THE EFFECT OF VARIABILITY ON HOST FEEDING AND REPRODUCTIVE SUCCESS IN PARASITOIDS

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We model the behaviour of a solitary parasitoid that can either eat a host or lay an egg on it. When the parasitoid does not die as a result of starvation, it should always lay an egg on a host. We compute the parasitoid's lifetime reproductive success in this case, and illustrate the effects of the mean time to find hosts and the variance in this time. We then develop a state-dependent model in which the decision to eat the host or lay an egg on it depend on the parasitoid's state. This model is used to explore the effects of variability in the time to find hosts on the parasitoid's lifetime reproductive success. It is shown that there can be a non-monotonic relationship between reproductive success and variability.

Introduction. Solitary parasitoid wasps search for insect hosts upon which they lay an egg. The immature parasitoid develops by feeding on the host, eventually killing it. Parasitoid wasps are important in the biological control of pests and this has resulted in intensive study of their reproductive behaviour. In recent years, the methodology of behavioural ecology has been applied to this study; in particular, the diet and patch models of classical foraging theory have been used to investigate host searching, host selection and clutch size (van Alphen and Vet, 1986; Waage, 1986; Godfray, 1987). While this approach has led to many insights into parasitoid biology, classical foraging models with time-independent parameters are inappropriate for the study of many aspects of parasitoid behaviour that are influenced by time-dependent factors such as egg load, energy reserves and the passage of the season. To study the evolution
of this type of behaviour, a dynamic optimization approach is required (Mangel, 1989).

An important aspect of the biology of many parasitoids is host-feeding; which occurs when a parasitoid feeds on a potential host (Jervis and Kidd, 1986). Some parasitoids feed from a host and then go on to use it for oviposition but the normal pattern is for a host to be used either for oviposition or as a source of food. The function of host-feeding may be either to obtain energy or to obtain protein and other nutrients necessary for the production of eggs. Host-feeding is important to the population dynamics of host/parasitoid interactions as it results in the death of hosts without the concomitant production of immature parasitoids.

Our aim in this paper is to study one particular aspect of host-feeding; how the optimal decision on whether to feed or parasitize a host is influenced by the distribution of hosts in the environment. We model different host distributions by allowing the distribution of the time between encounters to be a random variable specified by a probability distribution. If hosts are patchily distributed for example, then the distribution of inter-host intervals will have a higher variance than if hosts are randomly or regularly distributed. Those parasitoids that attack hosts feeding on evanescent resources such as fruit, dung or fungi, frequently emerge as adults some distance from suitable hosts. To investigate the effect this may have on host feeding we treat the interval from emergence to the discovery of the first host as distinct from subsequent inter-host intervals.

**The Model.** We assume that the function of host feeding is to provide energy for the searching parasitoid. The parasitoid's energy reserves are denoted by $x$. If energy reserves fall to zero, the parasitoid dies of starvation. We also assume that the parasitoid has an essentially unlimited number of eggs and that it cannot utilize eggs as an energy source (this behaviour, egg reabsorption, is found in some parasitoids). The parasitoid searches for hosts and the inter-host travel time, $T$, is a random variable with density function $f(t)$. If the parasitoid feeds on a host, its energy reserves increase by $e$ while reserves decrease (as a result of activity) at rate $b$ per unit of time. There is a constant mortality $m$ per unit of time.

On encountering a host, the parasitoid must decide whether to feed from it or oviposit in it. We calculate the optimal decision, as a function of energy reserves, on the assumption that natural selection maximizes the reproductive success of the insect. To do this we use the technique of stochastic dynamic programming. For reviews of the application of this approach to biological problems see McNamara and Houston (1986), Houston et al. (1988) and Mangel and Clark (1988) and, for particular applications to parasitoids, see Mangel (1987, 1989).