The many ecologies of behavior

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Gordon's claim that behavioral ecology forgets ecology may seem paradoxical given the name of the discipline but calls to a more explicit consideration of ecology in behavioral and evolutionary research are not new (Sutherland 1996; Houston and McNamara 2006; Dercole and Rinaldi 2008). Behavioral ecology has traditionally incorporated ecology as an immutable environment to which organisms adapt; but ecology considers environments as dynamic entities. In reality, the behavior of individuals not only has to respond to a dynamic environment but, for the most part, their environment will be modified by their behavior. Group structures, population sizes, species interactions, and resource dynamics are largely dictated by social, reproductive and foraging decisions.

Such an eco-evolutionary framework where behavior is not just viewed as an adaptation to the environment but as an integral part of it has 2 important advantages. First, it forces the logic of our arguments to be self-consistent (Houston and McNamara 2006). For example, if we were to say that wasteful foragers are adapted to abundant resources, but also deplete them, we would have to conclude that the behavior is not evolutionary stable because it prompts an environment to which it is not adapted. Although this may seem trivial in simple systems, it is not when further ecological complexity is considered. Foraging not only affects resources through consumption but also indirectly through its effects on competitor species or nutrient recycling. Acknowledging the ecological structure of the system is key to deduce the net effect of behavior on the environment it must adapt to.

A second advantage of integrating behavior and ecology is that it allows us to use the well-understood principles of adaptation by natural selection to grasp the intricacy of higher level ecological processes. Adaptation is what defines ecological interactions and hence it should be possible, at least in principle, to understand ecological systems as products of natural selection. I fully agree with Gordon's sentiment that ecology is not sufficiently ingrained on behavioral studies—neither is evolution on ecological ones—but I see the integration do better than merely complicate our simplistic view of the world. Although it is true that behavior is context-dependent and "the context constantly shifts," we also know that the context is in turn largely determined by behavior. We can use the power and elegance of evolutionary theory to predict how context and behavior will coevolve. This way, the range of possible ecological scenarios gets reduced to those consistent with adaptation by natural selection (Fussmann et al 2007; Uchida et al. 2007). Although ecology may appear to complicate the study of behavior; behavior, if understood as an adaptive process, can simplify ecology.

Addressing the mutual interdependence of behavior and ecology is not without precedents. Hamilton's rule is a clear example: it emerges from the explicit modeling of the bidirectional interaction between social behavior and its population-genetic environment (Hamilton 1964). Maynard Smith's evolutionary game theory also considers behavior–environment interdependence because the frequency of different behaviors in the population defines the social context to which behavior adapts (Maynard Smith 1979). Later the emphasis was extended to the population level where total densities, not just frequencies, affect and are affected by behavior (Houston and McNamara 2006). Gordon's claim is that the key is yet one step further: at the community level of species interactions. But why stop there? Why not consider the entire dynamics of the ecosystem? This may seem farfetched, but adaptive behavior can profoundly affect ecosystem processes. I will mention 2 examples. Chironomid antipredator behavior effects carbon cycling because their feces are more easily decomposed when scattered over the benthos than when accumulated in their hiding burrows (Stief and Hölker 2006). A more complex example is shown by the indirect effects spider hunting mode has on ecosystem primary production and mineralization through eliciting alternative feeding strategies in their grasshopper prey (Schmitz 2008).

The virtue of ecosystem science is that it defines the environment as a web of physiological and behavioral interactions between organisms and defines organisms by their effect on its different components. Seen this way, the properties of the environment directly emerge as consequences of the actions of organisms, to which we can apply an evolutionary reasoning. Moreover, ecosystem science brings a healthy tradition of respecting the principle of conservation of matter and energy, the ultimate requirement for self-consistency. Foraging studies model the disappearance of resources as animals consume them but where those resources disappear to remains unacknowledged. Ecosystem scientists know well that those consumed resources must eventually return to the resource pool; the question is how fast. The answer depends on variables such as assimilation, excretion, decomposition, and uptake rates: adaptations to the abundance and chemistry of resources that can be affected by behaviors as diverse as diet selectivity, antipredator responses, or reproductive decisions (Kay et al 2005; Fussmann et al. 2007). One could argue that linking the predictive power of evolutionary theory with the solid physicochemical principles of ecosystem science represents the ultimate mechanistic explanation in ecology. Of course we are not quite there yet, and the reductionist quest will benefit from a pluralistic approach that considers explorations at different levels of the ecological hierarchy. There is nothing wrong with assuming properties at certain levels as given while exploring variation at others. Learning requires such conditional simplifications.

I much welcome Gordon's teaser to view behavioral adaptations in the context of community ecology, just as I welcome a population or ecosystem approach. However, I argue that the main reason to do so is not to add phenomenological complexity but to increase logical consistency. Ecology provides the logic behind evolutionary processes, and interactions at a given ecological level must be consistent with their consequences at other levels. Self-consistent frameworks that ensure this have been applied to behavior in group or population contexts. Because their logic is level invariant, they can be used to understand behavioral adaptations in complex communities and ecosystems.

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