## Optimality — the biologist's tricorder

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The medical officers of *Star Trek* use a mysterious device called a tricorder to diagnose the condition of their patients. Unlike other sciencefictional technologies aboard Starfleet ships, we are never offered an explanation for the science behind this one. Nevertheless, watching starship medicos in action, we routinely witness the tricorder's efficacy. Carefully and systematically waved close to a living being, it reveals all we need to know about that body's physical and biochemical state. No needles, no knives, no pain, no waiting!

Perhaps we shall never have real tricorders, but I contend we already have something similar — and at least as interesting. Optimality theory (including game theory — the focus of this symposium) may not tell us about the DNA of any individual, but it can, without recourse to electrodes or scalpels, tell us about the thoughts of individuals and about the information in their thinking organs. Optimality can reveal the ultimate secrets behind their sexuality, their growth and shapes, their ageing and many other aspects of their phenotypes. It may not be able to determine the cause of any disease, but it can explain, without taking a single drop of blood, why organisms act the way they do and live the way they do. A fascinating example in this symposium: Understanding the deceptively risky way that sentinels expose themselves to view (Bednekoff 2001).

Of course, optimality studies cannot actually make conclusions available for particular indi-

viduals, only for groups of them. But that turns out to be another advantage. Looking at group consequences of individual behavior can reveal how behavioral decisions drive population dynamics. In this symposium for example, we learn that optimal behavior may destabilize single-species dynamics (McNamara 2001) and stabilize predatory dynamics (Brown *et al.* 2001). We also see it used to determine the frequency of stochastic dynamics, as well as the spatial scale at which population regulation occurs and within which habitat selection takes place (Morris 2001).

Optimality is nothing but practical natural selection. Darwin's Genie (to use Norman Myers lovely metaphor for natural selection) is too abstract to give us scientific explanations for the phenomena of life. As many have pointed out, its powers can be misinterpreted as tautology because it is too easy to express as 'the winners win, the losers lose'. It has certainly evoked many expansive and careless explanations, in fact, a whole cottage industry of adaptationist fable building that was meant to leave us thinking how smart and wise we were. Perhaps mimicry was the sole exception to this rule; a mimic surely has to resemble its model to succeed. But now, clothed with optimality, our attempts to understand the influence of natural selection have matured and become useful science.

The main problem with naked natural selection was inattention to constraints and tradeoffs.

Implicit in all adaptationist fables was the initial phrase, ceteris paribus, 'other things being equal'. But the evolutionist cannot ignore other things. Because of them, most changes have costs as well as benefits, and some strategies are simply impossible. Genetics constrains the possible strategies available to individuals. Phylogeny may too. And involvement of each single phenotypic property in multiple processes leads to trade-off constraints. Surely, the ultimate constraint is time itself — any behavior or function that occupies an organism's time may prevent it from spending that time some other way. The task of optimality theory is to model those constraints explicitly and thus to replace the adaptationist paradigm — which declares post factum why some trait is best — with the optimalist paradigm, which seeks the best strategy under the circumstances.

The symposium was rich in examples of such models. In particular, Mitchell and Porter (2001) show that the species diversity of optimal foragers will decline with increased travel and metabolic maintenance costs. And Bouskila (2001) creates a model of selective habitat use by rodents and rodent-eating snakes that allows for large variations in ambient conditions such as moonlight, competition and predation.

Like any scientific theory, an optimality theory swears to tell the truth — and nothing but the partial truth. Like any scientific theory, an optimality theory - in order to see what matters most — deliberately builds a simplified world from which to deduce its predictions. That is why we call scientific theories 'models'. And like all scientific theories, optimality theories are graded on the predictive accuracy of their halftruths. So it is not germane to criticize a particular optimality theory by pointing out that it omits some known feature of life, such as genetics. Genetics is but one of many constraints. The extent to which we can be accurate despite ignoring it, teaches us something about its ultimate influence.

Optimality theories are generally tested indirectly. Instead of directly measuring the optimality equations in the field or laboratory, we look at the tracks they leave, we ponder their shadows. Nowhere is this more apparent than in the experiments of Dall *et al.* (2001). They show that the search path of foraging gerbils becomes more random when foragers perceive a risk of owl predation.

Sometimes we say: If natural selection has done its job reasonably and we have appropriately modeled the significant constraints, then sex ratios ought to be such-and-such, foraging behavior so-and-so, life histories and mating systems like this, *etc.* If we are wrong, we conclude that our model is somehow defective and try to improve it. We do not suspect that natural selection has failed.

At other times, we want to discover what is in the mind of a forager. But we do not hook it up to a battery of electrodes, or slice and stain its brain. We deduce the optimal behavior given that the organism has information of a certain quality and quantity. We repeat our deductions assuming other qualities and quantities. Then we compare our predictions with data. In other words, we perform classical strong inference tests.

Our strategy of looking at the shadow of a variable, rather than directly into its face, is well established in science — so well established that it has even entered the popular literature:

"How (do) they locate invisible planets? ... the visible ones act in erratic and inexplicable fashion. Their orbits are ... warped. So you apply gravitational theory and a little geometry of moving spheres and you say, Aha, if there is a planetary body right *there* of such and such a mass and such and such an orbit, then all the random movements of the other planets become logical, even imperative" (MacDonald 1974: p. 85).

And so it is with well-evolved organisms. You apply optimality theory and a little tweak of environmental conditions and you say, Aha, if that environmental change produced such and such a cost or benefit to fitness, then all the patterns of behavior and phenotype become logical, even imperative.

Rarely in science does a paradigm get tested. Optimality, however, is one exception. The tenets of optimal foraging behavior claim that a forager should devote more effort to collecting food when and where such collection is more profitable. Adding competitors to a system should reduce profitability and so **reduce** foraging effort. But if a forager quits when it satisfies its nutritional requirements, then adding competitors should cause it to **increase** its effort. Two classical experiments with gerbils demonstrated the decrease (Mitchell *et al.* 1990, Hughes *et al.* 1994).

So, the enterprise of optimality studies is going astonishingly well. Perhaps its sole disadvantage is that unlike the tricorder, optimality does require waiting, waiting while analyses are developed and waiting while experiments to test them are conducted. Despite this imperfection, and in light of its successes and of the natural human desire to understand rather than merely to describe the world of life, funding agencies would be prudent to increase their emphasis on research that employs it. What a pleasure I had to sit at the symposium on which this volume is based and to see the current flowering of this work.

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