INTRASEASONAL MOVEMENT BETWEEN COLONY SITES BY CASPIAN TERNS IN THE GREAT LAKES

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Larids nesting in stable habitats tend to occupy the same breeding colony for many years, whereas those that occupy unstable environments shift colony sites frequently if nesting habitat becomes unsuitable (McNicholl 1975, Burger and Shisler 1980). The tendency of larids to return to the colony of previous breeding, providing environmental conditions remain favorable, is referred to as "site tenacity" (Austin 1949). Past studies on intercolony movement in the Great Lakes (Ludwig 1974, Morris and Hunter 1976, Southern 1977, Haymes and Blokpoel 1978, Southern and Southern 1979, Blokpoel and Courtney 1980) have focused on tenacity between seasons, but little is known about the movement of birds between colonies within a single breeding season. I examined seasonal colony site use patterns in Caspian Terns (Sterna caspia) nesting on five islands in northeastern Lake Michigan to answer the following questions: (1) do individual terns use more than one colony site during a single breeding season; and, if so, (2) what are the factors that influence intraseasonal colony site movement in this population?

STUDY AREA

During my study the resident Caspian Tern population in the Great Lakes was concentrated at 15 colony sites in the northern parts of lakes Michigan and Huron (the North Channel and Georgian Bay) and Lake Ontario. Shugart et al. (1978) estimated that the total 1978 Great Lakes breeding population was 3740 pairs. For logistic reasons I restricted my study area to five islands in northeastern Lake Michigan (Fig. 1). These colonies supported approximately 1100 pairs of Caspian Terns, representing about 30% of the Great Lakes population from 1976 to 1979. The colony sites were (1) the northeastern point of High Island, (2) High Island Shoal, (3) Hat Island, (4) Shoe Island, and (5) Ile aux Galets. Distance between colony sites ranged from 1 to 39 km (Table 1).

Colony site habitat in the Great Lakes varies in stability. The lakes are characterized by fluctuating water levels (Cohn and Robinson 1976), and these changes determine the quantity and quality of sites available to terns in each season (Shugart et al. 1978, Cuthbert 1981). When the lake level is above average, Shoe Island is submerged or so reduced in size that it is unsuitable as a breeding site. High Island Shoal also is unavailable for breeding by terns except when the water level is below or near average. The level of Lake Michigan in the month of June was above average for all years of this study except 1977 (U.S. Army Corps of Engineers, 1976–1979). Caspian Terns nested on High and Hat islands and Ile aux Galets during all four years of this study, on Shoe Island during 1977–1979, and on High Island Shoal in 1977. Historical records for this region (Hatt et al. 1948) suggest that a local population tends to use the same colony sites from year to year. However, because terns



FIG. 1. Study area in northeastern Lake Michigan.

were not color marked until my study, these earlier records indicate colony site use by the breeding population and not for specific individuals. A preference for traditional colony sites is indicated for the rest of the Great Lakes population as well (Ludwig 1962, 1965; Blokpoel and Fetterolf 1978).

METHODS

Data were collected during the breeding season (mid-April to mid-August) from 1976 through 1979. The islands were reached by float plane or boat; I visited the colonies on a rotational schedule every 3–7 days throughout each season. When I was not present, supplemental observations were made by investigators on High, Hat, and Shoe islands.

Capturing and marking techniques. — From 1976 to 1978, I captured and color marked 330 adult Caspian Terns. Initially, I used a cannon net (Southern 1972) to capture 254 terns (125 at Hat Island and 129 at Ile aux Galets). These birds were tagged with individually numbered vinyl-coated nylon patagial wing markers (Southern 1971) that were color-coded to colony site. After I observed that intensive cannon netting caused incubating terns to desert their nests (Shugart et al. 1978), I changed capture techniques. In 1978 an additional 76 adults were captured with a monofilament line nest snare (28 on High Island and 48 on Ile aux Galets) and banded with unique combinations of colored plastic leg bands. All adults also were banded with a USFWS leg band. To monitor the reproductive status of adult terns, I banded chicks with USFWS and plastic leg bands.

	High Island	High Island Shoal	Hat Island	Shoe Island	Ile aux Galets
High Island (45°45'N, 85°40'W)	0				
High Island Shoal (45°45'N, 85°40'W)	1	0			
Hat Island (45°47'N, 85°18'W)	28	27	0		
Shoe Island (45°48'N, 85°18'W)	28	27	1	0	
Ile aux Galets (45°41'N, 85°11'W)	38	39	18	17	0

TABLE 1
DISTANCE (IN KM) BETWEEN CASPIAN TERN COLONY STUDY SITES IN
NORTHEASTERN LAKE MICHIGAN

Intercolony movements. — From 1977 to 1979, I spent 1–6 h/day (>1200 h total) locating marked individuals at the Ile aux Galets and High Island colony sites. Observation time was divided equally between both sites. I spent 120 h looking for marked terns at Hat Island in 1977 and 1978 and 20 h on Shoe Island from 1977 to 1979. G. Shugart recorded marked individuals on Hat and Shoe from 1977 to 1979. I was unable to look for marked birds on High Island Shoal in 1977 as all terns took flight when the colony site was approached by boat. Therefore, the best data on intercolony movement are from the Ile aux Galets and High Island sites. Data collected on marked terns at each encounter included status (nesting, not nesting) and stage in the reproductive cycle (courtship, nest construction, incubation, chicks present, postnest failure).

Determination of reproductive status. — To examine the relationship between reproductive status and intercolony movement, I studied the nesting phenology of all color-marked terns at High Island and Ile aux Galets in 1978 and 1979. G. Shugart recorded reproductive status of marked birds observed on Hat Island. Nests were numbered and periodic inspection of their contents was made every 3–4 days from early incubation through banding of chicks. After chicks were marked, I observed color-marked parents and their offspring from blinds on the edge of the colonies to minimize disturbance. Causes of reproductive failure (e.g., storm washout, investigator disturbance, gull predation, unknown factors) were recorded during nest checks. Although both members of some pairs were color marked, data were collected and analyzed for individuals. Data on reproductive status and intercolony movement were analyzed using a chi-square test (Zar 1974).

RESULTS

Intercolony movements. — During each of three years of observation, two patterns of colony-site association emerged (Table 2): (1) 46–65% of the marked terns were observed at one colony site for the entire breeding season; and (2) 34–63% were recorded at one colony site for only part of the breeding season. The behavior of birds in the second group could be subdivided as follows: (1) 18–26% were noted at one site for part of the breeding season and then disappeared for the remainder of the summer; and (2) 16–37% were present in the breeding area all summer but were

 TABLE 2

 Number of Caspian Terns Observed at More Than One Colony in 1977–1979

	1977 (N = 220)	1978 (N = 114)	1979 (N = 68)
Observed at one colony for entire season	126 (57) ^a	74 (65)	31 (46)
Observed at one colony for brief period	58 (26)	22 (19)	12 (18)
Observed at more than one colony	36 (16)	18 (16)	25 (37)

a Percent of total.

seen at two or more active colony sites. These data indicate that intercolony movements occur regularly in this population of terns.

Causes of intercolony movement. — To determine factors that affect the movement patterns of terns, I categorized birds observed at two or more sites according to their reproductive status: (1) nesting birds with eggs or chicks, or (2) terns that were not nesting. Combining data from 1978 and 1979 (Table 3), I found that at the time observations were made 38 (88%) of the birds recorded at two or more sites were not nesting and only 5 (12%) had eggs or chicks at another colony site. When I examined reproductive status of marked birds observed at only one colony site for the entire season, I found that 98 (93%) were nesting birds and 7 (7%) were not nesting. Using 2 × 2 contingency table analysis, I tested and rejected ($\chi^2 = 96.23$, df = 1, N = 148, P < 0.001) the hypothesis that intercolony movement is independent of reproductive status. Terns with eggs or chicks associated almost exclusively with one breeding colony, and intercolony movement was most likely to occur in birds that were not breeding.

A more detailed examination of individuals observed at two or more sites showed that of the birds that were not nesting (N = 38), 55% had experienced reproductive failures earlier in the same season, 34% were involved in courtship or nest-site selection behavior, and 11% were nonbreeders for the entire season. Therefore, intercolony movement was precipitated by lack of a mate or nest site and by reproductive failure.

Observations on the 34 terns recorded for only part of the season at one site that subsequently disappeared for the duration of the summer (1978, 1979) provide further information on intercolony movement in this population. Twelve (35%) were courting for one to several days at one site during late April or early May. Another 12 (35%) were breeding birds that deserted the site following investigator disturbance or destruction of the nest contents by gull predation or storms. None of these individuals was recorded again for the duration of the season. Lastly, 10

TABLE	3

Reproductive Status of Individuals Observed at More Than One Colony in 1978 and 1979

	Percent of total $(N = 43)$
Terns that experienced reproductive failures	49
Unpaired terns involved in prenesting activities	30
Terns with eggs or chicks	12
Terns that were unpaired for entire season	9

terns (29%) that were observed briefly after early June all behaved as if they had lost eggs or chicks (i.e., stood on colony edge with a mate, performed nest site selection behavior, attempted to feed unrelated chicks). Some or all of these individuals may have finally nested at colony sites outside the study area.

Intercolony movement by birds involved in courtship or nest-site selection tended to be temporary, as most individuals eventually obtained a mate and chose a nest territory at a specific colony site. When actively searching for a mate, terns courted at the colony site of future nesting, at other active colony sites, or at communal resting spots such as sand bars or stretches of undisturbed beach along the shoreline of northern Lake Michigan. Some individuals visited several colony sites a day until they acquired a mate. Individuals often constructed a few nest scrapes with temporary partners; however, once an individual began to associate with an exclusive mate, the pair made many trial nest scrapes at from one to several colony sites in the study area. Once the nest was constructed and egg laying initiated, terns were rarely observed at colonies other than the one where they were breeding unless the reproductive effort was interrupted by prolonged disturbance or destruction of the nest contents.

During this study reproductive failures were caused by storms (55%) and gulls (3%) that destroyed nests, eggs, or chicks, and investigator disturbance (22%) that led to nest desertion. Unknown factors accounted for 20% of the failures. The typical response of terns to destruction of the nest or its contents was to remain in or adjacent to the nest territory for 2-7 days. After this time they usually deserted the colony and often renested at another colony or associated with several colonies as nonbreeders for the remainder of the summer; occasionally, individuals remained and renested at the original colony.

Insight into the impact of prolonged investigator disturbance on intercolony movement is provided by the results of an isolated incident in 1977. Approximately two-thirds (445 pairs) of the Caspian Tern colony deserted the Hat Island site after cannon netting activities in early June (Shugart et al. 1978). Eighty-one terns had been tagged with individually numbered wing markers. After the disturbance, 24 of the tagged birds continued to nest on Hat, 20 left Hat Island and either renested (11) or were observed (9) at High Island or Ile aux Galets, and 37 deserted Hat Island and were not recorded for the duration of the breeding season.

DISCUSSION

Intraseasonal movement of terns between colonies in northeastern Lake Michigan was common. The most accurate estimates are probably reflected in the 1979 data, as no new birds were marked during this season and no patagial-tag or color-band loss was known to occur. In addition this was the only season when extensive observations were made on colormarked individuals during the pre-nesting stage, a period when birds move between sites before selecting a mate and nest location.

In the area studied, intercolony movement within a season is probably confined primarily to the islands in northeastern Lake Michigan; however, terns may move to the colonies outside of this area but still within the range of the Great Lakes population. Color-marked birds occasionally disappeared after they were observed courting in early spring, and eventually may have nested on Gravelly Island, in northwestern Lake Michigan, or in one of the Canadian colonies. Ludwig (1968, 1980) reported some interseasonal movement of individuals between the lakes Michigan and Huron colonies but found a greater tendency of terns from the Canadian colonies to disperse to the Lake Michigan colonies than the reverse situation. I found that 8% (N = 119) of the previously banded birds captured during my study were banded at colonies in Lake Huron (Cuthbert 1981).

Documentation of intercolony movement is difficult to obtain because it requires (1) individually marked birds and (2) investigators to find them by regular visits to many or all colony sites within the range of a breeding population. Austin (1949) not only found that Common Terns (*Sterna hirundo*) often desert a colony site after experiencing reproductive failure, but he also established that these birds renested at other colonies within the Cape Cod area. Buckley and Buckley (1972) noted that some Royal Terns (*S. maxima*) deserted their breeding colony in response to colorbanding activities and subsequently were observed at an adjacent colony site. Finally, Southern (1977) reported wing-marked Ring-billed Gulls (*Larus delawarensis*) at colony sites different from the one where they were captured earlier in the season but stated that reasons for intercolony movement were unknown. In this study intercolony movement was recorded most frequently in terns that experienced reproductive failure. Similar patterns of intraseasonal intercolony movement may also occur in other populations of Caspian Terns as well as in other species of larids that breed in areas where alternative colony sites are available and reproductive failures occur frequently. Other investigators have documented terns deserting eggs or chicks in response to disturbances of breeding adults or destruction of nest contents. Examples include predation (Austin 1944), ectoparasites (Feare 1976), storm damage (Austin 1949, Hardy 1957), and human disturbance (Bergman 1953, Vaisanen 1973, Shugart et al. 1978).

Because courtship behavior in Caspian and other species of terns (e.g., Common Tern, Austin 1947; Sandwich Tern [*S. sandvicensis*], Langham 1974; Royal Tern, Buckley and Buckley 1972) may be performed at locations other than the breeding colony, some movement between colonies probably occurs wherever populations are divided into subgroups of individuals that breed at two or more colonies within a specific geographic area.

During the study period the most frequent cause of reproductive failure in this population was nest destruction due to storm damage (Shugart et al. 1978, Cuthbert 1981). This suggests that intercolony movement by individuals breeding in northeastern Lake Michigan probably is greatest during years of higher than average lake level. High water levels may also increase movement of birds during the courtship period. Although Caspian Terns from the Great Lakes population exhibit site tenacity to the colony of previous breeding (Cuthbert 1981), birds that return to a colony and find it submerged as a result of high lake levels will be forced to breed at a new location. Under these circumstances individuals may be less likely to pair with their mate from the previous year (Cuthbert 1985) and may visit several colony sites searching for a new mate.

Results of the present study suggest that unless extensive observations have been made on marked individuals, colony sites located within the local range of a breeding population should not be viewed as independent demes either within or between seasons. Because information on demographic patterns is essential to understanding the biology of colonial species, knowledge of the extent and causes of intercolony movement is important to investigators studying populations in which it is common.

SUMMARY

Colony-site use patterns were studied in Caspian Terns (*Sterna caspia*) nesting on five islands in northeastern Lake Michigan to address the following questions: (1) do individual terns frequent more than one colony site during a single breeding season; and (2) what are the factors that influence intraseasonal colony site movement in this population?

Intraseasonal movements of terns between colonies in northeastern Lake Michigan were common. Birds that were not nesting were observed significantly more often at two or more colonies than nesting terns, and intercolony movement was precipitated by lack of a mate or nest site and by reproductive failure (e.g., nest destruction by storms or predators and investigator disturbance). Intercolony movement during courtship and following reproductive failures probably is intensified during periods of flooding or high water in the Great Lakes.

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