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REPRODUCTIVE PERFORMANCE OF RING-BILLED GULLS IN RELATION TO NEST LOCATION

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ABSTRACT.—We evaluated the reproductive performance of Ring-billed Gulls (*Larus delawarensis*) nesting on the periphery and in the center of a colony in northern Lake Superior in 1976 and 1977. The center and periphery of this colony were not subject to flooding, predation or differential human disturbance. Egg-laying, clutch size, hatching and fledging success, and nest attentiveness did not differ significantly between peripheral and central clutches. The colony population has increased in size during the last five years and become stabilized, whereby peripheral and central areas are now being occupied simultaneously. In this study, reproductive performance was related more to the timing than the location of nesting.

The proportion of eggs hatched and young fledged often differ markedly in relation to nest location in colonies of many bird species. Birds nesting in the central part of a colony normally hatch proportionately more eggs and raise more young than do birds with nests on the periphery (Coulson 1968, Dexheimer and Southern 1974). We wanted to determine if such differences existed at an island colony of Ring-billed Gulls (*Larus delawarensis*) that has shown a rapid increase in size in recent years.

STUDY AREA AND METHODS

We conducted the study during the nesting seasons (May, June, July) of 1976 and 1977 on Granite Island (48°43′N, 88°29′W), Black Bay, northern Lake Superior. Granite Island is a rock outcrop 402 m by 201 m with a summit 30 m above the surrounding water. During the study the colony consisted of 1,900 pairs. The nesting habitat was described by Ryder and Somppi (1977). The central nesting area was on the summit of the island. The gulls nested in numerous shallow depressions in the granite rock surface. The dominant vegetation in the depressions was Kentucky bluegrass (*Poa pratensis*). The peripheral area formed the south and west edges of the central area and consisted of the same type of habitat. Immediately adjacent to the peripheral area, off the colony, was a forest, primarily of balsam fir (*Abies balsamea*), white cedar (*Thuja occidentalis*), and white birch (*Betula papyrifera*). No gulls nested in the forest.

We use the following terms: a "peripheral" nest was located on the edge of the colony, forming part of the border (Dexheimer and Southern 1974) and not surrounded by other nests. A "central" nest was located inside the border of the colony and was surrounded by other nests (Tenaza 1971). "Hatching success" was the percentage of eggs laid that hatched (Gilman et al. 1977). "Fledging success" was the percent of chicks that were estimated to fledge from eggs hatched (Gilman et al. 1977). A "fledgling" was a chick at least 21 days old (Dexheimer and Southern 1974). "Reproductive success" was the number of chicks fledged per breeding pair.

Daily nest histories were kept in 1977 for all clutches within the study area. We did not visit the colony during the hottest part of the day or during inclement weather because we assumed that such visits would hinder the survival of embryos. Nests were marked with a numbered wooden block placed beside the nest. Eggs were numbered, in the sequence they were laid, on the blunt end with a non-toxic felt pen. In 1977 we measured the distance to nearest neighbor for a total of 98 randomly chosen nests in order to assess the relationship of nest spacing to reproductive performance.

Chicks were marked at hatching with a numbered fingerling fish tag fastened through the foot web. We recaptured them at 7 to 14 days of age, when their legs were large enough to retain a U.S. Fish and Wildlife Service aluminum leg band. To facilitate recovery of the chicks, we erected a 30.5-cm fence of chicken wire mesh around the study area. Nisbet and Drury (1972) found that the effect of this type of fencing on breeding success was negligible in their study of Common Terns (*Sterna hirundo*) and Roseate Terns (*S. dougallii*). Additionally, they stated that Pearson (1968) and Langham (1968) had fenced Arctic Tern (*S. paradisaea*) and Black-headed Gull (*L. ridibundus*) nests, respectively, without detrimental effects.

We monitored attentiveness of early-nesting gulls in the center and periphery of the colony in both years using a camera mounted in a 5.5-m high observation tower located just off the colony. The camera was equipped with an automatic timer set for one shot every 3 min. In 1976, we determined from the film the presence or absence of attendants during early, mid and late incubation from 25 central and 25 peripheral nests that were started during the peak of egg-laying. In 1977 this procedure was repeated for 30 early central and 24 early peripheral nests. Additionally, in 1977 we recorded attentiveness at 16 late-starting central nests and eight late-starting peripheral nests.

RESULTS

In 1977, the peak of egg-laying in the center was 6–10 May, about one week earlier than on the fringe (Fig. 1). Birds in both areas,

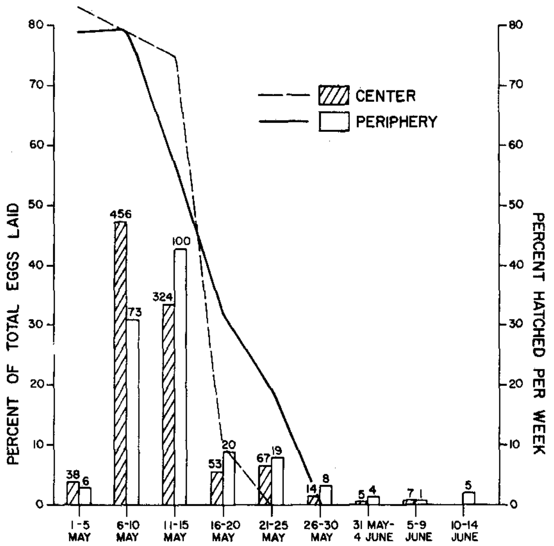

FIGURE 1. The relationship between egg-laying (bars) and hatching success (lines) of Ring-billed Gulls on Granite Island, 1977. The numbers of nests in each interval are given at the tops of the columns.

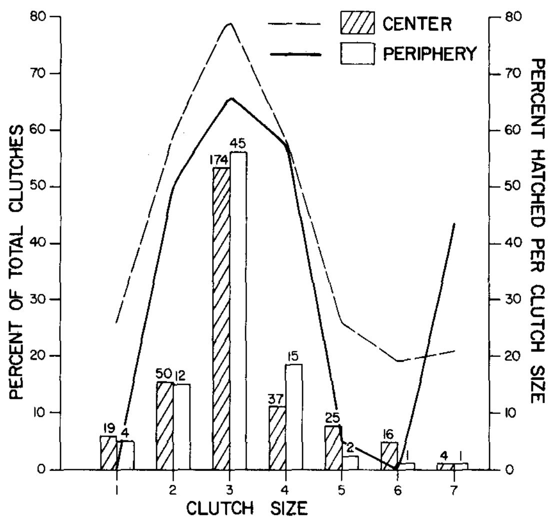

FIGURE 2. Clutch-size frequency (bars) in the center and periphery of the Granite Island Ring-billed Gull colony, 1977. The broken and solid lines correspond to hatching success in relation to clutch size. The numbers of nests in each interval are given at the tops of the columns.

however, started most of their clutches during week 2 (69% in the center and 55% on the periphery). Egg-laying extended from 1 May to 9 June in the center and until about a week later on the periphery (Fig. 1).

Average clutch size did not differ between central and peripheral nests (Table 1). The modal clutch size was three eggs in both areas (Fig. 2).

The modal date of hatching in the center was about a week earlier than on the periphery (Fig. 3), though hatching success was similar in both areas (Table 1). Hatching success of eggs laid at the peak of clutch initiation was about 80% in both the center and periphery of the colony (Fig. 1). Hatching success of eggs laid after the peak declined in both areas (Fig. 1). Three-egg clutches had the highest hatching success regardless of location (Fig. 2).

Some chicks were not recaptured or were found dead so we had to estimate the number that fledged. From a sample of 86 known-age dead chicks, we knew that 40 (46.5%) had died in less than one week and 53.5% died between one and three weeks of age. Consequently, if a chick was last seen at less than one week of age, we assumed that its chance of being alive was 53%; if a chick disappeared at one to three weeks, then its chance of being alive was assumed to be the reciprocal, 47%. To calculate fledging success, we added the number of chicks that we knew were at least 21 days old to the number of unrecovered chicks that we calculated to have fledged, based on the above proportions (Ryder and Carroll 1978). Table 1 shows that fledging and reproductive success did not differ significantly in either area. Proportionately more chicks fledged, however, from eggs hatched during the peak of hatching than from those hatched before or after this pe-

TABLE 1. Breeding success of Ring-billed Gulls on Granite Island, 1977.

Variable	Center	Periphery
Number of nests	325	80
Clutch size	3.19 ± 1.19[a]	3.08 ± 0.98
Hatching success[b]	59.5 (618/1038)[c]	58.5 (144/246)
Fledging success[b]	54.3 (335.4/618)	59.0 (84.9/144)
Reproductive success[b]	1.03 ± 0.75	1.06 ± 0.95
Inter-nest distance (cm)	74.9 ± 25.9 (70)[d]	95.8 ± 54.9 (28)

[a] $\bar{x}$ ± SD.
[b] Terms defined in Methods.
[c] % (raw data).
[d] $\bar{x}$ ± SD (sample size); t = 2.6, $P < 0.05$.

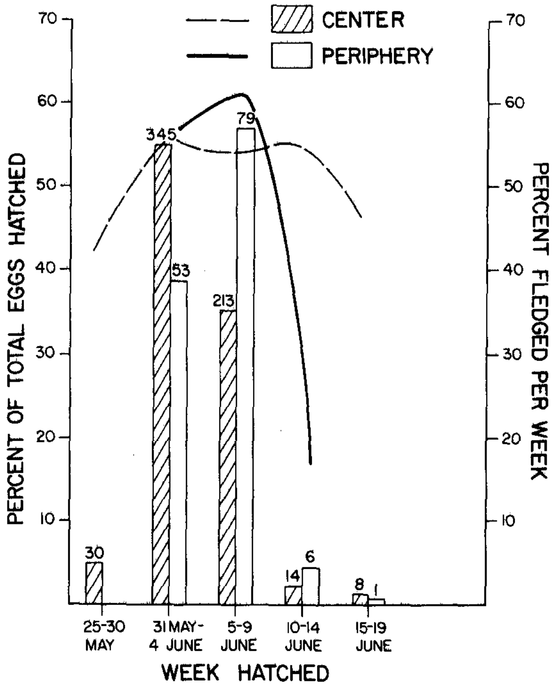

FIGURE 3. Frequency of Ring-billed Gull hatching (bars) in the center and periphery on Granite Island, 1977. The broken and solid lines correspond to fledging success in relation to date hatched. The numbers of nests in each interval are given at the tops of the columns.

riod. The relatively small sample of chicks hatched before and after the peak made it difficult to demonstrate statistically significant differences.

The average minimum distance between nests differed significantly between the center and periphery (Table 1). The distances, however, were not related to week of clutch initiation ($F = 2.45$, $df = 4,82$, $P > 0.05$), clutch size ($F = 0.43$, $df = 6,91$, $P > 0.05$), or hatching success ($r = 0.02$, $df = 96$, $P > 0.05$).

In both years, over 80% of the early-nesting gulls attended their nests over 90% of the time, regardless of nest location (1976, $\chi^2 = 2.45$, $df = 1$; 1977, $\chi^2 = 0.53$, $df = 1$). In 1977, significantly fewer (67%) late-nesting central and peripheral gulls were on their nests 90% of the time than earlier-nesting pairs ($\chi^2 = 4.16$, $df = 1$, $P < 0.05$).

DISCUSSION

The general similarity in reproductive performance of Ring-billed Gulls nesting on the periphery and in the center of the Granite Island colony agrees with the results of Dexheimer and Southern's (1974) study of Ring-billed Gulls at the Rogers City, Michigan colony. On both the Granite Island and Rogers City colonies neither the center nor the periphery was subject to flooding that has caused differences in breeding success at some other colonies (see Dexheimer and Southern 1974, Blus and Keahey 1978). The center and periphery of the Granite Island colony were not subject to differential predation, which may reduce the success of birds nesting on the fringe (Patterson 1965) or center of the colony (Montevecchi 1977, Burger and Lesser 1978), nor to differential human disturbance (Gochfeld 1980). No people visited Granite Island during our studies and we kept the number and time of our visits to a minimum. Additionally, during the last five years, the colony population has increased by 140%, from 800 pairs in 1973 (Ryder 1975) to 1,900 pairs in 1978 (Ryder and Somppi 1979). The colony boundary has expanded to the point where further growth would necessitate the gulls' nesting in the forest. We suggest that the colony boundary has become inflexible.

Although slightly more late-arriving, and possibly younger (Ryder 1975), gulls laid eggs on the periphery than in the center (Fig. 1), their numbers were too low to markedly reduce the overall success within the area. Our prognosis is that as the colony population stabilizes, differences in breeding success will be further reduced. Thus the differences in breeding success usually reported between central and peripheral birds should not be considered to exist a priori at every colony, because such differences may diminish with the growth and maturation of a colony (Nelson 1978). In our study, reproductive performance was related to timing of nesting more than location of nesting.

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RECENT PUBLICATIONS

Woodpeckers and the Southern Pine Beetle.—James C. Kroll, Richard N. Conner, and Robert R. Fleet. [1980]. Agriculture Handbook 564, U.S. Dept. of Agriculture. 23 p. Paper cover. Source: Supt. of Documents, U.S. Govt. Printing Office, Washington, D.C. 20402. Four species of woodpeckers are important predators of the southern pine beetle, which in turn attacks all species of southern pines. This booket describes the pertinent ecology of the birds and the beetle, and suggests forest management practices that would favor woodpecker populations. The use of birds as biological control agents and the consideration of non-game species in forest management represents a commendable new approach in forestry.

Relationships between hummingbirds and flowers in the Andes of Colombia.—David W. Snow and Barbara K. Snow. 1980. Bulletin of the British Museum (Natural History), Zoology series, Vol. 38, No. 2, 34 p. Paper cover. £ 5. Source: Publications, British Museum (N.H.), Cromwell Road, London SW7 5BD, U.K. This is a research report on the feeding ecology of hummingbirds in the subtropical and temperate forests of the Andes, where the greatest number and variety of species coexist. After presenting their observations at each of three study areas, the authors discuss ornithophily, coevolution between hummingbirds and flowers, and the foraging habits of hummingbirds. The article offers data and ideas in abundance. References.

Evolution of Social Behavior: Hypotheses and Empirical Tests.—edited by Hubert Markl. 1980. Dahlem Workshop Reports, Life Sciences Research Report No. 18, Verlag Chemie, Weinheim. 255 p. Paper cover. \$22.50. Source: Verlag Chemie Int., Plaza Centre, Suite E, 1020 N. W. 6th St., Deerfield Beach, FL 33441. Here are the proceedings of a workshop on the evolution of sociality in animals, held in Berlin in 1980. Nine formal papers are followed by four group reports: Methodology and sociobiology modelling, mechanisms of kin-correlated behavior, measuring fitness in social systems, and genetics and social behavior. On the one hand are the views of theoreticians and specialists in mathematical modelling, while on the other are those of students of animal behavior in the laboratory or the field. Although only one of the papers specifically concerns birds, the volume offers many ideas of interest to avian sociologists. The book can be considered a state-of-the-art report, thanks to the eminence of its contributors and the alacrity with which it was published. References, limericks, and indexes.

Behavioral Mechanisms in Ecology.—Douglass H. Morse. 1980. Harvard University Press, Cambridge, Mass. 383 p. \$25.00. This is a textbook "about the relationships of animals to their resources and about their relationships to one another through those resources." In order, it considers foraging efficiency and economics, habitat selection, avoiding predation, behavioral thermoregulation, reproduction, competition of different kinds, and sociality. Birds are used for many examples, their behavioral ecology being among the most-studied of all animals. The writing is admirably clear, a notable accomplishment in a field where much of it is not. Most chapters contain a concluding synthesis and the last chapter itself indicates future directions for research. Graphs, references, index.