Patch-leaving rules for parasitoids with imperfect host discrimination

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Abstract. 1. The solitary parasitoid *Anagrus delicatus* attacks hosts (plant-hopper eggs) that exist in distinct batches and that are readily detectable to the foraging parasitoid. However, *Anagrus delicatus* attacks only a small fraction of the available hosts within a batch of eggs and then disperses (Cronin & Strong, 1993a). Here we address the question: Why is *A.delicatus* abandoning seemingly high quality patches?

2. A parasitoid with an imperfect ability to discriminate between unparasitized hosts and hosts that it has attacked earlier within the same patch experiences a risk of self-superparasitism when attacking multiple hosts within a single patch. Self-superparasitism can incur costs in the form of lost time and eggs. Early patch leaving can be favoured as a means of avoiding the costs of self-superparasitism.

3. A simple static model demonstrates that patch leaving is favoured by low costs of travelling to a new patch, high error rates in discriminating previously self-parasitized hosts, and high levels of parasitism in the currently occupied patch.

4. A more detailed dynamic state variable model, parameterized for *A.delicatus*, demonstrates that this parasitoid's seemingly enigmatic behaviour can be explained under our hypothesis. In order for this to be the case, we predicted that *A.delicatus* cannot recognize previously parasitized hosts. Subsequent to our prediction, Cronin & Strong (1993b) demonstrated that experienced *A.delicatus* do not avoid ovipositing in previously self-parasitized hosts.

5. Optimal patch leaving rules can be highly sensitive to even very low host discrimination error rates, which may be widespread among parasitoids.

Key words. Optimal foraging, patch use, host discrimination, Hymenoptera, parasitoid, *Anagrus delicatus*.

Introduction

The theory of patch use has been applied to understanding the behaviour of insect parasitoids foraging for patchily distributed hosts (Cook & Hubbard, 1977; Hubbard & Cook, 1978; reviewed by van Alphen & Vet, 1986; Godfray, 1994). Classical patch use theory was developed for 'predators' that capture and consume prey items (or other resources) while foraging (Charnov, 1976; Stephens & Krebs, 1986). However, unlike foraging by predators, foraging by parasitoids involves search for, and oviposition in, hosts, and is thus a process that produces a spatial and temporal distribution of progeny in the environment.

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Attacked hosts are not consumed, but remain in the environment in a parasitized state as parasitoid progeny develop. Many parasitoids demonstrate increased probabilities of dispersing from a patch upon detection of previously parasitized hosts (van Lenteren, 1981, 1991; van Alphen & Vet, 1986; Hemerik *et al.*, 1993).

The linkage between parasitoid foraging and progeny distribution also means that factors influencing offspring survivorship can shape the selective forces acting on parasitoid foraging behaviour. Three such processes have been studied. First, if the searching behaviour of hyperparasitoids or predators that attack the immature stages of parasitoids responds to the distribution of parasitoid progeny, then optimal patch use behaviour by the primary parasitoid may be altered. For example, models developed by Ayal & Green (1993) and empirical studies

conducted by Mackauer & Völkl (1993) suggest that aphid hyperparasitoids that generate directly density-dependent mortality in primary parasitoid populations can decrease the optimal number of aphids that a primary parasitoid should attack before leaving a patch. Second, when the distribution of parasitoid offspring influences both the between-generation mean and variance of off-spring survival rate, and therefore parental fitness, 'bet-hedging' or 'spreading of risk' may be important, and could also select for earlier departures from host patches (Strong, 1989; Cronin & Strong, 1993a). Third, as noted by Yamada (1988), parasitoids foraging within a patch face the risk of self-superparasitism; this is one type of risk that is not encountered by foragers that consume their prey. Parasitoids attacking more than one host per patch may re-encounter hosts that they have already parasitized. Unless the ability to discriminate between these hosts and unparasitized hosts is perfect, there is a risk that additional eggs and time will be allocated to the same host without the increase in reproductive success that would be garnered from oviposition on a healthy host.

Our study was motivated by the reported behaviour of egg parasitoids in the family Mymaridae (Hymenoptera), which attack planthopper and leafhopper eggs (Homoptera). Several mymarids attack species of leafhoppers that deposit large batches of eggs in distinct patches, and in which host eggs are readily detected by the foraging parasitoid. For example, the parasitoids *Gonatocerus cinctipitis* and *Anagrus optabilis* do not leave a patch until all hosts have been attacked (Sahad, 1982, 1984). In contrast, the solitary parasitoid *Anagrus delicatus* attacks only a small number of hosts (in one study, parasitizing an average of six hosts out of eighty-one available) and then disperses (Cronin & Strong, 1993a). A number of potential explanations for this result, including the possibility that parasitoids were egg limited or that hosts were either unsuitable for parasitoid development or protected from attack, were experimentally rejected by Cronin & Strong (1993b). Furthermore, departure from patches was not precipitated by interference between foraging parasitoids or by frequent contacts with parasitized hosts, and occurred before patch depletion could depress the rate of oviposition. Here we address the question: Why is *A. delicatus* abandoning seemingly high-quality patches?

In particular, we propose that a parasitoid with an imperfect ability to discriminate between unparasitized hosts and hosts that it has attacked earlier within the same patch can benefit from early patch leaving. We first present a simple static model to explain the relationship between constraints on discrimination accuracy and patch leaving rules. We then present a more detailed dynamic state variable model, parameterized for *A. delicatus*, to explore the conditions under which this parasitoid's seemingly enigmatic behaviour can be explained under our hypothesis. Finally, we discuss the application of our results to parasitoids with different levels of host discrimination abilities.

Results

A simple static model

Consider a proovigenic (i.e. all eggs are matured prior to the onset of oviposition activity), solitary parasitoid that has deposited all of its eggs but two. The parasitoid discovers an unexploited (i.e. no prior parasitoids) patch of H hosts, with $H \gg 1$ (to be called patch 1), and lays an egg in one of these hosts. Thus, the proportion of hosts in patch 1 that is parasitized, p, is now $1/H$. Assume that all hosts in this patch and elsewhere are of equal value, and let the fitness increment from ovipositing any number of eggs in a single host be the same (1). That is, once one egg is laid in a host, no additional fitness is accrued from depositing additional eggs in that host.

Assume that subsequent foraging within the patch is random, such that if the parasitoid continues to search in the patch for a second host, the probability that the next host it encounters is the one just parasitized is p. (This assumption could easily be relaxed to incorporate other modes of search; for example, systematic search would depress the re-encounter probability below p, and area-restricted search would increase the re-encounter probability above p.) Let the probability that a parasitoid re-encountering the previously parasitized host fails to perceive that the host is parasitized be ε, the host discrimination error rate $(0 \leqslant \varepsilon \leqslant 1)$. Furthermore, assume that if the parasitoid discriminates successfully on the first re-encounter, it will not err on subsequent re-encounters.

Let the probability of parasitoid mortality from any source (e.g. senescence, predation) while foraging in patch 1 for the next host = m_{stay}, and let the probability of parasitoid mortality while travelling to some new patch (patch 2) and foraging within that patch to locate a host be m_{move}. Assume further that the parasitoid foraging in patch 2 has zero probability of encountering a host that it had previously parasitized.

Under what conditions should the parasitoid leave patch 1? The currency of our model is the fitness derived from the parasitoid's last egg. Two strategies are available. First, the parasitoid can stay in patch 1. In this case, the parasitoid will obtain a fitness increment of 0 if it re-encounters the already parasitized host and fails to recognize that the host is parasitized (probability = $p\varepsilon$), and will obtain a fitness increment of 1 if it first encounters an unparasitized host (probability = $1-p$) or re-encounters the previously parasitized host, successfully recognizes it as such, and therefore rejects it and moves on to an unparasitized host (probability = $p(1 - \varepsilon)$. Thus, the fitness value associated with staying is

$$V_{stay} = (1 - m_{stay})\{[p\varepsilon]\cdot 0 + [(1 - p) + p(1 - \varepsilon)]\cdot 1\}$$
$$= (1 - m_{stay})(1 - p\varepsilon). \tag{1}$$

Second, the parasitoid can leave to search for a host in patch 2, in which case the fitness value is

$$V_{move} = (1 - m_{move})\cdot 1$$
$$= (1 - m_{move}). \tag{2}$$

Parasitoids will be selected the leave patch 1 when $V_{move} > V_{stay}$. Substituting from (1) and (2), we obtain a condition under which leaving is favoured:

$$(1 - m_{move}) > (1 - m_{stay}) (1 - p\varepsilon)$$

$$(1 - p\varepsilon) < (1 - m_{move})/(1 - m_{stay}) \tag{3}$$

We define the cost of leaving c by $(1 - m_{move})/(1 - m_{stay}) = (1 - c)$. In general, $0 \leqslant c \leqslant 1$; if there is no travel cost $c = 0$, whereas if travel causes certain death $c = 1$. Substituting into (3) we have

$$(1 - p\varepsilon) < (1 - c)$$

$$c < p\varepsilon \tag{4}$$

Our simplest case model predicts that parasitoids will leave when the cost of leaving is less than the product of the level of parasitism in the current patch and the host discrimination error rate. Thus leaving is favoured by low costs of travelling to a new patch, high error rates in discriminating previously self-parasitized hosts, and high levels of parasitism in the currently occupied patch. Leaving is never favoured when the error rate is zero. For parasitoids with no ability to discriminate between parasitized and unparasitized hosts ($\varepsilon = 1$), we obtain a very simple result: leaving is favoured when the cost is less than the current parasitism rate.

Our development of this model for application to *A.deli-catus* was initially highly speculative because we lacked an estimate for the error rate, ε. However, Cronin & Strong (1993b) have recently reported detailed laboratory analyses of host acceptance behaviour by *A.delicatus* that demonstrate that this parasitoid has little or no ability to distinguish between unparasitized and freshly parasitized hosts (previously attacked by either the same or a different female). It seems highly improbable that the acceptance of previously parasitized hosts observed by Cronin & Strong (1993b) was adaptive (*sensu* van Alphen & Visser, 1990; Mangel, 1992); in at least some treatments, parasitoids had prior oviposition experiences in patches of unparasitized hosts, and still demonstrated no avoidance of parasitized hosts. Furthermore, *A.delicatus* has a limited fecundity, and appears frequently to be egg-limited in the field (Cronin & Strong, 1993a). Thus, it appears that *A.delicatus* is unable to recognize that a host has been parasitized, i.e. ε is very close to 1.

A state variable model

A parasitoid with a limited number of eggs such as *Anagrus delicatus* has a naturally defined physiological state variable. This allows us to focus on the interaction between the physiological state of the organism and the environment, as mediated by behaviour. Here we describe a simple dynamic state variable model (*sensu* Mangel & Clark, 1988; Mangel & Ludwig, 1992) that elaborates the simple static model discussed in the previous section.

We characterize the ecology as follows. Imagine a large number of identical patches, each containing H hosts.

Patches are physically separate and the travel time between patches is τ. Here the fundamental increment of time is the time it takes the parasitoid foraging within a single patch to locate and reject a previously parasitized host. Hence, travel time is a multiple of this rejection time. When the parasitoid moves between patches, the rate of mortality is q_m so that the probability of surviving a move between patches is $\exp(-q_m\tau)$. When the parasitoid stays in the patch, the rate of mortality is q_s.

Next, consider the physiology of the organism. We let $x(t)$ denote the egg complement of the parasitoid at the start of period t and let $y(t)$ denote the number of eggs already laid in the current patch. Both of these are constrained by the maximum number of eggs x_{max} that the parasitoid has upon eclosion or shortly thereafter. When the parasitoid encounters an unparasitized host, we assume that it will oviposit in that host and it increments its total lifetime reproduction by f. Oviposition requires time τ_{ovip}. When the parasitoid encounters a previously parasitized host we assume that there is a probability ε that is does not recognize the host as previously parasitized. If such recognition occurs, the host is rejected; otherwise the parasitoid oviposits, but because the host is already parasitized there is no increment in lifetime reproductive success associated with this host. For *Anagrus delicatus* it is most likely that $\varepsilon = 1$, but we develop the general model because the phenomenon we discuss is a general one.

Ecology and physiology are linked through the focus on expected lifetime reproductive success

$ERS(x,y,t) = $ Expected lifetime reproductive success from time t onwards, given that current egg complement is x and that y eggs have already been laid in the current patch (5)

We assume that there is a time T after which no more reproductive success is accumulated, so we set $ERS(x,y,T) = 0$ for all values of x and y. (Doing this is actually a technical consideration, because in the results that we consider below we allow T to be so large that behaviour is independent of time.)

For times previous to T we must compare the values, measured in terms of reproductive success, of moving to a new patch or staying in the current patch. The value of moving is

$$V_{move}(x,y,t) = \exp(-q_m\tau)ERS(x,0,t + \tau) \tag{6}$$

That is, if the animal moves, the probability of surviving the travel is $\exp(-q_m\tau)$, in which case it ends up in a new patch ($y = 0$) with the same number of eggs (x) at a later time ($t + \tau$, which we replace by T if $t + \tau$ exceeds T).

If the animal stays in the current patch there is a probability $p(y,H)$ that it will encounter a parasitized host. We assume that encounters are random so that

$$p(y,H) = y/H \tag{7}$$

If we assume that $H > x_{max}$ (generally the case for *Anagrus delicatus*) then the probability defined in (7) is

always less than 1.0. The value of staying then involves three kinds of events: an unparasitized host is encountered and attacked, a previously parasitized host is encountered and recognized as such, and a previously parasitized host is encountered but not recognized as such. Evaluating the expected reproductive success for each of these leads us to

$$
\begin{aligned}
V_{stay}(x,y,t) = {} & (1 - p(y,H))\{f + \exp(-q_s\tau_{ovip}) \\
& ERS(x - 1, y + 1, t + 1)\} \\
& + p(y,H)(1 - \varepsilon) \exp(-q_s) \, ERS(x,y,t + 1) \\
& + p(y,H) \, \varepsilon \exp(-q_s\tau_{ovip}) \\
& ERS(x - 1, y, t+1)
\end{aligned}
\tag{8}
$$

We then determine expected reproductive success according to

$$
ERS(x,y,t) = \max\{V_{move}(x,y,t); \, V_{stay}(x,y,t)\} \tag{9}
$$

The solution of (9) not only predicts expected lifetime reproductive success, but also oviposition behaviour, particularly the number of eggs to lay in a patch before moving to another one. When the difference between T and t is large, behaviour is independent of time and depends only upon physiological state (x) and the number of eggs laid thus far (y). We can then use the predicted behaviour to look forward (Mangel & Clark, 1988) in the following manner. Imagine that the parasitoid has just entered a new patch (so that $y = 0$) with current egg complement x. We then begin to decrement x and increment y until the predicted behaviour is to leave the patch. In this manner we can predict the number of eggs to lay before moving as a function of the current egg complement (Fig. 1). Note that the predicted behaviour of exiting patches after parasitizing a small number of hosts is consistent with that reported by Cronin & Strong (1993a).

The general case: parasitoids with imperfect host discrimination abilities

Anagrus delicatus is not unique in lacking host discrimination abilities. A similar inability to distinguish between unparasitized and parasitized hosts has been inferred for a variety of parasitoid wasps (Liu & Morton, 1986, and references therein). However, van Lenteren (1981) estimated that host discrimination had been demonstrated in 150—200 species of parasitoids in a broad array of taxa, and it seems clear that most hymenopteran parasitoids do possess some discrimination ability. Nevertheless, even in discriminating species, rejection of previously parasitized hosts rarely is complete (e.g. Cloutier *et al.*, 1984; Hubbard *et al.*, 1987; Micha *et al.*, 1992). In a few cases it has been shown that the occasional failure to reject a parasitized host is due to a breakdown in the mechanism of host discrimination. For example, the parasitoid *Leptopilina heterotoma* (= *Pseudeucoila bochei*) has a highly developed host discrimination ability, but will still accept a self-parasitized host if it returns to the host within 70 s and probes at a site distant from the previous site of oviposition (van Lenteren, 1981). This observation is consistent with a host-marking chemical that requires
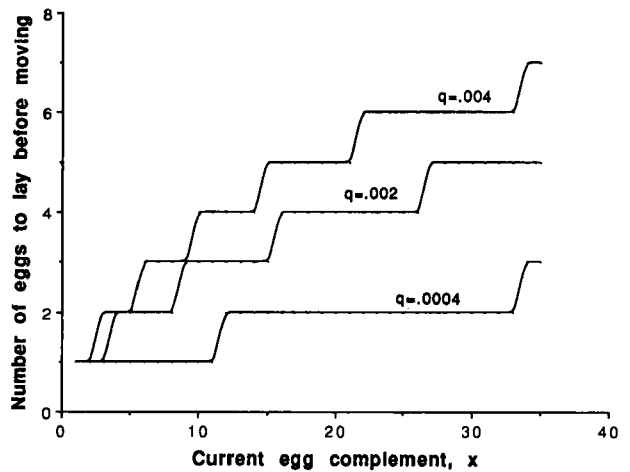

Fig. 1. Predicted number of eggs to lay before leaving a patch as a function of the current egg complement x and the rate of mortality. Here we have assumed, for simplicity, that $\tau_{ovip} = \tau = 5$ and that all of the mortality rates $(q$'s$)$ are equal. For reference, the value $q = 0.0004$ corresponds to a 0.998 probability of surviving a single oviposition or travel and a 0.932 probability of survival to lay all thirty-five eggs in a single patch: for $q = 0.002$ the respective values are 0.99 and 0.705; for $q = 0.004$ they are 0.98 and 0.497 respectively. Although the cost of moving between patches (defined on the spatial scale of individual leaves) has not been quantified formally for *Anagrus delicatus*, field observations suggest that the cost is small (J. T. Cronin, personal communication). $x_{max} = 35$; $H = 50$; $\varepsilon = 1.0$.

some time to diffuse through the host's body. Similar processes have apparently contributed to host discrimination errors in other parasitoids (Wylie, 1971; King & Skinner, 1991). In the parasitoid *Opius dimidiatus* host discrimination based upon a combination of externally- and internally-detected cues breaks down 3—4 h after parasitism (Nelson & Roitberg, 1993). However, it is in general frustratingly difficult to determine whether failure to reject a parasitized host represents a breakdown in the ability to discriminate or alternately a 'decision' by the parasitoid to oviposit in what is recognized as a parasitized host; adaptive superparasitism can occur even under conditions when parasitoids forage alone on patches with abundant, unparasitized hosts (Visser *et al.*, 1990). Overall, however, we suggest that non-zero error probabilities are likely to be widespread. Will low error rates have an important influence on optimal patch leaving rules?

Optimal patch leaving rules can clearly be highly sensitive to even very low error rates (<0.1), especially when the cost of moving between patches is small (Fig. 2). It is intuitive that if the mortality cost of moving between patches is sufficiently high, and if there are enough hosts in a single patch (so that the chance of encountering a previously parasitized host is sufficiently low), then there will be selection for staying in the current patch until all eggs have been laid. Our model allows us to quantify the costliness of moving and the density of hosts per patch necessary for selection to favour depositing all eggs in one patch (Fig. 3). It is likely, then, that the risk of self-
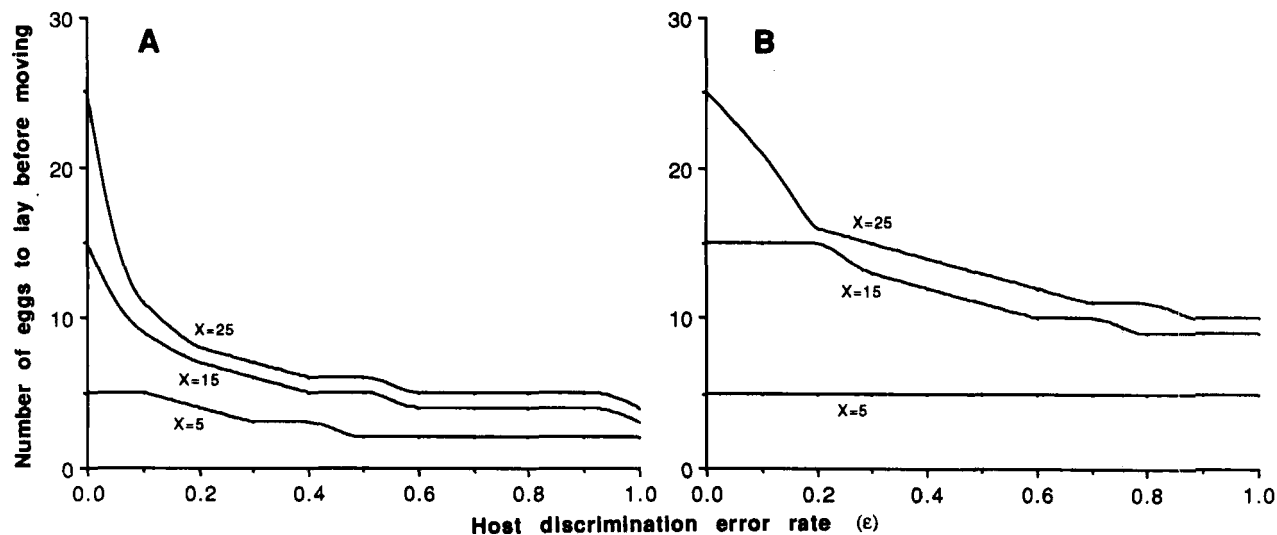
Fig. 2. Predicted number of eggs to lay before leaving a patch as a function of the probability ε of failing to recognize that a host is already parasitized and the current egg complement x. Here $\varepsilon = 0$ corresponds to perfect discrimination, in which case all eggs should be laid in a single patch. As ε increases, it is increasingly likely that a previously parasitized host will not be recognized. When $\varepsilon = 1$, this is certain (and is likely to be the case for *Anagrus delicatus*). We suspect, however, that for many other parasitoids, the value of ε is closer to $0-0.2$. (a) $q = 0.002$. (B) $q = 0.02$. All other parameters as in Fig. 1.
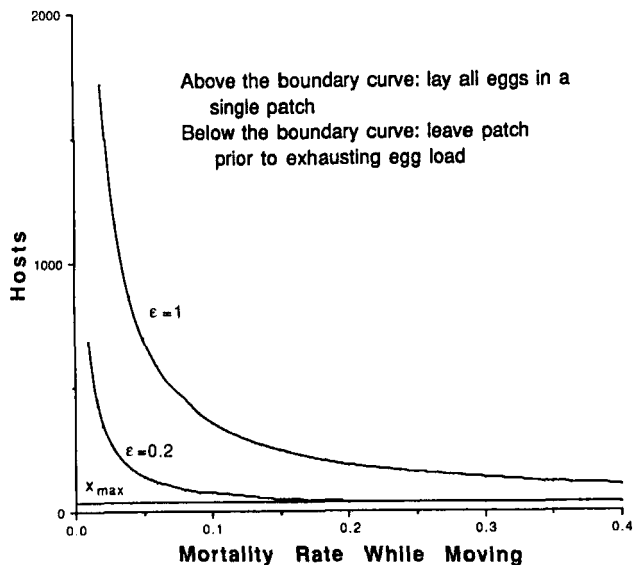

Fig. 3. Boundary curves separating the region in which all eggs are laid in a single patch from that in which patches are exited before all eggs are laid. Parameters are $x_{max} = 35$; $H = 50$; $q_s = 0.002$; and $\tau_{ovip} = \tau = 1$. When the original number of hosts in a patch is much larger than the total egg load (thirty-five eggs), the probability of self-superparasitism is small and parasitoids will not leave patches if the mortality rate while moving (q_m) is high. When there is some, but not perfect, discrimination, the host density needed for staying is lower.

superparasitism has shaped the foraging behaviour of a broad array of insect parasitoids, including those with a documented host discrimination ability, by favouring earlier departure from partially-exploited host patches.

Discussion

Anagrus delicatus, *Anagrus optabilis* and *Gonatocerus cinctipitis* are solitary mymarid parasitoids whose hosts (homopteran eggs) are deposited in distinct patches and are readily detectable by foraging wasps. *Anagrus delicatus* possesses little or no ability to discriminate between parasitized and unparasitized hosts, and leaves patches after ovipositing in only a few hosts (Cronin & Strong, 1993a, b). *Anagrus optabilis* and *G.cinctipitis* are able to avoid superparasitism (Sahad, 1982, 1984), and remain in the patch until all the hosts are attacked. Our analyses show that the cost of self-superparasitism is sufficient to promote the early departure from incompletely exploited patches that is observed in *A.delicatus*. Furthermore, even parasitoids with well-developed, but still imperfect, host discrimination abilities will be selected to depart from patches earlier than parasitoids with perfect host discrimination. The risk of self-superparasitism, which is a function of the host discrimination error rate and the current level of within-patch parasitism, is balanced against the cost of dispersal to a new patch of hosts.

Self-superparasitism by a solitary parasitoid entails two types of cost: the cost of the extra egg and the cost of the extra time which are allocated to an already-parasitized host. Thus the risk of self-superparasitism may be important for both time-limited and egg-limited parasitoids. For parasitoids like *A.delicatus*, which appears frequently to be egg-limited, both types of cost may be important. For other parasitoids that are rarely egg-limited, the time cost may be the more important.

Several hypotheses have been proposed to explain the incomplete exploitation of host patches demonstrated by

A.*delicatus* and other parasitoids. For A.*delicatus*, all off-spring within a patch die when the leaf bearing the hosts senesces; Strong (1989) and Cronin & Strong (1993a) have hypothesized that early patch leaving may be favoured as a means of bet-hedging. As pointed out by Godfray (1994), however, bet-hedging benefits have not been formally demonstrated empirically (by a study of across-generation reproductive rates) or with quantitative models. Furthermore, spatial variation alone does not give rise to bet-hedging, which instead requires temporal variation (Seger & Brockmann, 1987; Venable & Brown, 1988). A. Bouskila *et al.* (unpublished) have suggested that A.*delicatus* may be exploiting only the highest quality hosts within a patch, and then departing to search for additional high-quality hosts. This hypothesis is supported by the observation that A.*delicatus* probes and rejects many hosts; additional work is required, however, to determine what, if any, variable aspects of host quality are being detected by parasitoids. Although A.*delicatus* is not attacked by hyperparasitoids (Cronin & Strong, 1993a), for other parasitoids the influences of predators or hyperparasitoids attacking immature parasitoid offspring could also influence optimal patch use behaviour (Ayal & Green, 1993; Mackauer & Völkl, 1993). Our hypothesis that the risk of self-superparasitism promotes early patch-leaving complements these other hypotheses. Foraging parasitoids exploit resources, much as a predator does, but the exploited resources remain in the environment, unlike those used by a predator. Thus a larger array of ecological forces than has been considered for predator foraging may shape parasitoid patch use.

Our goal here has been to assess the functional consequences of imperfect host discrimination. Thus we have not considered the evolutionary question of why A.*delicatus* has not evolved an effective means of host discrimination. We have proposed that in the absence of host discrimination, A.*delicatus* enhances reproductive success by early departure from host patches. It is, of course, possible that some other process (not yet identified) has favoured a foraging strategy that leads to early patch leaving. Early patch leaving lessens the risk of self-superparasitism, and thus decreases the need for host discrimination. Nevertheless, the risk of conspecific superparasitism remains and should provide potent selection for the evolution of host discrimination (Strong, 1989). The explanation for the failure of A.*delicatus* to avoid superparasitism remains an intriguing question.

Acknowledgments

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