NEST SPACING, REPRODUCTIVE SUCCESS, AND BEHAVIOR OF THE GREAT BLACK-BACKED GULL (*LARUS MARINUS*)

RONALD G. BUTLER AND WAYNE TRIVELPIECE

Seabird Research Group, Mount Desert Island Biological Laboratory, Salsbury Cove, Maine 04672 USA

ABSTRACT.—A study of the relationship of nest spacing, reproductive success, and behavior of the Great Black-backed Gull (*Larus marinus*) was conducted during the 1979 breeding season. Egg production and hatching success were similar on territories in high and low density areas, but gulls in high density areas fledged significantly fewer chicks than those in low density areas. Adults breeding in high density areas engaged in significantly more bouts of agonistic interactions and chick-oriented vocalizations than pairs in low density areas, although there were no significant differences between the two groups in the frequency of long calls, choking bouts, or chick feedings. The results of this investigation are related to a model proposed by Hunt and Hunt (1976) that predicts that, in the absence of interspecific predation, larger territories may confer a reproductive advantage on some larids due to a decrease in conspecific interference. *Received 11 April 1980, accepted 18 July 1980.*

NEST spacing within seabird colonies is a direct function of the size of the breeding territories defended around the nest sites. Breeding territory size may be considered an adaptation responsive to selection pressures such as predation, competition for nesting habitat, and conspecific social and aggressive characteristics. As nest spacing exhibits the natural variability inherent in any evolutionary adaptation, it may be hypothesized, for a given set of environmental conditions, that reproductive success would be related to some optimal nesting density or territory size in colonial species. This hypothesis has been examined in the family Laridae with conflicting results.

Nesting density was not found to be related to chick survival in Glaucous-winged Gulls (*Larus glaucescens,* Vermeer 1963), Black-headed Gulls (*L. ridibundus,* Patterson 1965), Ring-billed Gulls (*L. delawarensis,* Dexheimer and Southern 1974), or Western Gulls (*L. occidentalis,* Hunt and Hunt 1975). Although Fordham (1964) demonstrated a positive correlation between nearest-neighbor distance and egg losses in the Dominican Gull (*L. dominicanus*), he was unable to establish a relationship between nearest-neighbor distance and chick survival in a later study (Fordham 1970). In contrast, Parsons (1971) observed that Herring Gulls (*L. argentatus*) exhibited maximum breeding success at median nesting densities, and Hunt and Hunt (1976) were able to show a positive correlation between the size of the breeding territory and chick survival in Glaucous-winged Gulls. Although the variability in these reported results may be due to methodological, environmental, and/or species-specific differences, it is clear that additional data (both reproductive and behavioral) will be necessary to clarify this problem. The objectives of the present study were to: (1) investigate the relationship between nest spacing and reproductive success in a colony of Great Black-backed Gulls (*L. marinus*), and (2) examine behavioral factors that might have been related to the reproductive success of pairs breeding in high versus low density areas.

METHODS

This study was conducted on Little Duck Island, Hancock County, Maine during the 1979 nesting season. Two pairs of Great Black-backed Gulls were first reported breeding on Little Duck Island in 1931 (Norton and Allen 1931), and approximately 325 pairs of *L. marinus* currently nest in two large

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meadows on this 35-ha, semi-forested island. Breeding habitat consisted largely of several species of grasses (*Gramineae*), stinging nettle (*Urtica dioica*), angelica (*Angelica lucida*), and raspberry (*Rubus idaeus*) and of exposed granite outcroppings. Little Duck Island supported no mammalian predators, although Herring Gulls and a pair of Common Ravens (*Corvus corax*) did breed there. The island is located several kilometers offshore and is uninhabited, so study animals were subject to disturbance only from the observers.

A blind was constructed during the early egg-phase of the Black-backed breeding cycle at the periphery of the study colony. The blind was constructed on masonary scaffolding that elevated the observer to 4 m to facilitate observation of nest sites over vegetation that generally averaged 1 m in height. The blind was approached via a path through the forest and entered from behind to reduce observer disturbance. We marked 24 representative nests that were close enough to the blind to be clearly observable for study, and the number of eggs laid and chicks hatched were monitored during several nest checks conducted during May–June. Twenty of these nest sites were selected for behavioral observation, and 17 incubating adults from those nests were captured, weighed, measured (culmen, head, and tarsus), and banded (USFWS and leg streamers) for individual identification. Adults were sexed on the basis of morphometry (the larger member of a pair was assumed to be the male) and behavioral parameters (e.g. copulations, begging, etc.). Chick survival at all 24 study sites was determined through observations from the blind to avoid observer disturbance in the colony and its potential detrimental impact on reproductive success. Chicks were considered "fledged" at 50–55 days following hatching and/or when they were observed to fly strongly in the vicinity of the colony.

Behavioral observations (350 observation h) were conducted between 0600 and 1200 on a daily basis from 29 May to 25 July 1979 (i.e. chick hatching to chick fledging). Four nests were selected as focal nests each day, and behavioral data were collected from each by switching sites every 15 min consecutively over the course of the observation period. The following data were recorded using binoculars, digital stopwatches, and portable cassette tape recorders: the frequency of and apparent stimulus for long calls, the identity of adults that engaged in long calls, chokes (given by both members of the pair simultaneously), low-level agonistic behaviors of a display nature (e.g. upright aggressive, moving upright aggressive, grass-pulling, etc.), high-level agonistic behaviors that resulted in an intruder fleeing (e.g. attack, chase, fight), yelps, mews, and chick feedings. Behavior patterns such as the long call, yelp, mew, upright aggressive, etc. were operationally defined to remain consistent with current literature (Moynihan 1958; Tinbergen 1959, 1960; Stout et al. 1969; Stout 1975). Behavioral data were collected only from those breeding territories that contained surviving chicks, and only those sites that were totally visible over the entire course of the season were included in the data analysis.

For the purpose of data analysis, Great Black-backed pairs were operationally defined as defending territories either in high density areas (breeding territories bounded by three or more contiguous territories) or low density areas (breeding territories bounded by two or fewer contiguous territories). Breeding territories were considered contiguous if adjacent adults engaged in agonistic interactions characteristic of territorial defense. Actual territory sizes were not measured during the breeding season in order to reduce disturbance to nesting birds in the colony. In addition, exact measurements of the sizes of low density territories would have been extremely difficult, because these pairs had, by definition, only one or two territorial neighbors, and boundary disputes rarely occurred. Following chick fledging, inter-nest distances were measured with an optical rangefinder, and rough estimates of individual territory sizes were obtained by using half of the mean inter-nest distance for each nest site as the radius of a circle. All data in this study were analyzed utilizing the Student's *t*-test, Chi-square, or Mann-Whitney *U* statistic.

RESULTS

Territory and reproductive parameters.—Gull pairs breeding at high densities nested much closer together (and presumably had much smaller territories) than did birds breeding on low density sites. The mean ($\pm$SE) number of contiguous territories bounding high density breeders was 3.6 $\pm$ 0.2, while only 1.8 $\pm$ 0.1 were adjacent to low density pairs. The mean nearest-neighbor distance for gulls on high density territories (4.7 $\pm$ 0.5 m) was significantly less than that for low density breeders (12.1 $\pm$ 1.2 m; $t = 6.587$, df $= 22$, $P < 0.001$), as was the mean inter-nest distance between contiguous territorial pairs (6.4 $\pm$ 0.6 m and 13.5 $\pm$ 1.0 m, re-

TABLE 1. Comparisons of reproductive success of Great Black-backed Gulls breeding on high and low density territories.

	High	Low	χ^2	P
Eggs/breeding pairs	41/15 (2.73)	25/9 (2.78)	0.001	NS
Chicks hatched/eggs	33/41 (0.80)	23/25 (0.92)	0.129	NS
Chicks fledged/chicks hatched	7/33 (0.21)	19/23 (0.83)	7.279	<0.001
Chicks fledged/breeding pairs	7/15 (0.47)	19/9 (2.11)	6.411	<0.05

spectively; $t = 6.501$, df $= 22$, $P < 0.001$). Estimates of territory size based on inter-nest distances yielded a mean of approximately 35.4 ± 6.8 m^2 for high density pairs and 149.9 ± 24.3 m^2 for low density birds.

Although clutch size and phenology were similar, birds breeding at high densities fledged fewer chicks than pairs on low density territories. High density breeders produced 2.73 eggs per pair, which did not differ from the mean of 2.78 eggs per pair for low density breeders (Table 1). The mean chick hatching dates for high and low density breeders in 1979 were 2 June and 4 June, respectively. Although there were no differences in terms of hatching success between the two groups (Table 1), high density Black-backed pairs fledged significantly fewer chicks (21%) than low density gulls (83%; $\chi^2 = 7.279$, df $= 1$, $P < 0.01$). To reduce disturbance, we did not enter the colony to look for chick carcasses. Two instances of chick mortality on high density sites were observed, however, and were directly attributable to adjacent, nonbreeding territorial pairs.

Behavioral parameters.—Adult *L. marinus* breeding in high density areas generally engaged in more bouts of agonistic behavior than gulls in low density areas (Fig. 1). High density birds exhibited more bouts of low-level agonistic behavior ($U = 24$, df $= 5,5$, $P < 0.01$) and high-level agonistic behavior ($U = 23$, df $= 5,5$, $P < 0.025$). Comparisons of high and low density territories, however, revealed no significant difference in the frequency of long calls given per hour (Fig. 1). Approximately 75% of the long calls given by both groups were directed either at overflying conspecifics or at landing, territorial neighbors; the remainder were given by or directed toward landing mates or chicks engaged in vigorous begging bouts around recumbent, resting parents. There was also no difference in the mean frequency of choking bouts recorded for high and low density pairs.

Approximately 71% of all agonistic encounters engaged in by gulls breeding on high density territories involved pairs that had lost their chicks (but were still occupying a territory) or incipient breeders (i.e. pairs that courted and defended territories but did not lay eggs). The remainder of the agonistic interactions (29%) involved adjacent territorial pairs. This ratio was significantly different from that recorded for gulls breeding in low density territories (51% and 49%, respectively; $\chi^2 = 8.585$, df $= 1$, $P < 0.01$). Fights were rare on high density territories (0.01/h) and always involved a nonbreeding, territorial bird. Fights were not observed on low density sites.

Gulls breeding in high density areas engaged in significantly more bouts of chick-oriented vocalizations than did low density adults (Fig. 1). High density pairs yelped ($U = 22$, df $= 5,5$, $P < 0.05$) and mewed ($U = 21$, df $= 5,5$, $P < 0.05$) while oriented toward their chicks significantly more often than did low density pairs. Although the frequency of feeding bouts per hour did not differ between the two groups (Fig. 1), adults on high density territories reconsumed regurgitated food
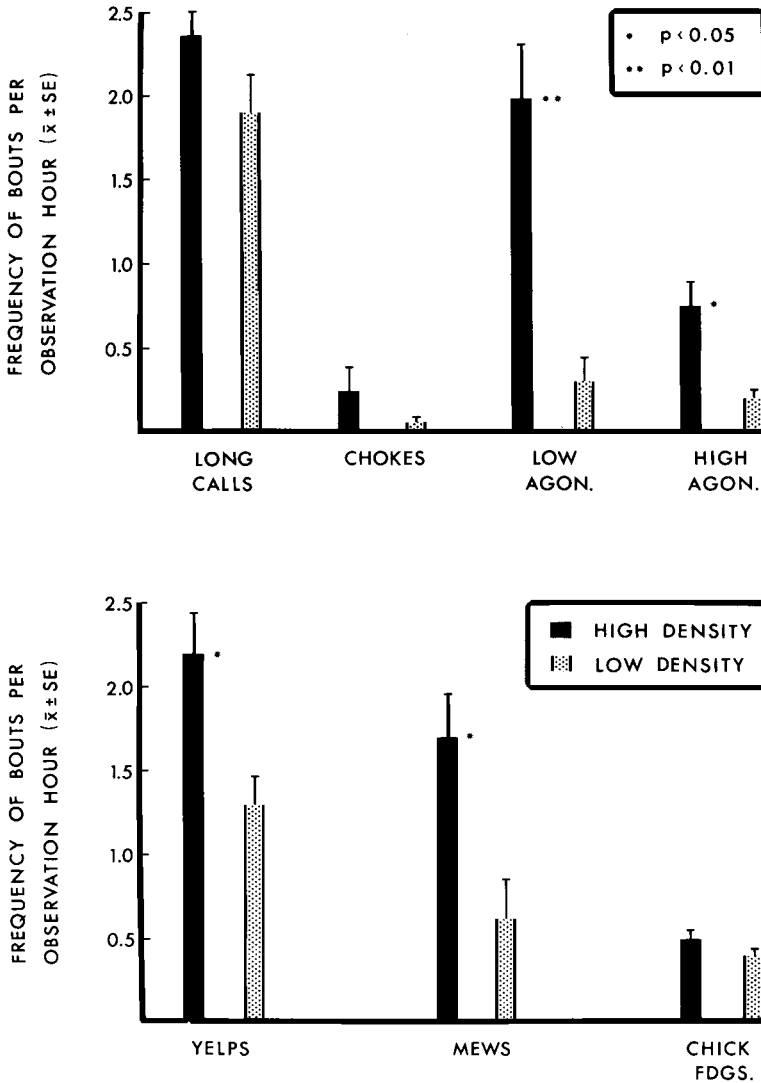
Fig. 1. Comparisons of the frequencies (mean ± SE) of selected behaviors of adult *L. marinus* in high and low density areas. Results of Mann-Whitney *U* tests are indicated.

significantly more often than birds on low density territories (21% and 9%, respectively; $\chi^2 = 5.647$, df = 1, $P < 0.05$). Prey items identified from the blind in 22% of the chick feedings included: fish (spp.), squid (*Loligo borealis*), crustaceans (spp.), mussels (*Mytilus edulis*), Common Eider chicks (*Somateria mollissima dresseri*), Herring Gull chicks, and goose-necked barnacles (*Lepas* sp.). There were no statistical differences in proportions of these items fed on high or low density territories.

Territory attendance.—Following hatching, one or both parents were in attendance on the territory continuously. As the season progressed and the chicks grew larger, the territory was sometimes deserted by both of the adults for varying periods of time (range <1 min to 5 h). At such times, the chicks on high density territories
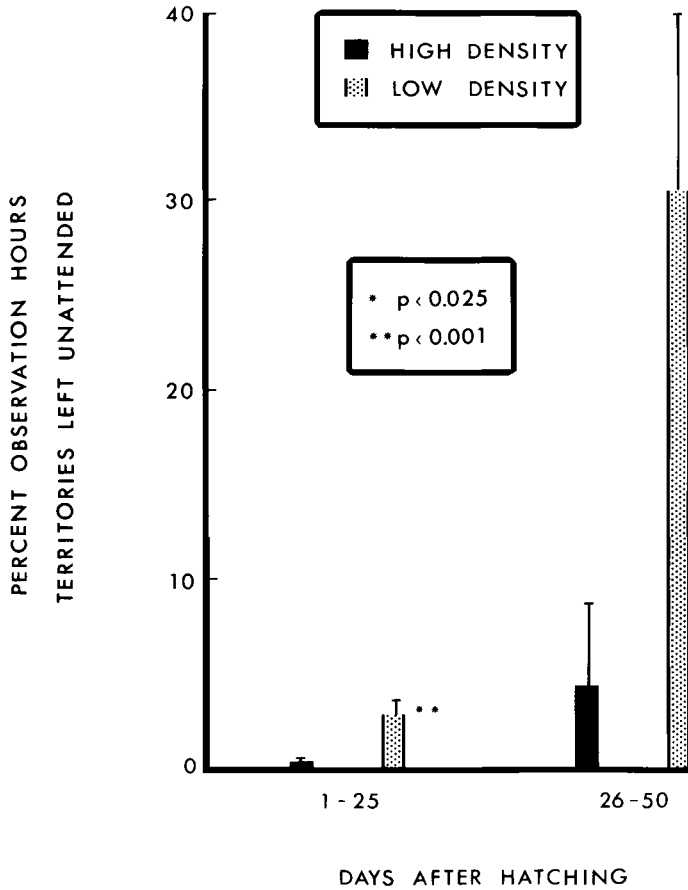
Fig. 2.   Comparisons of the percentage (mean ± SE) of observation hours that high and low density *L. marinus* breeding territories were left unattended (25 days and 26–50 days following chick hatching). Results of Mann-Whitney *U* tests indicated.

generally remained concealed in the vegetation, while the offspring of low density pairs were often out in the open pecking at substrate, preening, or resting. Incipient breeders or birds that had previously lost eggs or chicks sometimes intruded into these temporarily abandoned territories. During one such instance, a strange pair was observed to attack the undefended chick repeatedly and eventually to drive it off the territory. Usually, however, the intruding bird(s) directed mews at the hiding chick or engaged in agonistic behavior with adjacent territorial pairs. The latter were observed to drive intruders off unattended, adjacent sites on several occasions. Low density adults left their territories abandoned significantly more often than high density pairs during the first 25 days following hatching (means = 2.9 ± 0.9% and 0.1 ± 0.1%, respectively; $U = 40$, df = 4,8, $P < 0.001$), as well as days 26–50 following hatching (means = 31.2 ± 11.3% and 4.5 ± 3.7%, respectively; $U = 26$, df = 4,7, $P < 0.025$; Fig. 2). Males and females did not differ statistically in terms of the proportion of observation hours they spent on the territory at either high density (males = 55.0 ± 3.4%, females 52.1 ± 3.2%) or low density sites (males 54.4 ± 4.4%, females 45.0 ± 3.7%).

DISCUSSION

Hunt and Hunt (1976) proposed a model that predicts that in the absence of interspecific predation, conspecific interference (a source of chick mortality in large larids) may select for increased territory sizes. In that event, gulls breeding on smaller territories should be at a disadvantage in terms of reproductive success. The results of the present study of Great Black-backed Gulls breeding in high and low density areas are consistent with this model. Other potential explanations of the differential reproductive success observed between high and low density territories in the present study include asynchrony in the seasonal timing of egg laying and hatching (Paynter 1949, Vermeer 1963, Patterson 1965, Kadlec and Drury 1968), peripheral versus central nesting position in the colony (Coulson 1966, 1968; Tenaza 1971), or age differences between the two groups (Davis 1975). These explanations, however, may be discounted for the most part. First, the mean hatching dates of high and low density breeders did not differ statistically. Second, in terms of colony structure, the Great Black-backed Gull is one of the least "social" of the larid species and has even been described as a "solitary" nester (Harris 1964). Because inter-nest distances and territory sizes of *L. marinus* are generally greater than many of its smaller congeners (e.g. *L. pipixcan,* Burger 1974; *L. fuscus,* MacRoberts and MacRoberts 1972; *L. argentatus,* Parsons 1976), assignation of central versus peripheral status was sometimes difficult. By definition, however, the majority of low density nesters was peripherally located in the colony and fledged significantly more chicks than more centrally positioned, high density nesters. Third, although we have no data regarding the age structure of our study colony, it has been demonstrated for several species that nesting position in stable colonies is generally unrelated to age (Tenaza 1971, Nelson 1978). In addition, Davis (1975) has shown that young Herring Gulls tend to breed later in the season than older birds. Again, it must be emphasized that there was no statistical difference in the mean hatching dates of chicks from high and low density territories.

Comparisons of our reproductive data with those in the literature indicate that 1979 was a fairly "typical" breeding season. Overall, the Great Black-backed Gulls on Little Duck Island produced 2.75 eggs per pair, had a hatching success of 84%, and a fledging success of 59%. Previous reports of egg production range from 2.68 to 2.90 eggs per pair and hatching success from 39 to 76% (Harris 1964, Erwin 1971, McGill 1977, Verbeek 1979). Although McGill (1977) reported a fledging success of only 38%, the mean inter-nest distance in that colony ($\bar{x}$ = 4.9 m) was much lower than that in the present study. This fact may offer further support for the hypothesis that increased territory density is related to reduced reproductive success of *L. marinus*.

The difference in fledging success of pairs on high versus low density territories also did not seem directly related to increased frequency of chick feedings by the latter. Although feeding frequency has been reported to be one of the most important correlates of fledging success for Herring Gulls (Weaver 1970), there were no differences in the frequency of feeding by high and low density Great Black-backed pairs. These data may be misleading for two reasons, however. First, a regurgitated meal was generally consumed entirely by a brood of two or three chicks on low density territories unless the food item (e.g. a large fish or squid) was unmanageable and required further digestion by the parent. On high density territories, however, adults reconsumed freshly regurgitated food significantly more often than low density

parents, because either the chick was satiated or the feeding bout was interupted by the approach of a territorial neighbor. Presumably this same food was presented to the chick at a later time, and this may have inflated the feeding frequency recorded on high density territories. Second, behavioral data were recorded only from 0600–1200. It is possible that over the course of the entire day adults on low density territories did, in fact, feed their chicks more often than did high density pairs.

Analyses of behavioral data revealed several factors that may have been related to the reproductive differential between high and low density Great Black-backed pairs. There were more nonbreeding, territorial pairs (i.e. incipient breeders or pairs that had lost their eggs or chicks) in high density areas than in low density areas. High density breeders engaged in more bouts of agonistic behavior (i.e. low level, high level, and aggressive choking) than low density pairs, and more of these interactions were with nonbreeding, territorial pairs. Increased investment in territorial behavior may have decreased the investment high density pairs were able to place in other types of parental care. This is reflected by the fact that, following hatching, high density pairs left their territories unattended significantly less often than low density adults. Presumably both members of low density pairs were able to forage to feed their larger broods at these times. It is significant that Weaver (1970) found that reduced nest attentiveness was significantly correlated with increased brood size in the Herring Gull.

The increased level of agonistic behavior on high density territories may also have contributed to the significant decrease in chick survival on those territories. Heavy chick mortality (especially during the first few weeks following hatching) due to conspecific aggression has been documented in several larid species (Paynter 1949, Parsons 1971, Hunt and Hunt 1976). This phenomenon may be of more importance on high density territories during years of decreased food availability, as hungry chicks may be more likely to intrude into neighboring territories and be attacked by adult conspecifics (Hunt and McCloon 1975). Chicks on low density territories would be able to wander over a much larger area without intruding on a neighboring territory. This contention is supported by the fact that adults on high density territories engaged in significantly more bouts of yelping and mewing than low density pairs, even though the frequency of feeding bouts was the same between the two groups (despite the greater number of chicks on low density sites).

Stout (1975) indicated that the yelp of *L. glaucescens* was utilized in agonistic contexts, but he was unable to assign any clear function to this vocalization. Our observations of *L. marinus* suggest that during the posthatching period both the mew and yelp calls (often given together) appear in the context of locating chicks and/or attracting them to the vicinity of the parent (usually for the purposes of feeding). Adults were also observed to utilize a combination of yelping and mewing when their chicks approached a territorial boundary or when a chick was being approached by a territorial neighbor. Conceivably, the higher frequencies of yelps and mews recorded on high density territories were due to the fact that chicks wandering over such territories were more likely to come into close proximity to adult conspecifics on neighboring territories than were chicks of low density pairs.

Hunt and Hunt (1976) indicated that past attempts to relate reproductive success to either nesting density (in terms of nests per unit area) or mean nearest-neighbor distance have produced either negative or conflicting results, because neither of these parameters is an indicator of territory size *per se*. Our data suggest that, in addition

to territory size, the number of contiguous territories (i.e. territory density) may be important in determining chick survival. In other words, on those nest sites with only one or two territorial neighbors, chicks could, in fact, wander off their natal territories without intruding onto a neighboring territory. The relationship of conspecific interference, territory size, and reproductive success may be of more significance in those large larids in which interspecific predation is not a major source of mortality. In this context, Vermeer (1970) has suggested that the body size of a gull species may be inversely correlated to its aggregative tendency. This would explain negative or contradictory results in past attempts to investigate this problem in some of the smaller larid species. Given the large size of the Great Black-backed Gull, its relatively reduced social tendency (in terms of inter-nest distance and territory size), and the apparent disadvantage (in terms of fledging success) suffered by pairs breeding on high density territories, it is somewhat surprising that the majority of the breeding territories in our study site were of this type. Possible explanations of this fact may include a relatively recent freedom from interspecific predation pressure during the species' rapid southern expansion during the past 50 yr, a high population density relative to available breeding habitat, habitat constraints not readily apparent that prevented more pairs from nesting in low density areas, or some advantage accrued by the chicks of high density breeders that was not revealed in our 1-yr study of the problem.

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