



Commentary

Iwasa et al. (1984): On the cusp of a revolution in foraging theory

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Emlen (1966) and MacArthur and Pianka (1966), the first two studies to develop a mathematical theory of optimal diet, led to heady times in animal behavior, behavioral ecology, and ethology. The theory of these papers was based on either maximizing the rate of energy intake or minimizing the time to achieve a target energy intake (e.g. Schoener, 1971). The theory was exceptionally simple to derive and provided clear guidance to empiricists. For example, the rate-maximizing theory for predicting optimal diet requires that one measures the net energy content, handling time, and encounter rates with prey items and then ranks them by profitability of items (the ratio of energy per prey item to handling time per prey item). With these data and simple algebra, one constructs the long-term rate of energy intake according to which items are in the diet, beginning with the most profitable and including items in order of profitability until the rate of energy intake starts to fall ((Mangel, 2006), pp. 3–5), thus predicting the diet maximizing the long-term rate.

The rate-maximizing approach to behavior was used in the highly influential paper in *Theoretical Population Biology* by Charnov (1976) to characterize the behavior of an organism foraging in a patchy environment. The resulting theory, called the Marginal Value Theorem, requires that one measures the rate of gain of energy as a function of residence time in one of many identical patches and the travel time between patches. From these one predicts the patch residence-time that maximizes the long-term rate of energy gain; such predictions can be obtained using a simple graphical method (Mangel, 2006), pp. 5–8).

Rate-maximizing theory explained behavior of the birds (Krebs et al., 1977), the bees (Pyke, 1978), and many other organisms. These theories were highly successful, but they also had gaping holes. In particular, the theories lacked a treatment of mortality while foraging (all organisms face the challenge to obtain sufficient resources for reproduction without being killed) and ignored physiological state (very hungry organisms and sated organisms often behave in different ways).

Iwasa et al. (1984) filled these holes, using the method of Stochastic Dynamic Programming (SDP; see Mangel (2015) for a history relevant to biology). They illustrated the theory with the oviposition strategy of parasitoids, which lay their eggs in or on other insects and whose offspring complete development using the resources of the host insect. Iwasa et al. (1984) converted the diet choice problem into a question of host range (which hosts to attack, given a mixture of hosts in the environment) and used the methods of rate-maximizing to predict the range of hosts attacked. To include natural mortality, they computed the expected accumulated lifetime oviposition, which is a natural measure of Darwinian fitness, using SDP. They separated mortality while searching for hosts and mortality while ovipositing on a host of a particular kind. They derived the equation of SDP, which depends upon state (number of eggs remaining) and time, and computed the solution for the stationary (time independent) version of the equation under a variety of different assumptions about ecology and biology, such as the shape of the relationship between eggs laid and reproductive success, the number of host types, whether hosts are previously parasitized or not, and the rate of natural mortality.

The choice of parasitoids was brilliant. First, a female's remaining number of eggs is a natural physiological state that is also clearly connected to fitness through oviposition. Second, there is a class of parasitoids, called pro-ovigenic, which are born with all of their eggs and do not mature eggs during their lives (Mangel, 2006), pp. 133–135). Thus, an egg used at one time for oviposition in an inferior host is clearly not available at a later time if a superior host is encountered, making the tradeoff abundantly clear. Third, parasitoids are generally small insects subject to abiotic (e.g. rain storms) and biotic (e.g. spiders) mortality pressure almost constantly; their future is uncertain and the end is always near.

Iwasa et al. (1984) used the theory to predict the host range when mortality is included and compared it with the host range from the rate-maximizing theory, showing when the two led to the same predictions and when they differed. The discussion in their paper is rich and thorough.

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Iwasa et al. (1984) were on the cusp of a revolution of state dependent behavioral and life history modeling. I have called their Eqns 5 or 7 one of the two canonical equations of state dependent behavioral and life history theory (Mangel, 2015). A decade after their paper, at the meeting on entomophagous insects in Whistler, British Columbia, Canada, attendees stated almost uniformly that one had to think about physiological state when understanding insect behavior and life history.

At the current time, it is possible to find articles using state dependent behavioral and life history modeling implemented by Stochastic Dynamic Programming applied to all kinds of organisms, including humans (e.g. Clark and Mangel, 2000); space does not allow a full list). These methods are particularly appropriate for predicting responses to anthropogenic disturbance and environmental change (e.g. McHuron et al., 2017).

Even so, the paper of Iwasa et al. (1984) is not as well-known as it should be and it is worthwhile to explore why. First the paper is about insect parasitoids, and many researchers who worked on birds, bees, and fish may have not even bothered to read it because of the title. When McNamara and Houston (1986) and Mangel and Clark (1986) once again introduced the method of SDP, the foci were the small bird in winter (McN&H) and patch selection, butterflies, feeding offspring, and territorial defense (M&C). Thus, it is likely that the potential of SDP modeling did not emerge to most readers from Iwasa et al. (1984). Second, this was a stand-alone paper from the authors; the title (that this is part 1 of a series) suggests that more were to come but as far as I can tell they moved on to other work. It is rare that a single paper achieves a revolution (Elworthy, 2007). Third, although the analysis in Iwasa et al. (1984) was presented clearly, it would have been challenging for many biologists, especially empiricists (e.g. because the model is formulated in continuous time, it requires Landau order notation). Although the algorithm of SDP is easy to state one learns how to think backwards in time (Mangel, 2015), implementing it often requires computation, and computing was difficult in 1984. Within just a few years the desktop revolution had changed the access biologists had to computers. Today virtually all biologists compute, many using R,

which is sufficient for a majority of the models involving SDP. Finally, introducing a physiological state makes experiments more daunting and more work — one must both observe behavior and somehow determine state. For insects this requires dissecting and counting eggs, which is hard enough, but for other species it is even more complicated.

Hopefully, colleagues will return to this paper and give it the proper consideration that it deserves.

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