

TERRITORY SIZE DIFFERENCES IN RELATION TO REPRODUCTIVE STAGE AND TYPE OF INTRUDER IN HERRING GULLS (*LARUS ARGENTATUS*)

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ABSTRACT.—Breeding Herring Gulls defend three territory types, which vary in size depending on the stage in the reproductive cycle. Territory types are a function of the nature of the conspecific intruders and consist of a primary territory defended against neighbors, a secondary territory defended against non-neighbors, and a unique territory defended against all intruders under all conditions. In all three territory types, defense activity is highest at the nest. The unique area is smallest, the primary territory is intermediate in size and nonoverlapping with neighbors, and the secondary territories are largest and overlapping. The defense of each territory type is discussed in terms of the costs and benefits to the territory defender during each stage in the reproductive cycle. I suggest that one advantage of breeding synchrony within subcolonies is to prevent egg and chick loss due to territory size differences of the unsynchronized pairs. *Received 12 September 1979, accepted 6 March 1980.*

ORNITHOLOGISTS have been fascinated by the existence and adaptive significance of territory since Howard (1920) first described it. Although authors initially concentrated on documenting its occurrence, they later began classifying territories according to their use for foraging, nesting, or both (Nice 1941, Tinbergen 1953, Brown 1964). Many species of gulls breed in large colonies and defend breeding territories, but they obtain all their food away from the colony. Kirkman (1940) and Huxley (1934) suggested that the nesting territories of gulls resemble rubber discs, because their size varies under different conditions.

Subsequently, authors have shown that territory size varies as a function of age (Dhondt and Huble 1968, Ralph and Pearson 1971), time of day (Weeden 1965), and stage of the breeding cycle (Stenger and Falls 1959, Weeden 1965, Stefanski 1967, Falls 1969). Nonetheless, in most studies, territory size has been determined for a short period of time during only part of the reproductive cycle rather than from daily observations throughout the cycle. In gulls, territory size has often been obtained by measuring the distance to the closest neighbor. This distance may not be a good measure of territory size, because only in dense gull colonies might the nest be located in the center of the territory. Furthermore, territories are usually not round but are irregularly shaped.

Hunt and Hunt (1976) measured territory in Western (*Larus occidentalis*) and Glaucous-winged (*L. glaucescens*) gulls and found that it increased during the chick phase. Under some conditions, differences in territory size resulted in differences in reproductive success. Glaucous-winged Gulls with larger territories had higher reproductive success, as their chicks were not killed by neighbors. Hunt and Hunt did not mark the birds in their study for individual identification, however, and they determined territory boundaries on the basis of all encounters without considering whether they occurred with neighbors or non-neighbors. Furthermore, they did not look for specific territory size differences as a function of stage in the reproductive cycle.

Kirkman (1940), and later Patterson (1965), suggested that territory owners respond differently to conspecific neighbors than to non-neighbors. This aspect was

not stressed in either study, and their birds were not individually marked. Quantitative data on the reactions of gulls to intruding neighbors and non-neighbors are generally lacking in the literature. Investigators working with passerines have long known that males respond differently to the songs of neighbors as compared to non-neighbors (Weeden and Falls 1959, Emlen 1971). Such responses involve individual recognition, with the strength of the responses depending upon the location of the intruder relative to the territory and the territory-holder. These responses have not been directly related to shifts in territory size. The ability of gulls to recognize and respond differently to neighbors and non-neighbors could result in differences in how space is used and defended around nests.

In this paper I describe shifts in Herring Gull (*Larus argentatus*) territorial boundaries and territory size with respect to reproductive stage (pre-incubation, incubation, chicks) and type of intruder (neighbor, non-neighbor) and comment on the adaptive significance of these shifts. I hypothesize that territory owners would defend space differently depending upon their stage in the reproductive cycle and upon the type of intruder.

STUDY AREA AND METHODS

I observed the territorial behavior of Herring Gulls during 1976 and 1977 on Clam Island, New Jersey, where a colony of 800 pairs nested on *Spartina patens* and under bushes. Clam Island is a low salt-marsh island located behind a barrier beach in Barnegat Bay. Data from 1976 were used to generate hypotheses about the territorial defense of Herring Gulls to be tested in 1977.

In 1977, 15 color-marked pairs were observed from a blind for 8–12 h a day, 4 to 6 days a week, from before egg-laying (15 April) to fledging (15 July). Additional pairs that nested adjacent to the study area were color-marked so that the neighbors of all study animals could be determined. To color-mark gulls, I suspended a cup filled with dye from a small frame over the nest. A string connected to the cup allowed me to dump the dye on the gull once it resumed incubation. Gulls immediately flew, and I continued to pull the apparatus from beside the nest. Thus, the returning gull resumed incubation without any apparent effects. A neighbor was defined as either member of a Herring Gull pair whose territory abutted the primary territory of the pair being examined, while a non-neighbor was defined as any other conspecific.

I recorded the presence and location of every intruder on maps, the outcome of each encounter, the sex of the intruder when it was a neighbor, and the reaction and reproductive stage of all nearby territory owners. The sex of neighbors was determined by noting the copulatory position of all pairs observed to copulate at least twice. The sex of intruders was determined only when size differences were extreme. Aggressive interactions were recorded on data sheets listing the sex and status of the intruder and the outcome of the interaction. The exact location of each encounter was plotted on a scaled map. These daily maps of all territorial encounters could be related to the reproductive stage of each pair. Because the pairs were fairly synchronous, this resulted in about 10 pre-incubation, 20 incubation, and 32 post-incubation (chick phase) maps for each pair. During the entire study period, aggressive interactions varied from 2 to $60 \cdot \text{day}^{-1} \cdot \text{pair}^{-1}$ ($\bar{x} = 1.32 \pm 0.54 \text{ encounters} \cdot \text{pair}^{-1} \cdot \text{h}^{-1}$).

The areas of all individual territories were determined with a computer by tracing the defended areas onto a console that entered data directly into the computer. For the analysis, I drew a line that connected the outermost points of each territory type. This was straightforward for the unique and primary territory types, as these boundaries were relatively fixed and territorial clashes occurred at the boundaries. Furthermore, many nonattack defense behaviors (such as grass-pulling and upright posturings) occurred at the boundaries between neighbors. These defense behaviors confirmed the location of the precise boundary. The boundaries of secondary territories were less precise but could be computed, because the secondary boundary of one pair was the unique boundary of its neighbor. Furthermore, there were no points of defense for any pairs that were more than 2 m from other defense points. Such distant points were defended very early in the season (March), when territories were initially being established, but I did not include these data.

In order to test the hypothesis that territory size relates to the distance to the closest neighbor, I measured the distance from the center of a nest to the center of the four closest neighbors. The distance

TABLE 1. Behavior of territory owners with respect to reproductive stage and type of intruder. N = neighbor who is intruding, and NN = non-neighbor who is intruding. Shown are the types of intruders that a territory owner will chase as a function of stage.

Reproductive stage	Type of territory		
	Unique	Primary	Secondary
Pre-incubation			
Either member of the pair	N, NN	N, NN	NN ^a
Incubation			
Incubating bird ^b	N, NN		
Nonincubating	N, NN	N, NN	NN ^a
Chick phase			
Either member of the pair	N, NN	N, NN	NN ^a

^a Chases only when the neighbor whose primary territory the secondary territory overlaps does not chase it.

^b Chases only when its mate is not present.

of each of these neighbors (and combinations thereof) was then correlated with the computed mean primary territory size for each pair.

Data from 1976 generated the following hypotheses to be tested in 1977: (1) territory owners respond differently to neighbors than to non-neighbors, (2) three territory types are defended, and (3) these territory sizes vary with reproductive stage.

RESULTS

Three defended areas were discernible for each pair of Herring Gulls: a primary territory, a secondary territory, and a unique territory (Fig. 1). The primary territory was usually defended against all conspecific intruders. The secondary territory (larger than the primary territory) was defended against non-neighbors (except when the defender was incubating) whenever a neighbor did not chase the intruder. The unique territory, the smallest area, was defended against all intruders at all times. Table 1 summarizes the defense behavior of members of a pair, which varied seasonally depending upon reproductive constraints. Either member defended during the pre-incubation phase, while during the incubation period the nonincubating mate did the chasing. When its mate was not present, the incubating territory holder left its nest only to chase conspecifics (neighbor and non-neighbor) from its unique territory. During the chick phase, both members of each pair chased intruders from all defended areas. Territory owners chased intruders (only non-neighbors) from their secondary territory only when their neighbor (in whose primary territory the intruder landed) did not chase the intruder. Neighbors did not chase these intruders when only the incubating bird was present.

These interactions can be illustrated by an intruder that lands at X in Fig. 1: (1) If the intruder were a neighbor of pair 1, pair 1 would chase the intruder, because it would be in the primary territory of pair 1. (2) If the intruder were a non-neighbor, either a nonincubating bird from nest 1 would chase it, or (if no one from nest 1 chased it) a nonincubating bird from either nest 2 or 3 would chase it, as it would be in their secondary territories.

When plotted seasonally for the 15 pairs, the mean size of the secondary territory was always larger than that of the primary territory (Fig. 2), and the mean size of the unique territory was always smaller than that of the primary territory ($F = 28.6$; $df = 2, 161$; $P < 0.001$). Territories generally increased in size in early June following hatching. This was possible because one pair deserted its territory due to egg

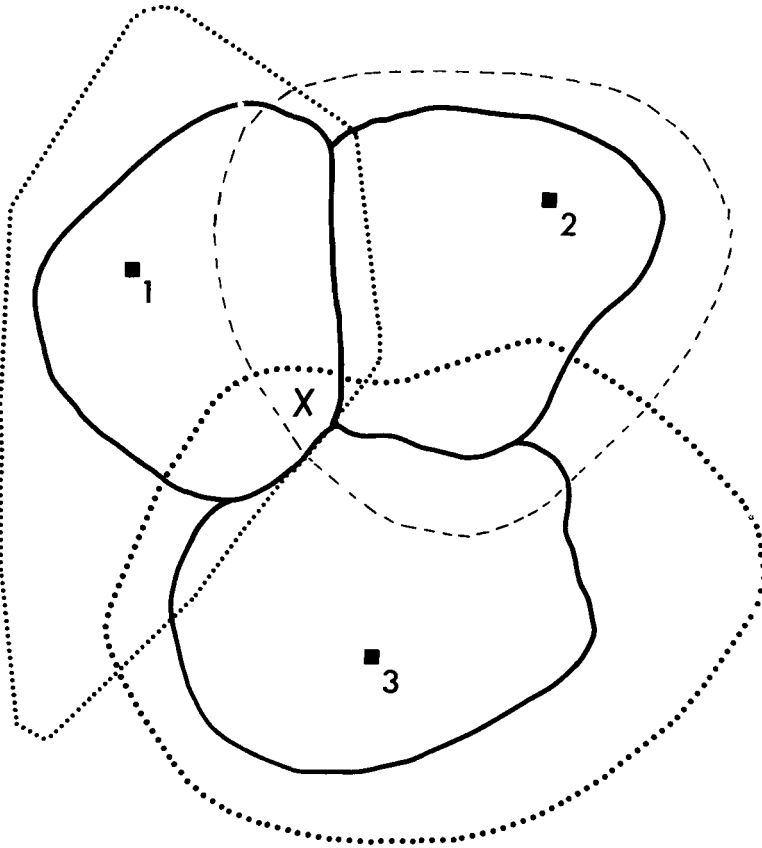


Fig. 1. Representation of territory types in Herring Gull. Solid line = primary territory; small dotted line = secondary territory of pair 1, large dotted line = secondary territory of pair 3, and dashed line = secondary territory of pair 2. The unique territory for pair 1 = the area bounded by the solid line on the left and the dashed and dotted lines within the solid line on the right. Square = the nest location; X = the point at which an intruder has landed (see text).

loss, and some previously unused space was occupied. Both events normally occur in gull colonies unless space is extremely limited.

Because mean territory size varied seasonally, gulls appeared to defend territories of different sizes at different periods in their reproductive cycle. To test this, I analyzed the data by reproductive stage (Fig. 3). Significant differences occurred within and among reproductive stages and territory types ($F = 53.9$; $df = 6,271$; $P < 0.001$). In general, all three territory types were significantly different in size during each reproductive stage (Table 2A). The variation in size as a function of reproductive stage for each territory type is shown in Fig. 3. Secondary territory size varied among all stages (Table 2B). The unique territory, however, was similar in size in the pre-incubation and incubation stages, and the primary territory was similar in size during the pre-incubation and chick phases (Table 2B).

Four pairs from nearby territories outside the study area lost their eggs to predators (crows and conspecifics) during the incubation period. All contracted the size of all three of their territories so that there were no significant differences among their primary, secondary, and unique territories ($F = 26.3$; $df = 1,50$; $P < 0.01$).

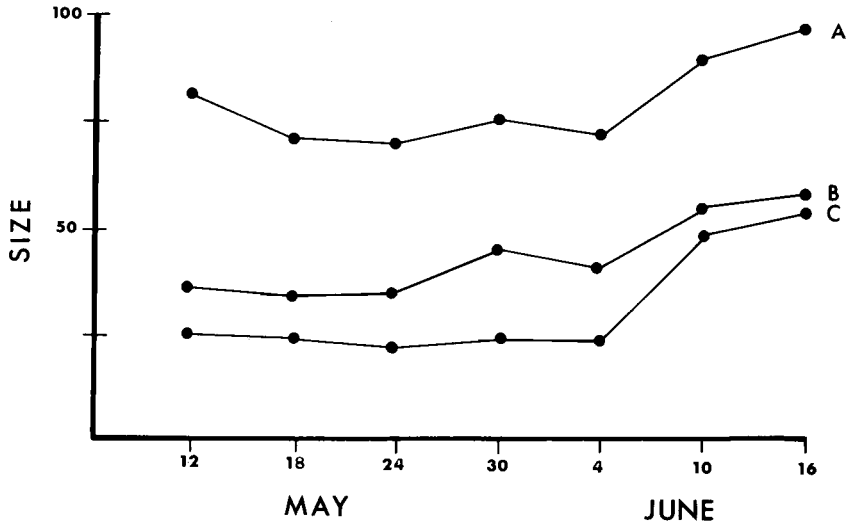


Fig. 2. Seasonal differences in primary (B), secondary (A), and unique (C) territories in Herring Gulls.

They reduced their unique ($\bar{x} = 20 \pm 5 \text{ m}^2$) and primary ($\bar{x} = 22 \pm 4 \text{ m}^2$) territory sizes to that of the unique territory of normally incubating pairs. The secondary territory stayed slightly larger ($\bar{x} = 26 \pm 8 \text{ m}^2$), as the birds still chased non-neighbor

TABLE 2. Statistical values for differences in the sizes of territory types defended as a function of reproductive stage and territory type.

Stage and type	t value	df	P <
A. Reproductive stage			
Pre-incubation			
Unique and primary	3.75	28	0.001
Unique and secondary	10.45	28	0.001
Primary and secondary	3.93	28	0.001
Incubation			
Unique and primary	0.67	28	NS ^a
Unique and secondary	3.06	28	0.005
Primary and secondary	2.65	28	0.05
Chick phase			
Unique and primary	4.83	26	0.001
Unique and secondary	13.42	26	0.001
Primary and secondary	9.12	26	0.001
B. Territory types			
Secondary			
Pre-incubation and incubation	6.86	28	0.001
Pre-incubation and chick	3.02	26	0.005
Incubation and chick	7.92	26	0.001
Primary			
Pre-incubation and incubation	3.81	28	0.001
Pre-incubation and chick	1.97	26	NS
Incubation and chick	4.95	26	0.001
Unique			
Pre-incubation and incubation	0.66	28	NS
Pre-incubation and chick	4.93	26	0.001
Incubation and chick	5.43	26	0.001

^a NS = not significant.

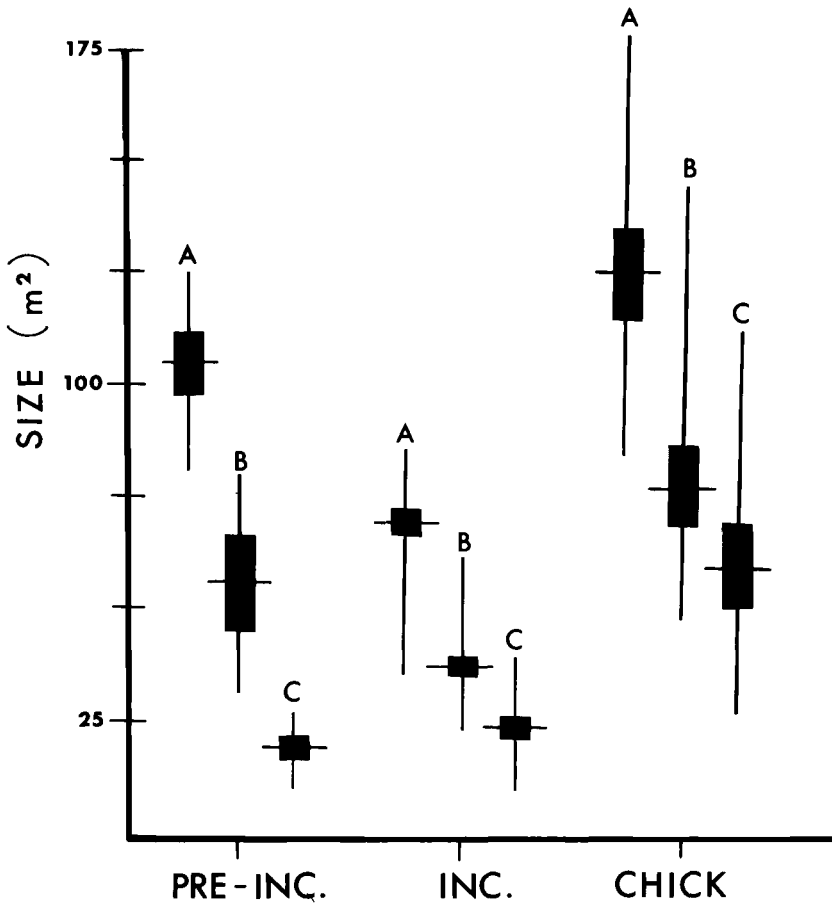


Fig. 3. Differences in primary (B), secondary (A), and unique (C) territory size as a function of reproductive stage. Shown are mean (horizontal line), range (vertical line), and SD (vertical bar).

intruders. These pairs reverted to courtship and did not concentrate on territorial defense until they had relaid. Once they had complete clutches, they again began defending a primary and secondary territory and attempted to enlarge these areas.

I then tested the hypothesis that territory area relates to the distance to the nearest neighbor, as is assumed in many papers on territoriality. The distance to the closest conspecific neighbor did not correlate with the primary territory size ($r = 0.174$). The best measure of the primary territory size for the 15 pairs was the distance to the second nearest neighbor in any direction other than that of the first nearest neighbor ($r = 0.831$, $P < 0.01$). The correlations of territory size with the mean inter-nest distance of the closest two neighbors ($r = 0.58$, $P < 0.05$) and closest three neighbors ($r = 0.64$, $P < 0.01$) were lower.

To determine the threat of egg cannibalism that neighbors provide to one another, I constructed 15 nests at the primary territory boundaries of 15 pairs in another area of the colony. Each test nest contained three Herring Gull eggs, and all were eaten within 2 h: 2% by crows, 11% by conspecific non-neighbors, and 87% by the resident territory owner (equally by both sexes).

DISCUSSION

I did not examine territorial behavior before pair formation or reformation (assuming most pairs had been paired in previous years), because it is difficult to mark individuals without making them shift locations. cursory observations indicated that secondary territories were very large and became distinguishable from primary territories when neighbors settled and were no longer able to displace the territorial pair.

Overall, the mean primary territory size for the 15 pairs examined did not correlate significantly with the distance to the nearest neighbor. My results indicate that the distance to the second nearest neighbor provides the best indication of territory size. Given the territorial requirements of Herring Gulls (adequate space to raise chicks), this is understandable. When the first nearest neighbor is very close (where dense vegetation or rocks present a visual barrier between nests; see Burger 1977), then the second nearest neighbor must be far enough away to provide adequate territory space. When the nearest neighbor is at an intermediate distance, then the second nearest neighbor is also at an intermediate distance. Thus, the second nearest neighbor provides the best measure of territory size.

In the present study, differences in the defense of the territory of Herring Gulls existed with respect to the type of intruder as well as to the stage in the reproductive cycle. These differences reflect the functions of the three territory types as well as the magnitude of the threat posed by the type of intruder. During the pre-incubation phase, the pair must establish a primary territory large enough for subsequent reproductive activities. Thus, they chased both neighbors and non-neighbors at greater distances than required for successful courtship and mating. It is adaptive for them to defend bigger secondary territories to prevent intruders from establishing a territory between the present neighbors. If an intruder established a station (future nest site) a few meters into a neighboring gull's primary territory, the new intruder would annex some of the defending gull's primary territory as well as some of its neighbor's. Thus, a gull is not defending a neighbor's nest but is protecting its own territory by creating a buffer zone. The defense of a secondary territory during the pre-incubation phase is required only when their neighbors are absent.

During the incubation phase, one member of each pair is always present and is incubating. At this time, their reproductive investment (eggs) is best protected by remaining on the eggs. But anticipatory to the chick phase, the pair must maintain an adequate primary territory. If the parents allowed the territory to shrink to the size of the nest, they might be unable to expand it to the necessary size required by mobile chicks. Adults remain on the eggs until violations of their unique territory occur. A larger secondary territory is maintained to prevent intruders from establishing territories. These intruders are not immediate threats to the nest and eggs, but they will be when the eggs hatch. Courting neighbors are ignored, as these neighbors will be incubating when the defending, incubating pair's chicks have hatched.

During the chick phase, all three territory types increase significantly in size. This is possible because of the loss of the chicks of one pair (and reduction of territory size) and the availability of some unused area. Both events regularly occur in a gull colony, and gulls normally expand their territory into these unused areas. During this chick phase, parents provide room for chicks to wander about without being killed by neighbors during territorial clashes or by non-neighbors who are canni-

balistic. Cannibalism is well known in Herring Gulls (Parsons 1971, Davis and Dunn 1976), and so it is advantageous for parents to chase all non-neighbors. Time and energy invested at this time directly relate to chick survival (see Hunt and Hunt 1976), particularly as it is too late in the season for pairs to relay (Burger, unpubl. data).

Methodologically, the computing of the three territory types depends upon the quantity of data recorded. The exact territory boundaries will become more precise with more data. Nonetheless, I found that after 6 or 7 days of recording territorial clashes during each phase (pre-incubation, incubation, chick) the territorial boundaries did not shift markedly with additional data.

In gulls, where cannibalism is often the most important cause of chick mortality, I suggest that breeding synchrony may be the result of the decreased mortality of eggs and young in synchronous areas as compared to asynchronous areas. As shown above, reproductive losses in Herring Gulls would be higher in areas of low synchrony directly as a result of egg and chick losses to neighbors and indirectly by the increases in aggression necessary to defend areas against courting pairs. During the egg-laying period, pairs often leave their eggs uncovered until they lay the second or third egg. Courting individuals often wander about the perimeter of their territory, and eat any uncovered eggs they encounter. I also found that males and females ate unattended eggs in their secondary territories. If marked differences in chick size facilitate parental recognition of chicks not their own, then asynchrony would contribute to chick cannibalism.

Biologists normally assume that breeding synchrony is a function of social facilitation during the pre-egg-laying phase (Darling 1938, MacRoberts and MacRoberts 1972, Burger 1979). The adaptive significance of synchrony relates to reducing the percentage of chicks taken by predators and to the early egg laying found in synchronous areas. In terns, the biomass of prey taken per day by nocturnal predators is constant throughout the breeding season, despite a hundredfold increase in biomass available (Nisbet 1975). If there is no recruitment of predators into the area (M. Gochfeld, pers. comm.), a high degree of synchrony results in an abundance of food for only a short period of time, making it impossible for predators to eat as high a proportion of young as under asynchronous conditions. Highest survival of chicks in early egg-laying gulls has been found by Paynter (1949), Paludan (1951), and Vermeer (1970), while highest survival in the mid-egg-laying period was found by Brown (1976) and Kadlac and Drury (1968). I suggest that in a species like the Herring Gull in which cannibalism accounts for most egg and chick losses, and neighbors account for much of the cannibalism, it is adaptive to be synchronous for protection against conspecifics, as well as for the usual antipredator devices.

ACKNOWLEDGMENTS

I thank M. Gochfeld for many discussions on synchrony and for helping with the computer analysis and the manuscript. M. Conover, G. Hunt, B. Murray, G. Shugart and J. Verner provided helpful comments on the manuscript, and I thank them. The research was funded by the Research Council of Rutgers University.

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