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COMMENTARY

TERRITORIALITY IN TREE SWALLOWS

Verner (1977) hypothesized that territoriality evolved for direct benefits such as attaining adequate food, nest sites, or escape cover. He also noted that once evolved, territorial behavior could serve as a mechanism of interference competition. By aggressively preventing conspecifics from breeding, an inhibitor would increase its relative contribution to future generations. Several authors quickly criticized this model (Colgan 1979, Getty 1979, Pleasants and Pleasants 1979, Rothstein 1979), asserting that unless inhibitory behavior were cost-free and population sizes were very small, such behavior could hardly increase in frequency.

In 1979, I published a study on Tree Swallows (*Tachycineta bicolor*) that documented the defense of an additional resource (a nest box) not needed for successful reproduction (Harris 1979). I suggested that these swallows fit Verner's model for the evolution of superterritories. In particular, Tree Swallow population sizes are small and there appeared to be no cost to excluding a potential breeder from nesting.

Robertson and Gibbs (1982) discussed my work and its conclusions. They stated that my hypothesis was that the force behind the evolution of territoriality in Tree Swallows was the "prevention of nesting by other potential breeders." These authors asserted that gene flow in Tree Swallows is such that effective population sizes are so large that they could not see how inhibition could have evolved. They concluded that the "superterritories" that I observed were experimental artifacts. Robertson and Gibbs presented their own work which suggested that Tree Swallow territory size was not a function of the number of easily defendable nest boxes and that these birds did not preferentially defend the compass direction towards the easily defendable nest box.

My view of the evolution of superterritories was that of Verner, i.e., territoriality evolved for certain direct benefits. Once territoriality had evolved to secure a nest hole, and assuming little or no cost to defending a nearby nest site, then selection would favor this inhibition.

Gene flow between populations may not prevent the evolution of inhibition. As Rothstein (1979) noted, the selection pressure (s) for inhibition is on the order of the frequency of breeding inhibitors in a population. For selection to be more effective than drift in changing gene frequencies, the inequality $4Ns > 1$ must hold, where N is effective population size (Fisher 1930, Wright 1931). Since s at the appearance of the inhibition trait is on the order of $1/N$, $4Ns$ is indeed greater than one, and drift would be overcome. The genotype for inhibition should increase when rare, regardless of population size. This case assumes that inhibitory behavior neither increases costs nor increases benefits to inhibitors. My observations suggested that both of these conditions held true in the population I studied. Indeed, the population turnover characteristic of Tree Swallows might favor the evolution of inhibition, since the likelihood of an inhibitor being related to another individual is low. The inclusive fitness of inhibitors depends on the degree of relatedness between inhibitor and those inhibited, and on the effect of that inhibition (Hamilton 1970).

Robertson and Gibbs (1982) failed to reject the null hypothesis of no difference in territory size between birds able to defend two nest boxes and those not able to defend extra boxes. It is important in such cases, however, to determine whether the power of the statistical analysis conducted was adequate to evaluate the model. Failure to reject a null hypothesis is only strong evidence for its truth when the statistical power of the test is high. The small sample size and the use of a more conservative nonparametric statistic, although perhaps appropriate, further biased the result toward accepting the null hypothesis and, perhaps, committing a type II error. Their experiment, although interesting, may not have been the critical test of the evolution of inhibition when the cost of inhibition is low. Further study in Tree Swallows that documents variation in inhibition within and between populations, perhaps as a function of relatedness of neighbors, its heritability, its potential costs, and its consequences for reproduction success, would be most interesting in this regard.

My conclusion in 1979 was that Tree Swallows may have evolved inhibition to prevent conspecifics from nesting when there was little or no cost in doing so. I see no reason to modify that conclusion.

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