SPECIAL FEATURE

When Predators Don't Eat Their Prey: Nonconsumptive Predator Effects on Prey Dynamics[1]

Predation has long influenced how ecologists think about ecological processes from the small to the large. At the microscale, predation-related stress can yield permanent changes in prey physiology or morphology; at the macroscale, altered predation regimes in grazer-dominated systems can profoundly alter ecosystem function.

Recently, many ecologists have become interested in the nonconsumptive effects (NCE) of predators; broadly, the consequences of defensive strategies employed by prey in response to predation risk. This body of research grew out of reductionist behavioral studies of how prey foraging tactics shifted in response to risk. As a result, this field of study has sometimes been considered a specialized offshoot of trophic or behavioral ecology. This is especially understandable in light of the difficulty in empirically distinguishing between NCE and consumptive predator effects. Understanding these effects is essential, however, since predator NCE on prey growth, life history, resource use, etc., can enhance or obscure consumptive effects and make it difficult to predict the community-level outcome of predator–prey and predator–prey–resource interactions.

The aim of this Special Feature is to show that NCE are often central to analyses of consumer–resource interactions, especially those that occur in spatially-structured multispecies systems. We build on the groundwork laid by a 2003 *Ecology* Special Feature that highlighted NCE research via a series of synthetic, theoretical, and empirically-based papers that explored individual trait plasticity in ecological communities. The intervening five years have seen an explosion of interest in and increased awareness of NCE by community ecologists, and recognition that their significance may extend well beyond trophic interactions.

This Special Feature explores some of the exciting advances in NCE research by reviewing our increased understanding of the central importance of NCE to ecological processes across multiple levels of organization. It includes papers examining NCE in "classic" predator–prey studies, their import to spatial ecology, and their effects on ecosystem-level processes. All three papers highlight the larger-scale consequences of nonconsumptive interactions between predators and their prey and illustrate that NCE may extend a predator's reach far beyond its immediate grasp.

The Special Feature starts with an article by B. Peckarsky and colleagues that reviews the role of NCE in several "textbook" examples of predator–prey interactions in order to introduce this concept to readers previously unfamiliar with the topic. They first explore the influence of NCE on the boreal lynx–hare cycle as well as in aquatic trophic cascades (both marine and freshwater). The available evidence suggests that NCE play an integral role that may be overlooked unless NCE affect prey in a direction opposite that expected from the consumptive predator effect (e.g., increasing rather than decreasing prey density). The classic predator–prey interaction between wolves and moose on Isle Royale has also demonstrated that the impact of NCE varies as a function of climatic conditions. NCE may also play an important role in keystone predation, in which a consumer species' effect on community structure is disproportional to their biomass. Some keystone predators may achieve this status by acting as "intimidators" whose relatively minor consumptive effects on prey biomass are magnified by community-wide responses to predation risk (i.e., predators scare many more prey than they eat). Peckarsky et al. conclude by highlighting the potential effects of NCE on other ecological processes such as delayed density dependence and predator-mediated prey coexistence, and they call for a more consistent integration of NCE into community-level research.

In the second article, J. Orrock and colleagues assess the importance of both predator consumption and NCE to metacommunity dynamics, a rapidly emerging field of research that

[1] Reprints of this 32-page Special Feature are available for $10.00 each, either as PDF files or as hard copy. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 1990 M Street, N.W., Suite 700, Washington, D.C. 20036 (esaHQ@esa.org).

addresses the interplay between spatial ecology and interspecific interactions. They use classic models of competition and metapopulation dynamics to explore the implications of predators that affect prey colonization rates (via decreased immigration to and increased emigration from predator-containing patches) as well as local prey density. They find that defensive changes in prey movement can alter the dynamics of predator-free patches in ways that lead to the predator's influence being felt throughout the habitat matrix. Predators can thus exert "remote control" over ecological processes within sites that they do not occupy. This phenomenon has the potential to profoundly alter spatially structured systems via predator-mediated changes in population persistence and susceptibility to habitat loss. These changes can, in turn, affect competitive hierarchies that structure community diversity. Shifts in the competition–colonization trade-off in response to predators may have similarly important consequences; even rare or spatially restricted predators can tip the balance between prey coexistence and competitive exclusion. Such predator-mediated shifts in spatial dynamics can also affect the chances of biological invasions and, intriguingly, the ability of communities to respond to anthropogenic habitat destruction. Throughout the article, Orrock et al. emphasize the potential for NCE to have subtle but profound impacts in spatially structured habitats.

The third article in the Special Feature takes a large-scale view of NCE and examines whether predation risk can affect ecosystem function. Oswald Schmitz and colleagues use a combination of case studies and syntheses to link predator-induced alterations in prey foraging behavior to changes in a variety of ecosystem metrics. In old-field systems, for example, predation risk from spiders with different hunting modes generate qualitatively different patterns of plant diversity, productivity, and nutrient cycling; in marine intertidal zones, predation risk alone leads to reduced energy transfer up the food chain via decreased prey growth efficiency. Importantly, these patterns are only understandable in light of NCE. This synthesis shows that NCE not only influence, but effectively control ecosystem processes in a range of systems. As a result, Schmitz and colleagues argue strongly that this linkage of evolutionary and ecosystem ecology possesses substantial explanatory power for resolving the often-contingent way ecological processes manifest themselves at a variety of spatial and temporal scales.

Ultimately, this Special Feature aims to introduce NCE to a broad ecological audience by emphasizing that its significance extends well beyond trophic interactions and has important implications for other ecological disciplines. We hope that these papers will spark awareness of and foster research interest into the impacts of these sometimes subtle but often powerful phenomena on a wide array of ecological processes.

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