On the Advantage of Being Different

Experiments with nest predation in birds show that patterns of species coexistence can mimic those formed by competition

Birds have long been the subject of study among ecologists, specifically relating to the factors that influence how communities are assembled. And within this particular context, data from field studies of birds formed much of the basis for the notion that competition was the principal factor affecting community assembly.

In recent years, however, ecologists have come to recognize that community assembly in general is the outcome of many different interacting influences, even though in different habitats a single factor may be dominant over the rest. Competition is now seen as just one of these factors, with predation being equally important.

It is fitting, then, that experimental data on bird ecology recently reported by Thomas E. Martin of Arizona State University should highlight the potential importance of predation in community structure. And even more fitting that the effects of predation—specifically, in how species divide up the environment among themselves—should mimic the pattern once thought to be the classic result of competition.

Ideas about the role of predation were developed principally from work on marine communities, with Joseph Connell of the University of California, Santa Barbara, leading the way. "Predation should be regarded as being of primary importance, either in directly determining the species composition [of a community]," he said a little more than a decade age. Most ecologists would wish to temper this somewhat, but would nevertheless agree with Robert Holt of the University of Kansas, who said recently: "It is clear that any general theory of ecological communities must incorporate predation as an important determinant of community structure."

Now, a predator that simply wipes out a prey species clearly has a dramatic impact on the composition of a community. And a predator can affect the overall composition of a community by preventing any one of a series of competing, potential prey species from becoming dominant. But what Holt and then Martin were concerned with is a more subtle effect. In the context of Martin's recent theoretical and experimental research it is this: how do you explain the coexistence of bird species whose resource requirements are different? The classic answer would be competition: only those species that use ecological resources differently can successfully coexist.

In different and complementary ways, first Holt and then Martin effectively said: that may be correct in some circumstances, but perhaps predation can also produce this same pattern, which is known as resource partitioning.

Martin chose to work on nesting behavior, partly because "nest predation is probably an important agent of natural selection for birds because such predation commonly is a primary limit on reproductive success." It has the additional advantage of being amenable to experimental intervention.

He needed to be able to demonstrate that predators' behavior is influenced by the effort and reward involved in preying on nests, specifically on eggs and hatchlings. If predators responded to the way birds distribute their nests throughout the environment—becoming more successful in some circumstances and less in others—then this in turn would present selection pressure on the birds' behavior.

During the last year's nesting season, Martin carried out two experiments: the first was to test whether predators' search intensity is influenced by the number of occupied nesting sites in a given area; the second focused on the efficacy of predation when a given density of nests was distributed among different types of nesting site as against a uniform nesting site.

The answers were quite clear-cut. Yes, predator search intensity does increase with increased occupation of potential nest sites. And yes, predation pressure is significantly greater when a given density of nests is distributed among a single type of nest site as against distinctly different nest sites. Searching among different potential nest sites reduces the predators' efficiency.

In other words, because MacGillivray's warbler and the black-headed grosbeak select different parts of a tree in which to construct their nests—low and high, respectively—they can coexist and suffer a lower predation rate than if either lived alongside species that used the same nest sites. "Predation, not competition, can therefore explain this kind of resource partitioning," concludes Martin. ■ **Roger Lewin**

ADDITIONAL READING

R. D. Holt, "Spatial heterogeneity, indirect interactions, and the coexistence of prey species," *Am. Nat.* **124**, 377 (1984).

T. E. Martin, "On the advantage of being different," *Proc. Natl. Acad. Sci. U.S.A.* **85** 2196 (1988).

Bird brains

Coexistence of bird species has often been explained in terms of competition; but the effects of predation can produce the same pattern.

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