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Mechanisms of local persistence in coupled host–parasitoid associations: the case model of *Maculinea rebeli* and *Ichneumon eumerus*

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SUMMARY

We examine a spatially explicit 'case model' for the interaction between the lycaenid butterfly, *Maculinea rebeli*, and its specialist parasitoid, *Ichneumon eumerus*. This butterfly lives in small, closed populations, rarely numbering over a few thousand individuals, and the parasitoid is found at only a small subset of butterfly-harbouring sites. We explore how parasitoid searching intensity and behaviour, and host refuges from parasitism affect the dynamics of the host–parasitoid couple. In the absence of explicit host refuges, the parasitoid persists only for a very restricted range of search rates and searching behaviours. Absolute refuges to parasitism, modelled as a cue-threshold phenomenon in the elicitation of intensive search for the host, expand the persistence conditions. We link these results to the more general problem of what inferences can be drawn concerning the association between population-level variation in the distribution of parasitism and the population dynamics of the system. The parasitoid's persistence depends importantly on heterogeneity in the vulnerability of the host caterpillars to encounter with parasitoids. Although the host's persistence is also enhanced by such heterogeneity, it is actually intraspecific competition within ant nests that dominates host dynamics. Deductions of the stabilizing power of parasitoids from measures of spatial heterogeneity in parasitism will be spurious without information about the respective density-dependent influences of the parasitoid and other limitation factors affecting the host.

1. INTRODUCTION

Despite the burgeoning literature on the population dynamics of host–parasitoid interactions (e.g. Bailey *et al.* 1962; Hassell & May 1973; Hassell 1978; May 1978; Chesson & Murdoch 1986; Murdoch *et al.* 1987; Reeve 1988; Taylor 1988; Hassell *et al.* 1991; Comins *et al.* 1992; Ives 1992*a*, *b*; Mangel & Roitberg 1992; Holt & Hassell 1993; Rohani *et al.* 1994; Hochberg & Holt 1995), and the increasing numbers of comparative (Hawkins *et al.* 1993; Hochberg & Hawkins 1994) and experimental (e.g. Jones *et al.* 1993; Lampo 1994; Reeve *et al.* 1994*a*) investigations of population dynamics theory involving parasitoids, there has been only scant consideration of how patterns in parasitoid searching behaviour may influence their persistence and population dynamics (e.g. Murdoch & Stewart-Oaten 1989; Godfray & Pacala 1992; Ives 1992*b*; Rohani *et al.* 1994).

In principle, parasitoid searching biology can influence parasitism patterns. A certain range of models show, in turn, how heterogeneity in parasitism can be associated with, or even responsible for, the population dynamics of tightly coupled host–parasitoid associations (e.g. Hassell & May 1973; Hassell 1978; May 1978; Chesson & Murdoch 1986; Hassell *et al.* 1991). Although a growing number of studies have identified situations in which the clarity of the relationships between heterogeneity in parasitism and population dynamics is qualified or even contravened (Chesson & Murdoch 1986; Murdoch & Stewart-Oaten 1989; Hochberg & Lawton 1990; Ives 1992*b*; Rohani *et al.* 1994), few investigations have attempted to tackle the methodological and statistical problems associated with testing such associations (Jones *et al.* 1993; Reeve *et al.* 1994*a*).

One way to investigate in detail how heterogeneity may be associated with population dynamics is to employ mechanistic formulations that are tailored to particular biological systems (Godfray & Waage 1991; Jones *et al.* 1993; Reeve *et al.* 1994*b*). Such 'case models' have the advantage of biological realism and provide the possibility of evaluating assumptions and validating predictions on a site by site basis.

We employ the case model approach to investigating the roles of parasitoid search behaviour and host refuges in the persistence and population dynamics of the hymenopteran parasitoid, *Ichneumon eumerus* (Wesmael), and its specific host, the lycaenid butterfly, *Maculinea rebeli* Hir. This butterfly lives in small, closed

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populations, usually numbering in the tens or hundreds of individuals (Wells *et al.* 1984; Munguiara 1987; Kockelke *et al.* 1994). The local rarity of *M. rebeli* (officially listed as 'vulnerable' Anon. 1990) must mean that its parasitoid is geographically at least as scarce, and is locally at least as vulnerable to extinction (Thomas & Elmes 1992; Thomas 1994). This type of system, involving small population numbers and high degrees of specialization in interspecific interactions, is likely to be as sensitive as any to small variations in species biology or the environment. It is therefore an appropriate scenario for evaluating how small-scale population processes influence the persistence of host–monophagous parasitoid interactions.

2. BACKGROUND TO THE *MACULINEA REBELI* COMMUNITY MODULE WITH PARTICULAR REFERENCE TO *ICHNEUMON EUMERUS*

The term 'community module' refers to small groups of species that interact either directly or indirectly, and whose dynamics can be understood to some extent, divorced from the context of the surrounding community (see Holt 1996). Our main interest in applying this concept to *M. rebeli* is to establish the minimal species set that contributes to the persistence and dynamics of this rare butterfly, and of the consumer which depends on it, *I. eumerus*. The biologies of the butterfly and its parasitoid have been reviewed elsewhere (Thomas *et al.* 1989, 1993; Elmes *et al.* 1991*a*, *b*; Hochberg *et al.* 1992, 1994; Thomas & Elmes 1993) and are briefly presented below.

Like its other four European congeners, *M. rebeli* is exceptional among the Lycaenidae in its degree of specialization in exploiting its two larval resources, the cross-leaved gentian, *Gentiana cruciata* L., and the red ant, *Myrmica schencki* Emery. The butterfly oviposits on or near the developing flowers of the gentian, irrespective of the presence of the host ant (Thomas *et al.* 1989). Despite moulting through three larval instars within the plant's flowers, the young caterpillars only gain about 1 % of their final biomass. Upon reaching the fourth and final larval instar they drop to the ground and are either found by a *Myrmica* worker (of any species) and brought back into its nest, or perish due to dessication or predation (Elmes *et al.* 1991*a*). It is, however, almost solely within the nests of *M. schencki* that the caterpillars can survive to adulthood, manipulating ant workers into feeding them for about 10 months of their annual life cycle (Thomas *et al.* 1989; Elmes *et al.* 1991*b*). Not all caterpillars entering *M. schencki* nests survive to become adults: many perish due to failed initial adjustment to life in the nest (Elmes *et al.* 1991*a*), competition with other *Maculinea rebeli* caterpillars within the same nest (Thomas *et al.* 1993) or – the focus of the present study – parasitism by *I. eumerus* (Thomas & Elmes 1993).

Ichneumon eumerus exhibits extreme behavioural, morphological and physiological adaptations that enable it to locate, oviposit in, and emerge from the specific *Myrmica* nests that support its specific lycaenid host (Thomas & Elmes 1993). The adult wasp emerges in late summer when *M. rebeli* caterpillars are feeding either on gentians or have already been adopted by *Myrmica* colonies. Female parasitoids systematically search the ground for *Myrmica* odours, apparently regardless of whether *G. cruciata* grows near. In laboratory experiments, the odour of any *Myrmica* species induces some reaction, but *I. eumerus* responds strongly only to *M. schencki* colonies, examining them further by inserting her head in the nest entrance. Having identified the ant species in which *M. rebeli* survives, the wasp can then detect which nests also contain caterpillars, and enters only those that do. Inside the ant nest, the wasp oviposits in the largest *M. rebeli* caterpillars present, thus selecting the individual hosts most likely to survive. She then marks the caterpillar, which prevents superparasitism for at least two days before the scent wears off; laboratory experiments suggest that she may mark the nest entrance too. Parasitized *M. rebeli* caterpillars are reared by *M. schencki* exactly like healthy ones, and pupate in the upper brood chambers 9 to 10 months later. A single adult parasitoid emerges from each pupa, and fights past the ants to the nest surface.

I. eumerus releases an allomone when entering and leaving ant nests which induces most workers to attack one another. The parasitoid is also fiercely attacked, but is heavily armoured and bludgeons past its attackers. Nevertheless, parasitoids in laboratory ant nests retreated to unoccupied cells to shed workers between attacking the well-protected *M. rebeli* caterpillars in the brood chambers (Thomas & Elmes 1993), and on two occasions a parasitoid was overwhelmed and killed (J.A.T. & G.W.E., unpublished work).

Little is known about the population dynamics of *I. eumerus* in the field, though laboratory observations indicate that it has an unusual population structure for an insect, with individual females seldom living to enter more than one ant nest, and laying very few eggs that, however, have a high chance of survival (Thomas & Elmes 1993). Small field samples from two sites from which *I. eumerus* is known indicate that it had successfully penetrated 22–35 % of *M. schencki* colonies examined supporting butterfly caterpillars ($n = 22$), killing 6–23 % of the *M. rebeli* population ($n = 128$), with 1–8 parasitoids emerging per ant nest ($n = 7$) (Thomas & Elmes 1993).

3. REVIEW OF PREVIOUS MODELLING STUDIES ON THE *MACULINEA REBELI* COMMUNITY MODULE

The present is the third in a series of empirically based, theoretical investigations of the *M. rebeli* module. The first two will hereafter be referred to as 'HTE' (Hochberg *et al.* 1992) and 'HCET' (Hochberg *et al.* 1994).

HTE explored a simple mathematical model of the butterfly population, constructed from phenomenological functions of survival and reproduction. Only the population of the butterfly could change from generation to generation, whereas those of the other potentially interacting species (the gentian, the red ant and the parasitoid) were kept constant. HTE showed that both the density and resilience of the butterfly population are strongly determined by the population of its definitive host, *Myrmica schencki*. Predicted butterfly density was also sensitive to the parameter determining the constant year to year mortalities inflicted by *I. eumerus*.

Based in part on the prediction by HTE that variation in the population of *M. schencki* is central to the dynamics of *Maculinea rebeli* itself, HCET developed a spatially explicit model that simulated both within and between season dynamics of the butterfly, of *Myrmica schencki* colonies, and of nests of other species of *Myrmica*. The model was much more mechanistic than HTE, incorporating, for example, a linear gradient in microhabitats which determined variation in yearly reproductive rates of the competing ant species. One of the major predictions of HCET was that, despite a large armory of biological mechanisms promoting the persistence of the butterfly, subtle changes in the microhabitat gradient could greatly affect the host ant's ability to recover from damage inflicted by the caterpillars, and thus the ant population's capacity to sustain the butterfly population. Again, as in HTE, HCET assumed the parasitoid population to be constant.

Neither HTE nor HCET consider the dynamics of the parasitoid, *Ichneumon* eumerus. Despite its presence on a number of *Maculinea rebeli* sites, it is not known how it persists nor what its effects are on other members of the *M. rebeli* community module. Our intention in extending the model of HCET to include this natural enemy is to understand how assumptions about its searching biology may affect its persistence and the repercussions for the dynamics of the *M. rebeli* module.

4. THE BASIC MODEL

Before expanding the model of HCET to include the dynamics of *I. eumerus*, we briefly recount its major properties (see HCET for details).

The numerical algorithm models a 1 ha square of 900 cells, over which a constant population of gentians is non-randomly distributed according to observed distributions. Each cell may contain at most one *Myrmica* nest. HCET developed in some detail the within-nest dynamics of *M. schencki* and an additional population of other *Myrmica* species, this latter population grouping *M. rubra*, *M. scabrinodis* and *M. sabuleti*. HCET simulated a one-dimensional gradient in the maximum yearly reproductive rate **R** (i.e. colony productivity) of both ant populations; this gradient corresponds to differences in soil humidity and associated grass cover, with cell-column 1 arbitrarily being the most humid (and grassy) and cell-column 30 being the hottest and driest (with the sparsest turf); each of these 30 points along the one-dimensional gradient have 30 cell-rows with the same habitat conditions (totalling, therefore 900 cells). For each ant species, **R** is a unimodal function of the position along the gradient, peaking at cell column 22 for *M.schencki* and at cell column 9 for 'other' *Myrmica*.

To reach adulthood, *Maculinea rebeli* caterpillars must survive (i) density-independent and then (ii) density-dependent mortalities while on the host plant (with at most one caterpillar surviving per bud), (iii) adoption into a nest of *Myrmica schencki*, and then (iv) density-independent followed by (v) density-dependent mortalities within ant nests (with at most one caterpillar surviving per 50 workers). HCET assumed a constant mortality inflicted by the parasitoid after these within–nest mortalities; in the present study these mortalities are variable due to the population dynamics of *I. eumerus* (see below).

Specifically, a given generation of *Maculinea rebeli* begins with the distribution of the egg population (a constant multiplied by the number of female butterflies) over the plants according to an empirically based distribution function. It is only when gentians and a nest of *M. schencki* co-occur within a cell that a proportion of these caterpillars, once having left their host plant, may be adopted into the nest. This proportion depends on colony size, a measure of the colonies' foraging range.

In parallel to butterfly dynamics, within-nest dynamics of the ants occur. Each year, both ant populations produce two broods, one ('vernal brood') that is potentially exploited by any caterpillar adopted in the nest, and the other which develops rapidly ('rapid brood') during periods when the caterpillars are either absent from nests or are too small to affect the survival of the ant brood. HCET assumed that caterpillars never survive to adulthood within nests of other *Myrmica* species, but nevertheless reduce the productivity of these nests by about half before their death.

Furthermore, each year there are size-dependent probabilities that a given ant colony will either disband and die, or bud into a vacant, adjacent cell. HCET assumed that the first nest to arrive in a given cell could not be displaced by neighbouring nests (i.e. colonies compete pre-emptively). Caterpillar adoption occurs after the completion of the yearly nest dynamics.

5. TEST OF THE BASIC MODEL

The HCET model has recently been tested at 12 independent sites (in addition to Panticosa) in the Alps and the Pyrenees, by estimating the seven of its 19 parameters possible for the 12 new sites (Elmes *et al.* 1996). We found that the predictions explain 86% of the variation in egg numbers over these sites, indicating that HCET is an accurate descriptor of this butterfly's population dynamics.

6. EXTENSION TO *ICHNEUMON EUMERUS*

In our extension of HCET, most of the dynamics of *I. eumerus* are restricted to adult females searching for fourth instar caterpillars of *Maculinea rebeli* within nests of *Myrmica schencki*. We make the following simplifying assumptions about the biology of *I. eumerus*. (i) Parasitism occurs once both density-independent and density-dependent mortalities have acted on caterpillars in the nests. (ii) Only one parasitoid larva can develop per host. (iii) Once parasitized, the parasitoid larva always survives to maturity within the host. And (iv) if two or more parasitoid adults enter a given nest, it is assumed that they do so sequentially (i.e. there is no interference between adult parasitoids).

Due to egg-limitation, and/or time-limitation, and/or host-limitation, the parasitoid will only be able to parasitize a finite number of hosts over its lifetime. Hence, there is the potential for natural selection to favour the use of cues leading to the caterpillars, so as to reduce losses in potential reproductive success as a consequence of inefficient search (van Baalen & Sabelis 1993).

We assume that every parasitoid can inspect, at random, a maximum of τ cells over her lifetime and that the value of τ is the same for every parasitoid in every generation; we will refer to this cell to cell prospection as 'extensive search'. During extensive search, if a parasitoid should locate a cell with cues indicating the potential presence of caterpillars, we assume that 'intensive search' is elicited. Once a constant number ζ of such 'cue cells' are encountered and searched (and caterpillars possibly attacked), the parasitoid is assumed to perish, even if she has inspected fewer than a maximum of τ cells (i.e. $\tau \geqslant \zeta$). If, when searching intensively within a cell, the parasitoid should enter a *M. schencki* nest with *Maculinea* caterpillars (see below), then she encounters them in a random sequence until a maximum ν are met; clearly, if fewer than ν caterpillars are in the nest, then all the caterpillars will be encountered. Encounters occurring in a random sequence is a reasonable assumption when the parasitoid is time-limited within the nest, as is ostensibly the case in this biological interaction (where the parasitoid is heavily attacked within the nest by ant workers). If an encountered host is already parasitized, then we assume that the encounter is wasted, in that either only one parasitoid progeny will survive within-host competition, or that no egg will be deposited (i.e. the parasitoid avoids within-host competition).

7. NUMERICAL SIMULATION METHODS

Since many of the model processes are based on probabilities, no two numerical simulations are exactly alike. With the aim of standardizing the simulation technique, we ran a series of 20 simulations in the absence of the parasitoid, each of 200 generations. At the beginning of each simulation (i.e. generation 1), the two ant populations were assigned to cells at random (with a 50% chance of a colony of either one occupying any given cell), and the gentians were distributed according to a negative binomial, with the clumping parameter, mean number per cell, and the number of flowers per plant determined from field data (HTE; HCET). The algorithm was then run for 50 generations until the ant populations equilibrated, both in terms of cell occupation and nest size. At the beginning of generation 51, a single fecund female *Maculinea* was introduced into the system and allowed to establish over a subsequent period of 150 generations; this was sufficient time for the population dynamics of the butterfly and the two ant species to reach a dynamic pattern without an obvious long-term trend in the populations. At the beginning of generation 201, we noted the full state of the system (i.e. all state variables involving ants, plants and the butterfly).

Because small to moderate variations in total plant numbers from run to run could have an effect (albeit a small one) on the population dynamics of the system (HCET), we chose as the baseline for further numerical studies that particular simulation from the 20 which most closely approximated the total number of gentians actually measured in the field (HTE). Figure 1 shows some of the properties of the baseline system at the beginning of generation 201. Notably, there is a negative correlation between gentians and *Myrmica schencki* nest size due to the negative impact of *Maculinea rebeli* on colonies of this ant (figure 1*c*; HCET). Note also that the occupation of nests sites in the warmer, dryer parts of the site by *Myrmica schencki* is a consequence of several factors: the gradient in this ant's reproductive rate, competition in intermediate areas with other *Myrmica*, and the negative impact of the butterfly on *M. schencki* nests (figure 1*d*; HCET). The same patterns presented below, albeit with more scatter, were produced when we did not standardize the simulations for the plant population, and rather ran each from generation 1 with the butterfly introduced in generation 51 and the parasitoid introduced in generation 201.

So as to ensure that the parasitoid did not go extinct in the first generation of its invasion (possibly reflecting stochasticities extraneous to its interaction with the host), we introduced 20 fecund females in generation 201, just after caterpillar adoption and survival from density-independent and density-dependent mortalities within ant nests.

For all simulations presented below, we employ the baseline model parameter values presented in table 2 of HCET, and $\tau = 100$. We vary only ζ, ν and the parasitoid's search pattern (see below). Other modifications to HCET are presented in the Appendix.

8. RESULTS

We simulated a series of search patterns of individual parasitoids with the aims of seeing how each affected the population trends of the four dynamic populations in the system (especially those of the butterfly host and the parasitoid), and how a straightforward measure of heterogeneity in the risk of parasitism is associated with diverse population indices of the system.

(*a*) *Random indiscriminate and random discriminate search*

We considered how different types of searching 'cues' could affect the persistence of the parasitoid and butterfly, always assuming that the parasitoid encounters cue cells at random.

Six different types of cue were simulated. The most basic kind of random search involves (i) no cues whatsoever – the parasitoid intensively searches a fixed number of cells, regardless of their contents. Another possibility is that the parasitoid searches indirectly for the caterpillar, exploring a cell intensively only when (ii) gentian plants are present. Alternative patterns of

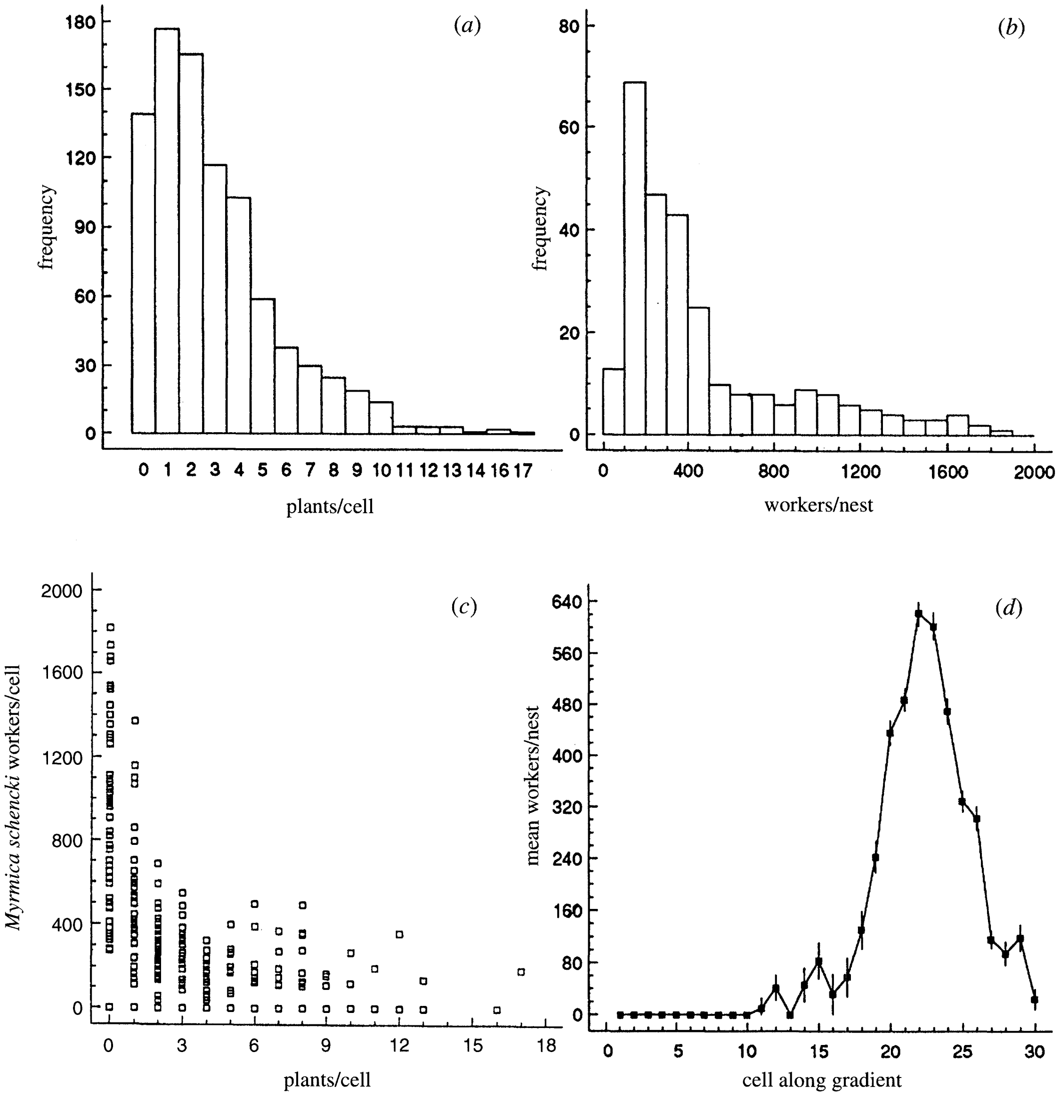

Figure 1. State of the system at the beginning of generation 201, just prior to the introduction of the parasitoid. (*a*) Frequency distribution of *Gentiana cruciata*; (*b*) frequency distribution of worker numbers of *Myrmica schencki*; (*c*) association between plant and host ant abundance for each of the 900 cells of the system; and (*d*) mean numbers of host ant workers per cell at each point along the habitat gradient (bars = s.e. of 30 cells).

search could either be to use (iii) red ants in general as a cue, or (iv) *M. schencki* in particular as a cue. Though still indirect, the use of the (v) joint presence of gentians and host red ants is, *a priori*, more likely to result in parasitism than the previous cases. The most direct form of search is to inspect intensively only (vi) cells containing *G. cruciata*, *M. schencki* and caterpillars of *Maculinea rebeli*.

For each of these six search patterns, there are areas in the ζ–ν parameter space resulting in parasitoid extinction because of insufficient exploitation of the host (area i, figure 2), persistence of the parasitoid with the butterfly (squares, figure 2), and extinction of both species due to the destabilization of the coupled population interaction by the parasitoid (area ii, figure 2). In general, the ability to attack more than three or four caterpillars per nest has little effect on the outcome, and searching more than about six cue cells always leads to extinction of both species if the number of caterpillars attacked per nest is not limiting (figure 2).

Using either gentian plants (figure 2*b*) or *Myrmica* nests (figure 2*c*) as cues makes little difference to the system outcome as compared to the case of no cues (figure 2*a*). It is only when the parasitoid uses *M. schencki* in particular as a cue that the outcome space is substantially altered, with persistent systems being restricted to fewer and fewer combinations of ζ and ν as the cue to the caterpillar becomes increasingly direct (compare figure 2*d*–*f*).

For instance, when potential reproductive effort is expended only whilst searching intensively in cells having caterpillar-harbouring nests, in order to persist the parasitoid need only find a single nest and potentially parasitize three caterpillars, or three nests and potentially parasitize one caterpillar in each (figure 2*f*). This makes sense, since the parasitoid must be able to attack at least two caterpillars during its life for its basic reproductive rate to exceed unity. (Two caterpillars because ν is always an integer, and we assume a 1 : 1 sex ratio of the parasitoid). Finally, under this same cue scenario, if the parasitoid is capable of attacking four or more caterpillars per nest, and locates two or more nests with caterpillars, then the extinction

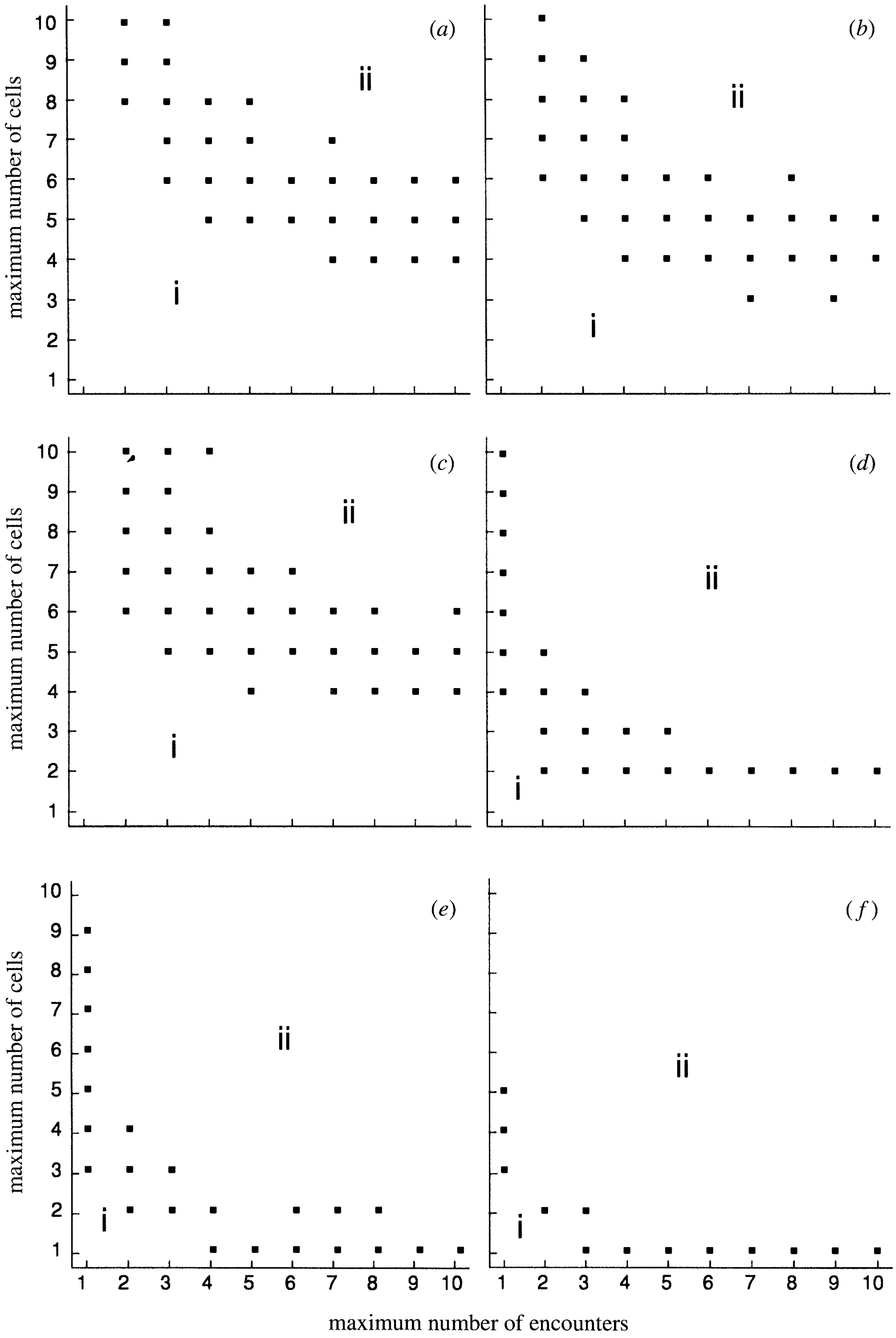

Figure 2. Joint effects of the maximum number of attacks a parasitoid can make per ant nest (ν) and the number of cue cells searched (ζ) on the persistence of the parasitoid and butterfly populations. Cue: (*a*) none; (*b*) presence of *Gentiana cruciata*; (*c*) presence of *Myrmica* nests; (*d*) presence of *Myrmica schencki*; (*e*) presence of *M. schencki* and *G. cruciata*; (*f*) presence of *Maculinea rebeli*. Approximate regions of each figure, based on a single simulation at each point in the parameter space: i = parasitoid does not establish; dots = both parasitoid and butterfly persist over the 200 generations of the simulation; ii = parasitoid and (usually) host go extinct following expanding oscillations. See text for numerical methods.

of both butterfly and parasitoid populations ensues (figure 2*f*).

Figure 3 presents the effects of random, indiscriminate search (i.e. figure 2*a*) on population parameters. For the same reasons evoked in the simulations of figure 2, the parasitoid persists for intermediate numbers of cue cells searched, ζ (figure 3*a*). The range of values of ζ over which the parasitoid persists increases and is shifted to higher minimum ζ as the maximum number of attacks per nest, ν, decreases (not shown). As long as the parasitoid can attack at least a single caterpillar per nest, the maximum level of parasitism attainable by adjusting ζ is *ca.* 80%. Finally, when ζ is sufficiently large, the parasitoid destabilizes the system, provoking its own extinction and (usually) that of the butterfly.

It is little surprise that the persistence of the parasitoid is associated with decreases in mean but-

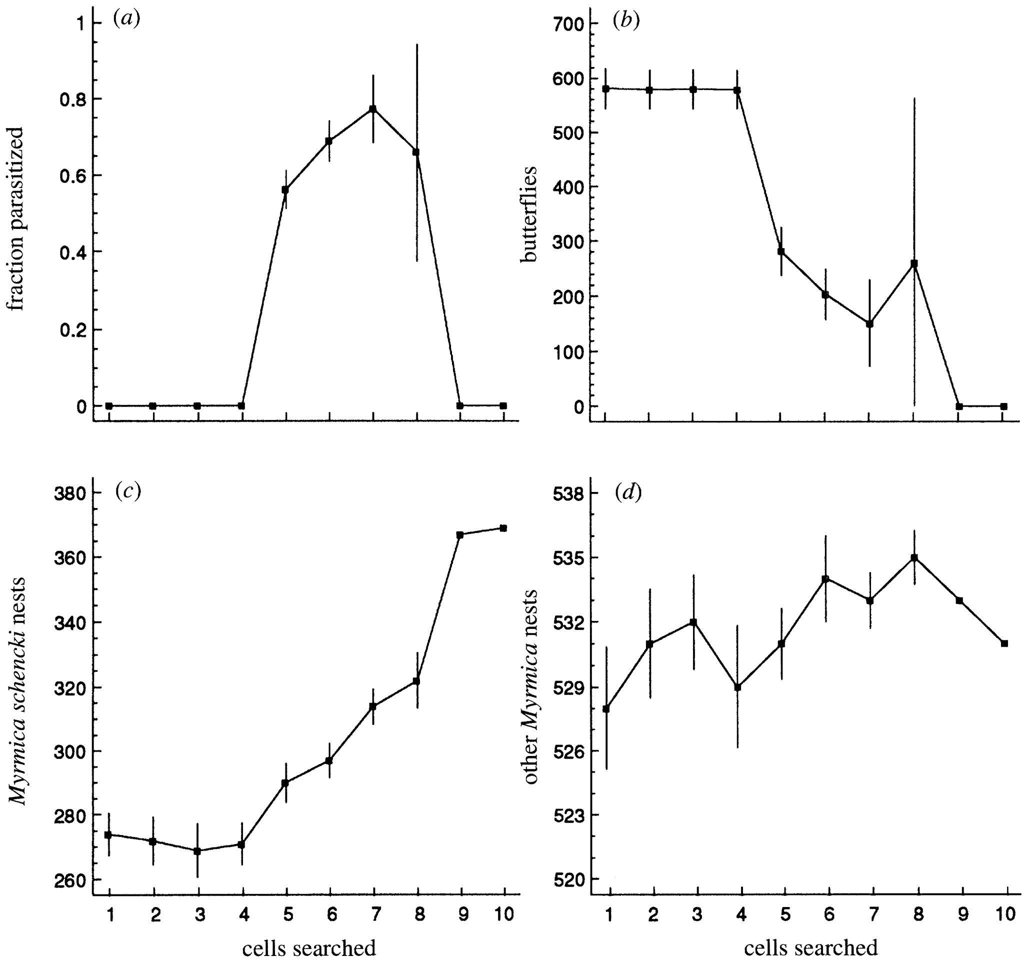

Figure 3. Effect of the number of cells intensively searched (ζ) with no cue on (*a*) percentage parasitism by *Ichneumon eumerus*, and the populations of (*b*) the adult butterfly, (*c*) *Myrmica schencki* nests, and (*d*) nests of other *Myrmica*. Bars indicate the standard deviations of the last 50 generations of each simulation. Other parameter value:$\nu = 5$.

terfly density (figure 3*b*), and as a consequence, modest increases in the density of *M. schencki* nests (figure 3*c*); the nest population of other *Myrmica* does not vary perceptibly with ζ (figure 3*d*).

Figure 4 illustrates typical simulations of the population dynamics of the butterfly and parasitoid. In the absence of the parasitoid, the butterfly persists at a mean of 589 adults with a temporal coefficient of variation of 6.24% (variation of the final 50 generations, averaged over 20 simulations; figure 4*a* illustrates one arbitrary simulation). Introduction of the parasitoid with a basic reproductive rate just above unity results in a very long approach of both species to their eventual more or less stable, but stochastically fragile, equilibrium (figure 4*b*). The mean population level of the parasitoid grows and that of the butterfly shrinks with increasing parasitoid basic reproductive rate (figure 4*c*), up to a point where the exploitation of the butterfly population induces cycles, and the eventual extinction of the parasitoid (and usually of the host as well) (figure 4*d*).

The above discussion is concerned with alternative methods of between-nest search by the parasitoid. Numerical studies of other modes of within-nest search not presented here indicate, for example, that when the parasitoid avoids costly encounters with already parasitized hosts, the conditions permitting persistence are further restricted than those illustrated in figures 2–4. In contrast, studies simulating true random search within nests (i.e. there is no memory in its choice of hosts as attacks proceed), indicate the expansion of persistence conditions as compared to the random sequential mode.

(*b*) ***Absolute refuges to parasitoid attack***

It is unrealistic to assume that there is no intrinsic variation whatsoever in the risk of being parasitized within the butterfly population. Such heterogeneity could arise from inter-individual variation in (i) the adult parasitoid population, in terms of its searching behaviour or intensity, and/or (ii) the host population, with respect to its escape from parasitoid detection, attack, or larval parasitoid development. As a first step towards exploring the role of refuges in host dynamics, we assume that the parasitoid searches intensively only in those cells which are at, or beyond, a cue threshold. Thus, for example, parasitoids may require a sufficient density of chemical cues emitted incidentally by worker ants to locate nest entrances or 'decide' to enter the nest, the density of the cue being a function of worker number.

To most clearly see the potential role of refuges in the system outcome (i.e. persistence or extinction of the

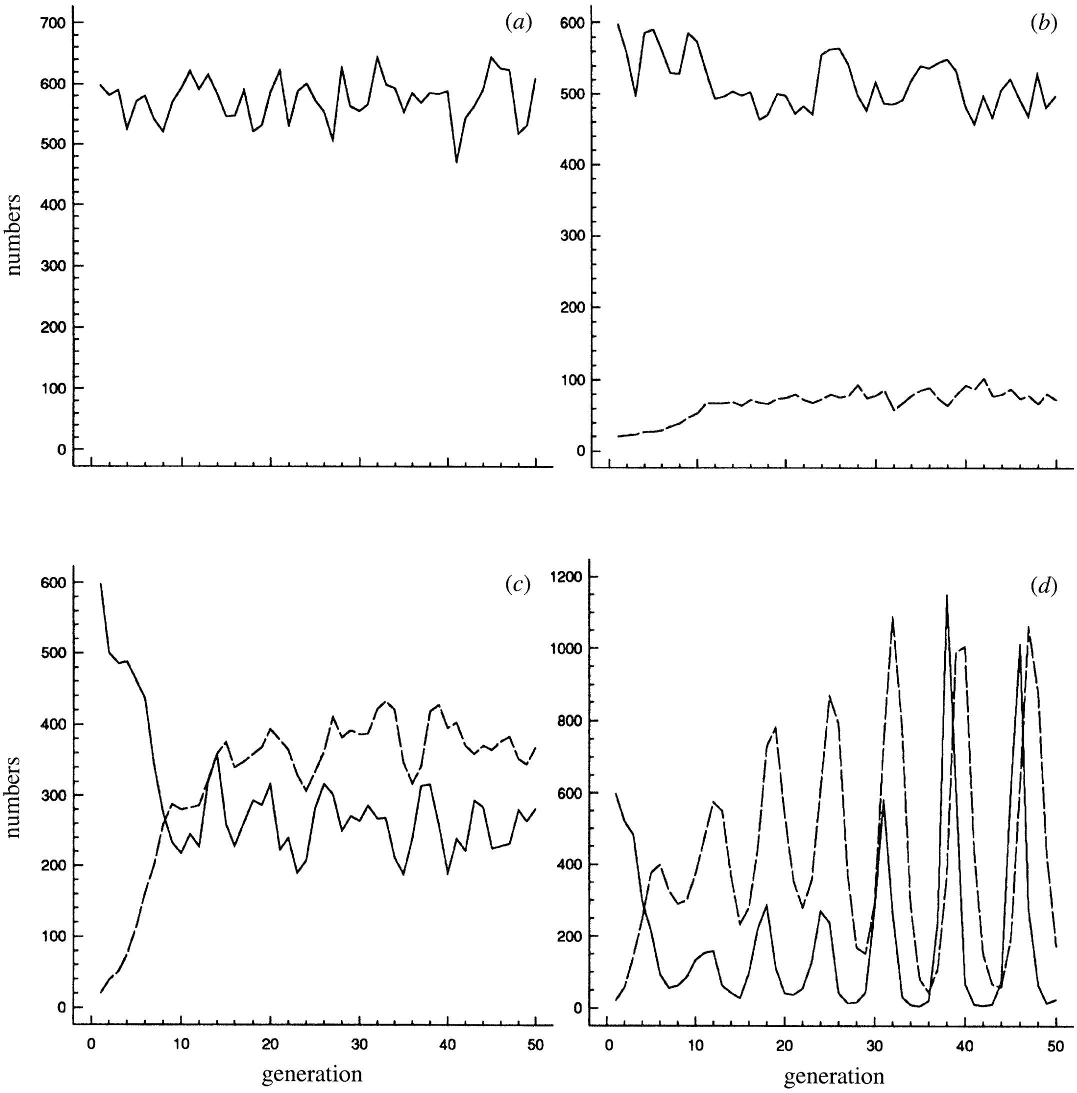

Figure 4. Population dynamics of the butterfly (solid line) and parasitoid (broken line) under the assumption of random, indiscriminate search. (*a*) parasitoid absent; (*b*) $\zeta = 13$; (*c*) $\zeta = 20$; and (*d*) $\zeta = 35$. Other parameter value: $\nu = 1$.

parasitoid and the host) we present simulations where the levels of ζ and ν are sufficient to put an indiscriminate, randomly searching parasitoid at the edge of provoking the extinctions of both it and its host (see figures 2 and 3). Figure 5 shows how four different types of cue threshold affect parasitoid persistence (i.e. mean per cent parasitism) and dynamics (variation in mean parasitism).

Increasing each type of cue threshold separately, and thus the propensity of hosts to be in refuges from parasitoid attack, generally increases parasitoid persistence and decreases parasitism levels (figure 5). System persistence is lowest for low cue thresholds – it is the invulnerable subpopulation of the caterpillar created by sufficient thresholds that promotes the persistence of both species in these simulations (see below). If the refuge is sufficiently, but not too, pronounced we observed that the parasitoid can establish and depress the host down to *ca.* 10% of its parasitoid-free levels (not shown). Finally, if the cue threshold is too high, then the parasitoid itself risks extinction from not having enough hosts to exploit (figure 5).

Specifically, parasitoid and butterfly persistence is ensured, no matter how high are ζ and ν, if intensive search is elicited for (i) $\geqslant 2$ plants per cell (figure 5*a*), (ii) $>$ *ca.* 375 workers per nest (figure 5*b*), or (iii) $\geqslant 20$ on the habitat gradient (i.e. parasitoid only searches in the driest microhabitats) (figure 5*c*), or (iv) the parasitoid only enters *M. schencki* nests with $\geqslant 2$ caterpillars (figure 5*d*).

(*c*) *Inferring the parasitoid's role in system dynamics*

Having considered how indiscriminate search, directed search and refuges can affect population persistence, we now turn to the parasitoid's role in the population dynamics of the system. This is important, for as we have seen in figures 2–4 the parasitoid has the potential to destabilize the system and provoke its own extinction as well as that of its host, the butterfly.

To explore the associations among readily measurable population parameters, we conducted one simulation for each of a series of threshold cue levels in *M. schencki* nest size (compare figure 5*b*). Simulations employing the other types of cues presented in figure 5

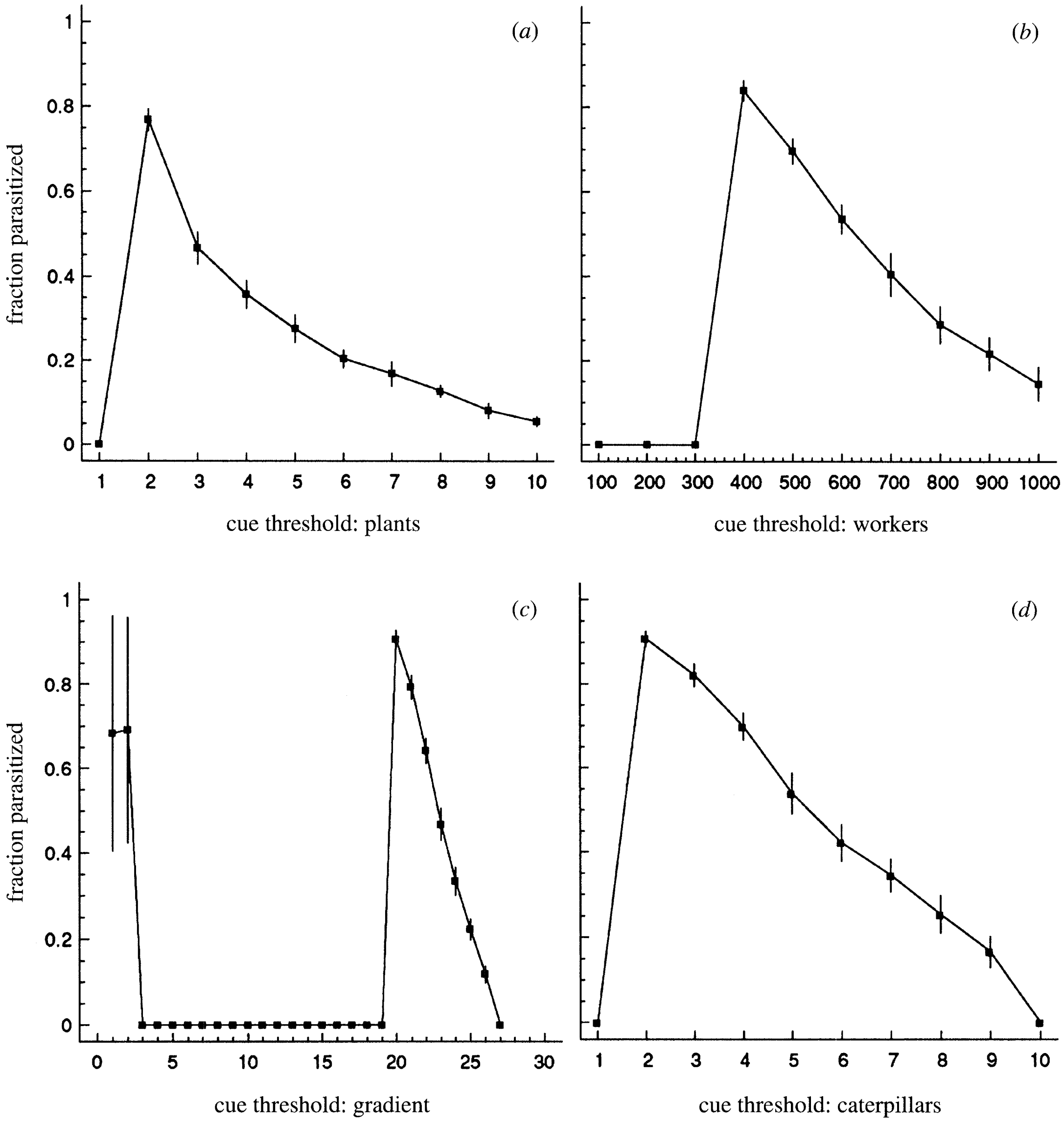

Figure 5. Effects of the threshold level of different cue types on percentage parasitism by *Ichnemon eumerus*. Bars indicate the standard deviations of the final 50 generations of each simulation. Parameter values: $\zeta = 8$; $\nu = 5$.

resulted in the same basic patterns presented below, as did simulations in which the parasitoid searched indiscriminately, but only the attack parameters (ζ and ν) were varied.

Figure 6 shows the population parameters as a function of the cue threshold, which is the host refuge from parasitoid attack. Nest to nest variation in parasitism levels varies positively with the host refuge (figure 6*a*). In contrast, the temporal variation in this index is U–shaped (figure 6*b*). Generation to generation variability in butterfly numbers is negatively related to the refuge (figure 6*c*), as is the parasitism rate (figure 6*d*). These patterns indicate the following.

1. Heterogeneity in parasitism is negatively associated with the temporal variability in host numbers (i.e. the common sense notion of 'stability', as used below) (figure 6*a* and *c*).
2. Heterogeneity in parasitism is negatively associated with mean parasitism rates (figure 6*a* and *d*).
3. The parasitoid always destabilizes the system to some extent (figure 6*c*).
4. The most stable systems occur when parasitism rates are low (figure 6*c* and *d*).
5. The reliability in sampling nest to nest variation as an index of dynamics is highest at intermediate to low levels of refuge (figure 6*b*).

9. DISCUSSION

(*a*) *Heterogeneity in parasitism and parasitoid persistence*

We predict that if the major constraint to the realised fitness of *Ichneumon eumerus* is survival within ant nests whilst searching for its lepidopteran host, then some form of heterogeneity in finding and/or accepting to enter nests of *Myrmica schencki* must exist if the interaction is to persist at local spatial scales (figure 2*d–f*). This is not to say that the evolution of parasitoid search is constrained by the population ecology of the interacting species, but that rather the costs of extensive search will lead to differential probabilities in perceiving cues for intensive search, and the costs to nest entry should lead to choosiness in which nests to enter.

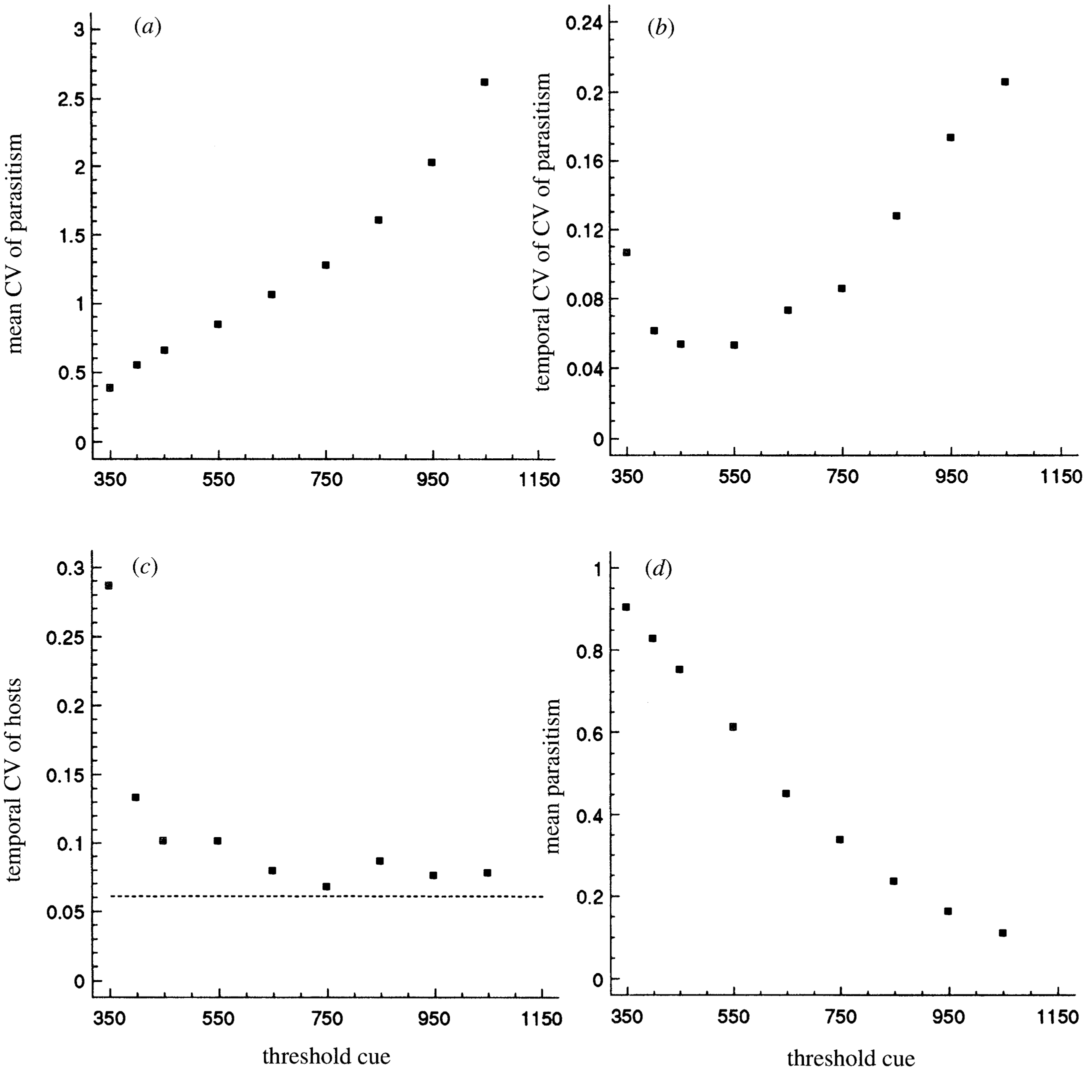

Figure 6. Relationship between threshold number of workers per nest above which the parasitoid perceives the ant's presence and exhibits intensive search (i.e. an absolute refuge) and (*a*) the mean coefficient of variation in parasitism over all *Myrmica schencki* nests harbouring caterpillars; (*b*) the temporal coefficient of variation of the estimates of the caption for (*a*) over the final 50 generations of the simulations; (*c*) the temporal coefficient of variation of butterfly numbers; and (*d*) mean parasitism rates. The means are calculated over the last 50 generations of each simulation. Horizontal dotted line in the caption for (*c*) is the coefficient of variation in butterfly dynamics when the parasitoid is absent (calculated as the mean of 20 simulations, each averaged over the final 50 generations). Parameter values: $\zeta = 8$; $\nu = 5$.

As we have illustrated using cue thresholds in the elicitation of intensive search, either form of heterogeneity promotes module persistence.

Given the limits in the reproductive capacity of the parasitoid and the concealment of its host within ant nests, the employment of cues may be essential to this parasitoid's persistence. Field observations suggest that *Ichneumon eumerus* uses ant trails to locate nest entrances (Thomas & Elmes 1993), but it is not known what kind of long-distance search cues may be employed, if any. Laboratory experiments have shown *Ichneumon* to distinguish host from non-host ants, and nests with caterpillars from those without (Thomas & Elmes 1993). Although in the laboratory, parasitoids were observed to exit nest boxes alive, field observations, involving much larger nests, show that the parasitoid may be repelled several times before succeeding at entry, and in some instances may abandon the attempt altogether; this implies that the parasitoid risks injury or death when it enters red ant nests. Taken together, along with our (unpublished) laboratory observations that female *I. eumerus* are relatively long-lived, we suggest that the major cost to the fitness of this parasitoid is its entry into, and host search within, *Myrmica schencki* nests (i.e. figure 2*d*). The more complex scenario suggested by laboratory trials, where the parasitoid only enters nests if caterpillars are present, remains to be verified in the field.

(*b*) *Heterogeneity in parasitism and host population dynamics*

The degree of coupling between host and parasitoid populations in our system depends on the relative density-dependent influences of resource limitation (i.e. *Myrmica schencki* abundance) and parasitism. In agreement with previous studies we found that pronounced spatial heterogeneity leads to high host populations (May 1978; Murdoch & Stewart-Oaten 1989; Murdoch 1989), and as a consequence, an increase in the impact of intraspecific competition on population dynamics (Hochberg & Lawton 1990). This means that when multiple density-dependent factors potentially affect the host, a single index (i.e. heterogeneity) cannot meaningfully reflect the stabilizing power of the parasitoid without corresponding information on its power to limit the host (Hochberg & Lawton 1990; Getz & Mills 1996).

Our employment of a particular measure of patch to patch variation in parasitism was not intended to establish a causal role of heterogeneity in population dynamics (for discussion, see Hassell *et al.* 1991), but rather to view it as an index of host population dynamics in the presence of the parasitoid. Two other measures of heterogeneity – one based on individual to individual variation in the number of encounters with parasitoids, and the other on nest to nest variation in the number of parasitoid entries – yielded similar patterns to that in figure 6*a*.

(*c*) *Comparison between theory and data*

The model most readily reproduces the levels of parasitism observed in the field (6–23 %, Thomas & Elmes 1993) when (i) there is sufficient variation in vulnerability from nest to nest, and/or (ii) the parasitoid is only capable of attacking one or at most a few hosts per nest. What little data we have support the roles of both these factors. The first is upheld given the high degree of variation in parasitism from nest to nest (coefficient of variance, c.v. = 1.49 based on the contents of 13 nests in the French Alps; c.v. = 1.99 in the nine excavated nests of Panticosa). We have insufficient data, however, to discern whether the variation in vulnerability is due to cue thresholds to nest location and entry, or simply because of the very low numbers of nests entered per parasitoid. The second factor is also supported by limited data, since in only one nest of the seven total parasitized by *Ichneumon* was there more than one parasitized host, despite 22 of the 24 total nests with hosts having more than one host to potentially parasitize.

10. CONCLUSION

Our results indicate that a monophagous parasitoid is unlikely to be the primary regulatory force of its host population, because increasing heterogeneity in the risk of parasitism has the effect of inflating the host population to levels where other forms of density dependence contribute to, or even dominate, host regulation. On the other hand, a monophagous parasitoid can be responsible for the destablization, and sometimes local extinction, of its host population, due to insufficient heterogeneity in parasitism. Without complementary information on the relative basic reproductive rates of host and parasitoid, commonsense measures of heterogeneity in parasitism can lead one astray from the role of the underlying heterogeneity in risk. The generality of these predictions to systems other than that treated in our case model should be tempered by two notes of caution. First, our model is concerned with host populations that are regulated to low numbers by other forms of density dependence in the absence of the parasitoid, and as such there is little 'room for manoeuvre' for the parasitoid to be the sole regulatory agent of the host. Second, we only considered 'absolute' refuges to parasitism. We do not know as yet how other types of refuge, generated for example by limited parasitoid dispersal (Comins *et al.* 1992), or by assuming a continuous probability distribution for cue cell location, would affect the general patterns produced by our model. We believe for these reasons that our findings merit further investigation to test their generality.

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APPENDIX

One process and one parameter are modified from the original HCET model. Neither of these modifications alters HCET's conclusions. First, to decrease the run time for each numerical simulation, we simplified the egg-laying behaviour of the butterfly by assuming that it distributes its eggs from plant to plant rather than from tiller to tiller, and that the eggs are equally distributed over the tillers of each plant. This modified assumption resulted in an estimated negative binomial clumping parameter of 0.39 (rather than the 0.25 for the tiller to tiller distribution of HCET). Second, to achieve independence between the data used to estimate the number of buds per tiller and the number of tillers per plant, we re-estimated the latter from a sample of 81 plants censured in July 1991 at the field site near Panticosa (Spain), resulting in a mean of 2.78 tillers per plant (standard error, s.e. = 0.192) (HCET employed a figure of 2.89, which was based on 107 plants). Finally, it should be noted that the stated value in Table 2 and in the text of HCET for the maximum nest size for disbandment to occur, Z_T, should not be 8, but rather 4.

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