



## Effects of habitat reduction on the persistence of *Ichneumon eumerus* (Hymenoptera: Ichneumonidae), the specialist parasitoid of *Maculinea rebeli* (Lepidoptera: Lycaenidae)

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Received 1 May 1997; revised and accepted 1 October 1997

The lycaenid butterfly, *Maculinea rebeli*, and its specialist parasitoid, *Ichneumon eumerus*, live in small, closed populations. Given the threatened status of the butterfly, it is reasonable to assume that its specialist parasitoid is even more vulnerable to local extinction than the butterfly host. Based on a mechanistic model recently developed for the tightly-woven community surrounding *M. rebeli* at a site in the Spanish Pyrenees, we investigate how the removal of habitat, and more particularly, specific habitat promoting the persistence of the butterfly, affects the population persistence of the parasitoid. Because of the relatively small impact of the parasitoid on the butterfly population in the Spanish Pyrenees, guidelines for conserving the parasitoid are only slightly more restrictive than those for its host. It is argued that at sites of more marginal quality for the butterfly than the reference site, achieving the dual aims of conserving both species will be more problematic.

Keywords: environmental gradient; extinction; conservation; persistence; parasite.

### Introduction

*Maculinea rebeli* Hirschke, 1904, like its congeners, exhibits high degrees of specialization in exploiting its two larval resources, the cross-leaved gentian, *Gentiana cruciata* L., and the red ant, *Myrmica schencki* Emery. In a previous study (Hochberg *et al.*, 1996) we investigated how the searching biology of the ichneumonid parasitoid *Ichneumon eumerus* Wesm., 1857, a specialist of *Maculinea rebeli*, could be expected to influence the population dynamics of its butterfly host. We found that because of the high maximum reproductive rate of the butterfly (estimated by Hochberg *et al.* (1994) to be at least ca 13 female butterflies produced by a single fecund female), the low levels of parasitism by the parasitoid observed in the field could only be achieved if the parasitoid had little impact on the host population. The biology of this butterfly has been reviewed elsewhere (Thomas *et al.*, 1989, 1993; Elmes *et al.*, 1991a,b; Hochberg *et al.*, 1992, 1994); that of the parasitoid is briefly recounted below (based on Thomas and Elmes, 1993; Hochberg *et al.*, 1996).

*Ichneumon eumerus* has at its disposal, behavioural, morphological and physiological adaptations that per-

mit it to locate, oviposit in, and emerge from its host. Each adult wasp emerges from a *Maculinea rebeli* pupa in the upper chambers of *Myrmica schencki* nests in late summer. This coincides with the imminent adoption of fourth instar *M. rebeli* caterpillars (the host instar attacked by the parasitoid) into ants nests; these caterpillars will be the new hosts for the parasitoid in the generation to follow. To locate these hosts, female parasitoids systematically search the ground for *Myrmica* odours. Laboratory experiments show that *I. eumerus* more readily enters *Myrmica schencki* nests than nests of other *Myrmica* species found in similar habitats. Once found, the parasitoid lays a single egg in each *M. rebeli* caterpillar, the number depending probably on how fiercely she is attacked by the ants. The parasitoid juvenile remains in the caterpillar for the next 9 or 10 months, finally killing the pupa prior to emergence.

Scant information is available concerning the population dynamics of *I. eumerus* in the field. Laboratory experiments and field observations suggest that the adult insect is long lived, probably succeeds in entering only one or a few ants nests, and generally does not parasitize more than one caterpillar in a given nest

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(Thomas and Elmes, 1993; unpublished data). Field samples from the three sites from where *I. eumerus* has been found indicate that it parasitizes ca 6–23% of the *M. rebeli* population ( $n = 133$  caterpillars and pupae).

Given the limited geographical distribution and local rarity of *M. rebeli* (Wells et al., 1984; Munguira, 1987; Kockelke et al., 1994), it is reasonable to suspect that its specialist parasitoid is geographically at least as scarce, and locally more vulnerable to extinction (Thomas and Elmes, 1992; Thomas, 1995). Our aim in the present study is to use the detailed mechanistic model recently developed by Hochberg et al. (1996) to investigate how two forms of habitat destruction could endanger the parasitoid and butterfly, and how attempts to introduce or reintroduce the parasitoid onto sites may or may not succeed, depending on the number of parasitoids released.

### The model

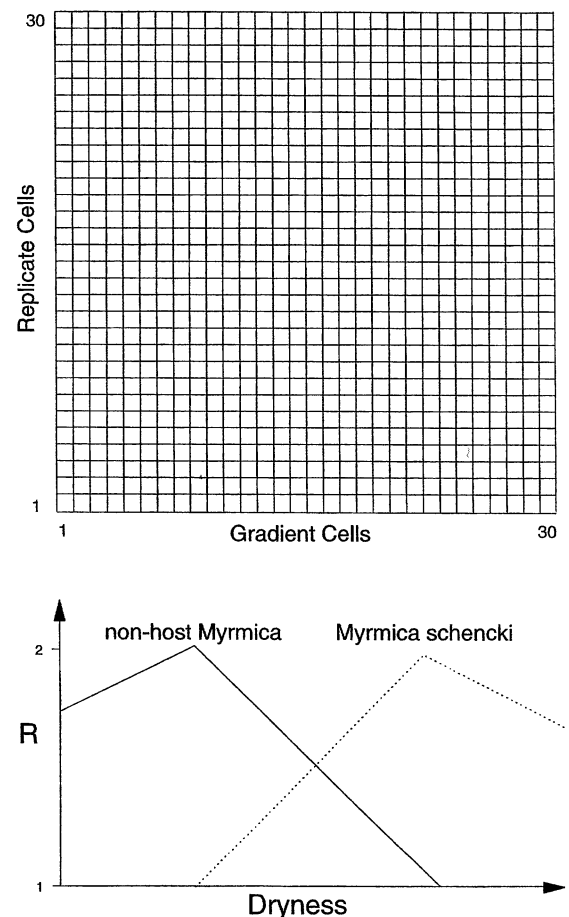
The numerical algorithm employed in this study considers the following as spatially and temporally variable populations: the butterfly *Maculinea rebeli*, its host ant *Myrmica schencki*, a single population lumping three other species of *Myrmica* (i.e. *M. rubra*, *M. scabrinodis* and *M. sabuleti*), and the parasitoid *Ichneumon eumerus*. The population of the intermediate host of *M. rebeli*, *Gentiana cruciata*, remains constant in time and in space. Every individual butterfly and plant is tracked in time and space, as is the density of every ant colony. The model, though parameter-rich, is based on a series of very simple assumptions.

Fourteen of the 20 model parameters are estimated from laboratory or field data, with the remainder being guesses based on unquantified observations. Most of the field-based estimates are from a single site in the Spanish Pyrenees (hereafter referred as 'S1', Elmes et al., 1996). The algorithm is presented in detail elsewhere (Hochberg et al., 1994, 1996), and the essentials recounted below.

#### The habitat gradient

The baseline model is a 1 ha terrain subdivided into 30 by 30 cells, each of 11.11 m<sup>2</sup> (Fig. 1). This corresponds to the estimated searched area by a very large *Myrmica* nest. Each of the 900 cells on the grid may contain at most one *Myrmica* nest, and each *Myrmica* nest has its own dynamics based on local environmental conditions (i.e. soil humidity and associated grass cover). These local conditions are assumed to remain constant

in time for any given cell, and are spatially represented as a one-dimensional gradient in the maximum yearly productivity,  $R$ , of ant colonies (Fig. 1). In the model, we designate cell-column 1 as the coolest and most humid (and grassy), and column 30 as the hottest and driest (with the sparsest turf). For each of the 30 columns along the gradient, there are 30 cells with exactly the same habitat conditions (called 'replicate cells'). The maximum productivity of each of the two ant populations is assumed to be tent-shaped, peaking at cell column 22 for *M. schencki* and at column 9 for other species of *Myrmica* (based on estimates of the peaks and slopes from model fits of field data at S1).



**Figure 1.** Schematic diagram of the full one hectare terrain modelled here. Tent-shaped distributions in lower graph indicate cells over which non-host and host *Myrmica* potentially persist if alone in system.  $R$  is the maximum yearly reproductive rate of ant colonies at different cells along the horizontal habitat gradient. Simulations in Figs 2–5 are conducted by removing rows and/or columns from this scheme.



### The host plant

The gentian population remains completely constant from year to year. The precise number, distribution, and flowering capacity of these gentians is based on data from S1. The gentian density was estimated at 2672 plants per hectare, with 2.778 tillers per plant, and a relationship between buds ( $b$ ) and tillers ( $t$ ) of  $b = 7.737t^{0.857}$ . The cell to cell distribution of gentian plants was slightly clumped, and fitted to a negative binomial distribution, yielding an aggregation parameter of 2.1.

### The butterfly

A given season begins with butterfly flight, during which eggs are laid over the gentian population. The estimated number of eggs surviving to hatch per female butterfly is 121, which, though probably an overestimate, has little importance to system dynamics (unpublished simulations show that above ca 25–30 eggs, system dynamics are little altered). A statistical fit to field data at site S1 shows the distribution of eggs over gentian plants to be aggregated, with the negative binomial parameter of 0.39. The eggs laid on any given plant are equally partitioned between the tillers of that plant. Of the hatching caterpillars, only a single one survives per gentian bud, and it is assumed that they disperse over the tiller's buds so as to minimize competitive mortality. Field experiments show that it is only when gentians and a nest of *M. schencki* are in proximity of one another (i.e. in the same cell) that newly moulted, 4th instar caterpillars may be adopted into the nest. We assume that the probability of being adopted increases in proportion to the square root of colony size, and that beyond a colony of 1200 workers, all caterpillars are adopted. Not all adopted caterpillars survive; laboratory data indicate that 88% survive initial nest adjustment and that thereafter one caterpillar survives for every 50 ant workers in the nest. The number of caterpillars rearable by a *Myrmica schencki* nest is the truncation of the vernal brood number, or  $\text{trunc}(0.5 Z/50) = \text{trunc}(Z/100)$ , where  $0.5 Z$  is the total ant brood exploitable by caterpillars (i.e. 'vernal' brood) and 50 is the number of brood required (and lost, see below) to rear one *Maculinea rebeli* caterpillar to maturity. It is only within nests of *Myrmica schencki* that *Maculinea rebeli* caterpillars develop to maturity; in nests of other *Myrmica* they perish. Finally, the only additional mortality afflicting the caterpillars in ant nests is from the parasitoid (see below).

### Host ants and non-host ants

The most complex population changes in the model involve ant nests. In any given year, ant colonies can grow, shrink, bud into adjacent cells, or perish. Ant dynamics occur in parallel to the butterfly's phenology. Between butterfly pupation (in May/June), and caterpillar adoption (in August), nests below a threshold of 200 workers may go extinct (in direct proportion to nest size). Extinction is probabilistic, and occurs if a nest is in unsuitable habitat (i.e. its  $R < 1$ ), or if butterfly caterpillars have damaged the nest sufficiently in previous generation(s) to lower its density below 200 workers. After these nest extinctions have all occurred, large nests potentially divide in two, with half the nest budding into an empty adjacent cell. The probability of a given nest budding is a linear function of its size, with budding being certain for nests of over 2000 workers. Once all budding is accounted for, nests begin to grow, producing two broods: 'vernal' brood (which is exploited by *M. rebeli* adopted in the nest), and 'rapid' brood which completes development during periods when the caterpillar is either absent or too small to affect ant-brood survival. We assume that half of the ant's brood (and therefore the potential number of *M. rebeli* caterpillars supported per nest) is of each type. Nest growth in gradient column  $j$  ( $\delta_j$ ) is governed by the simple relation:  $\delta = R_j / (1 + \theta Z_j)$ , where  $R_j$  is the maximum growth rate of a nest in column  $j$ ,  $Z_j$  is the nest size just after budding, and  $\theta$  is a constant reflecting intraspecific competition between ants ( $\theta = 0.0025$  for all nests). The function for  $\delta$  approximates compensatory self-limitation in ant colonies (Brian, 1965).

Harbouring *Maculinea* caterpillars always results in a lessening in the potential growth rate  $\delta$  of the parasitized ant colony. For *Myrmica schencki*, if more caterpillars are adopted (and survive initial adjustment) than are rearable then all of the vernal brood is destroyed; otherwise 50 times the number of caterpillars adopted (parasitized by the parasitoid or not) in vernal ant brood are eliminated. For other *Myrmica*, the damage is always  $0.5 \times 50 \times$  number of caterpillars adopted.

Thus, the only two differences in the model between colonies of *Myrmica schencki* and other species of *Myrmica* are (i) their productivities ( $R_j$ ) along the habitat gradient (Fig. 1), and (ii) the amount of damage a caterpillar does to the colony. With regard to the latter point, we assume that there are no differences in ant species' abilities to adopt caterpillars, but the damage done to other *Myrmica* colonies is 50% of that done to *Myrmica*



*schencki* nests (since caterpillars in the former eventually perish).

#### The parasitoid

The dynamics of *Ichneumon eumerus* are centred-around the adult female's search for fourth instar *M. rebeli* within nests of *Myrmica schencki*. A central feature of the model is that the parasitoid will be limited in the number of nests it can enter, and in the number of caterpillars it can parasitize per nest. This is ultimately a consequence of the fierce attacks inflicted by the red ants: we hypothesize that there will be strong selection pressure on the parasitoid to invest in entering nests and finding and parasitizing caterpillars, with costs to the number of eggs the parasitoid carries (Hochberg *et al.*, 1996). Because specializations towards this task will not be perfect, we suspect that many parasitoids will perish from injuries, thereby limiting the number of nests ultimately entered. Hence, natural selection should favour the use of cues leading to the caterpillars (i.e. use of gentians from a distance, *M. schencki* odours once in the vicinity of gentians, and *M. rebeli* once in host-ant nests).

Numerical simulations of this model indicate that the parasitoid can persist in the system at levels consistent with observed parasitism if its maximum population growth rate is ca two female parasitoids produced per female parasitoid (assuming a 1 : 1 sex ratio; Hochberg, unpublished simulations). There are a number of ways to achieve this figure, in adjusting parameters such as (i) the number of cells searched, (ii) the number of caterpillars parasitized within *M. schencki* nests, (iii) the cues used in searching cells (plants and/or *M. schencki* colonies), and (iv) habitat types most likely to harbour *Maculinea* parasitized ant nests (attraction to large nests, cells with many gentians, or dry habitats most likely to have *schencki* nests).

What little data we have on within-nest search of the parasitoid indicates that in most cases only a single parasitoid is produced per nest (Thomas and Elmes, 1993, unpublished observations). Thus, we assume in the model that only one caterpillar is parasitized per nest. We simulated the model to see how many *M. schencki* nests would have to be searched, and how large they must be to give mean parasitism rates of ca 10–20%, as was observed at the site in the Spanish Pyrenees. We found that five nests (harbouring or not harbouring *Maculinea*) of at least 380 ant workers gave this level of parasitism. We have no data to show that this reflects the level in the field, but it is at least a plausible prediction.

The model tracks the fate of every individual parasitoid in the system. The following rules are employed for the life-cycle of *Ichneumon eumerus* (based on Thomas and Elmes, 1993). The parasitoid enters *Myrmica schencki* nests once both density-independent and density-dependent mortalities have acted on *Maculinea* caterpillars within the nests, and parasitized caterpillars always survive to produce an adult parasitoid (at a 1 : 1 sex ratio). To achieve the ca 10–20% level of parasitism observed in the field, we allowed each parasitoid to enter five *Myrmica schencki* nests at random, but only if the nests contained at least 380 workers. Further, we assume the parasitoids enter nests sequentially (i.e. there is no interference between adults), and that each parasitoid attacks a single caterpillar within a nest. Finally, if the parasitoid adult encounters (at random) a host which has already been parasitized, then it wastes time handling it, and then leaves the nest without parasitizing any caterpillars.

#### Numerical procedure

Many of the ecological processes in the model are probabilistic, and so no two numerical simulations are exactly alike. We employed the same initial conditions of Hochberg *et al.* (1996), which correspond to our best estimate of the population ecology of all components in the model if the parasitoid were absent. We then removed rows or columns of cells from all areas (i.e. rows in Fig. 1) and/or from the driest areas (columns from the right of Fig. 1). Finally, 50 simulated years later (when butterflies, if present, and ants had settled down to a new trajectory pattern), we introduced a predetermined number of fecund female parasitoids into the system, and simulated the model for 50 additional generations.

#### Results and discussion

Figures 2–4 show for different numbers of introduced parasitoids that both butterfly and parasitoid are sensitive to the extent and quality of their habitat. They are assured of extinction 50 years after their introduction if the driest ca 37% of their habitat is absent (i.e. if categories 18–30 are removed in the simulation) and likely to go extinct if the driest ca 35% is missing. This is simply because *Myrmica schencki* only prospers in dryer microhabitats, and what few colonies are present in the wettest ca 63% of the baseline terrain are of insufficient productivity to support the butterfly population.

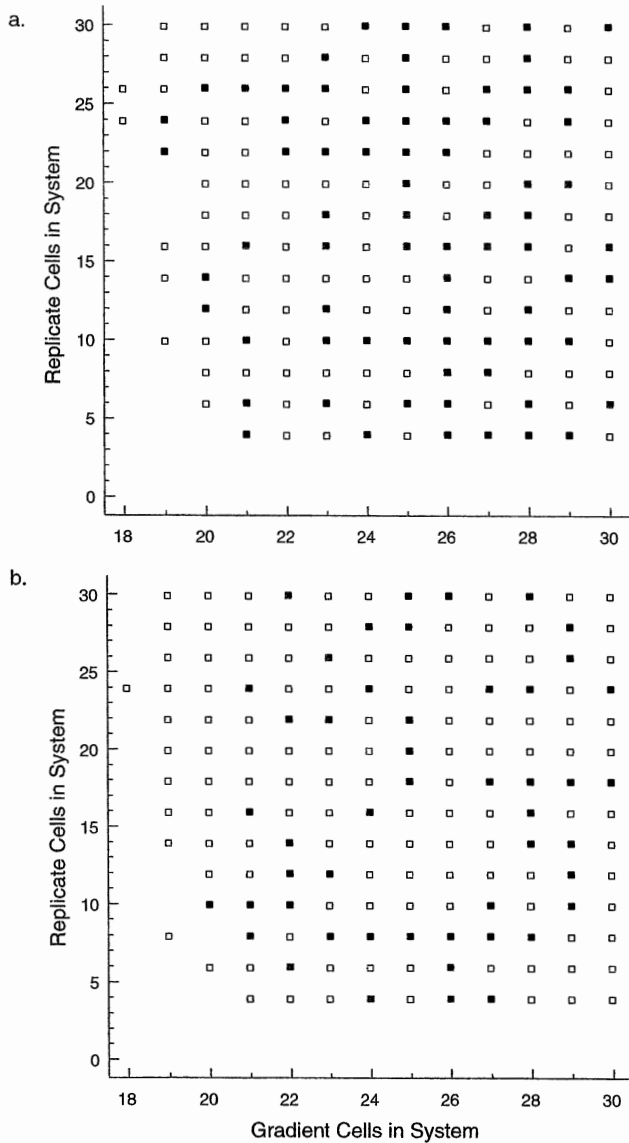
When only the quantity of habitat is limiting (i.e. when habitat rows are removed), both species gener-



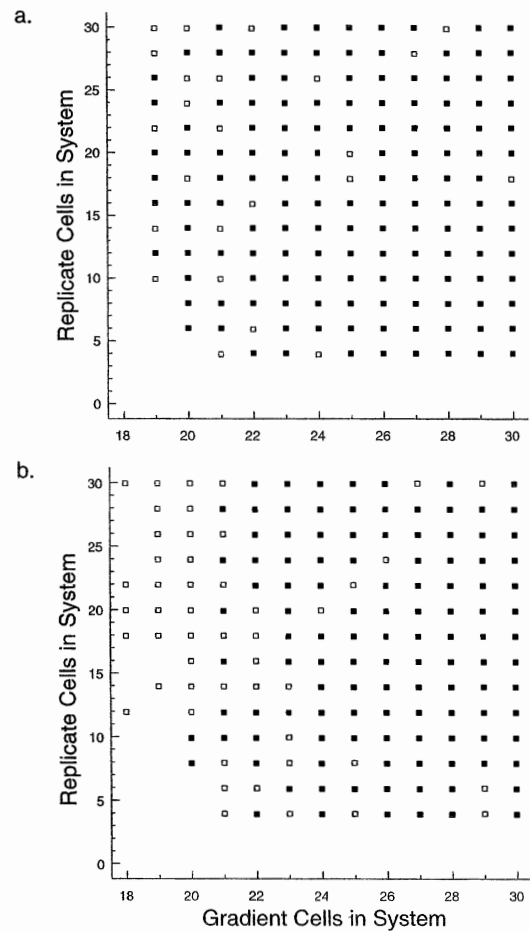
ally persist if at least ca 13% of the site is present; that is, ca 0.13 ha is the minimum size habitat which can support both populations if the site characteristics are

as at the reference site in the Spanish Pyrenees. Using a much simpler analytical model without spatially explicit characteristics, Hochberg *et al.* (1993) predicted that the butterfly should go extinct if the habitat size fell below ca 0.15 ha. Therefore, the essential characteristics of the simpler model are sufficient to predict butterfly persistence if habitat is removed from the system.

The minimum habitat quantity necessary for persistence is virtually the same for the butterfly and for the parasitoid (e.g. Fig. 4b). In other words, habitats showing the full range of qualities should be suitable for the parasitoid if they exceed ca 0.13 ha. In contrast, the parasitoid is slightly more sensitive to habitat *quality* than the butterfly: it requires the presence of ca 70% of the gradient whereas the butterfly needs ca 63%. Therefore, as long as sufficient numbers of parasitoids are



**Figure 2.** Effects of site characteristics on the persistence of the parasitoid and butterfly when only one fecund female is introduced. Horizontal axis is the number of gradient cells present in the system. Vertical axis is the number of cells of each gradient type (with a maximum type indicated on the x-axis) present in the system. (a) Status of both species after 10 years post-introduction of the parasitoid. (b) Status after 50 years post-introduction. Each position on this graph corresponds to a separate simulation. Solid squares indicate both host and parasitoid present. Open squares indicate that only the butterfly is present. Empty areas correspond to both host and parasitoid extinction.



**Figure 3.** Effects of site characteristics on the persistence of the parasitoid and butterfly when five fecund females are introduced. See Fig. 2 for details.

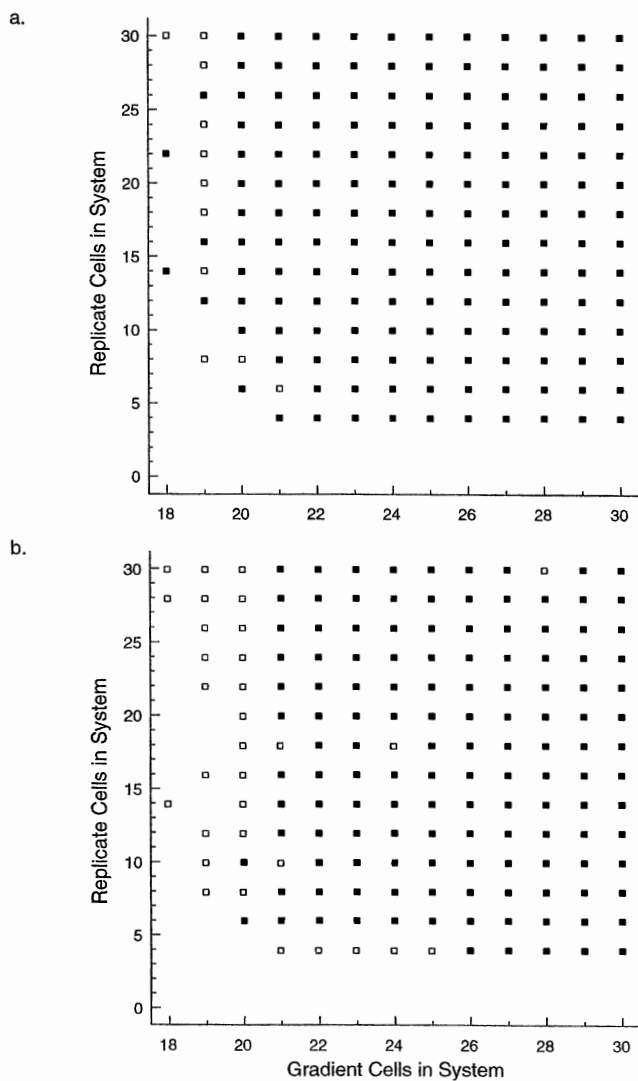


introduced into the system (see below), it can be concluded that site conditions similar to the Pyrenees situation promoting the host should be generally sufficient for the parasitoid as well.

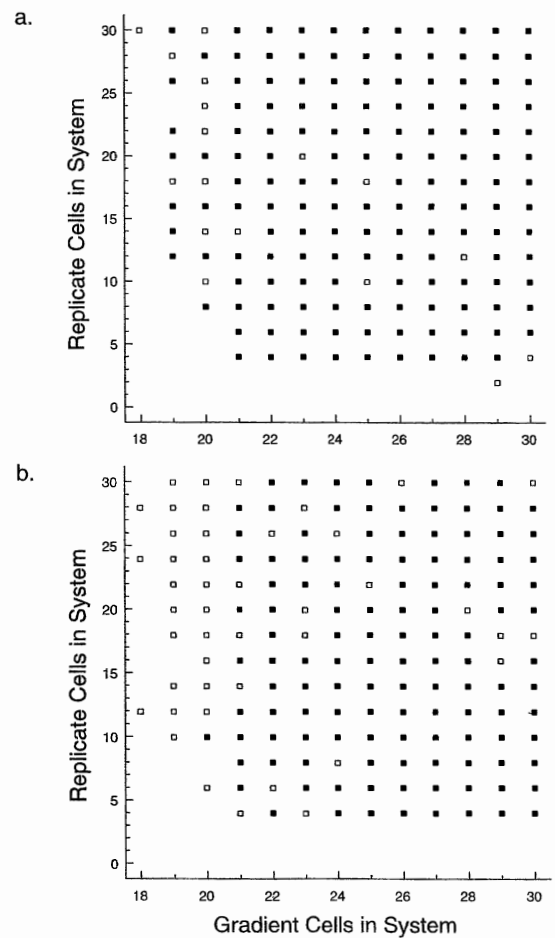
Figures 2–4 also show that the initial number of parasitoids introduced into the butterfly population can be critical to the success of the introduction. In particular, introductions of one or five parasitoids are rarely sufficient for the parasitoid to persist for 50 years (Figs 2 and 3), and an introduction of only a single fecund female rarely persists more than 10 years (Fig. 2a). Figure 2a shows that habitat size and quality has little to do with this latter result; rather, it is the strong

demographic stochasticity at low parasitoid densities which is responsible. Figure 4 (and simulations not presented here) illustrates that a release of 20 parasitoids is generally sufficient for persistence on a time scale of 50 years.

If an introduction programme has limited numbers of fecund females at its disposal in a given year, an alternative may be to introduce small numbers each year, over several years. Figure 5 shows how the introduction rate of parasitoids may affect the outcome of the programme. The simulations in Fig. 5 assume a single fecund female is introduced per year, for five consecutive years. This tactic has a slight propensity towards better establishment ten years after the first release as compared to the same numbers released all in a single year (Fig. 3), but the differences are virtually nil 40 years thereafter.



**Figure 4.** Effects of site characteristics on the persistence of the parasitoid and butterfly when 20 fecund females are introduced. See Fig. 2 for details.



**Figure 5.** Effects of site characteristics on the persistence of the parasitoid and butterfly when one fecund female is introduced in each of the first five generations. See Fig. 2 for details.



### Conclusions

This is the first study to our knowledge to employ a mathematical model to investigate conservation measures for a pair of antagonistic species, one of which is an insect parasitoid. The main result is that the small impact of the parasitoid, *Ichneumon eumerus*, on its rare host, *Maculinea rebeli*, should mean that conservation guidelines for the former species need only be slightly more stringent than those for the latter. The problem of parasitoid conservation is bound to become increasingly important in the years to come, both because of their stunning diversity (Hawkins, 1994) and because of their potentially precarious positions on the peripheries of trophic food chains (Holt, 1997).

The simulations vividly show how habitat destruction affects species persistence. Both *Maculinea rebeli* and *Ichneumon eumerus* have very specialized niches towards the end of the microhabitat spectrum at the sites where they are found, and as such the model predicts that they should tolerate far more non-specific habitat destruction than the loss of the driest habitats in the system.

It may seem surprising that such a specialized parasitoid is predicted to be only slightly more vulnerable to extinction than its endangered host. The reason is that the parasitoid's maximum reproductive rate is much less than its host's, and as such the former species is regulated by the latter (Hochberg, 1996). We predict that the parasitoid should be much more sensitive to local extinctions as compared to the butterfly on sites (prior to habitat removal) where (i) the parasitoid's maximum reproductive rate were closer to unity, or (ii) the butterfly's maximum reproductive rate were closer to unity. The first situation could arise if parasitoids were time limited, and host-ant nests were at low densities over the habitat. The second case implies that substantial habitat exists for the butterfly, but it is all of marginal quality (i.e. either wetter or dryer than optimal for *Myrmica schencki* nest growth).

Our study suggests that conservation programmes for the parasitoid, like the butterfly, must be particularly attentive to the abundance of microhabitats yielding productive *Myrmica schencki* colonies. Habitat size, though a concern, is less critical (as long as sufficient amounts are of high quality for *Myrmica schencki* ants). Reintroduction programmes of the parasitoid need to consider the following:

- (i) *The provision of a sufficient range of dry microhabitats for Myrmica schencki.* If the habitat is similar to that in the Spanish Pyrenees, then the actual area covered by the site is of relatively minor impor-

tance (we predict it can be as little as 0.13 ha). Elmes (1996) showed that for 13 sites in the French Alps and Spanish Pyrenees, most site to site variation in butterfly density could be explained by site to site variation in gentian density. Their analysis indicates that habitat gradients in ant productivity vary little from site to site. The only accurate way of assessing the quality of habitat gradients for conservation of the butterfly and its parasitoid is through the quantification of nest density and nest productivity (Petal, 1967; Hochberg *et al.*, 1992-1994).

- (ii) *The release of sufficient numbers of fecund adult parasitoids.* We predict that the release of ca ten or more fecund parasitoids over a few years running should be sufficient for establishment at sites of sufficient habitat quality. At present, *Ichneumon eumerus* has not been successfully cultured in the laboratory, but because of the long period between emergence from *Maculinea rebeli* pupae and search for caterpillars within *Myrmica schencki* nests, these parasitoids can be easily stored prior to release, once procured from sites where they flourish. It is not known to what extent *I. eumerus* mates successfully in the laboratory. Caution is therefore needed in interpreting the exact figures of our results (which assume the release of fecund females only). It is likely that larger numbers of unmated females than we recommend must be released together with male parasitoids to achieve sufficient numbers of searching fecund parasitoids in the field.
- (iii) *The possible re-inoculation of parasitoids in situations where its maximum reproductive rate is dangerously close to unity* (i.e. the threshold for persistence). Given the local rarity of the butterfly, maximum reproductive rates of the parasitoid approaching unity may mean that a programme of repeated inoculation is the only way to ensure its persistence. This will require the existence of one or more source sites of the parasitoid, and the ability to monitor their small numbers (via excavation of ant nests just prior to butterfly emergence). Given that all studied populations of *Maculinea rebeli* are highly sedentary (Kockelke *et al.*, 1994; Thomas and Elmes, unpublished observations), it is unlikely that persistence can be maintained exclusively by intermittent flows among metapopulations (Gilpin and Hanski, 1991).

We close with a cautionary note. Our model was calibrated to a site which supports a thriving population of the butterfly. Assuming that sites do exist in which the



butterfly is menaced by local extinction (i.e. sites composed uniquely by marginal habitat for *Myrmica schencki* nest growth), introduction of the parasitoid could induce the local extinction of *Maculinea rebeli* (Hochberg et al., 1996). This serves as a warning that conservationists must first assess the viability of the butterfly population before proceeding with the introduction of its natural enemy.

### Acknowledgement

We thank Irma Wynhoff and two referees for comments on the manuscript. This research was funded by the French Ministry of the Environment (program SRETIE), the French Ministry of Education (program ACC-7), and the Franco-Britannic Alliance Program. Identifications of *Ichneumon eumerus* were made by M.G. Fitton, M.R. Shaw and H. Hilpert.

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