Territorial Boundaries: An Economic View
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TERRITORIAL BOUNDARIES: AN ECONOMIC VIEW

Burger's comment (1981) is an interesting contribution to a difficult problem. My point is to suggest an alternative, more complicated, and I hope more realistic, formulation. The two explanations, however, are not inconsistent and will be integrated below. I will begin, however, with a model in which the bird, or whatever organism we are considering, does not engage in the Burger-type strategic calculation but simply selects the best area.

Assume an environment which is suitable for settlement of a particular bird and that at first only one bird, or one pair of birds, arrives. They should select their nest location in order to maximize their access to resources. Note that for the rest of this article, I will assume that the resource value of any given point in the area is known with certainty, thus ignoring the stochastic variables discussed in Tullock (1979). This is for simplicity only. A stochastic value of each point would be readily substituted but would make the mathematics more complicated.

From any nest location, the value of any given spot is shown by equation (1), in which A is the potential resource available from the area and D is the distance from the nest which has been selected.

$$V_j = A_j - f(D_j) \qquad j = 1, \ldots n. \tag{1}$$

The shape of the function $f(D_j)$ distance would depend on the use of the particular resource, for example, space for protective purposes would have a different functional shape than a food source which has to be harvested. It is, nevertheless, generally true that the farther away, the less valuable a given resource will be.

The basic problem, as shown in equation (2), is to maximize the value of the territory around the nest, the territory extending, of course, only through the domain of (3).

$$\text{MAX} \sum_{j=1}^{j=n} V_j = \sum_{j=1}^{j=n} A_j - f(D_j) \tag{2}$$

$$\text{Domain } A_j - f(D) \geq 0. \tag{3}$$

Also, the area must provide enough resources to ensure survival, which is shown by the constraint Z which is the minimum resource base which gives reasonable chance of survival and reproduction.

$$\sum_{j=1}^{j=n} V_j \geq Z \tag{4}$$

The area would be a perfect circle around the nest point if the resource were evenly distributed over space. If they were not equal, irregular shapes would presumably develop.

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Assume now that other birds arrive and select nest positions, and that two of the birds have chosen nest points such that the domain of (3) is satisfied for one spot for both birds. Under these circumstances conflict will occur, and each of the birds should be willing to invest in the fight up to the present value of this spot. Since I am assuming that the birds are equally big and tough (altering assumptions would be possible but make it more complicated) and that the value of any given point, that is A_j, is the same to all members of the same species, then each one would have a 50–50 chance of winning and, hence, would be willing to invest up to 50% of $A_j - f(D_j)$ in fighting over this point.

If we consider two birds whose nests are close enough together so that a number of areas satisfy domain conditions for both of them, then bird 1 will invest more resources in defense of areas nearer its nest than will bird 2; the converse holds for those areas closest to bird 2.

If we assume that the defense commitment determines the outcome, we would expect that a line would appear between the two parties connecting all points at which constraint equation (1) is the same for both parties, and that the points nearer to the nest of 1 would be completely under the control of 1 and those nearer the nest of 2 completely under the control of 2. There would be, however, conflict along the border and it seems reasonable that this conflict would be proportional to the value of the various points along the border to the individual bird. Thus, if we look at figure 1 and assume the dotted line shows the border of two birds, 1 and 2, which is the line of conflict between them, there would be less fighting at point N than at point M, because N is farther from the two nests and therefore less valuable to them even though the resource produced there might be the same as that at M. This hypothesis is, of course, readily testable.

The combat cost for 1 would be shown by

$$C = \tfrac{1}{2} \sum_{j=1}^{j=m} g[A_j - f(D_j)]. \tag{5}$$

Subject to the domain limitation of

$$\text{Domain } D_1' = D_2', \tag{6}$$

a bird, in selecting a location with other birds as potential competitors for space, would try to maximize

$$\text{MAX} \sum_{j=1}^{j=m} [A_j - f(D_j)] - \tfrac{1}{2} \sum_{i=1}^{i=m} g[A_n - f(D_i)]. \tag{7}$$

It is subject to constraint 2, but the domain would be more limited since part would be cut off by the line of conflict, hence the use of M instead of N.

$$m < n. \tag{8}$$

With this formulation we could expect irregularly shaped territories, either because resources are not evenly distributed or because the history of the arrival of birds, together with the fact that they are reluctant to move their nests once they have established them, would lead to irregularly shaped areas. (Note that

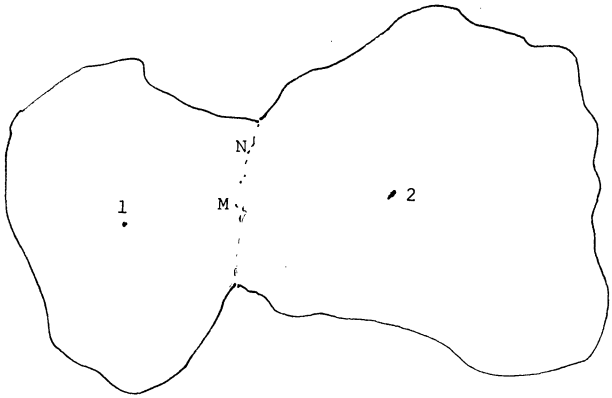

FIG. 1.—Two adjacent territories of conspecifics.

with even distribution of resources and nest movable without cost, the outcome would be the Losch system of hexagons.) It could also lead to gaps when two nests are far enough apart so that constraint 1 leaves a particular area unoccupied, but a bird settling in the area would not obtain Z. Note that if this expression is accepted, then in those years in which the bird population is low, individual territories would tend to be larger than in those years when it is large. This is also testable, but if I understand the empirical evidence, the hypothesis is already verified.

So far the model is quite different in spirit from the Burger model. Efforts, however, in selecting nest location and in deciding whether to defend any given area might lead to the kind of strategic calculations that she emphasizes. Turning to her figure 1*B*, in which there is an opening, bird B might choose a nest location a little closer to A than is otherwise optimal in order to make certain that the area which is potentially available for C is too small to support life. If bird C does appear, bird B might also choose to invest resources in fighting (which is irrational from the standpoint of eq. [7]), on the hypothesis that this would drive bird C away and, hence, fighting "irrationally" for one or two days would pay off in the future. I could complicate my equation to take these factors into account, but it seems to me that the first step is field observation to find out whether the behavior fits the equations I have given or whether Burger's more complicated strategic model is necessary.

LITERATURE CITED

Burger, J. 1981. Super territories: a comment. Am. Nat. 118:578–580.
Tullock, G. 1979. On the adaptive significance of territory: comment. Am. Nat. 113:772–775.

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