# REPRODUCTIVE SUCCESS AND COLONY-SITE TENACITY IN CASPIAN TERNS

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ABSTRACT.—Colony-site use by individually marked Caspian Terns (*Sterna caspia*) was studied at four breeding colonies in northeastern Lake Michigan during 1976–1979. I examined two related aspects of colony-site use: (1) colony-site preference in experienced breeders and (2) the relationship between reproductive success and colony-site tenacity. Terns showed a significant preference for the colony of previous breeding unless their preceding reproductive effort was unsuccessful. Caspian Terns tended to use the same colony site if young were produced but moved to a new location if reproductive success had been terminated or threatened at the traditional site. *Received 11 Feburary 1987, accepted 15 January 1988.*

SELECTION of breeding habitat is a crucial determinant of avian reproductive success. Many species of gulls and terns are ideal for the study of habitat selection because they often nest in dense colonies and exhibit site tenacity, or the tendency to return to the colony site or nest site of the previous year providing the habitat remains suitable (Austin 1949, McNicholl 1975, Burger and Shisler 1980). Breeding birds appear to select nesting habitat where individuals will have a high probability of maximizing their reproductive success. Natural-selection theory predicts that individuals producing offspring at a colony site should continue to breed at that location as long as it remains relatively unchanged, whereas birds that have site-related reproductive failures (e.g. storm washouts, egg and chick predation, human disturbance) should move to another breeding colony, use another nest site in the same colony, or start a new colony at another location for subsequent nesting attempts. I examined the relationship between reproductive success and colony-site tenacity in Caspian Terns (*Sterna caspia*) breeding in northeastern Lake Michigan.

Demonstrations of the adaptive value of habitat selection in colonial waterbirds are for the most part correlative, but reproductive success in Laughing Gulls (*Larus atricilla*) is related directly to nest location (Montevecchi 1978, Burger and Shisler 1980). More recently, Burger (1982) found that Black Skimmers (*Rynchops niger*) usually abandon unsuccessful colony sites but continue to nest at successful sites. Although several studies have demonstrated a relationship between nest-site tenacity (within the same colony) and previous success (Macdonald 1977, Brooke 1978, Ollason and Dunnet 1978), no study of larids or other colonial waterbirds has focused on the specific relationship between colony-site tenacity and the reproductive history of color-marked individuals. To determine if preference for colony site is influenced by whether chicks were raised to fledging at that location in the previous season, I studied colony-site preference in experienced breeders and the relationship between reproductive success and colony-site tenacity.

## STUDY AREA AND METHODS

The study area included four islands in northeastern Lake Michigan. Colony sites were located on the northeastern point of High Island (45°45'N, 85°40'W); Hat Island (45°47'N, 85°18'W); Shoe Island, a gravel bar 1 km south of Hat Island; and Ile aux Galets (45°41'N, 85°11'W). The distance between colonies ranged from 1 to 39 km. The study area is described in greater detail by Cuthbert (1985b). Approximately 1,100 pairs of Caspian Terns nested at these sites from 1976 to 1979. These birds represented about 30% of the Great Lakes population during this period; the rest nested on Gravelly Island (45°31'N, 86°43'W) in northwestern Lake Michigan or in the Canadian colonies located on islands in northern Lake Huron (North Channel and Georgian Bay) and Lake Ontario (Blokpoel and Fetterolf 1978, Shugart et al. 1978, Cuthbert 1985b).

The Great Lakes exhibit changes in water level (Cohn and Robinson 1976, Larsen 1985), and breeding larids are affected directly by these changing lake

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levels (Ludwig 1962, 1974; Morris and Hunter 1976; Southern 1977; Shugart et al. 1978; Shugart and Scharf 1983; Cuthbert 1985a, b). Relatively high water levels (above the 1900–1979 spring average) prevailed in all years of this study except 1977 (U.S. Army Corps Engineers 1976–1979, Shugart and Scharf 1983). Caspian Terns nested on High and Hat islands and Ile aux Galets during all 4 yr of this study and on Shoe Island during 1977–1979. When lake levels were above average, Shoe Island was submerged or so reduced in size that it was unsuitable as a breeding site, and portions of the other sites were flooded repeatedly by storm-driven waves during the breeding season.

Data were collected during the breeding season (mid-April to mid-August) from 1976 to 1979. I visited the colonies on a rotational schedule by float plane or boat every 3–7 days throughout each season. Field assistants supplemented my observations when I was not present.

*Capturing and marking techniques.*—From 1976 to 1978 I captured 449 adult Caspian Terns. About 25% (119) were banded at the time of capture, and information from the bands was used to determine previous nesting history. Initially, I captured 254 terns (125 on Hat Island and 129 on Ile aux Galets) using a cannon net (Southern 1972) and tagged them with individually numbered, vinyl-coated nylon patagial wing markers (Southern 1971) that were color-coded to colony site. Because of significant tag loss, I obtained an additional 76 birds (28 on High Island and 48 on Ile aux Galets) in 1978 using a monofilament line nest snare (Zwickel and Bendell 1967) modified to capture birds around the feet. I marked these terns with unique combinations of colored plastic leg bands; there was no evidence of leg-band loss within or between seasons. The bands were more reliable than the wing markers, and only data collected on terns color-marked with plastic leg bands were analyzed. Observations on colony-site use by individuals that retained wing markers provided supplementary information. To monitor adult reproductive success I banded chicks with a U.S. Fish and Wildlife Service aluminum leg band and plastic band color-coded to colony site.

During color-marking operations I recaptured 75 terns that had been captured and banded as breeding adults at least one time before my study. I obtained information on the location of previous captures from the U.S. Fish and Wildlife Service Bird Banding Laboratory.

*Intercolony movements.*—From 1977 through 1979 I spent 1–6 h/day (1,200+ h) locating marked individuals at Ile aux Galets and High Island; observation time was divided equally between the sites. I spent 120 h recording marked terns at Hat Island in 1977 and 1978; these observations were supplemented with data collected by G. Shugart from 1977 through 1979. I made only 20 h of observations at the Shoe Island site from 1977 through 1979.

*Evaluation of reproductive success.*—All nests of color-marked Caspian Terns were numbered individually, and periodic inspections (every 3–4 days) of nest contents were made from early incubation through banding of chicks. In 1978, 28 nests were monitored on High Island and 48 on Ile aux Galets. In 1979 the nests were distributed as follows: Hat Island (4), Shoe Island (7), High Island (18), and Ile aux Galets (25). After the chicks were banded (152 in 1978, 118 in 1979), I observed color-marked parents and their offspring from blinds on the edge of the colonies. Terns were considered to have had a successful reproductive season if one or more chicks survived to fledging (40+ days). I recorded cause of reproductive failure (e.g. storm washout, investigator disturbance, gull predation, unknown factors) for birds that produced no offspring in a season. Data on reproductive success and colony-site tenacity were analyzed using a Chi-square test (Zar 1974).

## RESULTS

### COLONY-SITE PREFERENCE IN EXPERIENCED BREEDERS

By analyzing colony-site use records for breeding adults banded before my study and recaptured during the study period, I established two records of site use for 62 terns and three records for 13 individuals. Thirty-six (58%) of the 62 birds with two colony-site records were nesting at the colony of first capture, and 26 (42%) were recaptured at a different colony (Table 1). Of the 13 individuals with three known breeding records, 9 (69%) had nested at the same site at least three times, 2 (15%) used the same site at least twice, and 2 (15%) nested at three different colony sites. Most (93%) of these birds were banded initially at colonies in the study area. Five (7%) were banded as adults at the Charity (44°01'N, 83°20'W) and Papoose (45°51'N, 81°20'W) island colonies in Lake Huron, approximately 175 and 150 km from the recapture site.

Caspian Terns from the northern Lake Michigan colonies often breed on the same island for more than one breeding season; over a number of years individuals may nest at two or more different colony sites. Recapture data collected periodically over a long period of time, however, cannot provide an accurate picture of colony-site use by individual birds because the data do not supply information on colony-site changes within a season or in consecutive breeding years. To avoid problems associated with analyzing recapture data, I attempted to follow colony-site use by individual terns

TABLE 1. Colony-site use by banded Caspian Terns captured as breeders in 2 years.

| Colony of first capture as nesting adult (before 1976) | Colony of recapture as nesting adult, 1976–1978 | | |
|---|---|---|---|
| | Original site[a] | Different site | Total |
| Ile aux Galets | 27 | 16 | 43 |
| Hat Island | 0 | 0 | 0 |
| Shoe Island | NS | 1 | 1 |
| High Island | 9 | 4 | 13 |
| Charity Island | NS | 4 | 4 |
| Papoose Island | NS | 1 | 1 |
| Total | 36 | 26 | 62 |

[a]NS = not sampled.

throughout two consecutive breeding seasons. In 1978 I recorded colony-site use by 76 terns wearing unique combinations of colored leg bands; I located 55 of these individuals in 1979. Of the 55, 36 (69%) nested at the site of previous breeding, and 16 birds (29%) bred at one of three additional colony sites in northeastern Lake Michigan (Table 2). One individual was a nonbreeder in 1979 and was observed visiting three different colonies for varying periods of time.

I analyzed colony-site use for 54 terns that bred at known sites in 1979 to test the hypothesis that individuals do not show a preference for the colony where they initially nested the previous year. Individuals originally banded on Ile aux Galets ($\chi^2 = 37.9$, $n = 34$, df = 3, $P < 0.001$) and birds from the High Island colony ($\chi^2 = 22.0$, $n = 20$, df = 3, $P < 0.001$) showed a significant preference for the colony of previous breeding. In 1979, 21 marked terns present in 1978 were not recorded during observations at the three largest islands. Several factors may account for their absence. A bird would not have been observed if it lost its color bands, died after leaving the colony in 1978, nested on Shoe Island where thorough observations were impossible, nested or was a nonbreeder at another colony in the Great Lakes outside the study area, or did not return to the Great Lakes for the 1979 breeding season. All terns were banded with 2–4 color bands, and there was no indication of band loss in any of the 55 color-marked adults that I located in 1979. The other four explanations may account for missing terns. Ludwig (1965) estimated an 11% annual adult mortality in the Caspian Tern population breeding in the Great Lakes. This suggests that 8 or 9 of the missing terns may have

TABLE 2. Colony-site use by nesting color-banded Caspian Terns in two consecutive breeding seasons.

| 1978 colony | 1979 colony | | | | |
|---|---|---|---|---|---|
| | Ile aux Galets | Hat Island | Shoe Island | High Island | Total |
| Ile aux Galets | 22 | 2 | 4 | 4 | 34 |
| High Island | 1 | 2 | 3 | 14 | 20 |
| Total | 25 | 4 | 7 | 18 | 54 |

died between the 1978 and 1979 seasons. Under the extreme assumption that the missing terns (14 from Ile aux Galets and 7 from High Island) nested at 1 of 9 other alternative colony sites (Cuthbert 1981), the colony of previous breeding would still be the colony of preference (Ile aux Galets: $\chi^2 = 36.17$, df = 4, $P < 0.001$; High Island: $\chi^2 = 20.96$, df = 4, $P < 0.001$). I believe that experienced terns do not select breeding sites randomly within the general breeding region. Although some individuals change sites in consecutive seasons, Caspian Terns tend to breed at the colony where they nested the previous year.

## Reproductive Success and Colony-site Tenacity

In 1978, 60 (79%) of the 76 birds raised at least 1 chick to fledging. In 1979, 37 (69%) of the 54 individuals recorded breeding in northeastern Lake Michigan raised at least 1 chick to fledging. A total of 33 nesting efforts failed in both years, and 15 (46%) attempted renesting (i.e. nest reconstructed, 1 or more eggs laid) within 2–3 weeks after the original nest contents were destroyed. Storms driven by winds exceeding 80 km/h caused most (55%) of the failures. My color-marking activities caused 7 (22%) birds to desert their eggs. Only 2 birds abandoned their nests in response to handling; the other 5 deserted after Ring-billed Gulls (*Larus delawarensis*) punctured their eggs while I was banding chicks in adjacent nests. Another 20% of the nests failed for unknown reasons; predation by adjacent nesting Herring Gulls (*L. argentatus*) accounted for only 3% of the failures.

Using two categories of nesting efforts, I determined if colony-site tenacity was influenced by previous reproductive success within a season (intraseasonal) or between seasons (interseasonal).

*Intraseasonal tenacity.*—Twenty (30%) color-

TABLE 3. Reproductive success of 75 color-banded Caspian Terns in 1978 and colony-site use in 1979.

| Nesting success at 1978 colonies | Breeding colony in 1979 | | Terns observed in 1979 | Terns not observed in 1979 |
|---|---|---|---|---|
| | Same | Different | | |
| Ile aux Galets | | | | |
| Successful | 23 | 7 | 30 | 11 |
| Unsuccessful | 1 | 3 | 4 | 3 |
| High Island | | | | |
| Successful | 13 | 3 | 16 | 2 |
| Unsuccessful | 1 | 3 | 4 | 5 |
| Total | 38 | 16 | 21 | |

marked terns experienced reproductive failures during their first nesting attempt in the year and then renested within the same breeding season. Sixteen (21%) of the 76 color-banded terns lost the contents of their nests in 1978. Of the 54 color-banded birds located in 1979, 17 (32%) failed in their initial breeding attempt. None of these individuals had failures in both seasons. These 33 birds responded to the nest failures in a number of ways: 6% renested at the original colony, 6% remained at the original colony but did not renest, 36% deserted the original colony and were not observed for the rest of the season, 39% renested at a different colony, 9% were observed making a nest scrape at a different colony but renesting was not established, and 3% moved to a different colony but did not renest. Most frequently, birds that failed responded by deserting their breeding colony. Of those that were known to renest within the same season, 87% relocated at a different colony site and 12% remained at the original colony.

*Interseasonal tenacity.*—In 1979 I located 46 color-banded individuals that had raised at least 1 chick to fledging the previous year (Table 3). More than 75% of these successful birds (36) nested at the colony they used in 1978; 10 bred on a different island. Eight of the 16 birds that failed in 1978 bred in 1979. Two nested at the same colony, and 6 bred elsewhere. I rejected the hypothesis that colony-site use was independent of reproductive success for Ile aux Galets ($\chi^2 = 4.38$, $n = 34$, df = 1, $P < 0.05$) and High Island ($\chi^2 = 4.82$, $n = 20$, df = 1, $P < 0.05$).

Site-use and reproductive-success data were reanalyzed incorporating data on missing terns. I made the extreme assumption that all missing birds nested at another colony. A test of heterogeneity of both samples indicated that the samples were homogeneous ($\chi^2 = 1.49$, df = 1, $P < 0.10$), and I used pooled data to test the null hypothesis that site use is independent of reproductive success. It was rejected ($\chi^2 = 11.83$, $n = 75$, df = 1, $P < 0.001$). As long as the proportion of the unobserved birds assumed to have renested is equal for both successful and unsuccessful terns, other analyses that adjust for death and nonbreeders will also result in rejection of the null hypothesis.

## DISCUSSION

### COLONY-SITE PREFERENCE IN EXPERIENCED BREEDERS

Recaptures of banded birds and observations of color-marked individuals indicate that experienced Caspian Terns in northeastern Lake Michigan tend to nest at the colony where they bred the previous year. Staav (1979) found that Caspian Terns from the Baltic population also show strong tenacity to the colony of previous breeding. McNicholl (1975) proposed that the selective advantage of site tenacity may be the reduction of susceptibility to predation and other negative factors by familiarizing the bird with its surroundings. Several additional benefits are possible. For example, birds that return to the same colony each year may spend less time searching for a colony and nest site and therefore may breed earlier than individuals that change colony sites. This advantage would be strengthened if mate retention was enhanced by birds returning to a colony site. Terns that use a colony in consecutive seasons also may become familiar with productive fishing areas in the vicinity. McNicholl (1975) suggested that strong site tenacity would be disadvantageous if it promoted the continued use of poor sites or sites that changed rapidly or deteriorated, and he hypothesized that the degree of site tenacity exhibited by individuals in a population may reflect the stability of the nesting habitat. The relationship between habitat stability and site tenacity has been observed in larids that breed at several sites of variable stability in the Great Lakes. Ring-billed Gulls that nest on inundation-prone islands in northern Lakes Huron and Michigan tend to change colony sites frequently (Ludwig 1974). In contrast, Ring-

billed Gulls from this same population that nest on a well-protected breakwall in northern Lake Huron exhibit a high degree of colony-site tenacity (Southern 1977).

### Reproductive Success and Colony-site Tenacity

Caspian Terns that raised at least 1 chick to fledging significantly preferred the same colony during the subsequent year, whereas terns that experienced reproductive failures tended to nest at a new colony site on their next attempt. Sample sizes of unsuccessful birds were too small to detect a difference among responses of birds to different causes of reproductive failure, but terns that experience a disturbance that potentially threatens adult survival may be more likely to desert their nests quickly and permanently. Immediate desertion of colony sites by Caspian Terns has been observed or suspected following investigator disturbance (Bergman 1953, Shugart et al. 1978), military operations (Väisänen 1973), duck hunting adjacent to the colony (Bergman 1980), and egg-collecting activities (Väisänen 1973, Bergman 1980). Desertion has been reported in other species of terns; reasons include food shortage in a colony of Sandwich Terns (*S. sandvicensis;* Marples and Marples 1934), predation on Common Terns (*S. hirundo*) by rats (*Rattus norvegicus*), and desertion by Sooty Terns (*S. fuscata*) as a result of heavy infestation of virus-infected ticks (*Ornithodoros capensis*) (Feare 1976). All of these examples involved factors that potentially have direct influence on the survival of the adult birds.

Although Caspian Terns responded to reproductive failures by moving to new colony sites, exceptions occurred. Two individuals whose nests were destroyed by high waves in 1978 did not change colonies, and both nested on the same beach ridge as the previous year. Failure to change nest or colony sites despite repeated failure and potential hazards has been observed in other populations of larids and has often puzzled investigators. For example, Common Terns continued to nest at the same colony site where flooding caused frequent nest failures (Austin 1940), and Southern et al. (1985) reported that even after 9 years of fox predation, small colonies of gulls persisted despite total or nearly total annual reproductive failure. The fact that birds continue to breed at traditional locations despite reproductive failures demonstrates that selection of breeding habitat is influenced by multiple factors. In addition to reproductive success, these may include previous experiences at the colony site (e.g. predator or human disturbance, relationship with mate), local environmental conditions, and availability of alternative breeding sites. Additional studies on the behavior of individually marked birds that use adjacent colony sites are needed to enhance our understanding of this complex issue.

### Acknowledgments

I thank H. B. Tordoff, E. C. Birney, M. W. Weller, and J. L. D. Smith for commenting on earlier drafts of this manuscript. The manuscript was improved by comments from H. Blokpoel and an anonymous reviewer. I am grateful to W. E. Southern for discussion on colony-site tenacity in Ring-billed Gulls and to J. P. Ludwig, who generously shared his banding data on Caspian Terns. I thank G. W. Shugart, who contributed to this study in many ways. I am especially grateful to my field assistants, E. Donnelly and A. Kraupa, for friendship and enthusiasm throughout each field season and to D. DeRuiter, floatplane pilot.

I thank the many people in the Michigan Department of Natural Resources who provided assistance in numerous ways. The University of Michigan and Central Michigan University biological stations provided equipment, lodging, and transportation. Norma Essex prepared the final manuscript.

This research was funded by: Bergstrom Award (Northeastern Bird Banding Association), Frank M. Chapman Fund (American Museum of Natural History), Dayton Natural History Fund (Bell Museum of Natural History), Department of Ecology and Behavioral Biology (University of Minnesota), National Audubon Society, Society of Sigma Xi, and Wilkie Fund for Behavior and Evolution (Bell Museum of Natural History).

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