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COLONY STABILITY IN LEAST TERNS

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ABSTRACT.—I examined colony site tenacity, turnover rates, and causes of reproductive failure in Least Terns (*Sterna antillarum*) nesting in coastal New Jersey from 1976 through 1982. During this period Least Terns used 44 colony sites, although only 17–29 (mean = 22) sites were used in any one year. Population levels ranged from 942 to 2,469 birds (mean = 1,817, SD = ±513). The number of breeding terns increased significantly during the study period. Annual turnover rates varied from 0.16 to 0.30 (mean = 0.22, SD = ±0.05), and were intermediate to low compared to those for other coastal-nesting terns, gulls (*Larus* spp.), and Black Skimmers (*Rynchops niger*). Reproductive success for the Least Tern colonies in New Jersey averaged 0.48 young per pair (SD = ±0.22). The causes of reproductive failure were similar among colonies, except that colonies with over 80 birds suffered higher losses due to predators than colonies with fewer than 80 birds. I suggest that the large, mainland colonies are more vulnerable to predators because they are more stable (making their presence known to predators) and predators have easy access. Human disturbance accounted for over half of the reproductive failures of Least Tern colonies. The low turnover rate and high loss to human activity suggest that reproductive success can be improved by increased protection.

Colonial seabirds often use the same sites for years or decades, a behavior termed "colony site tenacity" (see review in Southern 1977, Southern and Southern 1982). Most seabirds nest in inaccessible places where they are safe from predators (i.e., offshore islands). Other species, such as the Black-billed Gull (*Larus bulleri*; Beer 1966), Franklin's Gull (*L. pipixcan*; Burger 1974), Laughing Gull (*L. atricilla*; Montevecchi 1978), and Black Skimmer (*Rynchops niger*; Burger 1982), shift colony sites frequently, particularly when changing water levels render previous colony sites unsuitable. McNicholl (1975) noted the relationship between habitat stability and colony site tenacity, and suggested that larids exhibit either high or low tenacity depending on their habitat. Several authors have subsequently reported that a given species may either retain colony sites or shift them depending on proximate cues (Morris and Hunter 1976, Southern 1977). Furthermore, reproductive success in one year may influence whether birds return and breed at the same site the following year (Burger 1982).

Studies on colony site tenacity have generally dealt with only one or two colonies (but see Burger 1982), and the specific environmental factors that caused abandonment or lowered nesting activities were not examined (but see Southern and Southern 1982). In this study I examined colony site use by Least Terns (*Sterna antillarum*) in coastal New Jersey in order to determine colony site tenacity, report on the relationship of reproductive success to colony site shifts in some colonies, and compare the causes of reproductive failure in large and small colonies. Because of the effects of greater numbers of nesting birds on early warning and antipredator behavior (Kruuk 1964), I hypothesized that large colonies would be more successful than small colonies.

Along the east coast of North America Least Terns breed on sandy beaches, often facing the oceanfront. Their preference for beaches is often in direct conflict with people who want to use these places for bathing, homes, marinas, fishing docks, or other recreational and business facilities. In recent decades human activities have led to massive habitat loss for the terns and rapid declines in their numbers (Galli 1978a). New Jersey has placed Least Terns on its state endangered species list, and the California Least Tern (*S. a. browni*) is on the federal endangered species list (Massey 1974). The suggestion that Least Terns shift colony sites frequently (Nisbet 1973) because of habitat instability (McNicholl 1975) may result in a general lack of protection of known nesting sites. Wildlife managers may assume that there is no use protecting a specific site since the colony may re-form a few hundred meters or more down the beach. Hence, an additional objective of this study was to determine the degree to which specific colony sites were re-used from year to year.

STUDY AREA AND METHODS

The entire coastline of New Jersey was censused from 1976–1982 either by aerial surveys

TABLE 1. Adult Least Tern populations at New Jersey colony sites (north to south). Given are the maximum number of adults reported during any one census. The number following the colony name refers to Figure 1.

Colony name		1976[a]	1977[b]	1978[c]	1979[d]	1980[e]	1981[f]	1982[g]
Port Newark	1	30	10					
Global Terminal (Bayonne)	2						8	60
Newark Airport	3	80						
Sandy Hook South	4	250	60	147	140	344	364	300
Ortley Beach	5		16	30				
Pelican Island	6	47	300	250	250	60		
Island Beach South	7						95	
Barnegat Inlet	8	67	70	40	100	320	90	45
Cedar Bonnet	9		80	140	70	75	70	
Parker Island	10		35	8				
Big Creek	11		2					
Holgate	12	74	55	250	160	150	268	650
Little Beach	13			50				
Peter's Beach	14	300	65	28	68	92	6	12
Brigantine Pier	15					14		
Absecon Inlet (Brigantine Beach)								
No. 1 (North)	16	125	25	96	125	258	75	140
No. 2 (South)	17				60	112	57	140
Altantic City Expressway	18							4
Absecon Blvd.								
West	19	12		30	5	12	13	14
East	20	12		20	32	16	12	20
Longpoint Blvd.	21			38	8	8	34	
Ventnor City	22	10	4					
Anchorage Point	23			8				
Longpoint Sodbanks	24	10	7	35	12	2	24	24
Seven-eleven	25			20	28			
Bass Harbour	26	2	6					
Drag Island	27	10						
Corson's Inlet								
(North)	28	47	70	190	250	500	700	800
(South)	29				10	8	2	60
Whale Creek	30			50				
Whale Beach	31	20	4		30	18	2	
Sea Isle City								
#54	32			9	1			
#74	33			6	3			
Avalon	34	4		25	40			
Gaven Island	35			3				
Seven Mile Beach								
(Stone Harbour Point)	36	44	40	150	40	A-60 B-86	80	50
Two Mile Beach								
I	37	10	8	22	65		6	
II	38	16		50				
South Cape May	39	50	85	140	60	20	105	80
Cape May								
Meadow	40				60			40
Magnesite Plant								
#1	41	14		72				
#2	42			10	8	4		
Ferry Slip (Cape May)	43	34			40	10		
Glades Sand Plant	44	120		12	85	30	40	20
Number of colonies		24	19	29	26	22	20	17
Total number of birds		1,388	942	1,929	1,750	2,199	2,051	2,459

[a] R. Kane and R. B. Farrar, 1976.
[b] R. Kane and R. B. Farrar, 1977.
[c] J. Galli, 1978b.
[d] J. Galli and R. Kane, 1979.
[e] J. Galli, 1980.
[f] J. Galli, 1981.
[g] Unpublished data from J. Burger, A. Galli, J. Gallagos, B. Jones, J. Jones, and R. Kane; Welty 1982.

(Kane and Farrar 1976, 1977, Galli and Kane 1979) or by ground surveys (Galli 1978b, 1980, 1981, Welty 1982; and unpubl. data, see Table 1). The surveys were undertaken to determine the populations of colonial birds in New Jersey, to contribute data for a general survey of these species along the East coast of North America, and for management and protection purposes by the Division of Fish, Game and Wildlife of the New Jersey State Department

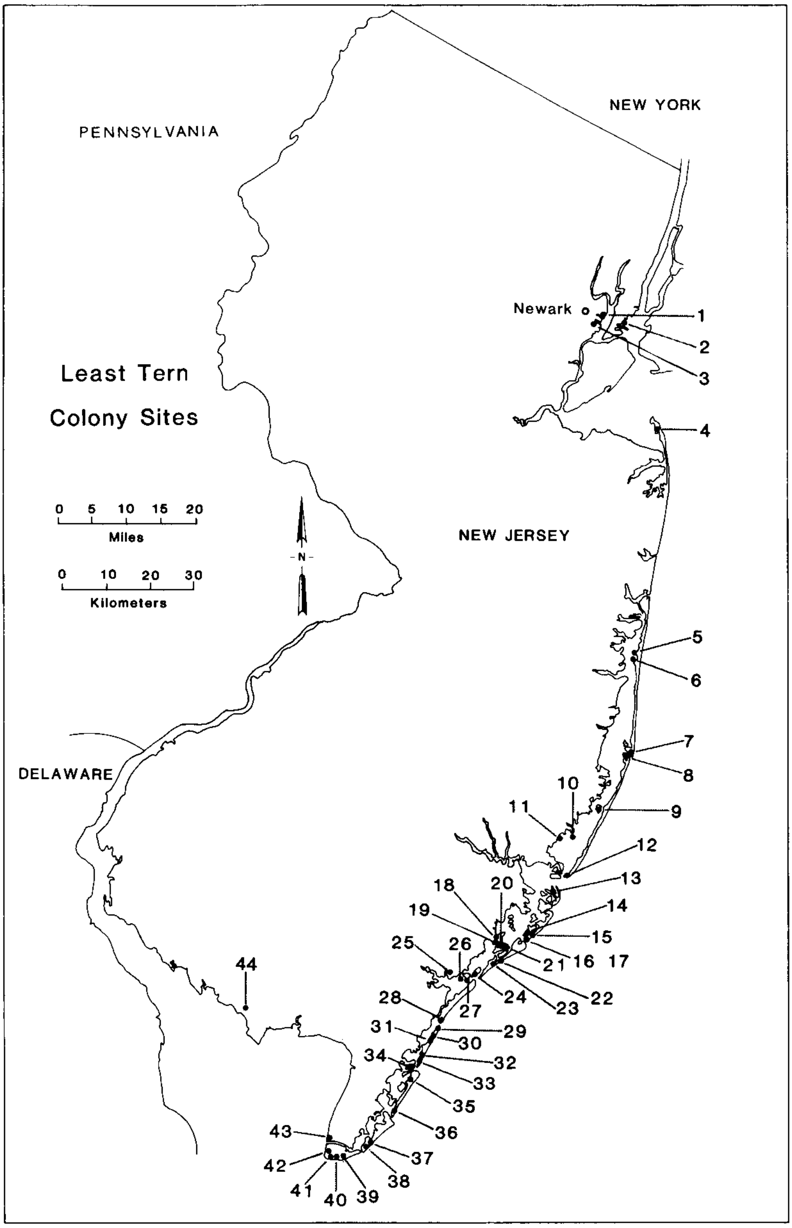

FIGURE 1. Location of Least Tern colony sites described in Table 1. Numbers correspond to Table 1.

of Environmental Protection (Galli 1978a). The surveys were conducted by the same group of people each year.

Aerial surveys were conducted from 1–15 June, and ground surveys were conducted several times during the reproductive season (late May–early July). For the ground surveys, several reliable observers cooperated so that all colonies along the coast were monitored. Specific colony locations are shown in Figure 1. During the census the number of adult terns present at the colony site was recorded. I feel justified in using both ground and aerial surveys because Erwin (1980) found a high correlation between aerial and ground estimates for counts for Least Terns in Massachusetts (coefficient of determination, R^2, of 0.99).

One-year turnover rates were computed by using the formula presented by Erwin and Erwin et al. (1981):

$$T = \tfrac{1}{2}(S_1/N_1 + S_2/N_2)$$

where S_1 = number of sites occupied only on the first census, N_1 = total number of sites during first census, S_2 = number of sites occupied only on second census, and N_2 = total number of colonies on the second census.

Turnover was measured between successive

TABLE 2. Colony numbers, turnover rates and reproductive success of Least Tern colonies in New Jersey.

	1976	1977	1978	1979	1980	1981	1982	1976–1982 mean (SD)
Number of terns	1,388	942	1,929	1,750	2,199	2,051	2,459	1,817 (513)
Number of colonies	24	19	29	26	22	20	17	22 (4)
Mean number of terns (SD)/colony	58 (75)	50 (67)	67 (73)	67 (69)	100 (135)	103 (168)	145 (232)	84 (34)
Percent of colonies with less than 80 birds	76	84	72	73	64	64	72	72 (7)
Number of colonies								
Used previous year		15	14	21	20	17	15	17 (3)
Not used previous year		4	15	5	2	3	2	5 (5)
Lost from previous year		9	5	8	6	5	5	6 (2)
Turnover rates		0.30	0.26	0.24	0.16	0.19	0.19	0.22 (0.05)
Reproductive success								
All New Jersey colonies			0.4	0.4	0.6	0.8	0.2	0.48 (0.23)
Barnegat Bay colonies	1.0	0.8	0.8	0.7	0.3	0.4	0.0	0.57 (0.35)

years. From 1976 to 1982, I regularly censused five Least Tern colony sites in Barnegat Bay, Ocean Co., New Jersey. I visited these colonies three to eight times yearly to determine the number of nests, reproductive success (number of fledged young/pair), and the causes of reproductive failure. Predators could be easily determined, and were usually rats (evidenced by burrows and trails) and crows (observed eating eggs). Three of the colonies examined in detail were on domed dredge-spoil islands (Ortley, Pelican, Barnegat Inlet), one was on a flat sandy (dredge spoil) area on a salt marsh island (Cedar Bonnet), and one was on the sandy barrier beach of Island Beach State Park.

Data on causes of reproductive failure were obtained from the census reports, and from my observations of the Least Tern colonies in Barnegat Bay. Reproductive success (number fledged/pair) was determined by counting the number of flying young and dividing by the number of pairs. The number of pairs was determined by dividing the largest reported number of adults (shown in Table 1) by two. For the purposes of this paper I defined a "small" colony as containing fewer than 80 birds; and a "large" colony as containing 80 or more birds. This separation was based on the mean colony size for the study period (see Results below).

RESULTS

POPULATION SIZE

In the seven years of the study Least Terns occupied 44 different colony sites, although in any one year the terns occupied only 17–29 sites ($\bar{x} = 22.4$, SD = ± 3.6; Table 1). The total number of birds on colony sites ranged from 942 in 1977 to 2,459 in 1982 ($\bar{x} = 1{,}817$, SD = ± 513; Table 2). I found no relationship between the year and number of colonies (Kendall tau = 0.47, $Z = -1.50$, $0.05 < P < 0.07$) or between the number of colonies and number of birds (Kendall tau = 0.24, $Z = -0.75$, $P > 0.20$). However, the number of terns significantly increased with advancing years (Kendall tau = ± 0.71, $Z = 2.25$, $P < 0.02$). The number of terns per colony ranged from 50 (1977) to 145 (1982) with a mean of 84.3 (SD = ± 34) terns per colony for the seven-year period (Table 2).

TURNOVER RATES

Only nine colony sites were occupied for all seven years, and three other colony sites were used for six years (Table 1). In all years of the study some colonies were abandoned from one year to the next, and new colonies formed on sites not used the previous year (Table 2). One-year turnover rates (see Methods) ranged from 0.09 to 0.22 (mean = 0.13, SD = ± 0.05).

REPRODUCTIVE SUCCESS AND CAUSES OF COLONY FAILURE

Reproductive success could be computed for all Least Tern colonies in New Jersey for only five years. The terns raised 0.46 young/pair (SD = ± 0.22, Table 2). For the five colonies I examined in Ocean County, reproductive success was slightly higher ($\bar{x} = 0.66$, SD = ± 0.24), but decreased in successive years (Table 2).

The relationship among reproductive success, human disturbance and predation pressures is shown in Table 3 for five colonies examined over eight years. The other colonies were not checked during the pre-laying period, and so I could not determine if birds returned to the sites before abandoning them. Successful colonies (those producing more than 0.5 young/pair) were always reoccupied the following year. Terns returned to colonies that were moderately successful (0.25–0.49 young/

TABLE 3. Reproductive success in five Ocean County Least Tern colonies. S = successful (over 0.5 young/pair), s = 0.25–0.49 young/pair, — = no birds returned to the colony, R = birds returned (even if briefly) but did not nest, P = nests destroyed by predators, H = nests destroyed by human disturbance, U = used but success unknown, X = not used by terns.

	1975*	1976	1977	1978	1979	1980	1981	1982
Ortley	U	—	S	s, P	R	R	—	—
Pelican	U	S	S	S	S	P	R	—
Barnegat Inlet	U	S	s, P	P, H	s, P, H	P, H	s, H	R
Island Beach	X	X	X	X	X	X	s, P	R**
Cedar Bonnet	U	S	s, H	S	S	S, H	S, H	R**

* From unpublished data, but reproductive success not obtained.
** Returned briefly but did not settle on colony site.

pair) except for the Island Beach colony, which was used only one year (Table 3). Terns even returned and nested at colonies that were completely wiped out the previous year by predators or human disturbance when the colony site had been in use for several years. Although Least Terns lay two eggs, pairs usually either raise one young or fail. Thus a reproductive rate of 0.25 young/pair usually means that only 25% of the pairs raised any young.

Since social factors often have been implicated in colony dynamics and reproductive success (see Discussion), I examined the causes of failure (<0.25 young/pair) in large and small colonies (Table 4). Large and small colonies had similar causes of failure, although small colonies suffered higher losses from human disturbance. Large colonies, however, suffered significantly more predation than small colonies (Table 4).

DISCUSSION

COLONY STABILITY

Least Terns generally nest on sandy areas (Downing 1973, Wolk 1974), which are often unstable either because of their location (ocean front) or their subsequent succession (encroaching vegetation on dredge spoil). In New Jersey, where Buckley (1978) examined Least Tern use of dredge spoil, 27% of the colonies were located on dredge spoil, but only 48% of the birds nested on it. The ephemeral quality of Least Tern habitat, coupled with its desirability for human recreation, suggest that colony site turnover rates could be high. Least Terns are notorious for colony shifting and relocation, both within and between colonies (Nisbet 1973).

In my study, turnover rates for Least Terns varied from 16–30% (mean = 22%). There was an average of 22 Least Tern colonies each year, nine of these occurred on the same site every year, and another three were on the same site for six of the seven years. Erwin (1977) reported turnover rates of 9% for Least Terns (1976–1977) in Massachusetts. Using the average of these two values as an indication of stability indicates that about 15% of the colonies are either new or are abandoned.

The real value of the turnover rate, however, is that it allows comparisons among years, habitats and species. In addition to Least Tern, five other species of terns, gulls and skimmers also nest in coastal habitats (see Table 5). Turnover rates for Least Terns are less than half those for these other species that are often considered to have high colony and nest site stability (see Bongiorno 1970).

Turnover rates usually are computed for groups of birds that have already laid eggs. However, in order to understand colony site tenacity one should also examine whether birds return to the site early in the season and subsequently abandon it because it is unsuitable. For the five colony sites examined intensively (see Table 3), the Least Terns always returned to the colony site in the year when they abandoned it. The presence of predators, human activities, or vegetation often rendered the site unusable. Thus site fidelity is high, and the birds merely respond appropriately to environmental cues by changing sites when the old site is unsuitable.

REPRODUCTIVE SUCCESS

During this study, reproductive success for the colonies along the New Jersey coastline varied

TABLE 4. Major causes of Least Tern colony failure* (1976–1982) in New Jersey. Shown are number of colonies destroyed by each cause.

	Under 80 birds	80 birds and over	χ^2	*P*
Unknown	4 (13%)	4 (17%)	0.20	NS
Flooding	7 (23%)	6 (25%)	0.00	NS
Human disturbance (and habitat loss)	18 (58%)	7 (29%)	2.59	
Predators				
Birds		2 (8%)		
Mammals	2 (6%)	5 (21%)	4.05	<.05
Total colonies that failed**	31	24	7.04	<.01

* Failure = fewer than 0.25 young/pair.
** χ^2 based on number of colonies of that size. There were 116 small colonies, and 45 large colonies.

TABLE 5. Turnover rates* in eastern coastal colonies of gulls and terns: a = marsh habitat, b = barrier beach (sand habitat).

	Virginia	New Jersey	Massachusetts
Herring Gull (*Larus argentatus*)	0.18[a]	0.32[a], 0.23[b]	0.10
Laughing Gull[a] (*L. atricilla*)	0.10	0.20	
Forster's Tern (*Sterna forsteri*)[a]	0.47	0.36	
Common Tern (*S. hirundo*)	0.44[a], 0.18[b]	0.20[a]	0.03
Least Tern[b] (*S. antillarum*)		0.22	0.09
Black Skimmer (*Rynchops niger*)	0.49[a], 0.15[b]	0.36[a]	

* After Erwin 1977, Erwin et al. 1981 (1976–1977), this study (1976–1981).

from 0.0 to 0.8 young fledged per pair per year, and in Barnegat Bay it varied from 0 to 1.0 young fledged per pair per year. Although these values may be low, in a long-lived seabird they may be sufficient to maintain population levels assuming there is no subsequent human persecution (Nisbet 1973, pers. comm.). Furthermore, Least Tern populations in many areas (such as New York) appear to be stable at present (see Buckley and Buckley 1980), although they have declined elsewhere (Downing 1980, Brubeck et al. 1981). Least Tern populations increased during this study.

I had expected differences in the causes of reproductive failure as a function of colony size, because larger colonies should be less vulnerable to predation, having more early warning and anti-predator behavior (see Kruuk 1964, Veen 1977, Burger 1981). Large colonies, however, suffered more failures and more predation than did smaller colonies. Rats accounted for all of the colonies destroyed by mammalian predators in this study. Rats are nocturnal predators that are fairly large (over 300 g) compared to Least Terns (45–55 g, M. Gochfeld, unpubl. data). Gulls' lack of antipredator behavior toward nocturnal predators has already been noted (Southern and Southern 1978, Southern et al. 1982). When rats arrive at a colony, it would seem advantageous for Least Terns to leave so as to protect themselves, rather than stay and try to protect their eggs or chicks. My preliminary observations with a night-vision scope indicate that Least Terns do leave their nests when rats and cats are in the colony. Large colonies may be more vulnerable simply because there are more prey to attract predators to these colonies, and they are more stable (occupied for more years). In New Jersey, the stable colonies attacked by predators are often situated on mainland or barrier-island beaches where vegetational succession does not take place. Such colonies are vulnerable to rats and cats that can survive the winter on the mainland or barrier beaches. Furthermore, rats and cats can easily reach these sand beach colonies.

Habitat loss usually resulted in the colony site being abandoned, rather than lowering reproductive success. The decrease in colony sites is potentially a problem because it raises the likelihood that overall production could be very low if one or two of the large colonies suffer heavy losses due to flooding or predators. The data indicate that the number of sites is decreasing and the mean colony size is increasing. Twenty-five of 55 (45%) colonies that failed did so because of human disturbance (21 colonies) or habitat loss (3 colonies). Most of this loss was due to off-road vehicles and people walking through the colonies, as happened before the desertion of the Barnegat Inlet colony. Much of this destruction can be prevented by education and adequate posting or patrolling (see Galli 1978a). Protective measures have worked in California with their Least Tern program (B. Massey, pers. comm.).

The relatively high colony stability over seven years reported in this study along 360 km of coastline (data are not available for any other similarly-sized region in the U.S.) suggests that Least Tern colonies are likely to form year after year in the same place. Protective measures (fencing and posting colonies) should be undertaken in the stable colony sites before the birds return in the spring to minimize human disturbance.

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LITERATURE CITED

BEER, C. G. 1966. Adaptations to nesting habitat in the reproductive behaviour of the Black-billed Gull *Larus bulleri*. Ibis 108:394–410.

BONGIORNO, S. 1970. Nest-site selection by Laughing Gulls (*Larus atricilla*). Anim. Behav. 18:434–444.

BRUBECK, M. V., B. C. THOMPSON, AND R. D. SLACK. 1981. The effects of trapping, banding and patagial tagging on the parental behavior of Least Terns in Texas. Colonial Waterbirds 4:54–60.

BUCKLEY, F. G. 1978. Colony site selection by colonial waterbirds in coastal New Jersey. Proc. Colonial Waterbird Group 2:17–26.

BUCKLEY, P. A., AND F. G. BUCKLEY. 1980. Population and colony-site trends of Long Island waterbirds for five years in the mid 1970's. Trans. Linn. Soc. N.Y. 9:23–56.

BURGER, J. 1974. Breeding adaptations of Franklin's Gull (*Larus pipixcan*) to a marsh habitat. Anim. Behav. 22:521–567.

BURGER, J. 1981. A model for the evolution of mixed-species colonies of Ciconiiformes. Q. Rev. Biol. 56: 143–167.

BURGER, J. 1982. The role of reproductive success in colony-site selection and abandonment in Black Skimmers (*Rynchops niger*). Auk 99:109–115.

DOWNING, R. L. 1973. A preliminary nesting survey of Least Terns and Black Skimmers in the East. Am. Birds 27:946–949.

DOWNING, R. L. 1980. Survey of interior Least Tern nesting populations. Am. Birds 34:209–211.

ERWIN, R. M. 1977. Population and colony site dynamics in selected Massachusetts Waterbirds. Proc. Colonial Waterbird Group 1:19–25.

ERWIN, R. M. 1980. Censusing waterbird colonies: some sampling experiments. Trans. Linn. Soc. N.Y. 9:77–86.

ERWIN, R. M., J. GALLI, AND J. BURGER. 1981. Colony site dynamics and habitat use in Atlantic Coast seabirds. Auk 98:550–561.

GALLI, J. 1978a. New Jersey's colonial waterbirds. Proc. Colonial Waterbird Group 2:92–98.

GALLI, J. 1978b. Research and management of endangered species (Least Terns). New Jersey Div. of Fish, Game and Wildlife, Trenton.

GALLI, J. 1980. Research and management of Least Terns. New Jersey Div. of Fish, Game and Wildlife, Trenton.

GALLI, J. 1981. Distribution and nesting locations of Least Terns. New Jersey Div. of Fish, Game and Wildlife, Trenton.

GALLI, J., AND R. KANE. 1979. 1979 Colonial waterbird populations of New Jersey. Occas. Pap. No. 139, Records of N.J. Birds 7:38–42.

KANE, R., AND R. B. FARRAR. 1976. 1975 Coastal colonial bird survey of New Jersey. Occas. Pap. No. 125, N.J. Audubon 2:8–14.

KANE, R., AND R. B. FARRAR. 1977. 1977 Coastal colonial bird survey of New Jersey. Occas. Pap. No. 131, N.J. Audubon 3:188–194.

KRUUK, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull (*Larus ridibundus* L.). Behaviour Suppl. 11:1–129.

MASSEY, B. W. 1974. Breeding biology of the California Least Tern. Proc. Linn. Soc. N.Y. 72:1–24.

MCNICHOLL, M. K. 1975. Larid site tenacity and group adherence in relation to habitat. Auk 92:89–104.

MONTEVECCHI, W. 1978. Nest site selection and its survival value among Laughing Gulls. Behav. Ecol. Sociobiol. 4:148–161.

MORRIS, R., AND R. HUNTER. 1976. Factors influencing desertion of colony sites by Common Terns (*Sterna hirundo*). Can. Field-Nat. 90:137–143.

NISBET, I. 1973. Terns in Massachusetts: present numbers and historical changes. Bird-Banding 44:27–55.

SOUTHERN, L. K., AND W. E. SOUTHERN. 1978. Absence of nocturnal predator defense mechanisms in breeding gulls. Proc. Colonial Waterbird Group 2:157–162.

SOUTHERN, L. K., AND W. E. SOUTHERN. 1982. Effect of habitat decimation on Ring-billed Gull colony- and nest-site tenacity. Auk 99:328–331.

SOUTHERN, L. K., S. R. PATTON, AND W. E. SOUTHERN. 1982. Nocturnal predation on *Larus* gulls. Colonial Waterbirds 5:169–172.

SOUTHERN, W. E. 1977. Colony selection and colony site tenacity in Ring-billed Gulls at a stable colony. Auk 94:469–478.

VEEN, J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (*Sterna s. sandvicensis* Lath.). Behaviour Suppl. 20:1–193.

WELTY, M. 1982. Research and management of Least Terns. New Jersey Div. of Fish, Game and Wildlife, Trenton.

WOLK, R. G. 1974. Reproductive behavior of the Least Tern. Proc. Linn. Soc. N.Y. 72:44–62.

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