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STATUS AND REPRODUCTIVE SUCCESS OF THE CASPIAN TERN (Sterna caspia)
IN THE U.S. GREAT LAKES

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Caspian Tern (Sterna caspia) breeding colonies exhibit a disjunct distribution on all continents except South America where they apparently do not nest. On the North American continent, breeding colonies are located in at least 6 geographical regions which are separated by more than 500 km (see Voous 1960, Martin 1978). Current evidence for Caspian Terns (Ludwig 1968, in prep.) and other larids (Austin 1940, Mills 1973, Harrington 1974, Ludwig 1968, Chabrzyk and Coulson 1976, Southern 1977) is that offspring tend to return to the region of their natal colony to breed. This tendency, and the geographical separation between Caspian Tern breeding areas in North America suggests there is little mixing between areas, and that birds in each region comprise a population that maintains itself primarily through reproduction. It is conceivable, therefore, that one population could decline dramatically because of local perturbations while other populations were unchanged. The possibility of a local decline would be greatest for small, discrete populations particularly if the birds nested at only a few colonies.

In 1975, a review of the Caspian Tern breeding status in the U.S. Great Lakes indicated that 1 of 4 colonies failed (Shugart 1975, Michigan Audubon Society 1976). Under these circumstances, and because the Caspian Tern met the above criteria as a species that could decline on a local scale, the Michigan Department of Natural Resources (1978) placed this species on its list of rare birds. This was an acknowledgment that the species "is extremely uncommon in Michigan and deserves further study and monitoring."

Since an initial year of study in 1975, we have accumulated sufficient data during 1976 to 1978 to answer several questions concerning the Caspian Tern's status in the U.S. Great Lakes including: (1) What is the current population? (2) Are the colonies producing an adequate number of young to maintain themselves? and (3) What factors now and in the immediate future will have major impacts on the population and on the continued use of the U.S. colony sites?

We realize that the U.S. Great Lakes population is a subset of the larger Great Lakes population, and that Caspian Terns do not respect international boundaries. We provide some data for the entire Great Lakes; but, for further information concerning the status of Caspian Terns in Canada, consult Martin (1978). Also, a study of Caspian Tern reproductive biology in Lake Huron is being conducted by J. Quinn of Brock University. J. Ludwig (in prep.) is updating banding data for Great Lakes Caspian Terns.

METHODS

Data for this paper were collected while Scharf and Shugart conducted surveys of the U.S. Great Lakes colonial bird populations in 1976 to 1977 (Scharf et al. 1978, in press); and while Shugart, in 1975 to 1978 (Shugart 1977a,b) and Cuthbert in 1976 to 1978 separately conducted thesis research with this species.

Censusing.--To determine the size of initial nesting populations at U.S. colonies, we directly counted all nests containing eggs at active colonies with the exception of Gravelly Island. Direct counts were conducted during the last week prior to first hatching at Hat and High Islands and Ile aux Galets in 1976 to 1978; and Shoe Island in 1978. In 1976 to 1978, nesting pairs at Gravelly Island were determined by counts of sitting (i.e. incubating) birds from aerial photographs. We realize that aerial photography is generally imprecise for estimating colonial bird nesting populations (Blokpoel 1976, Buckley et al. 1977). Counts of sitting birds eliminated much of the error and our counts of Caspian Terns had less than 5% error when checked against ground counts at 2 islands. This degree of accuracy was possible because there was no vegetation

in the colonies to hide birds, and photos were taken in early morning when blind observations indicated that mates of most incubating birds were gone from the colony. If mates were present, the low angle of the sun cast a shadow that permitted easy determination of standing versus sitting birds.

Canadian colonies were censused on 5 to 6 June 1978 by Cuthbert and an assistant. Two independent simultaneous counts were done and differences in totals of less than 3% indicated a high degree of accuracy.

Renests were counted during the last week of June or the first week of July at Hat and High Islands, and Ile aux Galets in 1976 to 1977; at Shoe Island in 1976 to 1977, and High Island Shoals in 1977. A renest is one that is initiated after 15 June.

Reproductive data.--Data were collected to assess average colony productivity and to permit identification of major causes of mortality. More detailed analysis of intraspecific variation in reproductive success as related to age, pairing, and nest-site location will be addressed in later papers.

Specific colonies and years of study are indicated in Table 1. At these colonies, nests were counted directly as indicated above and sections were mapped so the number of nests and eggs lost to storms or other causes could be determined. All nests were marked in 1977 to 1978.

The number of eggs present were recorded during censuses and clutch-size = total eggs in nests/total nests. Egg mortality or embryo mortality refers to eggs abandoned after disturbances or after they were washed from nests. Unless otherwise indicated, egg and chick mortality from other causes are combined.

Chick survival to flying was determined by counting the number still living when the first chicks from the initial nesting were able to fly. Young from initial clutches were 4 to 7 weeks old at this time and were counted easily and accurately when all formed an alarm creche (see Buckley and Buckley 1972). Young produced by renesters were determined in 1977 only, by visiting colonies on 8 August. Counts represent accurately the number that will fly from the colony as few young die after 3 weeks of age (Soikkeli 1973, Penland 1976).

Gull-tern interactions from 1975 to 1978, and species of prey delivered to tern chicks at Hat Island in 1977 and 1978 were determined by blind observations.

RESULTS AND DISCUSSION

Colonies and nesting pairs.--Initial nesting attempts of the season in the U.S. Great Lakes were confined to 4 islands in Lake Michigan during 1976 and 1977, and 5 Lake Michigan islands in 1978 (Table 1). All sites had been used previously (Ludwig 1968), but Shoe Island had not been used since the water level in Lake Michigan rose in 1969 (U.S.A.C.E. 1969) and periodically inundated it. This island became suitable for nesting as the Lake Michigan water level began dropping in 1977 and the island re-emerged from the lake (see U.S.A.C.E. 1968 to 1978 for water level data). One other formerly used colony site in Lake Huron (Ludwig 1968) was awash during the study period, and probably had been unusable since 1969 when water levels increased (U.S. A.C.E. 1969). Specific island and colony descriptions were detailed in Scharf et al. (1978, in press).

From 1976 to 1978, approximately 1600 pairs (Table 1) nested in the U.S. Great Lakes. This represents at least a 12% increase from 1435 nesting pairs found in a 1967 census (Ludwig 1968) of the same area. The increase in pairs nesting at Lake Michigan colonies was probably slightly larger than 12% because we have not accounted for the loss to the Canadian colonies of some pairs that nested on the inundated Lake Huron colony. This site was equidistant between the Lake Michigan and Canadian colonies, and birds probably distributed themselves among available sites.

Currently, 44% of the Great Lakes Caspian Tern breeding population nests at U.S. sites in Lake Michigan (Table 2). The proportion of the total has decreased from 56% in 1967 owing to a 70% increase in the number of pairs nesting at Canadian sites. Relatively faster growth in Canada does not appear to be a general trend, but can be attributed to increases at 4 of the 9 sites, 2 of which have doubled in size since 1967, and 2 others that have increased from a few pairs (Martin 1978) to a combined total of 410 pairs in 1978.

Reproductive success.--Clutch size averaged 2.4 eggs/nest in 2170 initial nesting attempts over the 4 year period (Table 3). We believe this represents the average number laid as counts were done after the initial clutches were completed and evidence suggests a few eggs were lost during normal incubation. For instance, during censuses each year, we found less than 2% of the total eggs or shells out of the nests; inclusion of these in calculations does not change the average clutch size to the precision we have indicated. Also egg loss due to egg predation by adjacent gulls or terns is minimal in Caspian Terns because this species begins incubation with the

TABLE 1

Nesting pairs at U.S. Great Lakes colonies

Island	Lat.-Long.	1975	1976	1977	1978
Ile aux Galets	45 41-85 11	280*	315	300	280
Hat Island	45 47-85 18	500 ¹	730*	685*	125*
Shoe Island	45 47-85 18	w	r	r	350*
High Island	45 45-85 40	d	10	20	315
High Island Shoal	45 45-85 40	w	w	r	w
Gravelly Island	45 31-86 43	p	560	550	580
Little Gull Island	45 30-86 43	0	0	r	0

¹Visual estimate; w - awash; r - re-nested upon; d - destroyed; p - present. Totals are rounded off to the nearest 5 pairs. *Study colonies.

TABLE 2

Total pairs initially nesting in the Great Lakes

Year	U.S. colonies	% of total	Canadian colonies	% of total	Total
1965	1145 ¹	57	860 ²	43	2005
1966	1285 ¹	55	1045 ²	45	2330
1967	1435 ¹	54	1215 ²	46	2650
1976	1605	--	--	--	--
1977	1555	--	--	--	--
1978	1640	44	2100 ³	56	3740

¹From Ludwig 1968. ²From Ludwig 1968, Blokpoel 1976. ³All sites were censused except South Limestone Island (J. Quinn, pers. comm.) and Pigeon Island (Martin 1978). Pigeon Island total is from 1977.

first egg (Bergman 1953, Soikkeli 1973). This is unlike gulls which do not begin full incubation until the clutch is completed (Drent 1970) and experience some egg loss of the exposed eggs during laying and early incubation. No potential egg predators other than gulls and terns (Soikkeli 1973) were observed on the study islands.

While initial clutch size variation in a single Caspian Tern population has not been noted previous to our report, differences between populations are common. Populations can be categorized as those most frequently laying 1 to 2 eggs, or 2 to 3 eggs. One and 2 egg clutches were common in Lake Winnipeg, Manitoba (O'Donoghue and Gowanlock 1919, Evans et al. 1970), California (DeGroot 1931, Miller 1943), Texas (Pemberton 1922), and Florida (Dunstan et al. 1975). Clutch sizes of 2 to 3 eggs are common in the Great Lakes (VanWinkle 1893, Ludwig 1965, this study), Washington (Penland 1976), and northern Europe (Bergman 1953, Soikkeli 1973). We assume these differences reflect proximate conditions of food availability, as suggested by the variation in clutch sizes within the Great Lakes population, (Table 3), rather than interpopulation genetic differences. Similar variation has been recorded for the Arctic Tern (*Sterna paradisaea*); and in this species, the variation has been related to food availability (Hawskley 1957, Evans and McNichol 1972, Lemmetyinen 1973).

Chick survival as a proportion of eggs present (hereafter referred to as chick survival) in initial breeding attempts was 39% averaged over 4 years (Table 4). This value represents a lower

TABLE 3

Initial nesting attempts at selected Lake Michigan colonies

Colony, year	Eggs/nest				Clutch size	Nests/eggs abandoned (a), washed out (w)	Chicks surviving to flying stage No. (% eggs)/(pair)
	1	2	3	3<			
Ile aux Galets, 1975*	15	136	125	5	2.4	20/ 50 (w)	420 (57)(1.5)
Hat Island, 1976**	57	243	418	14	2.5	140/ 355 (w)	890 (47)(1.2)
Hat Island, 1977**	47	244	386	9	2.5	445/1125 (a)	325 (19)(0.5)
Hat Island, 1978***	18	93	12	1	2.0	0	112 (46)(0.9)
Shoe Island, 1978*	44	152	150	1	2.3	100/ 270 (w)	360 (45)(1.0)

¹Rounded to nearest 5. Asterisks: an equal number indicate clutch size distribution that is not different ($p > 0.05$), an unequal number indicate a difference ($p < 0.01$).

TABLE 4

Summary of initial nesting attempts in 1975 to 1978 with and without effects of perturbations

	Nests ¹ /eggs ¹	Chicks surviving to flying stage No. (% eggs)/(pair)
With perturbations	2170/5350	2110 (39)(1.0)
Without perturbations ²	1465/3550	2110 (59)(1.4)

¹Rounded to the nearest 5. ²This represents the reproductive potential of Lake Michigan Caspian Terns under optimum conditions, i.e. when abandoned and washed-out nests are not considered in the total.

extreme in chick survival which was caused partially by 33% total egg (i.e. embryo) mortality. An upper limit or extreme in average chick survival can be approximated by subtracting from the total those nests and eggs that were lost due to local perturbations (Table 4). When this is done, we estimate that under more optimum conditions, chick survival as a 4 year average was 59%. These upper and lower limits correspond to 1.4 chicks/pair and 1.0 chick/pair, respectively.

When the effects of egg mortality due to perturbations are subtracted (Table 4), chick survival of 59% at Lake Michigan colonies during this study is similar to 58% at Great Lakes colonies in 1963 and 1964 (Ludwig 1965), and to Finnish colonies where chick survival was between 60% and 65% (Soikkeli 1973). Chick production per pair between studies is also similar because clutch sizes in initial attempts averaged 2.5, 2.8, and 2.5 eggs/nest, respectively. Comparison of these average values indicates that Lake Michigan colonies studied from 1975 to 1978 would have produced the expected number of chicks if they were not affected by perturbations that caused considerable egg mortality.

Renesting.--It could be argued that failure of initial nesting attempts has no effect on the dynamics of a population because the initially failing pairs go on to renest. However, this argument is untenable because the proportion of the population that renests has reduced reproductive potential relative to initial attempts.

When initial failures are considered as a group, reproduction is reduced relative to initial attempts because not all birds renest. The proportion that actually does renest was difficult to determine as we could not get to all colonies every year to assess losses, and because many birds relocate before renesting. In 1977, however, these problems were minimized because the Hat Island colony was the only colony in eastern Lake Michigan to experience a large number of initial failures. Since this was the 1977 study site, we had accurately censused the colony by sections, and therefore could determine losses. Losses totaled 465 nests and were concentrated between 31 May

and 2 June. Assuming the time from failure to renesting is similar to 12+ days found for other larids (Paludan 1951, Brown 1967, Parsons 1975), renesting by the birds that failed began at Hat and surrounding colonies on 15 June and continued through the first week of July. We counted 310 active renests during the last week of June and the first week of July (Table 4). If all 310 renests were from Hat, then 66% of the initially failing pairs renested. This probably is an overestimate as Soikkeli (1973) found that 10-17% initial attempts failed to hatch any eggs under normal conditions.

Relative to initial attempts, further reduced productivity per pair from the proportion of the population that does renest can be expected because of smaller clutches (Soikkeli 1973, Langham 1974, Parsons 1975). Lake Michigan Caspian Terns that we studied conformed to this general rule and laid an average of 1.8 eggs/renest (Table 5) as compared to 2.5 egg/initial attempt (Table 3). Laying a smaller clutch upon renesting reduces the number of chicks a pair has to feed, and apparently is an adaptation to reduce intrabrood food competition and favors survival of at least 1 chick (Perrins 1970, Parsons 1975).

Chick survival of renesters was determined only in 1977 at 4 colonies. Percent chick survival was equivalent to initial attempts at 3 colonies and was reduced at the 2 other sites (Table 5). Reasons for these differences between colonies were undetermined. A likely cause could be a scarcity of food late in the summer, but this can be dismissed as each of the colonies that did poorly was within 15 km of one of the more successful sites. The colonies in 1977 that had reduced survival of chicks relative to initial attempts appear to be exceptions as chick survival of renesters usually is not reduced (Langham 1974, Parsons 1975). Chick production per pair, however, is lower than in initial attempts because of smaller clutches.

TABLE 5

Renesting attempts at eastern Lake Michigan colonies in 1977

Colony	Eggs/nest				Clutch size	Total nests	Chicks surviving to flying stage No. (% eggs)/(pair)
	1	2	3	3<			
Hat Island	5	10	0	0	1.7	15	0
Ile aux Galets	18	45	3	0	1.8	66	19 (16)(0.3)
High Island		N.D.			N.D.	100	36 (N.D.)(0.4)
Shoe Island	8	32	9	2	2.2	53	63 (55)(1.2)
High Island Shoal ¹	7	33	2	0	1.9	42	55 (58)(1.3)

¹Approximately 80 nests were washed out before censusing. N.D. = not determined.

Causes of nesting failure.--We have shown that chick production per pair and chick survival at Lake Michigan Caspian Tern colonies would have approached expected levels if perturbations had not caused losses of eggs and chicks. In an attempt to understand the present and future impact of perturbations upon the Lake Michigan colonies, we separately discuss each factor, including: (1) wash-outs, (2) human disturbance, and (3) predation.

Wash-outs.--The most frequent cause of reproductive failures was gale force winds (75+ kph) which generated large waves that washed eggs from nests. Wash-outs occurred at 3 of the 5 study sites on areas within 20 m of, and less than 0.5 m above Lake Michigan. Twelve percent (260) of all initial nesting attempts (Table 3) were washed out. An undetermined number of initial attempts also were destroyed by wash-outs at Hat Island in 1975, Ile aux Galets in 1976 and 1978, and at Gravelly Island in 1976. Judging from the number of eggs and eggshells that were piled at the water line at these islands, the loss was probably 10% or more of the total. In 1977, 20 renests were washed away at Shoe Island, and about 80 of 120 renests at High Island Shoal similarly were destroyed.

It would seem that selective pressures would develop a mechanism in Caspian Terns which would permit selection of safe nest sites. This probably is true, as 88% of the total nests were not washed-out. It appears that placement of the remainder of the nests in areas subject to wash-outs was not a simple matter of choice but was caused primarily by earlier occupation of nest sites by gulls which limited the available nesting area for terns.

The first larid species to nest in northern Lake Michigan is the Herring Gull (Larus argentatus) which begins occupation of territories about mid-March and lays eggs during the last 3 weeks of April. Ring-billed Gulls (Larus delawarensis) begin colony occupation 1 to 2 weeks later, and they lay eggs beginning the last week of April and peak during the first week of May. Caspian Terns begin arriving at the colonies around mid-April and lay initial clutches during the first 3 weeks of May (see Scharf et al. 1978, in press, for further details). Based on this chronology, we suggest that gulls arrive at the colonies first and usurp much of the safe nesting sites. The early terns get the higher nest-sites, and later arriving terns are attracted to established nesting groups (Langham 1974, Veen 1977), but the only available area is low ground close to the water. The first gale washes these nests away.

In Lake Michigan, Herring Gulls are most important in limiting area as they nest earlier and are incubating eggs and defending territories when the terns arrive. Observations from hides during 4 seasons indicate that territorial Herring Gulls win in encounters with Caspian Terns, while Caspian Terns usually displace Ring-billed Gulls in interspecific encounters. Since Ring-billed Gull colonies are still in the prelaying or early laying period when the terns arrive, and because Caspian Terns can displace Ring-billed Gulls, they have less of an effect in limiting nesting area. Similar displacement of Common Terns (Sterna hirundo) has been noted by earlier nesting Herring Gulls (Crowell and Crowell 1946, Nisbet 1972) and also by Ring-billed Gull (Ludwig 1962, Morris and Hunter 1976).

Assuming the above is true, the amount of area available to nesting terns could be influenced additionally by the following interacting factors which require further study and clarification: (1) Succession on bare beach areas of annual plants (primarily Brassica sp., Barbarea vulgaris) that remain as dead mats and clumps through the winter. These objects tend to make beach areas more attractive to Herring Gulls (see Burger and Shisler 1978) the following spring which decreases area available to terns. (2) Winter storms and spring ice-pushes overturn and scour beaches and return them to the bare beach stage of succession. (3) Great Lakes water levels fluctuate up to 1-m over periods of 10 years or longer (Cohn and Robinson 1976) and in doing so alter island size and beach area.

The number of wash-outs that occurred during the study period suggest that Caspian Terns in Lake Michigan were approaching a limit in the number of pairs that could nest within the boundaries imposed by earlier breeding gulls. If gull populations remain relatively stable in Lake Michigan, we expect continued increases in the number of terns at existent sites in the future. Increases in gull populations in Lake Michigan would result in a stable or decreasing number of terns as some terns are forced to find sites that are not full in other lakes. A correlation can be drawn to the Caspian Terns in the State of Washington where earlier nesting by large gulls, and projected increases in gull populations at the Caspian Tern nesting sites were identified as major future impacts on the Caspian Tern breeding population (Penland 1976).

Human disturbance.--The greatest single cause of reproductive failure during the study period was egg abandonment after disturbance associated with Cuthbert's cannon netting activities on Hat Island. Abandonment is not a singular response of Caspian Terns to cannon netting, as this technique was used with no adverse affect in 1976 at the Hat Island colony. In 1977, Cuthbert netted the Hat Island colony after the initial census, and a second census on 10 June indicated only 240 (35%) of 685 initial nests still were attended. Criteria for attendance was that eggs and nests were dry after a rainstorm on 9 June which indicated nests were attended through the storm. Assuming that 10 to 17% of the pairs at this colony would not have hatched eggs (Soikkeli 1973), a minimum loss of 325 (45% of the total) could have been attributed to netting and associated disturbance.

The different responses of the colony in 1976 and 1977 most likely were related to earlier and repeated disturbance associated with netting in 1977 and to the chronological state of the colony at the time of netting. Asynchrony in 1976 was indicated by hatching which began on 2 June at one end of the colony and progressed to the other end by 24 June. In 1977, hatching began 31 May, and was completed in unabandoned nests by 16 June; but developmental stages of 45 of the abandoned clutches indicated hatching would have continued until 20 to 23 June. Therefore, the colonies were equally asynchronous in both years. Netting on 11 June 1976 occurred when all pairs had incubated at least 2 weeks. In 1977, netting was done on 31 May and 1 to 2 June; and even though hatching had begun in one area of the colony, many pairs had incubated less than 2 weeks. Greater nest-site attachment and decreased chance of abandonment as hatching nears generally is well known (Kruuk 1964, Drent 1970, Buckley and Buckley 1976). A contributing factor to 1977 abandonments was that many of the birds in the colony had not incubated long enough to prevent abandonment when disturbed.

A second contributing factor to different responses of the colonies to disturbance in 1976 and 1977, was a greater number of disturbances in 1977. Associated with each day of netting was 1 disturbance of 15 to 30 minutes to set the net, and 45 to 90 minutes of disturbance to process captured birds after each firing. One firing was done in 1976; while 1 or 2 were done each of 3

days in 1977, for a total of 5 disturbances.

There are numerous anecdotal accounts describing Caspian Tern abandonment following disturbance (Ward 1908, O'Donoghue and Gowanlock 1919, Bergman 1953, Cullen 1958, Viäsänen 1973, Penland 1976). Cullen (1958) argues that abandonment of disturbed nest-sites and re-nesting elsewhere is a breeding adaptation common to the crested tern group (Moynihan 1959) which includes the Caspian Tern. A lack of actual data makes this interpretation tentative for the Caspian, but such an interpretation is valid for the smaller crested terns (Kale et al. 1965, Buckley and Buckley 1972, 1977; also see McNichol 1975).

The abandonment at Hat Island, while unplanned, illustrates what may happen in the future as a result of disturbance from the general public, and perhaps from investigators using inappropriate techniques. To assist other investigators, we can suggest tentative guidelines regarding the frequency and duration of disturbance. Based on examples above and accounts in the literature, we urge cautious use of techniques at Caspian Tern colonies that require extended periods of disturbance (i.e. cannon netting, mass chick banding), particularly at large asynchronous colonies. Instead of long periods of disturbance, we recommend the use of several shorter periods (20 minutes or less) spaced at hour intervals within the guidelines of Buckley and Buckley (1976).

Our observations indicate that recreational boating is increasing particularly around the eastern Lake Michigan islands where 4 of the 5 colonies are located. This most likely will lead to increased visitation and disturbance to the colonies by the general public. While such visits can be advantageous in developing public appreciation for this and other species, they can be harmful if prolonged or if they coincide with critical periods of the nesting cycle (Buckley and Buckley 1976). In the future, it will be necessary to limit access to the colonies to guard against poorly timed visitation and disturbance. Similar views were expressed by Penland (1976) for Caspian Tern colonies in the State of Washington and by Martin (1978) for large Canadian colonies.

Predation.--A third factor clearly identified as a cause of mortality was Herring Gull predation of tern chicks in 1978 at the Hat Island colony (Table 3). Prior to 1978, we had observed sporadic Herring Gull and Ring-billed Gull predation on eggs and chicks only when the adult terns were off their nests during disturbance. In undisturbed situations, Ring-billed Gulls were chased away by the Caspian Terns. Herring Gulls elicited a different response. As a Herring Gull approached the tern colony, terns on the edge gawked from the nest, and mates of incubating or brooding birds flew up and swooped repeatedly at the gull. In colonies of normal density (i.e. 0.5 to 1.5 nests/m²) enough terns were present to halt the approach or induce retreat of 52 Herring Gulls that approached the tern colony edge during the study period.

In 1978, 1 Herring Gull that was previously color-marked developed into an effective tern predator, and it captured and ate 22 chicks up to 10 days of age. All predation that was observed occurred in the absence of disturbance as the gull attacked an adult tern on the edge of the colony, drove it from the nest, and grabbed the exposed chick. While Herring Gull predation was not a problem in other years, it is a potentially significant mortality factor because several gulls with similar predatory abilities could remove a large portion of the young from a colony.

Food supply.--The future of the colonies in Lake Michigan depends on factors discussed with the addition of food supply. During our study, food availability appeared adequate as chick deaths due to starvation as described by Soikkeli (1973) were not evident.

Caspian Terns usually captured live fish in the 5 to 15 cm length range. Of 1219 prey items brought to young by 6 pairs in 1977 and 15 pairs in 1978, 57% (697) were alewives (*Alosa pseudoharengus*) and 34% (415) were smelt (*Osmerus mordax*) (Table 6). Smelt were common up until mid-June when they left the shallows after breeding (Scott and Crossman 1973). After mid-June, alewives were captured more frequently (Table 6) as they entered the shallow water around the tern colonies to begin breeding (Scott and Crossman 1973).

In 1963 and 1964, alewives represented 78% (132), smelt 16% (27), and other prey 11% (16) of 169 prey items in a pooled stomach and regurgitation sample from colonies in Lake Huron and Lake Michigan (Ludwig 1965). It appears that the percent frequency of species have not changed substantially since 15 years ago.

The common prey species were not native to Lake Michigan. Smelt were introduced in 1912 and became very abundant with periodic fluctuations after 1930 (Christie 1974). Alewives immigrated from the lower Great Lakes into Lake Michigan by 1953 (Smith 1970, Christie 1974). This species was very abundant by 1960, and was the most abundant fish prior to this study (Scott and Crossman 1973, Christie 1974). At present, smelt stocks have stabilized after numerous oscillations as the population adjusted to the Great Lakes (Van Oosten 1947, Scott and Crossman 1973, Christie 1974). Alewife stocks may decline as the species adjusts to the fresh water ecosystem or because of predation from increasing stocks of re-introduced salmonids (Smith 1972, Brown 1972, Christie 1974).

Even though alewives were most common in both sample periods, it does not necessarily mean

that the Caspian Terns are dependent on this species, but only that alewives were captured most easily. Therefore, if alewife stocks remain at present levels, the food supply will be sufficient in the future to support the Lake Michigan colonies. The effect on the tern colonies of a decline in alewives are not predictable without additional information about the availability of other prey species.

Population trends.--From 1965 to 1967, the number of pairs nesting at U.S. sites increased about 15% per year until approximately 1435 pairs were present in 1967 (Ludwig 1968). Similar increases in the Canadian portion of the population indicates immigration minimally affected growth. In our census, we found the number of nesting pairs fluctuated around 1600 which suggests a stable state (Table 2). While the number nesting in Lake Michigan during our study was stable, there were 12% more pairs than in 1967. Evidently the number of pairs increased through 1967 then the rate of increase slowed to zero by 1976.

Because 12% of the terns nested on suboptimum areas (i.e. those that were washed out), it follows that nest sites were limited and only about 1600 pairs could nest under existing conditions. Limitation of nesting area probably was affected in the late 1960's by crowding as the number of nesting pairs increased, and by a reduction in safe nesting sites as water levels in Lake Michigan gradually increased 1 m from 1964 to 1969, and remained at record high levels until 1976 (U.S.A.C.E. 1964 to 1978, Cohn and Robinson 1976). If the number of pairs nesting in Lake Michigan continued to increase at 15% per year after 1967, then the current number of 1600 pairs was attained in 1969 at the latest after which space was limited and potential recruits either existed as floaters or nested at available sites in Lake Huron. Probably the rate of increase was slowed after 1967 because of reduced productivity due to wash-outs as later levels progressively rose after 1964.

Future trends can be predicted from current productivity. During 1975 to 1978, sample productivity averaged 1.0 young/pair surviving to leave the colony. This was above the 0.6 young/pair needed to maintain a stable population with an estimated 10% yearly adult mortality and 50% mortality of young between leaving the colony and breeding (Ludwig 1968). Assuming mortality has not changed, the pairs in Lake Michigan produced more young than will be able to obtain safe sites under existing conditions. This apparent limit will be eased as water levels decline through 1981 (Cohn and Robinson 1976) and make more safe nesting sites available. Therefore, the number of terns nesting in Lake Michigan will increase slightly in the future.

Effects of crowding from Herring Gulls should be reduced because the number nesting in Lake Michigan has remained stable or slightly decreased from 1962 (Ludwig 1962) to 1977 (Scharf et al. 1978). From the same estimates, Ring-billed Gull numbers have increased substantially; but this will have minimal effect on competition for breeding sites because of similar nesting chronology and interspecific dominance of Caspian Terns. In the future, human disturbance will probably cause periodic failure of colonies and reduced productivity of others. The magnitude of human disturbance effects cannot be predicted.

As in 1975 (Shugart 1975), we found that Caspian Terns nesting in Michigan and U.S. waters of the Great Lakes are not numerous and are concentrated on only 5 colonies. This species, therefore, is susceptible to perturbations. Monitoring of the status of Caspian Terns in the Great Lakes should be continued in the future to guard against population declines.

TABLE 6
Percent frequency of prey delivered to young in 1977 and 1978

Period	Smelt	Alewives	Other ¹	Days observed
1-15 June	51 (217) ²	31 (131)	18 (78)	19
16-30 June	34 (187)	63 (348)	3 (17)	24
1-15 July	5 (11)	90 (218)	5 (12)	15
Total	34 (415)	57 (697)	9 (107)	

¹Includes: Longnose Gar (Lepisosteus osseus), minnows, (Cyprinidae), shiners (Notropis sp.), bullhead (Ictalurus sp.), Ninespine Stickleback (Pungitius pungitius), sunfish (Lepomis sp., Micropterus sp.), Yellow Perch (Perca flavescens), and crayfish (Cambarus sp.). ²Number.

SUMMARY

During 1976 to 1978, about 1600 Caspian Tern pairs nested at 5 sites in the U.S. Great Lakes. All colonies were in Lake Michigan. There were about 11% more pairs in the U.S. Great Lakes than were nesting in 1967. The rate of increase in this region has changed from 15% per year during 1965 to 1967 to a stable state during 1976 to 1978.

Clutch size for initial nesting attempts prior to hatching was 2.5 eggs/nest in 2170 clutches sampled during 1975 to 1978. Chick survival from these nests was 39% as a proportion of the total eggs present, and averaged 1.0 chick/pair living to flying. Renesting did not recoup all losses resulting from initial failures.

Compared to other studies, the success of Lake Michigan colonies was low because storms washed eggs from nests; and eggs were abandoned after disturbance. Egg loss due to wave action indicates that a proportion of the terns nested on suboptimal sites. Terns apparently nested on suboptimum sites because earlier nesting gulls usurped many higher safe sites. Earlier nesting terns nested on the remaining sites and group adherence resulted in later arriving terns nesting on low areas next to established groups. Nest and egg abandonments occurred in a large asynchronous colony that was subjected to prolonged disturbance when many pairs had not incubated long enough to develop strong nest site attachment.

In the future, it appears that the tern population in Lake Michigan will continue to be affected by earlier nesting Herring Gulls, fluctuating water levels, and human disturbance. Because of the small number of nesting pairs concentrated at a few colonies, we recommend continued monitoring of Caspian Terns nesting in the U.S. Great Lakes to guard against population declines.

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