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TERRITORY SIZE IN WESTERN GULLS: IMPORTANCE OF INTRUSION PRESSURE, DEFENSE INVESTMENTS, AND VEGETATION STRUCTURE

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Abstract. Variation in territory size in a low-density colony of Western Gulls (Larus occidentalis) was analyzed in terms of costs and benefits accruing to owners. Spatial variation in intrusion rate per unit area best explains variation in territory size; the highest intrusion rate and smallest territories occurred near undefended gathering spots. Killing of chicks by neighbors was more frequent on small territories than on large territories. However, owners of large territories spent more time in territorial defense and more time per act of defense than owners of small territories. Intrusion elicited aggression from owners more frequently on small territories than on large territories, and intruders remained on large territories for longer periods of time.

Territory size was positively correlated with the amount of visually obstructive vegetation. This correlation was apparently a result of gathering spots occurring in areas with little cover.

Key words: aggression; chick mortality; coloniality; defense costs; gulls; intrusion pressure; Larus; territory size; vegetation structure; visibility.

INTRODUCTION

Territory size is a recurring topic in ecological literature because it usually affects spacing patterns of populations. Spacing patterns, in turn, influence the distribution, abundance and evolution of organisms (Brown and Orians 1970). One approach to understanding the determinants of territory size is to investigate correlations between territory size and environmental variables.

Territory size is negatively correlated with density of food for a variety of animals during both breeding (Pitelka et al. 1955, Stenger 1958, Holmes 1970, Cody and Cody 1972, Lyon 1976) and nonbreeding seasons (Smith 1968, Wolf 1969, Gill and Wolf 1975; Simon 1975, Gass et al. 1976, Kodric-Brown and Brown 1978, Gass 1979). However, it is often difficult to determine proximate causal mechanisms for these negative correlations. Do these correlations occur because a smaller area is needed to satisfy food requirements when abundance of food is high? Or does increased food availability cause increased intrusion rate (e.g., Gibb 1956, Ewald and Carpenter 1978) which in turn causes decreased territory size?

Myers et al. (1979) investigated this question with territoriality of wintering Sanderlings (Calidris alba). They showed that the negative correlation between food abundance and territory size was no longer statistically significant when the effects of food on intrusion pressure were eliminated. Partial correlations between territory size and intrusion pressure were statistically significant, but partial correlations between territory size and food availability were not. Furthermore, when intrusion pressure declined seasonally without a decline in food availability, territory size increased. Krebs (1971) documented a similar situation in Great Tits (Parus major); territory size was not correlated with the amount of food on the territory but was negatively related to the number of neighbors and the population density.

The present study investigates variation in size of breeding territories in the low-density colony of Western Gulls (Larus occidentalis) on Santa Barbara Island, California, USA. This system may offer insights into territory size that differ from those of the above investigations because Western Gulls do not forage on these territories. An earlier study of this population (Hunt and Hunt 1975) found no statistically significant relationship between territory size and increased reproductive benefits. We therefore made observations to evaluate three hypothetical relationships between costs of territorial defense and territory size.

1) Variation in territory size could be caused by variation in intrusion rate throughout the colony. Variations in intrusion rate could be caused by such factors as proximity to gathering spots or variations in quality of some unknown resource throughout the colony. This argument has been developed theoretically by several authors (Dill 1979, MacLean and Seastedt...
1979, Myers et al. in press, Schoener and Schoener in press).

2) Variation in territory size could result from some owners investing more in defense than others. In Red Grouse (*Lagopus lagopus*) territory size is positively correlated with an index of aggression by owners (Watson 1964, Watson and Miller 1971). However, their index incorporated frequency of victory as well as expenditures in aggression.

Varying levels of aggressiveness could be caused by age, environmental factors, or genetic variation. Genetically based variation could be maintained through evolutionary time by changing selective pressures. In some years owners of larger territories might reap benefits that outweigh the extra defense costs. Owners making smaller aggressive investments might do better in other years. For example, Hunt and Hunt (1976) showed that territory size of Glaucous-winged Gulls (*Larus glaucescens*) was correlated with chick survival when food availability appeared to be low. The correlation was not statistically significant in a different year when food availability appeared to be high. The optimal amount of aggressive investment might be difficult for gulls to determine at the time of territorial establishment because benefits accrue later during the egg and chick stage (e.g., in terms of decreased predation on offspring by neighbors).

3) High density of vegetation might obstruct an owner’s vision or movement. In such a situation an owner could: a. chase a smaller proportion of intruders, b. make a greater investment in defense to seek out and remove intruders, or c. defend a smaller territory.

Several investigators have found negative correlations between territory size and the amount of topographical obstruction on the territory. Watson (1964) and Burger (1974) showed that territory size was negatively correlated with visibility in Red Grouse and Franklin’s Gulls (*Larus pipixcan*) respectively. However, Watson’s statistical treatment suggests that visibility has a less important influence on territory size than variations in aggressiveness.

In many cases variation in physical structure may affect territory size by influencing other variables (e.g., intrusion pressure, availability of breeding sites) as well as by obstructing vision or movement. Orians (1961) reported that territories of Red-winged Blackbirds (*Agelaius phoeniceus*) increased in size after marshes were burned and then decreased as the marshes grew back. Kodric-Brown (1978) showed that addition of rocks to territories of pupfish (*Cyprinodon* sp.) caused reductions in territory size. Similarly, Zucker (1974) documented decreased territory size in fiddler crabs (*Uca terpsichores*) as the density of rocky breeding shelters increased.

**METHODS**

We measured territory size on 18 territories before eggs were laid but after the available “real estate” had been claimed (16 April–17 May 1975). By using this period we avoided ambiguities in territorial boundaries associated with neighbors intruding on and defending each other’s territories when owners were incubating. Ten of the 18 territories were used in all analyses. The other eight were included whenever appropriate variables were measured for these territories.

In general, observations were made before 1200 and after 1700 during similar times of day for all territories. Large and small territories were observed alternately on a day-to-day basis to avoid seasonal effects on correlations between territory size and territorial behavior. Mean amount of observation time per territory was 36.5 h.

Birds were marked with color bands or by spreading a paste of Rhodamine B crystals and vegetable oil on the rim of a metal can (10 cm diameter x 14 cm long) containing food. Feathers contacting the dye remained colored for approximately 10 d.

Grids of wooden stakes were laid out on each territory to record accurately locations of interactions. Territorial boundaries were deduced by plotting locations of intruders that elicited aggression from the owner (while neighbors were present) and connecting the outermost points to form a convex polygon. Since territory sizes from this type of mapping depend on the number of observed aggressions (see Odum and Kuenzler 1955, Stenger 1958), we randomly eliminated data points from territories with larger data bases until all territories were based on the same number of aggressions (17). Reducing the data base in this manner reduced territory size slightly.

To measure variations in intrusion pressure one must first choose appropriate dimensional units. When intrusions on a two-dimensional territory occur at the territorial boundary, one-dimensional units such as intrusion rate per unit perimeter are appropriate. However, at the gull colony on Santa Barbara Island, intrusion pressure seems to be measured more precisely by intrusion rate per unit area; intruders usually dropped down from the sky onto the territory, landing prior to their expulsion. Furthermore, interactions were not clustered near territorial boundaries. Rather, they were evenly distributed within each territory. We therefore quantified intrusion pressure by dividing number of intrusions by both the territory size and the total observation time.

In Western Gulls, territories are defended by both sexes, defense by males comprising a greater proportion of total defense than that of females (Pierotti 1975). Males and females were not distinguishable for all territories in this study. We therefore calculated the total seconds spent in defense per territory and divided this value by two to obtain the mean amount of time spent in defense by the two owners. The proportion of observation time that an owner was present on a territory was calculated analogously.
Percent of territory covered with vegetation sufficiently tall to obstruct a gull's vision (i.e., *Suaeda californica*, Chenopodiaceae) was computed from vegetation maps that were made in the field.

**RESULTS**

If variation in territory size were caused by variation in intrusion pressure throughout the colony, territory size ($A$) should be inversely related to intrusion rate per square metre ($I$). Fig. 1 shows that a strong inverse correlation exists between $A$ and $I$. ($P < .01$, two-tailed Spearman $r_s = -.79$).

The data in Fig. 1 are presented with two reference curves. The dashed curve shows the expected relationship if variation in territory size were caused by variation in intrusion pressure, and if intrusion rate per territory were constant over all territory sizes. In this case

$$A = R/I$$

where $R$ is a constant, set equal to the mean intrusion rate per territory over all territories ($R = 2.499$ intrusions per territory per hour). There was not a statistically significant relationship between territory size and intrusion rate per territory ($P > .1$, $N = 18$, two-tailed Spearman $r_s = .07$).

The weakness of using $R$ to approximate territorial costs is that costs per intrusion vary with territory size (Fig. 2). As territory size increased, time spent per act of aggression increased (Fig. 3a) and a lower percentage of encountered intruders was chased (Fig. 3b). The proportion of time that owners were present on their territories was highly variable (Fig. 3c). These three factors were incorporated into a temporal index of territorial costs: "proportion of time spent in defense" ($D$). This index is obtained by dividing total time spent in defense by total observation time for each territory. The index does not incorporate the amount of time intruders spend on the territory. Although intruders spend more time per intrusion on larger territories (Fig. 3d), the relevance of this correlation to the fitness of owners is uncertain.

The solid curve in Fig. 1 represents the expected relationship if variations in territory size were caused by variations in intrusion pressure $I$, and if $D$ were constant for all territories. In this case

$$\text{SP} = -0.00967A + 0.000906A \log A = D/I \quad (2)$$

(see Appendix for derivation). A value for $D$ was obtained by calculating the mean proportion of time spent in defense for all territories in which time spent in defense was measured ($D = 0.00249$).

To compare quantitatively the fit of the data points to these two hypothetical curves, the mean deviation of the points from the curves ($\bar{d}$) was calculated for each curve.

$$\bar{d} = \frac{\sum |d_i|}{N}$$

$d_i$ is the difference between the actual territory size and the size expected from the curves. The mean deviations from the dashed curve (98 m$^2$) and the solid curve (85 m$^2$) are not significantly different ($P > .1$, two-tailed Randomization test, Siegel 1956), deviations from dashed and solid curves were paired for each territory.

$D$ is not necessarily a better estimate of territorial costs than $R$. Although more time is spent in aggression per intrusion on large territories (Fig. 2), this extra time may be insignificant relative to other costs associated with each intrusion that are independent of territory size (e.g., hormonally mediated metabolic costs, or risk of injury). If $R$ is a better measure of territorial costs than $D$, then the dashed curve is a more accurate representation of how territory size would vary solely as a function of $I$. Alternatively, if $D$ is a better measure of territorial costs, the solid curve is a more accurate representation.
Fig. 3. Relationships between various characteristics of territorial defense and territory size. (\(r\) is Spearman's rank correlation coefficient.) (a) Mean seconds spent per aggressive act vs. territory size; \(r_s = .62, P < .025\), one-tailed. (b) Percentage of intrusions on a territory that elicited aggression vs. territory size. Intrusions that occurred while both owners were absent from the territory were not included in this analysis: \(r_s = -.66, P < .05\), two-tailed. (c) Percentage of observation time an owner was present on the territory vs. territory size; \(r_s = .26, P > .05\), two-tailed. (d) Mean time that intruders remained on the territory versus territory size; \(r_s = .75, P < .01\), two-tailed.

If the variation in territory size were caused by owners spending different amounts of time in defense, \(A\) should be positively related to \(D\). A positive relationship does exist between \(A\) and \(D\) (Fig. 4, \(P < .05\), two-tailed Spearman \(r_s = .66\)). The curve in Fig. 4 is the expected relationship if variations in territory size were caused entirely by owners spending different amounts of time in defense, and if intrusion rate per unit area were constant throughout the colony. In this case, \(A\) should increase as \(D\) increases according to Eq. 2; \(D\) is now the variable and \(I\) is constant. A value for \(I\) was obtained by dividing the total number of intrusions on all 10 territories by the total area. This quotient was then divided by the total time \((I = 0.00702 \text{intrusions} \cdot 10^{-2} \cdot \text{h}^{-1})\).

The mean deviation from the curve in Fig. 4 (246 \(\text{m}^2\)) is greater than the mean deviations from the solid curve (98 \(\text{m}^2\)) and the dashed curve (85 \(\text{m}^2\)) in Fig. 1. \((P < .05\) and \(P < .02\) respectively, two-tailed Randomization test; deviations were paired for each of the 10 territories common to both figures). Thus, the hypothetical curves in Fig. 1 account for variations in territory size better than the curve in Fig. 4.

Proximity to gathering spots could cause variation in intrusion pressure and therefore territory size. To evaluate this idea we grouped territories according to distance from the nearest 'club'. (Clubs are locations in the colony where gulls frequently gather; see Tinbergen 1960.) All territories under observation were either >200 m or <50 m from the nearest club. Territories >200 m from a club were always larger than those within 50 m (Table 1). This relationship was not simply an effect of peripheral vs. central location in the colony. A test using only peripheral territories also yielded a statistically significant difference with no overlap in territory size \((P < .005, N = 12\), two-tailed Mann-Whitney U test). If variation in the amount of obstructive vegetation caused the observed variation in territory size, territory size should be negatively correlated with percent cover. The data do not support this idea. In fact a statistically significant positive correlation exists (Fig. 5, \(P < .02\), two-tailed Spearman \(r_s = .81\)). The preceding results analyze relationships between territory size and costs of territorial defense. To understand the causes of variation in territory size on
Santa Barbara Island, relationships between territory size and territorial benefits must also be analyzed. Hunt and Hunt (1975) gathered data from 37 territories on Santa Barbara Island to determine whether territory size was negatively correlated with killing of chicks by neighbors. Territories in which no chicks were killed were larger than territories in which one or more chicks were killed. \( (P = .187, \text{one-tailed Mann-Whitney } U \text{ test}) \). However, this test did not incorporate the number of chicks killed relative to the number of chicks that could have been killed. In the following test of the same data, territories were grouped according to size in 50-m\(^2\) intervals, and the total number of chicks killed was divided by the total number of chicks hatched for each interval. The results (Fig. 6) show a weak inverse relationship between killing of chicks by neighbors and territory size \( (P < .06, \text{one-tailed Spearman } r_s = .57) \).

**DISCUSSION**

Proximate causes of variation in territory size

The close fit between the theoretical curves and data in Fig. 1 supports the idea that variation in intrusion pressure is a primary cause of variation in territory size. However, note that all large territories \( (> 500 \text{ m}^2) \) have rates of intrusion greater than expected under the assumption of constant temporal costs per territory \( (i.e., \text{all points lie to the right of the solid curve in Fig. 1}) \). Small territories \( (< 500 \text{ m}^2) \) are more evenly distributed about the expected values. This positive correlation between territory size and time spent in defense is shown more clearly in Fig. 4. However, the discrepancy between the actual data and the curve in Fig. 4 is evidence that variation in aggressive expenditures is not a primary cause of variation in territory size. Note also that if variation in aggressive expenditure were the sole cause of variation in territory size, the expected relationship in Fig. 1 would be a vertical line \( (I = 0.00702 \text{ intrusions}\cdot \text{m}^{-2}\cdot \text{h}^{-1}) \).

What causes the variation in intrusion rate per unit area throughout the colony? The clustered distribution of small territories near clubs, with larger territories at greater distances (Table 1), suggests that proximity to clubs is a factor; areas closer to the clubs sustain a greater intrusion pressure due to gulls approaching, leaving or observing the clubs.

We did not find a negative correlation between territory size and amount of obstructive cover. The positive correlation was due to the four largest territories...
having more cover than the seven smaller ones (Fig. 5). The former were >200 m from the clubs while the latter were within 50 m. Since clubs generally occur in areas of sparse vegetation (see also Tinbergen 1960: 45), the correlation in Fig. 5 is probably a secondary effect of smaller territories occurring near clubs. Our territories contained <12% cover (Fig. 5). Comparison of territories equally distant from clubs containing higher amounts of cover might yield a negative correlation between territory size and percent cover. Nevertheless, decreased visibility (or maneuverability) due to obstructive vegetation does not help explain variation in size of the relatively unobstructed territories of this study.

A fourth variable, not measured in this study, could have influenced territory size. Individuals with greater fighting ability or experience might be able to defend larger territories either because they have (1) more time and energy to spend in defense, or (2) lower defense costs per unit space. For example, first-year White-crowned Sparrows (Zonotrichia leucophrys) and Great Tits (Parus major) defend smaller territories than older birds (Dhondt and Hulé 1968, Ralph and Pearson 1971). If fighting ability (or age) were a major cause of variation in territory size on Santa Barbara Island, one would have to explain why better fighters (or older birds) tended to settle far away from the club. One possibility is that better fighters settle there preferentially because these areas have lower intrusion pressure and hence a greater net benefit. However, even if this were true, variations in fighting ability would explain only part of the variation in territory size.

Ecological and evolutionary stability

The results of this study help explain why some owners defend larger territories than others. When intrusion pressure is low, the cost of defending a large territory is outweighed by decreased killing of chicks by neighbors. When intrusion pressure is high, defense costs of a large territory are greater than the benefits of decreased chick mortality.

However, if the benefits and costs described above were the only ones important in this system, the ecological stability of the system would be questionable. For example, consider an owner of a large territory (low intrusion rate per square metre) that reduced its territory to the size of one of the small territories in the colony. This owner would incur the same level of neighbor-caused chick mortality as on the small territory, but would have lower defense costs. The net benefit on the reduced territory would therefore be greater than that of the small territory. We have assumed above that owners defend large territories under low intrusion pressure because a large territory provides a greater net benefit than a reduced territory would provide. By this reasoning, the net benefit from large territories in this system would be greater than the net benefit from small territories.

This result presents a theoretical problem. In theory animals should settle where their net benefit in fitness will be greatest (Orians 1969, Fretwell 1972). If the costs and benefits investigated in this study were the only ones influencing territory size, gulls should attempt to settle preferentially on large territories. The cost of usurping area from a large territory should be less than the cost of usurping the same amount of area from a small territory because large territories should be more compressible (Huxley 1934). Furthermore, an area seized from a large territory should be associated with lower defense costs due to the lower intrusion rate per unit area (Fig. 1). Preferential settling on large territories should continue until net benefits to settlers are equal over all sizes of territories.

This problem would be resolved if there were some benefit associated with proximity to clubs. Increased frequency of mating is one possibility. Pierotti (1975) observed males copulating with females that were not their mates, on the same clubs used in the present study. Close proximity to clubs could also provide better detection and avoidance of predators.

When food is a territorial benefit, it is often difficult to determine whether increased availability of food causes decreased territory size directly, or indirectly by causing increased intrusion pressure. This ambiguity should not exist when the territorial benefit is increased mating or predator avoidance. Increased food abundance could cause shrinkage in territory size directly because an owner can only eat a certain maximum amount of food. In contrast, the upper physiological limit to the number of copulations is probably much less approachable for male gulls. Predator detection and avoidance is not a simple increasing function of territory size, as is food availability.

An alternate explanation of the results presented here exists in the literature. Brown (1964) suggested that “as long as counterselection against aggressiveness were weak, aggressiveness per se would be maintained in the population merely by the exclusion of less aggressive birds from breeding.” Extending this idea, Verner (1977) proposed that defense of territories that are larger than those yielding optimal net reward could be maintained through evolutionary time if the high level of aggression “prevents others from obtaining a territory and breeding, or forces them into suboptimal habitats.” However, owners of such “super-territories” would have a lower fitness than individuals that (1) owned the optimal size territory, and (2) could resist aggression by owners of “super-territories.” Although the results of the present study conform in some respects to Verner’s model, the model’s evolutionary instability weakens it as a realistic interpretation. Rothstein (1979) and MacLean and Seastedt (1979) present more in-depth analyses of Verner’s model.
PROSPECTUS

This study has shown that spatial variation in intrusion pressure best accounts for variation in territory size in a low-density colony of Western Gulls. Differential investment is of secondary importance if "investment" is measured by time spent in territorial defense (D). However, if "investment" is measured by intrusion rate per territory (R), differential investment does not help explain variations in territory size. The amount of obstructive vegetation does not appear to be important in determining territory size.

Now that many variables are known to be correlated with territory size, three directions seem most probable for future investigations: (1) Relative inputs of different variables can be deciphered by statistical methods (e.g., Watson 1964, Watson and Miller 1971, Myers et al. 1979). (2) Inter- and intraspecific comparisons could be made between populations that do and do not contain intercorrelations of the troublesome variables (e.g., this study). (3) Variables can be experimentally manipulated (e.g., Krebs 1971, Philobosian 1975, Simon 1975). Each approach requires careful consideration of alternative explanations, because even variables with high correlation coefficients may be of only minor importance in determining territory size (e.g., see Fig. 4).

A theoretical framework for understanding territory size from a cost-benefit perspective is now becoming available (Schoener 1971, Dill 1979, MacLean and Seastedt 1979, Myers et al. in press, Schoener and Schoener in press). To determine the applicability of this framework, systems are needed in which (1) environmental variables can be altered independently of each other, and (2) costs and benefits of territorial defense can be estimated in common units to determine relative inputs from the different variables.

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**APPENDIX**

**Derivation of Eq. 2**

If one expresses territory size in terms of temporal costs,

\[ A = \frac{D}{T}. \]

\( D \) is the "proportion of observation time spent in defense," a unitless quantity. \( T \) is the proportion of observation time that an owner must spend in defense per unit of defended area. Units of \( T \) are \( m^{-2} \).

\[ T = ISPH \]

\( I \) is number of intrusions per square metre per hour present on the territory. \( S \) is mean number of seconds spent in aggression against an encountered intruder. \( P \) is the proportion of observation time spent on the territory. The constant \( H \) converts units of seconds per hour into a unitless proportion \( (H = 2.78 \times 10^{-4} \text{ h/s}) \). Fig. 2 shows that the quantity \( SP \) is positively correlated with \( A \). The least squares "predictive regression" (see Ricker 1973) describing the data in Fig. 2 is

\[ SP = -3.48 + 3.26 \log A. \]

Substituting Eq. 5 into Eq. 4, and Eq. 4 into Eq. 3, we obtain

\[ A = DI((-0.000967 + 0.000906) \log A). \]

Eq. 5 yields Eq. 2 upon rearranging.