

Cognition as an Independent Variable: Virtual Ecology

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On close examination, human cultural artifacts bear the unmistakable impress of the structure of the human mind; our tools, habitations, and methods of communication have been molded to suit the strengths and limitations of the human cognitive system (Norman 1988). It has not commonly been emphasized, however, that similar shaping processes have taken place over the course of biological evolution in response to the cognitive features of other, non-human species (Bonner 1980; von Frisch 1974). Cognitive influences are particularly evident in the modifications of the color pattern and behavior of prey species that reflect biases and constraints in the perceptual systems of their principal predators. For example, avoidance learning by predators contributes to the evolution of aposematic, or warning, coloration in many distasteful or poisonous species (Guilford 1990; Schuler and Roper 1992), and Batesian mimicry (Bates 1862), in which palatable prey evolve to imitate the appearance of aposematic species, takes advantage of the predator's tendency to stimulus generalization (Oaten et al. 1975). But perhaps the most striking illustration of the effects of predator cognition on prey appearance is the large number of species of cryptically colored insects that are polymorphic, with a single species occurring naturally in a variety of disparate forms.

Cryptic prey polymorphism is common among grasshoppers, leafhoppers, and walking-sticks, but it is particularly characteristic of lepidoptera (Poulton 1890). Many moths have evolved cryptic coloration to avoid bird predation while they rest on tree trunks during the daytime, and polymorphism is pervasive among these species. In North America, roughly 45% of the Noctuid moths in the genus *Catocala* are polymorphic, with some species occurring in as many as nine different morphs (Barnes and McDonnough 1918). In other branches of the same family, the degree of morphological variation can be even more extreme: Adults of the army cutworm, *Euxoa auxiliaris*, are almost continuously variable in appearance. In 1890, Poulton remarked on the high frequency of polymorphism among cryptic insects and formulated a remarkably perceptive explanation for the phenomenon. He said that in polymorphic species, "the foes have a wider range of objects for which they may mistake the moths, and the search must occupy more time, for equivalent results, than in the case of other species which are not polymorphic" (Poulton 1890, p. 47). His implications are, first, that polymorphism is an adaptive response to the foraging behavior of the predator, and by extension of the cognitive processes that determine successful visual search. And secondly, that the selective advantage of polymorphism results from the fact that it is harder and more time-consuming to search for several things simultaneously than to search for only one.

The cognitive process involved appears to be a transitory increase in a predator's ability to detect cryptic prey when items of a similar appearance are encountered in rapid succession (Pietrewicz and Kamil 1979; Bond and Riley 1991; Reid and Shettleworth 1992), a phenomenon that has been termed "hunting by searching image" (Tinbergen 1960). As a result of the shift in detectability, visual predators tend to search for only a limited number of prey types at any moment in time, focusing on the most common prey available and effectively overlooking the others (Tinbergen 1960; Bond 1983; Bond and Kamil 1999). The ecological consequence of this perceptual bias is known as apostatic selection (Clarke 1962, 1969), and it has been suggested to be the primary mechanism for maintaining stable prey polymorphism. If predators tend to search most effectively for prey types they have recently found, then the more common any given prey type is the more heavily it will be preyed upon. Thus as a prey type becomes more common, predation on it increases, while the predation pressure on rarer types declines. Common morphs experience relatively higher predation rates and decline in numbers, while rarer ones become more common. The outcome should be a stable configuration of prey types with a much higher degree of morphological diversity than would have been the case in the absence of predatory cognitive biases.

Apostatic selection is an elegant theory, but until recently empirical support has only