



Statistical decision theory and evolution

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Two recent articles by Geisler and Diehl use Bayesian statistical decision theory to model the co-evolution of predator and prey in a simple, game-like environment. The prey is characterized by its coloration. The predator is characterized by the chromatic sensitivity of its visual system and its willingness to attack. The authors demonstrate how the coloration of prey and the perceptual system of the predator co-evolve, converging to a Nash equilibrium for both species.

The visual systems of organisms are highly specialized [1] and it is tempting to conclude that each specialization must confer an advantage on the organism possessing it, an advantage that ultimately translates into 'reproductive success'. The balance between predator and prey, for example, can hinge on the prey's ability to hide from the predator or the predator's ability to ferret out the prey. Exactly how predator and prey co-evolve over time or how this co-evolution shapes the characteristics of each is the subject of two recent articles by Geisler and Diehl [2,3].

In these articles, Geisler and Diehl develop a model of predator-prey interaction in a tiny environment where prey differ only in the match between their coloration and the typical background colors (camouflage) and predators differ in the chromatic sensitivities of their visual systems. They investigate how natural selection would shape both the chromatic sensitivity of the visual system of the predator and the coloration of the prey.

Box 1 describes an organism that has already broken out of the simple framework of Geisler and Diehl's world. It can alter its coloration to match its background in one part of the spectrum while simultaneously signaling in another. However, as Geisler and Diehl amply show, there is much to be learned in studying the simple example of co-evolution they have selected. The mathematical framework that they use is statistical decision theory [4–6], a set of mathematical methods for playing stochastic games well that was developed during and just after the Second World War. One article [3] consists of detailed simulations and analyses, whereas the other [2] presents an overview of the work, relating it to other theoretical viewpoints within psychology.

The prey in Geisler and Diehl world are little more than loaves of bread, unable to move, to see, or to act. They exist and, if they exist long enough, they reproduce asexually. Their children exhibit minor, random differences in coloration from their parents and, depending on predation, some will survive longer than others. Their continued existence depends on the match between their coloration

and the background of their world – as seen through the predator's eyes. The life of the prey is a hard life.

Predators have a distinctly more interesting *Lebenswelt*. They have a minimal visual system capable of registering chromatic differences in the environment that might correspond to the presence of prey. They also can act, choosing to 'attack' or 'not attack' a possible prey. If they attack successfully, they gain 'reproductive units' by ingesting prey. If they attack unsuccessfully, they waste energy that ultimately translates to a loss in reproductive units. Each predator is, in effect, a signal-detection observer (see Box 2) where the presence of the prey within striking distance is the signal and the criterion for action is fixed. The outcome of many signal-detection trials is scored in terms of reproductive fitness. Each predator is completely characterized by two numbers that determine

Box 1. Camouflage and signaling

The female crab spider (*Misumenia vatia*) can change its coloration to match a range of yellow to white backgrounds, effectively camouflaging itself (Figure 1) from insects whose visual sensitivity falls in the short- and middle-wavelength parts of the human visible spectrum and the ultraviolet. The two large red patches on its abdomen spoil the camouflage for human observers. Hinton conjectures that these patches serve to warn off potential predators (birds) with visual sensitivities that include the long-wavelength part of our visual spectrum [9]. The crab spider effectively hides itself in one part of the electromagnetic spectrum while signaling in another.



Figure 1. A female crab spider camouflaging itself in its surroundings. Illustration reproduced with permission from [10]; © Facts on File Inc.

Box 2. Signal-detection theory

In the simulations of Geisler and Diehl, the predator is a signal-detection observer [11]. Signal-detection theory is a collection of mathematical techniques for deciding whether a signal (the prey in this case) is present or not. The methods are over half a century old, grew out of statistical-decision theory, and serve as a simple but complete illustration of statistical decision theory.

The predator has two possible actions, *attack* or *not attack*. Correspondingly, he can make two different kinds of errors. If he has hallucinated a prey that isn't really there, then he committed a **false alarm** by attacking. If he fails to attack a prey that is really there, he has **missed** the signal (Figure II). There are two kinds of successes as well, attacking a prey that is really there and ignoring one that isn't. In the world of Geisler and Diehl, the two kinds of error have different costs and the two kinds of successes have different rewards. A false alarm leads the predator to waste energy, a miss leads him to overlook a readily-available prey, and the opposite in the cases of success.

Signal-detection theory is a way of computing the optimal trade-off between different errors and successes given the distributions of signals and non-signals, the costs and rewards associated with each, and the prior probability that there is a prey out there at all. In the specific form used by Geisler and Diehl, the signal-detection observer is characterized by the ability of the sensory apparatus to discriminate the presence of the signal (**signal strength**, denoted d') and by the criterion used to decide if the evidence is strong enough to warrant action (**criterion**, denoted c).

	Prey	No prey
Attack	+	-
Don't attack	-	+

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Figure II. Matrix showing the possible successes (+) and costs (-) of the predator attacking or not attacking. If there is no prey, then to attack is a false alarm (top right). Not attacking when there is prey is classed as a miss (bottom left).

the chromatic sensitivity of its visual system and its willingness to attack (criterion). These two parameters are intrinsic to a predator. They are nature, not nurture.

The predator's signal strength d' as a signal-detection observer depends on the predator's chromatic sensitivity *and* the match between the background of the world and the coloration of the prey. For a prey with a particular coloration, there is a choice of chromatic sensitivity that maximizes the predator's ability to detect the prey and the optimal predator for this prey has this chromatic sensitivity. But, of course, there are other prey with other colorations. Moreover, the net effect of the predator's predations is to reduce the likelihood that the prey it can most readily detect will reproduce.

The choice of criterion is, in effect, a threshold on the sensory evidence needed to justify an attack. If it is too low, the predator will waste itself attacking phantoms. If too high, the predator will starve surrounded by riches. Success, from the predator's point of view, depends upon

signal strength and a wise choice of criterion, but signal strength depends on the mix of prey currently available.

To summarize, we cannot say whether a particular predator will prosper until we discover what the typical colorations of its prey are. And these colorations depend, of course, on past predation which depends on the colorations of past prey.... Predator and prey are locked into a co-evolutionary cycle with no clear indication of what mixture of predators and prey will evolve over time. Geisler and Diehl evaluate this co-evolutionary dance for several choices of starting position and assumptions about possible prey and possible predators and show how the two species settle into stable coexistence (a Nash equilibrium in game-theoretic terms [7,8]). Once the stable mixture of prey coloration and predator chromatic sensitivity is reached, any prey of a different coloration, or any predator with a different chromatic sensitivity, is at a disadvantage. The co-evolution of the species dictates the chromatic sensitivity of predator and the coloration of prey, at least until the typical colors of the background change.

The articles by Geisler and Diehl are, of course, only a beginning. The approach that they take, though, is potentially of great value. Evolutionary explanations of aspects of biological perception are too often *post hoc* fairy tales. We explain what we already know in terms of a rich and flexible set of possible assumptions and our theory, such as it is, always evades the wicked witch of falsifiability, living happily ever after.

At a minimum, we might hope that simulations such as those of Geisler and Diehl could generate interesting predictions about visual perception, predictions that have not yet been verified experimentally. A predictive, mathematical model of visual function in an evolutionary context could serve as a valuable tool in guiding experimental research.

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