

Sexual selection forms the structure and dynamics of ecological communities

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The fields of community ecology and evolutionary ecology have in the past, to a large extent, been moving along separate paths. However, occasionally the two fields do meet, as in the article by Doherty *et al.* (1) in this issue of PNAS, in which the authors interpret new and exciting results obtained through statistical analysis of ecological monitoring data (2) within the framework of sexual selection (3). Through a powerful statistical analysis of data collected by volunteers, the authors are able to show, at a continent-wide scale, that sexual selection is associated with higher local extinction and turnover rates in natural bird communities, which affects biodiversity across the continent (Fig. 1). The insight thus obtained is both novel and highly interesting from an ecological point of view. In addition, the results reported (1) might have important implications for our understanding of the ecological dynamics and evolution of biotic communities, as well as for how we are to best protect threatened species.

The article by Doherty *et al.* (1) uses several advances within the currently very active field of statistical modeling of ecological data (2, 4). The paper specifically addresses the dynamics of communities, through the analysis of extinction and turnover rates estimated from North American Breeding Bird Survey (BBS) data (5, 6), a database that in the past primarily has been used to address pure ecological questions (see, e.g., ref. 6). BBS data include observations on the presence/absence of bird species along a large number of predefined routes that are surveyed annually by a horde of amateur ornithologists across the North American continent.

A general problem in analyzing such data is heterogeneity in detectability among species and survey routes. Doherty and coauthors (1) have, to a large extent, overcome this problem by using the jackknife estimator of Burnham and Overton (7) and the estimators of extinction and turnover rates cleverly developed by Nichols *et al.* (8). Thus, the local extinction rate is estimated as the proportion of species observed in a given survey route at year t but not in year $t + 1$, taking into account heterogeneity in detectability. Similarly, local



Fig. 1. Sexual selection accounts for the occurrence of elaborate displays such as the bright plumage color of the male hooded warbler *Wilsonia citrina* (Upper). The intensity of sexual selection is apparently much weaker in species such as the Canada goose *Branta canadensis* (Lower), where the sexes have similar plumage colors. In this issue of PNAS, Doherty *et al.* (1) demonstrate that sexual selection can have dramatic effects on the structure and dynamics of North American bird communities: sexually dichromatic species experience much higher local extinction and turnover rates than monochromatic ones. (Photograph taken by Paul Doherty.)

turnover rate is estimated as the proportion of species observed at year t but not in year $t - 1$. This method has recently been applied to a variety of ecological systems (e.g., refs. 6 and 8–13). Nevertheless, the application of this approach to estimating community dynamics parameters is little used at present, but, we are sure, it will be much more used in the years to come. Doherty *et al.* (1) elegantly demonstrate the power of this approach.

The study of sexual selection is an old and well established discipline within evolutionary biology. Darwin (14) was

puzzled by the existence of a class of elaborate, often sexually dimorphic, traits that seemed to reduce an organism's chances of survival. Conspicuous sexual displays, such as the colorful tail of the male peacock, were difficult to understand as the products of natural selection, because such features would seem to make their bearers less fit in terms of survival. This apparent paradox led Darwin to suggest that a distinct selective force is responsible for the evolution of such characters, namely sexual selection that "depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction" (14). Thus, despite the fact that such characters may reduce survival, they are favored in evolution because the bearers, on average, do typically leave more descendants through the advantage the traits ensure them in the acquisition of mates.

During the last few decades, we have witnessed an explosive growth in process-oriented studies of sexual selection, resulting in many new insights regarding the evolutionary and ecological implications of sexual selection at the individual and population levels. For instance, as suggested by Darwin, sexually selected traits do indeed incur a mortality cost on individuals (15, 16). The suggestion that the mortality cost associated with sexual selection might increase local extinction rates has to some extent been supported by natural experiments involving the fate of introduced birds to oceanic islands (17). However, building on the recent advances in the field of statistical modeling of ecological data (see, e.g., ref. 2), Doherty *et al.* (1) take the crucial next step along this line of research by demonstrating that sexual selection may have continent-wide consequences for local extinction risk in natural ecological communities.

However, sexual selection is certainly not only a destructive force incurring higher individual mortality and higher local extinction rates within ecological communities. Evolutionary biologists, for instance, have long been aware of

See companion article on page 5858.

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the creative potential of sexual selection in promoting speciation (18). Indeed, intensity of sexual selection has been found to be positively associated with species richness (19–21). The basic idea is that sexual selection can easily cause populations to diverge in mate recognition systems, thus leading to rapid evolution of prezygotic barriers between populations (22).

Interestingly, the results of Doherty *et al.* (1) suggest that an increased local extinction rate is not necessarily translated into an overall loss of sexually selected species. In their study covering a 21-year time span, a higher turnover rate of these species was found to compensate for the increased local extinction rate. Hence, sexual selection may indeed be a potent force shaping the composition and dynamics of ecological communities at both ecological and evolutionary time scales. We may, for instance, have underestimated the importance of sexual selection in promoting speciation, because the increased extinction risk (1) has not been accounted for in previous pattern-oriented studies (19–22). Moreover, the higher turnover rate of sexually selected species (1) might imply that the sexually selected species that endure increased local extinction risk have compensating life history properties, such as rapid population growth and/or high dispersal abilities.

Yet another highly interesting result documented by Doherty *et al.* (1) is the regional differences in extinction and turnover rates across the North American continent. Southern Texas and the prairie pothole region of the north-central part of North America stand out as having much more stable community structures than other regions by exhibiting markedly lower differences in extinction and turnover rates between dichromatic and monochromatic species. The authors briefly discuss some hypotheses

that could potentially influence meta-community dynamics at this level. Clearly, however, a major challenge for future studies would be to unravel the underlying ecological processes that determine the relative stability of communities.

Doherty *et al.* (1) provide an excellent demonstration of the potential power of using long-term ecological monitoring data to address key problems in community ecology and evolution. Conceptually, the study raises interesting questions that warrant further investigation. A pattern that now begins to emerge is that sexual selection may be a force that affects communities at both ecological and evolutionary time scales. On the one hand, sexual selection may be an important species generator at an evolutionary time scale (see ref. 18 and references therein for a critical review). On the other hand, sexual selection may drive populations away from their survival optima, thereby contributing to increased local extinction rate at an ecological time scale (1, 15–17). Novel hypotheses related both to community structure and dynamics and evolutionary biology may emerge when we consider the net effect of sexual selection at both evolutionary and ecological time scales. For instance, species with limited dispersal abilities and life histories that result in slow population growth would typically have rather local distributions and low turnover rates. Such species would probably be more sensitive to the increased local extinction risk of sexual selection than species with life histories that pave the way for wide distributions and high turnover rates. Hence, species may differ in their ability to endure when exposed to the increased local extinction risk associated with sexual selection, and this may in turn affect species compositions of commu-

nities at an evolutionary time scale. This is but one example in which the study of Doherty *et al.* opens up novel perspectives for the interface of community ecology and evolution.

The results reported by Doherty *et al.* (1) do have important implications for the protection of sexually selected species. Such species apparently experience frequent local extinction, followed by recolonization. This pattern may suggest that such species depend more heavily than others on dispersal and recolonization for their

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local dynamics. Allowing maintenance of a fluid metapopulation dynamic (23) might therefore be especially important for such highly sexually selected species. Environmental changes that limit effective dispersal may have severe effects on such species through reduced turnover rates, thereby increasing the risk of global extinction (1, 24).

In sum, the scientific crossing of the ecology and evolution paths, with advances in parameter estimation exemplified by Doherty *et al.*'s study, shows how we can obtain important new insights. Pattern-oriented studies like this (1) may shed valuable light on and extend the insight earlier obtained on the basis of more process-oriented experimental studies (see, e.g., refs. 15–17). To us, this crossing of fields demonstrates the value of joining forces among various blends of biologists in efforts aimed at better understanding the structure and function of the natural world around us.

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