

TERRITORIALITY AND BEHAVIORAL CORRELATES OF REPRODUCTIVE SUCCESS OF GREAT BLACK-BACKED GULLS

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ABSTRACT.—Territorial characteristics and behavioral correlates of reproductive success were examined in a population of Great Black-backed Gulls (*Larus marinus*). Territories were defended from the preincubation through the postfledging periods, and 53% of the territories under observation increased in size following chick hatching. Territorial adults displayed significantly more high-level agonistic behavior toward non-neighboring intruders than they did toward neighboring intruders. Most agonistic interactions, however, occurred between adjacent territorial neighbors, and only small segments of territorial boundaries were consistent sites of intense agonistic interaction.

Chick mortality was not related to percent vegetative cover, nearest-neighbor distance, territory size, or intrusion pressure. Chick mortality was positively correlated, however, with both the number of contiguous territories and the frequency of agonistic interactions of male gulls. Both post-hatch frequencies of neighbor intrusions and intrusions by non-neighboring conspecifics were positively correlated with the number of contiguous territories, but were not related to territory size. Finally, the time that adults left their territories abandoned during the posthatch period was negatively correlated with the frequency of intrusions (by both neighboring and non-neighboring conspecifics) and positively correlated with the number of chicks fledged. Received 20 May 1981, accepted 18 August 1981.

THE importance of territoriality and nest spacing in avian reproductive biology has long been recognized (Howard 1920). Recently, several authors have examined relationships between reproductive success in gulls and social and/or environmental factors associated with larid spacing systems. For example, Hunt and Hunt (1976) suggested that in the absence of interspecific predation, larger territories may be advantageous to Glaucous-winged Gulls (*Larus glaucescens*) because of a concomitant reduction in conspecific interference and associated chick mortality. Ewald et al. (1980) conducted a cost/benefit analysis of territory size of the Western Gull (*L. occidentalis*) and found that chick mortality was greater on small territories, but that adults that defended larger territories invested significantly more time in agonistic behavior. In addition, this study indicated that intrusion pressure, proximity to clubs (i.e. large aggregations of gulls), and vegetative structure were all important correlates of territory size. In contrast, Butler and Trivel-

piece (1981) suggested that the number of contiguous territories around each nest site might be a more important determinant of fledging success than territory size *per se* in Great Black-backed Gulls (*L. marinus*). Finally, Burger (1980) described three different-sized territories defended by Herring Gulls (*L. argentatus*) that were contextually dependent upon the phase of the reproductive cycle as well as upon the identity of the intruder. Whether or not these observations of *L. argentatus* may be extended to other species remains to be determined, as does the significance of such differential defense in terms of reproduction.

It is clear that the dynamics of territorial spacing and the role of this phenomenon in larid breeding ecology may be more complex than originally pictured by early investigators. The objectives of the present study were to: (1) describe some of the characteristics of territoriality in Great Black-backed Gulls, and (2) examine some of the more important behavioral correlates associated with reproductive success in this species.

METHODS

This study was conducted on Little Duck Island, Hancock County, Maine, between April and October

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1980. Approximately 500 pairs of *L. marinus* nested in two large meadows in habitat that consisted largely of several species of grasses (*Gramineae*), stinging nettle (*Urtica dioica*), angelica (*Angelica lucida*), and raspberry (*Rubus idaeus*); the area also included exposed granite outcroppings. The island supported no mammalian predators, although Herring Gulls, a pair of Common Ravens (*Corvus corax*), and at least one pair of Black-crowned Night Herons (*Nycticorax nycticorax*) bred there. The island was also uninhabited, so study animals were subjected to disturbance only from the observers.

A blind was erected on masonry scaffolding at the periphery of the colony during the preincubation stage of the Great Black-backed Gull breeding cycle. We marked 51 representative nests that were close enough to the blind for us to monitor for the presence of chicks. The number of eggs laid and chicks hatched was determined during nest checks conducted during May–June. Chick survival at all nest sites was determined via observations made from the blind in order to avoid observer disturbance 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.

Adults on a total of 30 nest sites were color marked and sexed on the basis of copulations and size differences. Behavioral observations were conducted systematically between 0500 and 2100 from May to August 1980 (3,578 nest-hours). These data were supplemented with limited nocturnal observations and data collected during the preincubation and postfledging periods. The frequency, apparent stimulus, and identity of adults engaged in a variety of behaviors were recorded, but only the following were analyzed in the present study: long-call, grass-pull, upright agonistic, face-off (i.e. squat-and-freeze), jab, attack, fight, charge, chase, and choke (in an agonistic context). All behavior patterns were operationally defined to remain as consistent as possible with previous literature (Moynihan 1958, Tinbergen 1959, Stout et al. 1969, Stout 1975). Data collection was facilitated with binoculars (10×), digital stopwatches, super-8 mm movie cameras, and aerial photographs taken in May 1980. Behavioral data from the posthatch period were collected from only those territories ($n = 19$) that were still entirely visible over dense vegetation and that had both adults in attendance for the entire season.

Boundaries where agonistic interactions occurred were mapped on aerial photographs. The remaining territorial boundaries at each site were determined by drawing lines that encompassed areas of less intense defense as well as consistent sites of adult and chick activity. Interne distances, territory sizes, and percent vegetative cover over 60 cm in height were measured using both aerial photographs and measurements made with an optical rangefinder. In-

trusions by adjacent neighbors (usually boundary-related) and non-neighboring conspecifics were recorded whether or not the territorial pair was in attendance. All data in the present study were analyzed using the Chi-square statistic, Wilcoxin signed-ranks test, or the Spearman's rank correlation coefficient and associated t -statistic.

RESULTS

Phenology and reproductive success.—In 1980, *Larus marinus* adults were observed in the vicinity of and on their breeding territories in early April, and nest construction began as early as 10 April. The first clutch was initiated on 24 April, the mean (\pm SE) clutch initiation date was 4 May (± 2 days), and the mean clutch size was 2.98 eggs per breeding pair. The first chick hatched on 22 May, and hatching success was 95%. Chick fledging occurred between 14 July and mid-September. Breeding pairs fledged 1.53 chicks per pair, which was 54% of the chicks hatched. By comparison, this population had a fledging success of 62% in 1978 and 59% in 1979.

Territoriality.—In 1980, the mean (\pm SE) nearest neighbor distance (6.7 ± 0.8 m), the mean area of primary territories during the posthatch period (78.6 ± 18.8 m²), and the mean number of contiguous territories bounding each nest site (2.5 ± 0.2) were similar to 1979 data. Territorial defense by adults occurred from preincubation through the postfledging period, and could generally be divided into two categories: low-level agonistic behaviors of a display nature (e.g. upright agonistic, face-off, grass pull, choke) that rarely escalated into more overt types of aggression, or more high-level aggressive acts (e.g. charge, chase, jab, attack) that often resulted in one adult's flying away or, occasionally, in a fight. Adults on their territories reacted very differently depending on whether they were engaged in an interaction with a neighboring, territorial conspecific (62% of all agonistic interactions), or were defending against an intrusion by a non-neighboring gull. Neighbor intrusions resulted in more low-level agonistic responses (82.9%) and fewer high-level responses (17.1%). In contrast, intrusions by non-neighbors resulted in fewer low-level responses (31.6%) and significantly more high-level agonistic interactions (68.4%; $\chi^2 = 261.374$, $df = 1$, $P < 0.001$). There were no significant differences in these ratios during the pre- and posthatch phases of

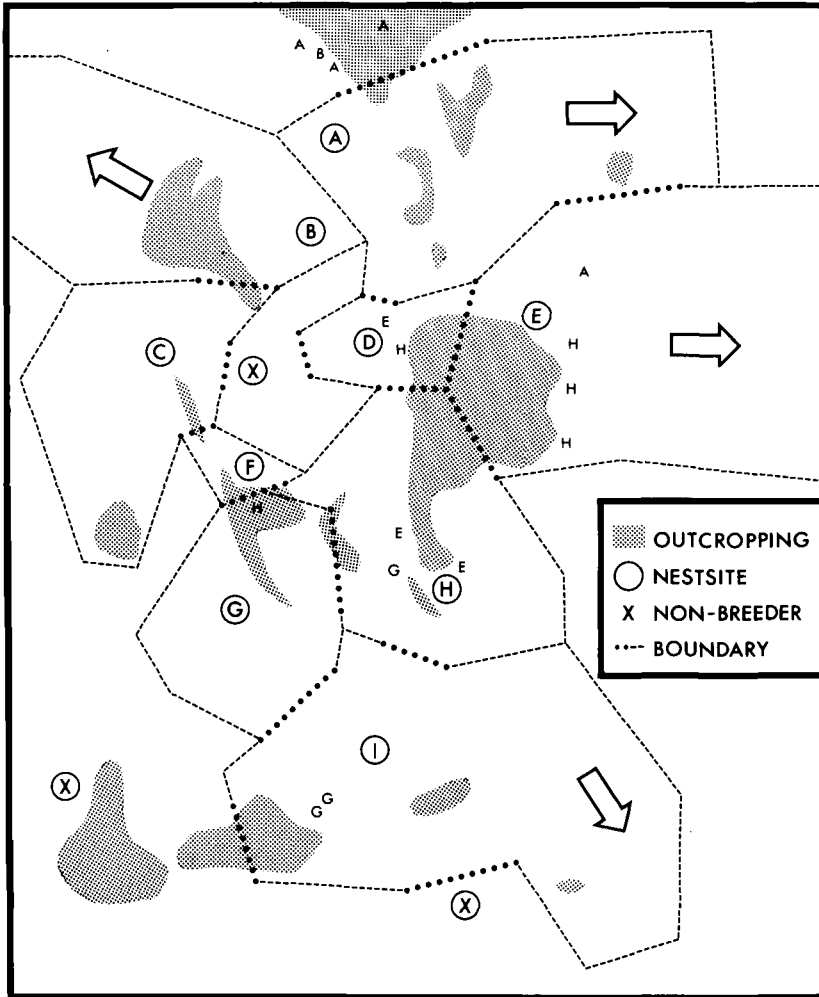


Fig. 1. Map of representative group of *Larus marinus* breeding territories, illustrating segments of intense agonistic interaction on boundaries (heavily dotted lines) and the significance of rock outcroppings. Because territorial interactions were infrequent elsewhere, lines were drawn that encompassed areas of adult and chick activity. Large letters indicate nest locations, and small letters represent sites of defense against non-neighboring conspecifics outside of the primary territory. Arrows show direction of posthatch territorial expansion, and all areas in white represent vegetation.

the breeding cycle. There were also very few statistical differences in the pre- and posthatch frequencies of high-level agonistic behavior for either sex (Butler and Janes-Butler MS). Although males did not show seasonal differences in low-level agonistic behavior, females demonstrated significant increases in the frequency of posthatch low-level agonistic acts ($\bar{x} = 0.23 \pm 0.05/h$), as compared to prehatch frequencies ($\bar{x} = 0.03 \pm 0.01/h$; $T = 30$, $n = 19$, $P < 0.01$). Females also exhibited signifi-

cant increases when the pre- and posthatch frequencies of long-calls were compared (means = $0.05 \pm 0.01/h$ and $0.53 \pm 0.08/h$, respectively; $T = 0$, $n = 19$, $P < 0.001$), as did males (means = $0.11 \pm 0.04/h$ and $1.0 \pm 0.17/h$, respectively; $T = 0$, $n = 19$, $P < 0.001$).

During the first 20 days following hatching, one or both parents were generally continuously in attendance on the territory. As chicks grew older, however, both adults frequently left the territory abandoned for varying periods

of time. When the territory was left unattended, we assumed that both adults were out foraging, although chick feeding frequency was not correlated with the percentage of observation hours that territories were abandoned. Chicks less than 30 days of age were generally inactive in dense vegetation during the adults' absence, while chicks 40 days and older were observed to defend the territory against both intruding adults and chicks. Chicks that had been flying for as long as 25 days (i.e. 74 days following hatching) roosted on the territory at night with adults, spent long periods alone on the territory during the day, and were often fed there by their parents. Large numbers of adults and fledged young were still observed on the shoreline of the breeding colony as late as 24 October 1980.

Over 80% of the agonistic interactions between neighboring adults at our study site took place over relatively small segments (9–39%) of the irregular territorial boundaries (Fig. 1). This was due to the fact that 40–90% of the total area of all territories under study was covered by dense vegetation during much of the posthatch period, and agonistic interactions across densely vegetated boundaries were rare. Only later in July did adult and chick activity begin to flatten vegetation significantly. Approximately 85% of all territories surveyed contained exposed granite outcroppings, and these outcroppings were frequently (69%) shared by one or more territorial pairs. Because many parent-chick feeding interactions took place on exposed rock surfaces, and because territorial neighbors were highly visible to each other on shared outcroppings, these areas were also frequent sites for boundary disputes between neighboring territorial adults. The other sites of intense interaction between adjacent territorial adults were areas in which vegetation was generally sparse or less than 60 cm in height. The locations of sites of intense interaction between adjacent pairs in 1980 were consistent with those observed for these same pairs in 1979.

Ten of 19 territories measured during the pre- and posthatch phases increased in size from one phase to the next. Some territories with few contiguous neighbors or slightly earlier hatching dates expanded by as much as 100% during the posthatch phase. Much of this expansion seemed related to increased mobility of the chick and the tendency of adults to

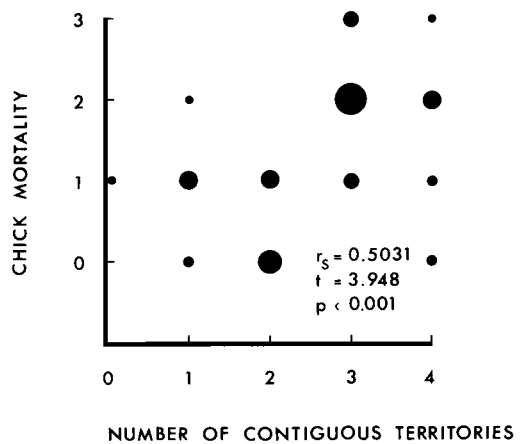


Fig. 2. Scattergram and Spearman's rank correlation coefficient of the relationship between chick mortality and the number of contiguous territories surrounding each nest site. Diameter of circles is proportional to the number of data points ($n = 51$).

maintain contact with their offspring. Boundaries of intense interaction, however, did not change over the course of the season, and territorial expansion was directed toward undisputed areas. Territories that possessed 3, 4, or 5 territorial neighbors expanded very little (if at all) following hatching. Territorial interactions outside the primary territory were too few (less than 2% of all post-hatch agonistic interactions) to allow us to determine the possibility and extent of defense of either secondary or unique territories (after Burger 1980). Acts of territorial defense by both males and females outside of the primary territory (even including defense of nest-sites on adjacent territories), however, were always directed at non-neighboring intruders, were confined to the posthatch period, and usually (85%) occurred in the absence of territorial neighbors.

Behavioral correlates.—Most chick mortality (91%) occurred within 20 days following hatching. Although few chick deaths were actually observed (and the study area was not entered for examination of carcasses), several cases were directly attributable to attacks by adjacent territorial conspecifics. Chick mortality was not observed to be related to the percent vegetative cover over 60 cm in height on the territory. Moreover, no significant correlations were found between chick mortality and either nearest-neighbor distance, territory size, frequency of neighbor intrusions ($\bar{x} =$

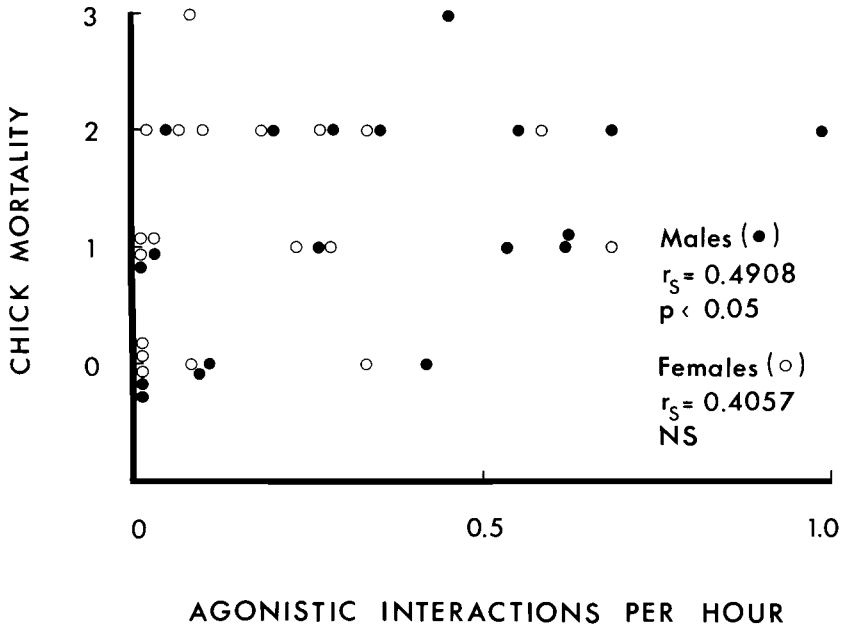


Fig. 3. Scattergram and Spearman's rank correlation coefficients of relationships between chick mortality and mean frequencies of male and female agonistic interactions during the posthatch period.

$0.16 \pm 0.04/h$), frequency of intrusions by non-neighbors ($\bar{x} = 0.10 \pm 0.03/h$), or the combined frequencies of intrusion divided by territory size ($\bar{x} = 0.009 \pm 0.003/h/m^2$). Chick mortality, however, was significantly correlated with both the number of contiguous territories ($r_s = 0.5031$, $t = 3.948$, $P < 0.001$; Fig. 2) and the posthatch frequency of male agonistic interactions ($r_s = 0.4908$, $t = 2.323$, $P < 0.05$; Fig. 3).

The relationships between territory size, frequency of agonistic interactions, and intrusion pressure were also examined for possible correlations. Posthatch territory size (primary) was not significantly related to either the frequency of male ($\bar{x} = 0.32 \pm 0.07/h$) or female ($\bar{x} = 0.17 \pm 0.05/h$) agonistic interactions (based on time in attendance on the territory), or to the frequency of intrusions by either neighbors or non-neighbors (based on total observation time). However, the frequencies of posthatch intrusions by neighbors ($\bar{x} = 0.16 \pm 0.04/h$; $r_s = 0.7237$, $t = 4.324$, $P < 0.001$) and by non-neighboring gulls ($\bar{x} = 0.10 \pm 0.02/h$; $r_s = 0.6864$, $t = 3.332$, $P < 0.01$) were positively correlated with the number of contiguous territories (Fig. 4). Finally, the percentage of observation hours that both adults

left the territory abandoned ($\bar{x} = 18.4 \pm 3.5\%$) following chick hatching was negatively correlated with the intrusion frequency (neighbors and non-neighbors combined; $r_s = -0.6935$, $t = 3.850$, $P < 0.01$) and positively correlated with the number of chicks fledged ($r_s = 0.5248$, $t = 2.466$, $P < 0.05$; Fig. 5).

DISCUSSION

Past investigation of the Great Black-backed Gull has concentrated largely on reproductive biology rather than behavioral ecology (Harris 1964, Erwin 1971, Verbeek 1979). The results of the present behavioral study suggest that territoriality in *Larus marinus* exhibits both similarities and differences with the spacing systems that have previously been described for the Herring Gull (Tinbergen 1956, Burger 1980), the Glaucous-winged Gull (Vermeer 1963, Hunt and Hunt 1976), and the Western Gull (Hunt and Hunt 1975, Ewald et al. 1980). Unlike the Western Gull, territory size was not related to percent vegetative cover, intrusion pressure, or chick mortality. The number of contiguous territories surrounding each breeding pair was a much more significant factor in terms of both chick mortality and investment in agonistic behavior. This supports previous

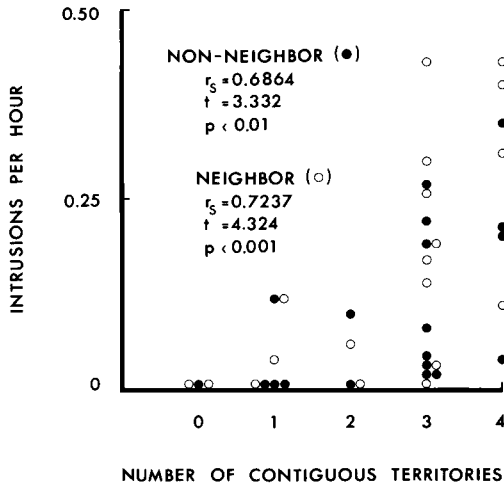


Fig. 4. Scattergram and Spearman's rank correlation coefficients of relationships of the mean frequencies of both neighbor and non-neighbor intrusions to the number of contiguous territories during the posthatch period.

observations of Great Black-backed Gulls that indicated that nesting density was an important determinant of reproductive success (Butler and Trivelpiece 1981). Although it was not surprising to find a relationship between the frequency of neighbor intrusions and the number of contiguous territories, it is interesting to note that the frequency of intrusions by non-neighboring birds was also significantly correlated with the number of contiguous neighbors. Presumably this may be explained by an attraction of strange birds (either juveniles, unmated adults, or unsuccessful breeders) to areas of high nesting density. Unlike the Western Gulls observed by Ewald et al. (1980), our study animals did not nest in the vicinity of clubs.

Larus marinus breeding territories did tend to expand during the posthatch period, as has been reported for *L. occidentalis* (Hunt and Hunt 1975), *L. glaucescens* (Hunt and Hunt 1976), and *L. argentatus* (Burger 1980). Rather than an actual increase in territory size, however, an alternative explanation for this apparent posthatch expansion may be a change in territorial utilization patterns by breeding pairs. Prehatch defense of largely unutilized and undisputed areas of a territory may not confer any advantage to incubating adults. This would account for the facts that posthatch

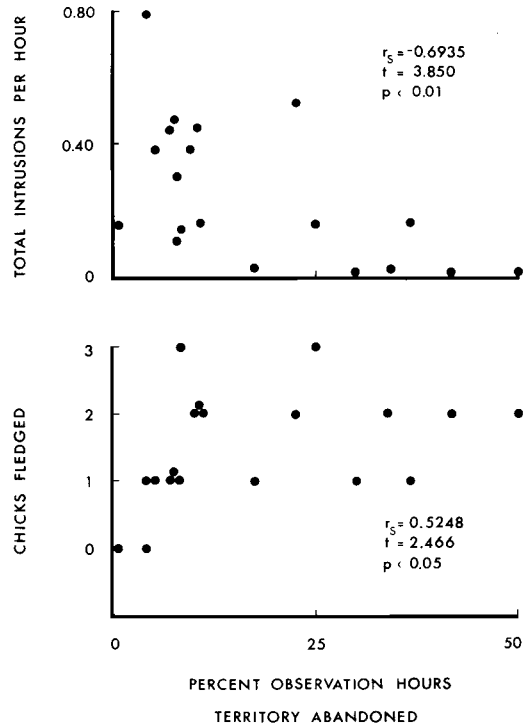


Fig. 5. Scattergrams and Spearman's rank correlation coefficients of the relationship between the percent of observation hours that breeding territories were left unattended by adults during the posthatch period and the mean frequency of total intrusions (by both neighboring and non-neighboring conspecifics) (above) and chicks fledged (below). Intrusion rates were combined under the assumption that the risk of chick mortality associated with adult aggression was independent of the identity of the intruder.

territorial expansion generally occurred in the direction of previously undisputed habitat, and that boundaries of intense interaction did not change over time. The problem of territorial expansion may be one of definition (i.e. a territory is any defended area), and may be resolved with data concerning the constancy of such expansion by individual pairs for several breeding seasons.

Burger (1980) has reported that Herring Gulls defended three discrete types of territories, the boundaries of which were contextually dependent on the identity of the intruder. Certainly *L. marinus* adults were more overtly aggressive toward non-neighboring intruders than they were toward intrusions by neighboring conspecifics. In addition, adult territory holders

were only observed in agonistic interactions outside of the primary territory with non-neighboring intruders. The applicability of Burger's classification (i.e., primary, secondary, and unique territories) to the Great Black-backed Gull spacing system, however, remains speculative due to the paucity of observed interactions that occurred outside of the primary territory. In our study animals, at least, charging or attacking conspecifics outside of the primary territory may simply have been an opportunistic investment on the part of the defender. Driving a non-neighboring intruder from an adjacent territory (in the absence of that territory's owner) may be adaptive in terms of a reduction in potential risk to the defender's chicks due to conspecific interference (Paynter 1949, Parsons 1971, Hunt and Hunt 1976). The fact that such acts were generally performed in the absence of a territorial neighbor and occurred largely during the post-hatch period supports this contention. Alternative explanations include both species-specific differences in territorial defense as well as nesting densities and agonistic interaction rates that were too low to facilitate mapping of a secondary territory.

The structure and complexity of habitat (e.g. vegetation) has been demonstrated to be a significant factor in the territorial systems of Franklin's Gull (*L. pipixcan*; Burger 1974), Laughing Gulls (*L. atricilla*; Burger and Beer 1975), and Western Gulls (Ewald et al. 1980). Although Ewald et al. (1980) found that the percentage vegetative cover was positively related to territory size (and hence to chick mortality), this relationship was confounded by the proximity of some nest sites to gathering places for aggregations of gulls (i.e. clubs). Much of the area of gull territories at our study site was densely vegetated, and percent cover was unrelated to territory size. Habitat structure was an important factor, however, as the locations of rock outcroppings and sparsely vegetated areas were clearly significant in determining boundaries and borders of more intense agonistic interaction. This was due to the importance of outcroppings as foci for much of the parent-offspring interaction that occurred early in the posthatch period, as well as the fact that these sites provided areas of high visibility between adjacent territorial pairs. The importance of the outcroppings diminished later in the posthatch period as chicks flattened

trails and resting places in the more heavily vegetated areas of the territories. The role that outcroppings play may be reduced in less densely vegetated colonies. It should be noted that McGill (1977) reported a fledging success of only 38% in an *L. marinus* population in which vegetative cover and internest distances were much lower than those in the present study.

Increased posthatch frequencies of long calls (in agonistic contexts) by both sexes were probably related to both increased chick mobility and the frequency of adult overflights associated with foraging trips to feed chicks. Males were consistently involved in more agonistic interactions than were females, and males failed to display, overall, major post-hatch increase in frequencies of agonistic behavior. In contrast, females exhibited a significant increase in the frequency of agonistic interaction. This may be explained by decreased female investment in incubation and a concomitant increase in "opportunities" to engage in agonistic interaction associated with the posthatch period (Butler and Janes-Butler MS). Overall, the frequency of posthatch agonistic interaction in 1980 was lower than that recorded in 1979 (Butler and Trivelpiece 1981). This was probably due to the fact that a number of territories defended by incipient pairs (i.e. pairs that displayed courtship behavior and regularly defended a territory, but did not lay eggs) in 1979 possessed nests with eggs in 1980. As most agonistic interactions occur between territorial neighbors, and incipient pairs were involved in more interactions than breeding pairs, the reduced frequency of agonistic behavior in 1980 is not surprising.

The significance of temporary territorial abandonment by adult *L. marinus* is not yet clear. As has been reported for Herring Gulls (Weaver 1970), abandonment in the present study was positively correlated with brood size (in terms of chicks fledged). Despite the fact that there was no correlation between chick-feeding frequency and abandonment, we assumed that during the adults' absence both members of the pair may have been out foraging to feed their significantly larger broods. As has been pointed out previously (Butler and Trivelpiece 1981), observed feeding frequencies for single-chick broods may be inflated due to the number of food items reconsumed by adults that are presented to their chicks at

a later time. In contrast, regurgitated food was reconsumed less often by adults with 2- or 3-chick broods. The percentage of observation hours in which territories were left unattended was also inversely correlated with the combined frequency of intrusions by both neighboring and non-neighboring gulls. The risk of chick loss on territories where the potential for conspecific interference is greater may force adults to remain in attendance, and therefore prevents simultaneous foraging. This fact may also result in increased chick mortality, as hungry chicks are more likely to wander into the adjacent territories of aggressive adult neighbors (Hunt and McCloon 1975).

Conspecific interference may take the form of either attacks on chicks that have intruded into the territories of neighboring gulls or attacks on chicks on their natal territories by intruding adults. Over the course of four breeding seasons, relatively few chick deaths were actually observed. Although both types of conspecific interference have been recorded, direct observation and chick carcass examination suggest that attacks by neighboring conspecifics on intruding chicks and exposure are the major sources of mortality in this population. This would in part account for the fact that, although chick mortality was correlated with both the frequency of male agonistic interactions and the number of contiguous territories, it was not directly related to the frequencies of intrusions by neighboring or non-neighboring adults. In other words, it was intrusions by chicks that most often resulted in mortality, rather than attacks from intruding adults. The relationship observed in the present study between the number of contiguous territories and chick mortality is a reflection of the greater risk that such chicks run of intruding into an adjacent territory. Most of the breeding territories in our study area were relatively large and heavily vegetated. We may hypothesize that in colonies in which nesting density is greater and/or habitat complexity reduced, this risk of chick mortality would be increased. Under such conditions, territory size may be more closely related to larid fledging success.

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