no one is yet paired) or very late (all are paired) stage. I established plots with only singles, only pairs, or pairs and singles (Table 1).

The terns' responses were not randomly distributed ($\chi^2 = 21.3$, $P < 0.001$); they preferred to land in the plot with singles and pairs 1.5 m apart, followed by the plot with the singles and pairs at 0.5-m intervals (Table 3). In the two plots with singles and pairs of decoys, both solitary and paired terns preferred the decoys that were more separated rather than those that were dense. Of the all single decoys or all paired decoys, the terns preferred to land in the plot with the single decoys. In this experiment terns were given a choice of paired, single, and paired plus single decoys; and they preferred the singles and pairs that were spaced at 1.5-m intervals rather than 0.5 m. Thus given a choice, the terns preferred the social status that most nearly approaches the conditions in nature, supporting prediction 4.

DISCUSSION

METHODOLOGICAL PROBLEMS

Birds could not be individually marked because they were new recruits to these colonies. Thus, it was impossible to determine if one bird landed 10 times or if 10 birds landed once. However, this problem was inherent in all the islands, for all the plots, and the results were compared among plots. All plots were the same size. Although the spatial area covered by decoys differed, the same air space was used to measure birds flying over. For each day, the results were significant as a function of treatment (i.e., 10 vs. 20 decoys). Thus, the results were not limited to 1 or 2 days. It was impossible to identify sexes since Least Terns are not sexually dimorphic. Thus it is impossible to know whether only males, only females, or both sexes were attracted.

GROUP SIZE, SPACE AND MATING STATUS

The combined results of these experiments indicate that terns prefer large groups of dispersed birds, and of singles and pairs rather than pairs or singles alone. These results were generally consistent among colonies.

The preference for large rather than small groups was general, and occurred in every experiment where there was a choice of group size. Within the confines of these experiments it was not possible to test for larger group sizes, but this clearly should be done. Nesting in a larger colony may be beneficial for a number of reasons (Wittenberger and Hunt 1985). Larger colonies have (1) more eyes for effective early warning of predators (Hamilton 1971), (2) more individuals for effective mobbing and antipredator behavior (Darling 1938; Hoogland and Sherman 1976; Gochfeld 1979, 1980), and (3) abundant eggs and chicks for effective predator swamping (Nisbet 1975). Thus, being able to assess colony numbers and select a site within a larger group could increase reproductive success.

Choosing an open spacing pattern may allow a tern to usurp space from already established or nesting terns with a minimum of territory overlap (and thus territorial aggression), while leaving a low amount of unoccupied space (preventing new territory seekers from landing). When terns are tightly packed, prospecting terns may not be able to introduce themselves within the prospective colony; there simply may be no more space for territories within such a colony. Thus individual spacing may be an important factor in the attractiveness of a colony. In nature, Least Terns nest in colonies with mean internest distances ranging from 0.5 to 6.8 m (Goodrich 1982; Burger, unpubl. data). Further experiments should test for preferences regarding even less dense nesting (over 2 m between decoys). Terns may prefer to be even more spread-out in the available space.

Spacing patterns are a compromise between spacing out for crypsis and clumping for effective antipredator behavior (Tinbergen 1960, Kruuk 1964, Patterson 1965, Tinbergen et al. 1967, Hunt 1975, Hunt and Hunt 1976, Ewald et al. 1980, Burger 1985). Least Terns are particularly vulnerable to predators because they nest on barrier islands where people are present and mammalian predators have easy access. Increases in people increase the number of nonnative mammals (cats, dogs, rats) as well as providing food for natural predators such as foxes and gulls.

Selecting sites in colonies where there are other single birds would increase the potential for mate acquisition or for selection of a high-quality mate. If unmated males are seeking territories and mates they may benefit from landing amidst single birds because (1) it will be easier to usurp a spot where there are fewer neighbors to chase them, (2) it might be easier to find a mate in a place where other terns are also seeking mates, and (3) it may be easier to steal an already mated female when her mate is absent. Additionally, there is an advantage to being at a similar reproductive stage as your neighbors in terms of effective antipredator behavior (Nisbet 1975). For a single bird seeking a territory and a mate, a colony with all paired birds may be unacceptable because the opportunities for mating are low. Indeed, when given a choice, the terns were not very attracted to plots with only paired birds.

Preference for a colony with both paired and single birds reflects conditions in nature. Most colonies have both paired and single birds on territory at any point in time. Single birds could be unmated males soliciting females (Hunt 1980), unmated females waiting for unmated males, mated females waiting for mates to return with fish to courtship-feed them (Nisbet 1973), or incubating parents whose mates are foraging. Pairs usually represent established units already engaged in reproductive activities. They indicate colony stability and attachment to the site. Thus, a newly arriving bird can be assured that the colony will continue to exist for the duration of the season.

The results of these experiments indicate that colony size, spacing patterns, and mating status are important components of social attraction in Least Terns. These factors allow individuals to choose a colony and nest size where they can maximize their fitness opportunities in terms of mate acquisition and antipredator behavior.

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