

Empirical tests of specific predictions made from a spatial model of the population dynamics of *Maculinea rebeli*, a parasitic butterfly of red ant colonies

G. W. Elmes (*), R. T. Clarke (*),
J. A. Thomas (*) and M. E. Hochberg (†)

(*) Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, Dorset BH20 5AS, UK.

(†) École Normale Supérieure, Université Pierre-et-Marie-Curie, Laboratoire d'Écologie (CNRS-URA-258), 46, rue d'Ulm, 75230 Paris Cedex 05, France.

Summary

We test the ability of a complex spatial model to predict the size of *M. rebeli* populations in two mountain ranges. The published model was based on nineteen parameters that described the population dynamic interactions between the butterfly, its initial food plant *Gentiana cruciata*, its subsequent host *Myrmica schencki*, and other competing non-host species of *Myrmica*. All original model parameters were measured on one site in the Spanish Pyrénées. In this study we measured seven of these parameters, concerning gentians and their habitat, at 12 new sites in the French Alps and at another in Spain. We show that model predictions using these values explained 86% of the variation in *M. rebeli* egg numbers, independently measured on the other sites. Three other (non-intuitive) model predictions were also partly confirmed: (i) *A priori*, our model (which had been parameterised from a single, atypical site with very high gentian densities) predicted a close, indirect, non-linear relationship between gentian and butterfly densities, with egg-numbers being negatively correlated at high gentian densities and positively correlated over low densities. The prediction would be unusual for phytophagous butterflies and is counter-intuitive for a species which experiences only moderate competition on its food plant before spending most of its life inside ant nests, where it is regulated by strong, density-dependent competition. Although this was not fully tested due to a lack of new sites supporting high gentian densities, the empirical results showed a very close positive relationship between egg numbers and gentian densities on sites supporting < 1200 gentians per hectare. Furthermore, our original mechanistic model also accurately predicted both the slope and the range of the positive relationship found at low densities. (ii) Annual fluctuations in populations of *M. rebeli* are exceptionally small. The fit between observed and predicted egg densities was significantly closer than expected if *M. rebeli* populations are assumed to fluctuate with the amplitude of the least variable phytophagous British butterfly. (iii) *Myrmica schencki* populations on the new sites occurred at the low densities predicted by the model as a consequence of parasitism by the butterfly. The accuracy of these predictions over a wide range of sites encourages us to apply the model to simulate the effects of different conservation options for *M. rebeli*.

Keywords: Community module, *Gentiana cruciata*, *Myrmica schencki*, oviposition, temporal-variability, simulation, Alps, Pyrénées, parasitism, population dynamics, *Maculinea rebeli*.

Résumé

Nous avons testé l'aptitude d'un modèle spatial complexe à prédire la taille de populations de *M. rebeli* dans deux chaînes de montagnes. Le modèle publié est fondé sur dix-neuf paramètres décrivant les interactions entre les dynamiques des populations du papillon, de sa plante nourricière initiale *Gentiana cruciata*, son hôte ultérieur la fourmi *Myrmica schenki*, et d'autres espèces de *Myrmica* non-hôtes en compétition. Tous les paramètres du modèle original ont été mesurés sur un site dans les Pyrénées espagnoles. Dans cette étude-ci, nous avons mesuré sept de ces paramètres, concernant les gentianes et leur habitat, sur 12 nouveaux sites dans les Alpes françaises et un autre en Espagne. Nous montrons que les prédictions du modèle utilisant ces valeurs expliquent 86% de la variation du nombre d'œufs de *M. rebeli*, mesurée indépendamment sur les autres sites. Trois autres prédictions (non-intuitives) du modèle ont aussi été partiellement confirmées : (i) *a priori*, notre modèle (qui a été paramétrisé à partir d'un seul site atypique ayant des densités de gentianes très élevées) prédit une relation étroite, indirecte, non-linéaire entre les densités de gentianes et de papillons, les nombres d'œufs étant corrélés négativement à de fortes densités de gentianes et positivement pour de faibles densités. La prédiction serait inhabituelle pour des papillons phytophages et est contre-intuitive pour une espèce qui ne subit qu'une compétition modérée sur sa plante nourricière avant de passer l'essentiel de sa vie dans des nids de fourmis où elle est régulée par une forte compétition densité-dépendante. Bien que cela n'ait pas été complètement testé en raison du manque de nouveaux sites à fortes densités de gentianes, les résultats empiriques montrent une relation positive très étroite entre les nombres d'œufs et les densités de gentianes sur les sites comportant moins de 1200 gentianes à l'hectare. De plus, notre modèle mécaniste original prédit aussi avec précision la pente et l'amplitude de la relation positive trouvée aux faibles densités. (ii) Les fluctuations annuelles des populations de *M. rebeli* sont exceptionnellement faibles. L'ajustement entre les densités d'œufs prédites et observées est significativement plus étroit qu'on ne pourrait s'y attendre en supposant que les populations de *M. rebeli* fluctuent avec l'amplitude du papillon phytophage britannique le moins variable. (iii) Sur les nouveaux sites, les populations de *Myrmica schenki* sont présentes aux faibles densités prédites par le modèle, résultant du parasitisme par le papillon. La précision de ces prédictions pour une grande variété de sites nous encourage à appliquer ce modèle à la simulation des effets de différentes options de conservation concernant *M. rebeli*.

INTRODUCTION

A largely unexplored area of community ecology is whether the dynamics of small groups of interacting species can be isolated from the potential influences of the local environment in which they live. If this is the case, a modular approach (*sensu* HOLT, in press) to understanding community structure would be a realistic objective for certain systems. Unfortunately, few field studies exist which attempt to evaluate the constancy of interspecific interactions in space and time, and in no case known to us has a model of a community module been tested in the field by comparing its predictions with independent population measurements made on other sites.

In an attempt to follow this approach, we developed two models to explore the population-level consequences of interactions within a community module of four interacting species. The community comprised the Large blue butterfly *Maculinea rebeli* (Hir.), its early larval foodplant the Cross-leaved gentian *Gentiana cruciata* (L.), and Red *Myrmica* ants, which adopt and feed this butterfly's caterpillar during its final instar. *Myrmica schencki* (Emery) is the specific host of *M. rebeli*,

but colonies of other *Myrmica* species adopt caterpillars with equal alacrity and support them for a few months. Our first model was a simple phenomenological one (HOCHBERG *et al.*, 1992). The second (HOCHBERG *et al.*, 1994; hereafter referred to as HCET) was more realistic in being a mechanistic model that incorporated small-scale stochasticity in interactions that occur spatially within and between populations of the four species. It also expressed habitat quality as a variable.

One objective of developing the HCET model was to explore how the basic ecologies of several interacting species influence their population dynamics and persistence. A secondary goal was to apply the model to identify attributes that make certain sites important for the conservation of *Maculinea rebeli*, which is classed as "Vulnerable" on the IUCN world list (ANON., 1990). But as it stands, the HCET model is parameterized for a single site (S1) in the Spanish Pyrénées. We did not know if the mechanistic foundations on which it was based worked in the same quantitative way on other sites and in other mountain ranges, a reservation that was heightened when we found S1 to be atypical in supporting exceptionally high densities of *G. cruciata*.

In this study we examine the robustness of the HCET model as a predictor of the population processes of its component species on 13 other sites in two mountain ranges. We test its ability to predict butterfly numbers on other sites as well as three more specific predictions: (1) A close, albeit indirect, relationship exists between gentian and butterfly densities. (2) Populations of *M. rebeli* experience smaller annual fluctuations than typical phytophagous species of butterfly. (3) *M. rebeli* alters the competitive balance between ants to such an extent that the host ant will be substantially outnumbered by other *Myrmica* species on sites occupied by the butterfly.

These predictions alone – and the extent to which we could test them – do not constitute a full test of the accuracy of all population processes underlying our model. But they would, if confirmed, support the status of this system as a community module, and allow us to use the model with increased confidence to make further predictions in pure and applied ecology.

THE *Maculinea-Myrmica-Gentiana* SYSTEM

Biology

Most Lycaenidae have associations with ants (MALICKY, 1969), but *Maculinea* species are unique among European butterflies in their extreme adaptations to living with *Myrmica* and in the fact that their caterpillars harm the ant colonies. The biology of *Maculinea rebeli* and its associated species is described by ELMES and THOMAS (1987 *a, b*), THOMAS *et al.* (1989, 1991), ELMES (1991), ELMES *et al.* (1991 *a*); ELMES *et al.* (1991 *b*), THOMAS (1992 *a, b*, 1994), HOCHBERG *et al.* (1992, 1994), THOMAS and ELMES (1993), THOMAS *et al.* (1993), and KOCKELKE *et al.* (1994). The following details are relevant to this paper and to the HCET model.

M. rebeli is univoltine. Adults fly in July and oviposit on the flowers of *Gentiana cruciata*, regardless of whether these grow near colonies of the host ant or any other species of *Myrmica* (THOMAS *et al.*, 1989). The eggs experience small density-independent mortalities, or hatch after a week (THOMAS *et al.*, 1991).

Caterpillars feed in *G. cruciata* flower buds for two weeks, experiencing density-independent then density-dependent mortalities caused, respectively, by predation and because individual flower buds seldom support > 1 caterpillar (ELMES & THOMAS, 1987 *a*; HOCHBERG *et al.*, 1992). They develop quickly through three instars on *G. cruciata*, but gain < 2% of their final biomass (ELMES & THOMAS, 1987 *a*; ELMES *et al.*, 1991 *a*; THOMAS, 1992 *b*). On reaching the fourth and final instar, caterpillars drop to the ground and await discovery by *Myrmica* workers; they cannot detect ant nests themselves and die if their gentian is beyond the short foraging range (c.1.5 m) of a colony (ELMES *et al.*, 1991 *a*). Workers of all the *Myrmica* species foraging beneath gentians find and carry caterpillars back to their nests with an equal probability, but it is almost exclusively in *M. schencki* nests that caterpillars survive to emerge as adults 11 months later (THOMAS *et al.*, 1989; ELMES *et al.*, 1991 *b*; HOCHBERG *et al.*, 1992). Inside the nest, caterpillars mimic the behaviour of ant grubs, and are preferentially fed by the worker ants. However, there are high mortalities even in *M. schencki* nests: caterpillars frequently experience contest competition when nests adopt more individuals than the workers can support (THOMAS *et al.*, 1993), and caterpillars may be parasitized by a host-specific ichneumonid parasitoid, which selectively enters *M. schencki* nests to oviposit in its host (THOMAS & ELMES, 1993).

Typical *M. rebeli* sites consist of discrete sub-alpine calcareous meadows, from which the adult butterfly seldom emigrates. At Panticosa (S1), where the HCET model was parameterized, the number of *Gentiana cruciata* flower buds per tiller is correlated with the number of tillers per plant, the number of tillers per plant has a truncated Poisson distribution with a mean > 1, and the plants themselves are non-randomly distributed following a negative binomial. Feeding by *M. rebeli* has no discernible impact on the population of *G. cruciata*, which has been very stable in space and time. The niche of the plant (and of the adult, egg and early larval butterfly) is much broader than that of any single *Myrmica* species, and ranges from moist patches with tall grass cover inhabited by *Myrmica rubra* L. and *Myrmica scabrinodis* Nyl., through intermediate zones where *M. rubra*, *M. scabrinodis*, *Myrmica sabuleti* Meinert and *M. schencki* compete, to short sparse arid turf where *M. schencki* is dominant. A typical *Myrmica* colony forages over about 10 m² and is highly dynamic, with small colonies frequently going extinct and vacant nest sites being colonised by offshoots from large neighbouring colonies (ELMES, 1991). *M. rebeli* caterpillars reduce the size of all the *Myrmica* colonies that adopt them – and hence increase colony extinction rates – by out-competing the ant brood reared in autumn and spring (ELMES *et al.*, 1991 *b*); however, they are more damaging to *M. schencki* nests because they seldom survive beyond winter in the nests of other *Myrmica* species.

The HCET model (HOCHBERG *et al.*, 1994)

The model was constructed to explain the population interactions of the *M. rebeli* community in Pyrénéan grassland at Panticosa (S1). It is cellular automata in type and highly mechanistic, incorporating 19 parameters measured at S1 or in the laboratory; some general features are described below.

The numerical algorithm models a 1 ha square of 900 (30 × 30) cells, over which a constant population of gentians is non-randomly distributed. The area of each cell approximates to the foraging range of a large *Myrmica* colony, and

contains at most one ant nest. Habitat variation is represented by a linear gradient along one axis (j) of the grid, changing from cool-moist to warm-dry grassland in 30 discrete steps; each point along the gradient therefore has 30 cells with the same habitat conditions (thereby totalling 900 cells).

HCET developed in some detail the within-nest dynamics of *M. schencki* and an additional population of non-host "other *Myrmica*" species, obtained by grouping *M. rubra*, *M. scabrinodis* and *M. sabuleti*. The habitat gradient directly affects the reproductive rates (R) of each *Myrmica* "species" (fig. 1). Colonies of *M. schencki* can persist only in cells $j = 9 - 30$ (where $R > 1$) and have maximum productivity (R_{\max}) at $j = 22$; other *Myrmica* species persist across $j = 1 - 22$ of the habitat gradient, with maximum productivity at $j = 9$. Thus the habitat gradient contains three major zones (each easily recognised in the field): hot-dry turf where the only ant is *M. schencki* (type 1), cool-moist turf where only non-host *Myrmica* live (type 3), and intermediate turf where *M. schencki* and other *Myrmica* species compete (type 2). The value of R_{\max} for each *Myrmica* "species" (fig. 1) was indirectly estimated to give the best fit to the relative ant densities measured across the habitat gradient at S1, although the model gives a closer estimate of the actual *M. rebeli* population size there if the values of R_{\max} are increased by 2% and 6% for other *Myrmica* and *M. schencki* respectively.

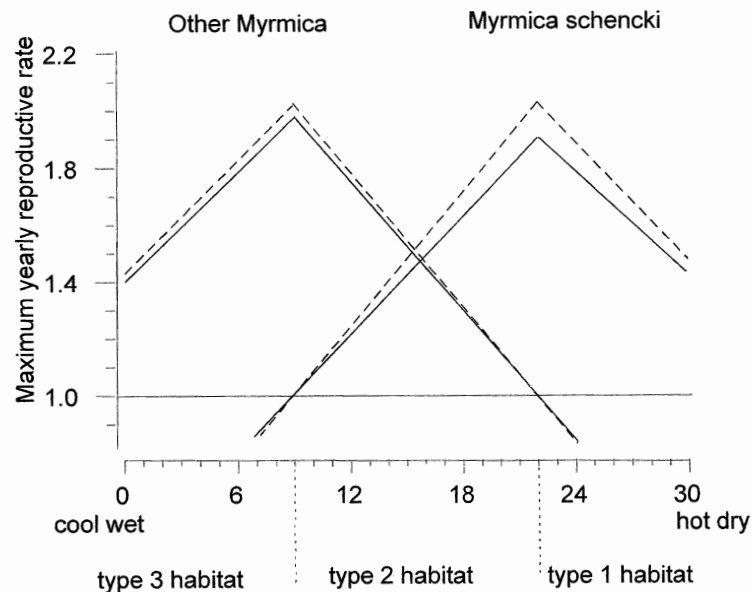


FIG. 1. - Change in maximum yearly reproductive rate (R) of colonies for *Myrmica schencki* and other *Myrmica*, across the gradient of 30 cells. The solid lines indicate the values used in HCET and are the default values used here; $R > 1$ is required for colony growth. Colonies of *M. schencki* do not grow below cell 9 and R peaks in cell 22 ($R_{\max} = 1.91$); colonies of other *Myrmica* do not grow above cell 22 and R peaks in cell 9 ($R_{\max} = 1.98$). The dotted lines indicate the alternative maximum growth rates ($R = 2.025$) for both species required to optimise the predicted to observed egg numbers at S1.

The model is seeded with ants and run for 30 “years”, allowing the two species to reach a dynamic balance. A mated female *Maculinea rebeli* is then introduced. A given generation begins with adult flight, during which eggs are laid from gentian tiller to tiller according to an aggregated negative binomial distribution. To reach adulthood, each individual must survive (1) density independent then (2) density dependent mortalities on the host plant, (3) adoption into a nest of *Myrmica schencki*, and (4) density independent followed by (5) density dependent mortalities within ant nests, with at most one caterpillar surviving per 50 workers. HCET finally assumed a constant mortality (6) from the parasitoid. Eggs laid on gentians in cells containing no *Myrmica* colony never survive beyond step (2) and those in cells containing non-host *Myrmica* nests cannot live beyond (4).

In parallel to the butterflies’ dynamics both within and between nest dynamics of the ant nests occur. Each year, both ant species produce two types of brood in quantities that vary with the colony size and its position along the habitat gradient (fig. 1). One type of brood develops in summer when caterpillars are absent from nests, but the other (vernal) brood can be exploited by any caterpillar adopted. The extent to which this reduces the next generation of ants in a nest depends on the number of caterpillars adopted and how long they survive, and hence is greater, on average, in *M. schencki* nests. There is also a probability each year that a given nest will either disband or divide and bud into a vacant adjacent cell, with both events depending on nest size. HCET assumed that the first nest to arrive in any vacant cell could not be displaced by neighbouring nests, and that caterpillar adoption occurs after the completion of the annual nest dynamics.

THE MODEL PREDICTIONS TESTED

HCET showed that both direct (two species) and indirect (chains of species) interactions had major impacts on the population dynamics of *Maculinea rebeli*, *Myrmica schencki* and the non-host species of *Myrmica*. At Panticosa (S1), the key factor determining the size and persistence of the butterfly population was the competitive balance between the populations of *M. schencki* and other *Myrmica*, with this balance being altered directly by the butterfly (which disproportionately weakens its host ant colonies) and indirectly by the distribution of gentians.

We tested how closely HCET predicted *M. rebeli* population size on other sites and examined three non-intuitive model predictions.

1) Butterfly and gentian densities are closely related

HCET predicts that a close relationship exists between gentian and butterfly densities, with both populations being positively correlated at densities of < 1200-1600 gentians ha⁻¹ and negatively correlated at higher foodplant densities (fig. 2, curves *a*, *b*). This was surprising because *M. rebeli* lives just 4% of its life on *G. cruciata*, gains < 2% of its biomass from eating it, and has no detectable effect on gentian densities. Moreover, caterpillars suffer comparatively small mortalities on gentians (< 20% total K), with much the heaviest, and most strongly density dependent, mortalities occurring in ant nests. However, the model indicates that

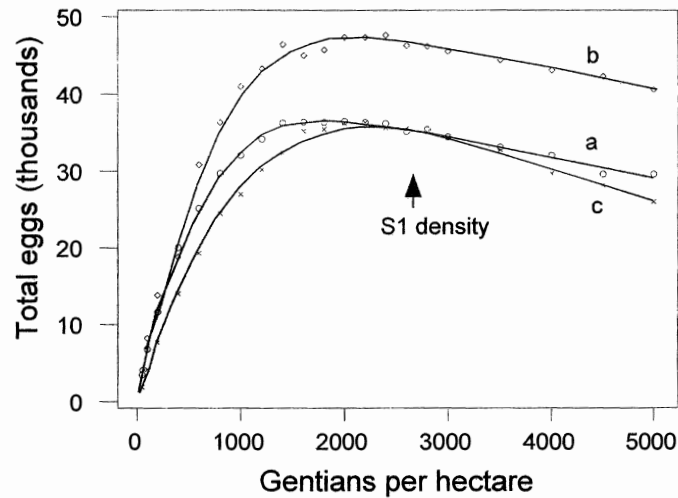


FIG. 2. – The mean number of *Maculinea rebeli* eggs/ha predicted by a series of simulations for different gentian densities using the HCET model: a) uses the original S1 default parameters (circles); b) as (a) but with $R_{\max} = 2.025$ (diamonds); c) as (a) but using the clumping relationship in equation 2 (crosses). The lines are smoothed fits to the simulated results.

the relationship between butterfly and foodplant populations is indirect, reflecting the mechanism by which final instar *M. rebeli* caterpillars enter particular *Myrmica* nests. Since neither the ovipositing adult *M. rebeli* nor its caterpillars can detect ant nests, it is the distribution of gentians that primarily determines the proportion and species of ant colonies that adopt the butterfly. At high gentian densities (e.g. the 2672 gentians ha⁻¹ at S1 where HCET was parameterized), so few *M. schencki* colonies escape parasitism that their carrying capacities are repeatedly depressed and many are supplanted by other *Myrmica* species. In this situation, the model predicts that a reduction in the gentian population would allow *M. schencki* to recover and ultimately would result in more butterflies. But at low gentian densities, any increase in the foodplant would benefit the butterfly until, at c.1200 gentians ha⁻¹, there is maximal butterfly yield from *M. schencki* colonies.

2) *M. rebeli* populations exhibit smaller annual fluctuations than phytophagous lepidoptera

Strong temporal stability of *M. rebeli* populations was predicted because the young stages avoid enemies so effectively in gentian buds (for 2 weeks) and in ant nests (11 months) that populations have a high intrinsic rate of increase, resulting in a rapid recovery following any perturbation. But as a *M. rebeli* population approaches (or exceeds) its site's equilibrium level, high mortalities arise from intraspecific competition for food, because most *M. schencki* colonies near gentians adopt more caterpillars than they can support. Powerful contest competition results in a fixed number of individuals surviving for a given ant nest size (THOMAS *et al.*, 1993), which quickly stabilises the butterfly population.

3) *M. rebeli* reduces host ant colonies to predictable low densities

This was predicted because the greater damage inflicted by caterpillars on *Myrmica schencki* makes individual colonies more likely to become extinct, and the vacant nest sites more likely to be colonised by fitter colonies of other *Myrmica* species. HCET specifically predicted that *M. schencki* will coexist with just 21%-38% of the gentian population on *M. rebeli* sites, with the exact percentage depending on gentian density (*see* fig. 5, dashed line). Furthermore, about one third of the *M. schencki* colonies that do grow near gentians are expected to contain too few workers to find and adopt caterpillars (*see* fig. 5, solid line).

METHODS TO TEST MODEL PREDICTIONS

The other sites investigated

In August 1993, nine HCET model parameters describing gentians, ants, *M. rebeli* (eggs), habitat and area were measured on six more sites (table I) to compare their values and variance with model predictions. The most accurately and easily measured of these described gentians and butterfly eggs: both are conspicuous, and the latter remain attached to the plant for some weeks after hatching (*see* photographs in ELMES & THOMAS, 1987 *a*; THOMAS *et al.*, 1991). We defined the area of each site by the limits of the distribution of *G. cruciata*. This was simple to map because the food plants were clumped in obvious patches, each separated by several hundreds and usually thousands of metres from the next field containing gentians. Mark-recapture experiments indicate that adult *M. rebeli* live in predominantly closed populations (unpublished data, M. L. MUNGUIRA, pers. comm.; KOCKELKE *et al.*, 1994), and that each study site was sufficiently isolated for the number of butterflies recorded on it to be taken as a true measurement of the indigenous population.

One site (S2) was c. 5 km from the original Pyrenean site (S1), and five (F1-5) were 550 km away in the French Alps near Gap; F1, F2 and F4 were close to Saint-Bonnet and F3 and F5 were about 20 km from them in a separate valley near Saint-Étienne. We also used unpublished data collected in 1984 from a fourth site near Saint-Bonnet (F6), and from early, less comprehensive sampling of six sites in France (table I). Two small sites (F9 and F10) in the St. Bonnet region were studied in 1982, and two (F11 and F12), that were near but separate from F6, were studied in 1984. Sites F7 and F8, which were surveyed in 1988, were on the same hillsides as the 1993 sites of F3 and F5. Each site had considerable areas of recently abandoned arable land adjoining it in 1988, which had been colonised by gentians, *Myrmica* and the butterfly by 1993. We considered both the changes in site characteristics and the time interval sufficient to treat the earlier estimates of F7 and F8 as independent of F3 and F5.

Predicting *M. rebeli* population size and testing for a relationship with gentians

Parameters measured

We measured seven HCET parameters describing the abundance, distribution and growth-form of gentians, and the underlying habitat on each site. A negative binomial provided a good description of the frequency distribution of gentians in 3×3 m quadrats, which approximated to the cell size in HCET. On small sites or where gentians were rare, the position of every gentian was mapped, from which we calculated the negative binomial clumping parameter (K_G) at the scale of 3×3 m. On larger sites, the abundance of gentians in a random sample of 50 3×3 m quadrats was measured, providing estimates of both gentian density and K_G .

On most sites supporting > 50 gentians, a random sample of 50 plants was selected and a count was made of the number of tillers, and of the number of flower buds and *M. rebeli* eggs per tiller. This provided estimates of four more HCET model parameters: mean number of tillers per plant, the

parameters of the logarithmic regression between total flower buds and tiller numbers per plant, and the negative binomial clumping parameter for eggs per tiller.

The proportion of the 50 gentians growing in each of the three main habitat types was also recorded. However, in the HCET model the habitat is arranged as a linear gradient in quality which can not be altered. The model was scaled therefore, by the relative abundance of gentians in each habitat type, which at S1, we approximated as 1:1:1 (HCET). Here we followed the same procedure, the abundance of gentians was divided by the corresponding area of each habitat type at the site to give the density of gentians in each habitat type, and was included as the seventh site-specific parameter in model simulations (table I and see below).

Finally, we made an absolute count of the egg population of *M. rebeli* on each site, or obtained an accurate estimate from the number of eggs counted on 50 or more gentians.

Model simulations

We ran the HCET model to predict the density of *M. rebeli* eggs expected on each site, and compared each prediction with the actual density observed there. Three sets of simulations were made: (i) Using the seven site-specific parameters measured on each site. (ii) Using site gentian density as a variable and the other parameters averaged for all sites, with K_G estimated from equation 2 (below). (iii) Using site gentian density as a variable, but with other parameter values as in the original model (*i.e.* using values recorded at S1). We also repeated each set of simulations with the ant growth rate $R_{\max} = 2.025$ (*see* fig. 1), making a total of six sets. All other parameters were as listed in HCET (table II *ibid*), except that the maximum size of nest for disbandment to occur (Z_T) was 4 rather than 8, as was erroneously typed (but not used) in HCET.

Since each numerical simulation of the HCET model gives a unique time series of population indices, results were expressed by averaging over 20 runs. For each simulation run, the spatial distribution of gentians was generated independently and then held constant over the simulated period (*see* HCET). The model was run for 30 years before the introduction of a single female butterfly, after which a further 70 years were simulated. Ant and butterfly populations fluctuate around equilibrium values, after an initial explosion in butterfly numbers. Estimates of these were made by first calculating mean equilibrium values for the last five years of each simulation and then averaging these over the 20 runs. Standard errors of these mean predicted egg numbers (and ant density estimates) were generally < 2%, but increased to 13% at densities of < 50 gentians ha⁻¹.

Statistical comparisons

Let O_i and P_i denote the observed and model prediction of *M. rebeli* egg density at site i . The simple correlation (r_{op}) between $\log O_i$ and $\log P_i$ was not used because, if the model tended to consistently over or under-predict egg density, a strong (linear) relationship might be observed and predicted, despite the model being a poor predictor of absolute egg density at any site. Instead, the accuracy of P_i was assessed more rigorously, as the proportion (F_{mod}) of the total variation between the n sites which is explained by the model where:

$$(1) \quad F_{\text{mod}} = 1 - \frac{\sum_{i=1}^n (\log O_i - \log P_i)^2}{\sum_{i=1}^n (\log O_i - m_0)^2}$$

where $m_0 = \frac{\sum_{i=1}^n \log(O_i)}{n}$.

In other words, how much P_i deviates from the 1:1 line expected if the model was a perfect predictor of O_i . The logarithmic transform is used because both estimation errors and temporal variation in observed butterfly egg densities are usually considered to be proportional to the site average egg densities (THOMAS *et al.*, 1994).

Do *M. rebeli* populations fluctuate less than other butterflies?

The magnitude of annual fluctuations in populations of various phytophagous species has been derived from the British Butterfly Monitoring Scheme (BMS) for 1976-1992 (POLLARD & YATES, 1993; THOMAS *et al.*, 1994). POLLARD and YATES (1993) showed that migratory and multivoltine species experience much greater fluctuations than species which, like *M. rebeli*, have colonial and univoltine life-styles. The BMS had data for 12 colonial-univoltine-phytophagous species for which sufficient populations were adequately sampled for unbiased calculation of the standard deviation of \log_{10} of their abundance values ($SD \log_{10}$) (THOMAS *et al.*, 1994; D. MOSS, pers. comm.). The mean value of $SD \log_{10}$ for these 12 species was 0.37, and that of the least variable species (Meadow brown, *Maniola jurtina* L.) was 0.29, equivalent to mean annual Coefficients of Variation (CV) of 104% and 75% respectively, assuming log normal distributions.

To test the prediction that *M. rebeli* populations have small fluctuations, we first assumed that the HCET model gave a perfect prediction of the long-term average egg density at each of the study sites and that, in any year, a site's population would fluctuate around its long-term average with a $SD_{\log 10}$ equal to either the overall average for UK univoltine species or the value for *M. jurtina*. We then generated "simulated observed" egg densities for each site by drawing random samples from log-normal distributions with the model's predicted means and the assumed $SD_{\log 10}$. From 1000 sets of such data, we calculated the proportion of cases that the "simulated observed" values gave a better fit (F_{mod}) or higher correlation with the model predictions than the actual observed values. In other words, we estimated the probability of obtaining, by chance, the observed fits if *M. rebeli* populations fluctuated annually around their means with the same amplitude as either a typical phytophagous British butterfly or the most stable known species.

Does *M. rebeli* reduce host ant populations to predictable densities?

Each of the 50 gentians selected for plant parameter measurements was baited with sugar during the peak foraging periods for *Myrmica*. Each bait was analogous to a *M. rebeli* caterpillar awaiting adoption beneath its gentian, and gave a realistic estimate of the proportion of caterpillars that would be adopted by *M. schencki* on each site (ELMES *et al.*, 1991 *a*). Baits were set once on most sites and on three occasions on S1 and S2. Sites F6, F7, F10-12 were not sampled for ants. The results were compared with values predicted by HCET for the probability of caterpillar adoption, given the density and mean clumping of gentians recorded on the study sites.

RESULTS

General observations

Table I presents parameter estimates for the source site of the HCET model (S1), 13 additional sites in the Pyrénées and Alps, and the mean values of the eight best-studied sites (S1, S2, F1-F6). *M. rebeli* densities, which ranged from 1.1 (F9) to 56.1 (S2) thousand egg ha^{-1} , are listed in table II.

Several parameters were surprisingly constant across sites, considering that estimates were made over a 10 year period and in two mountain systems. Those that differed most were site area and gentian density. All new sites were considerably smaller than S1, and their gentian densities ranged from 38 to 1645 plants ha^{-1} , compared with 2672 plants ha^{-1} at S1. But there was no evidence for any relationship between site size and the density of gentians supported; nor that parameters describing the log regression between buds and tillers or tillers/plant were related to plant density.

TABLE I. - Parameters measured at 14 sites supporting populations of *Maculinea rebeli*. S1 = the original (1990) HCET site in the Spanish Pyrénées; S2 (5 km from S1) and F1-F5, in the French Alps, were measured in 1993. Other sites, all in the Alps, were measured in 1982 (F9, F10), 1984 (F6, F11, F12) and 1988 (F7, F8). Mean parameter values were calculated from sites S1, S2 and F1-F6; geometric means were used for parameters (e.g. clumping) which are distributed exponentially. Suffixes: (1) Not measured but estimated from equation 2. (2) Not measured so equal density assumed. (3) Estimated from a sample of only 10 gentians. (4) Ratio of habitat types (1, 2, 3) approximated to 1:1:1 in HCET and to 1:2:1 in runs with mean parameters. (5) M. schencki present but not estimated accurately. (#) Identifies the 7 site-specific parameters used to test model.

	S1	S2	F1	F2	F3	F4	F5	F6	Mean	F7	F8	F9	F10	F11	F12
Gentians ha ⁻¹ , #	2672	1222	1049	171	930	46	741	432	908	284	167	38	42	783	1645
Gentian clumping parameter#	2.10	0.66	0.48	0.11	0.55	0.05	0.25	0.75	0.62	0.20 ¹	0.12	0.03 ¹	0.03 ¹	0.80	0.70
Area of site (ha)	> 1	0.44	0.55	0.47	0.48	0.67	0.45	0.20	0.45	0.45	0.24	0.85	0.24	0.06	0.08
Mean Tillers/gentian#	2.89	2.70	3.60	2.04	1.92	4.03	2.54	2.21	2.74	2.00 ³	1.87	3.50 ³	2.60	1.98	4.90 ³
Bud/tiller=A/(tillers) ^β															
A#	7.74	16.60	11.06	9.13	15.10	16.83	15.88	9.58	12.23	19.04 ³	15.04	7.74 ²	7.74 ²	10.86	17.63 ³
B#	0.857	0.856	1.012	1.517	1.011	1.141	1.069	1.400	1.108	0.922	0.876	0.857	0.857	1.979	0.017
Clumping parameter for eggs on gentians#	0.25	0.84	0.71	1.28	0.77	0.22	0.56	0.80	0.59	0.83 ³	0.72	27.5 ³	1.31	0.67	0.45 ³
Relative plant density in habitats#															
type 1	0.72 (1) ⁴	0.92	0.25	0.88	1.00	0.67	0.04	0.56	0.63 (1) ⁴	1.0 ²	1.0 ²	1.0 ²	1.0 ²	0.33	0.43
type 2	1.00 (1)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00 (2)	1.0 ²	1.0 ²	1.0 ²	1.0 ²	0.59	1.00
type 3	0.85 (1)	0	0.83	0.73	0.51	0.25	0.37	0.36	0.49 (1)	1.0 ²	1.0 ²	1.0 ²	1.0 ²	1.00	0
Proportion of gentians with M. schencki on baits	0.18	0.24	0.32	0.24	0.24	0.25	0.12	0.5	0.20	0.21	0.20	0.20	0.5	0.5	0.5

There was, however, a negative correlation between the clumping parameter for *M. rebeli* eggs on plants and gentian density ($r_{df=12} = -0.56$, $P < 0.05$), and a positive correlation between the clumping of gentian plants (K_G) at the 3×3 m scale and gentian density ($r_{df=6} = 0.923$, $P < 0.001$ -estimates of gentian clumping were obtained from only eight sites). Taken together these imply that, on sites with the lower densities of foodplant, gentians tend to be more aggregated at the 3×3 m scale and the butterfly eggs are more evenly dispersed between the plants. Regression analysis between gentian density and K_G gave no evidence for an intercept value significantly different from zero. The best fit was

$$(2) \quad K_G = 0.000701 \quad (\text{Gentians per ha})$$

which was used as an estimate of K_G at sites F7-F10 where no field estimates were obtained (table I).

Overall sites averaged habitats 1-3 in the proportions 0.35:0.40:0.25 rather than the 0.27:0.46:0.27 used in HCET (rounded proportions observed at S1). Most sites contained the full range of microhabitats described at S1, apart from S2 and F8 which had no habitat type 3 (dominated by other *Myrmica* species). Gentians were present in all three habitat types at each site although generally, intermediate habitat (type 2: where *M. schencki* and other *Myrmica* compete) supported the highest density of *G. cruciata*. Overall, the results suggest that an approximate ratio of 1:2:1 between relative gentian densities in the three main habitat types (1-3) is more typical of *M. rebeli* sites as a whole than the 1:1:1 HCET model assumption derived from S1 (table I).

Predicted versus observed egg number

The observed egg density on each site and the predicted egg densities from simulations for each of the six sets of parameters tested are listed in table II. The proportion (F_{mod} , eqn 1) of inter-site variation explained by each simulation is given for the 13 additional sites alone (*i.e.* excluding S1), and for all sites.

There is a statistically significant relationship between observed and predicted egg number for all six parameter sets tested (table II), with the seven gentian and habitat parameters measured on individual sites explaining 86-87% of the observed variation in *M. rebeli* population size between sites (fig. 3; table II: Act.lo and Act.hi). The best overall fit was obtained using average site parameter values, especially with ant growth R_{max} set at the higher value. This explained 91% of the variation in observed egg numbers on the 13 additional sites (table II: Avg.hi).

It is also remarkable that, by varying gentian density alone, the original HCET model explains 82% of the observed variation in *M. rebeli* density between sites (table II: S1.lo) although optimising R_{max} to fit S1 explains only 69% of the observed variation (table II: S1.hi). Clearly gentian density was the key parameter among those measured (*see below*); but the other six parameters are not negligible: inclusion of their site-specific values explains a further 22-71% of the residual variance not explained by gentian density (table II: Act and Avg).

TABLE II. – Observed (Obs) and predicted egg numbers (thousands) per hectare at 14 sites for *Maculinea rebeli*. Predictions were based on the HCET model originally parameterized at S1. Six predictions were made: Actual (Act) used 7 site-specific parameters (table I) plus 12 default parameters from S1; Average (Avg) used the actual gentian density combined with the average estimates for the other 6 site-specific parameters (table I) and 12 default S1 parameters; Default (S1) used actual estimates of gentian density (table I) and 18 S1 parameters. Two values of R_{\max} were used (see fig. 1); $l_0 \approx 1.9$ (default value HCET) and $h_i = 2.025$ (optimised to fit S1 observed eggs). F_{mod} = the proportion of between site variation in the (log) observed egg numbers explained by the (log) predicted values (see equation 1). (**) Sites where every egg was counted to obtain *M. rebeli* population size, (*) > 70% egg population was counted to estimate *M. rebeli* population size, remaining sites 10-40% sampled.

Site	Obs.	Act.lo	Act.hi	Avg.lo	Avg.hi	S1.lo	S1.hi
S1	47.6	36.1	47.1	34.4	44.8	35.5	45.9
S2	56.1	31.5	37.3	28.7	34.4	38.4	44.6
F1	32.1	17.9	22.7	26.6	31.7	33.9	41.5
F2*	4.8	6.6	7.5	5.9	6.8	10.3	12.2
F3	13.7	26.3	32.7	24.1	28.4	31.6	39.8
F4**	1.2	2.4	2.7	1.9	1.9	3.0	3.7
F5	18.0	8.3	10.3	20.9	24.0	28.8	35.6
F6**	34.6	17.6	22.2	13.0	17.1	21.4	27.4
F7	7.5	10.9	12.1	9.6	11.9	14.9	19.3
F8*	7.7	6.2	8.1	5.3	6.6	9.9	12.3
F9**	1.1	1.5	1.7	0.9	1.6	2.3	3.3
F10*	1.7	1.6	2.1	1.4	1.8	2.8	3.7
F11**	24.7	20.3	25.3	20.8	26.9	30.6	35.6
F12	41.8	28.9	36.8	31.6	40.4	36.1	46.4
F_{mod} (excluding S1)		0.86	0.87	0.89	0.91	0.82	0.69
F_{mod} (including S1)		0.87	0.88	0.90	0.92	0.83	0.72

Effect of gentian density

The close fit between observed and predicted egg numbers when only gentian density is varied (table II: S1.lo) confirms the (indirect) relationship between the butterfly and its foodplant predicted by HCET for densities < 1 200-1 600 gentians ha^{-1} (fig. 2 curves *a*, *b*; curve *c* is obtained by using the gentian clumping equation derived from eight sites). Neither the slope nor intercept of the observed linear regression between gentian (G) and egg (E) densities for the additional sites –

$$(3) \quad \log_{10} E = 0.965 \log_{10} G + 1.59 \quad (r_{df=11} = 0.955, P < 0.001)$$

were significantly different ($P \geq 0.09$) from the regression for the same gentian densities (fig. 4) predicted from the HCET model as parameterized at S1-

$$(4) \quad \log_{10} E = 0.764 \log_{10} G + 2.055 \quad (r_{df=11} = 0.959, P < 0.001)$$

Several sites contained sub-area with gentian densities in the range 2000–4000 ha^{-1} , but we were unable to find any site other than S1 with overall densities > 1 650 gentians ha^{-1} , and therefore could not test the prediction that increasingly higher foodplant densities eventually depress the butterfly population.

Are *M. rebeli* populations unusually stable?

If the HCET prediction of high temporal stability within *M. rebeli* populations was false, we would expect only a loose fit between observed and predicted *M. rebeli* densities, even if the model was a perfect predictor of each site's equilibrium level. In fact, the fit was significantly closer than that expected to be obtained from single censuses of populations of any species that fluctuated with the same amplitude as phytophagous butterflies. We calculated that, with the same average annual fluctuations of UK colonial-univoltine-phytophagous butterflies (fig. 3, dashed lines), we would expect a closer fit by chance, with the 1:1 model prediction (fig. 3, dotted line) on < 1% of occasions. Indeed, all observed values are well within the 95% confidence limits expected if *M. rebeli* populations showed the same temporal variation as the most stable of all known butterfly species (fig. 3, solid lines) and we would expect a closer fit to the 1:1 line on < 5% of occasions. Furthermore, the correlations between observed and predicted egg densities are significantly higher than expected ($P < 0.01$ and $P < 0.05$ respectively). We therefore conclude that *M. rebeli* populations experience smaller annual fluctuations around their equilibrium levels than phytophagous butterfly species.

Predicted versus observed covariation between ants and plants

If *M. rebeli* were absent from S1, HCET predicted that ant populations would reach a dynamic equilibrium with 48% of nests sites (=cells) occupied

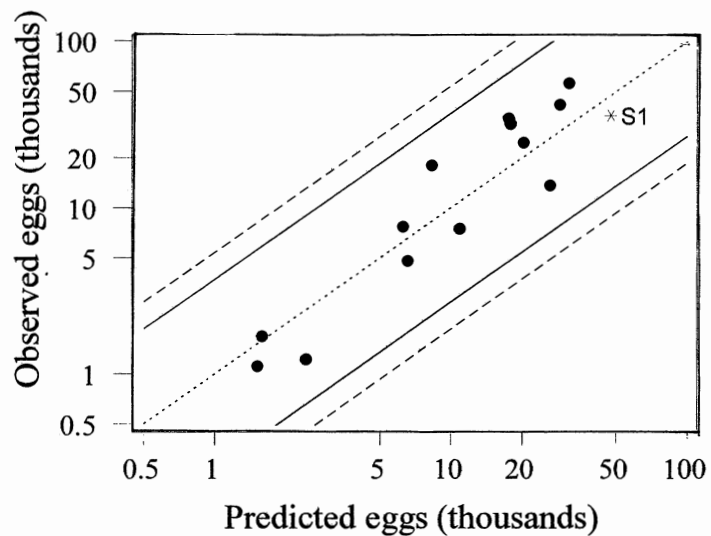


FIG. 3. – The observed *Maculinea rebeli* egg densities at the 14 sites investigated, plotted against the prediction from the HCET model using the 7 site-specific parameters (table II: Act.10). The dotted line indicates the expected (1:1) relationship if the model was a perfect predictor of egg density. Dashed lines represent the 95% confidence limits around the 1:1 line, expected if *M. rebeli* populations had the same temporal variability as the average univoltine British butterfly species ($SD_{\log 10} = 0.37$). Solid lines indicate the 95% confidence expected if *M. rebeli* had the same temporal variability ($SD_{\log 10} = 0.29$) as the least variable of all British butterflies.

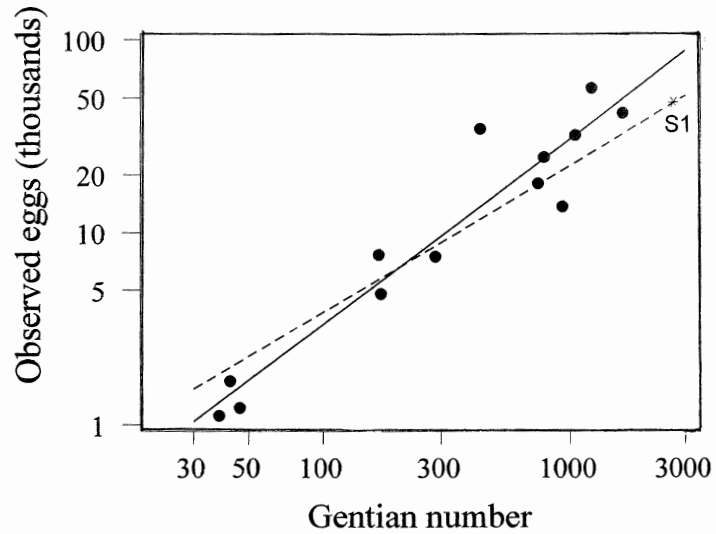


FIG. 4. – The density of *Maculinea rebeli* eggs (thousands ha^{-1}) observed at 13 new sites, plotted against the observed density of gentians. The solid line is the observed least squares regression and the dotted line is the regression of the values predicted from the HCET model (parameterized at the original site S1) with the observed gentian densities.

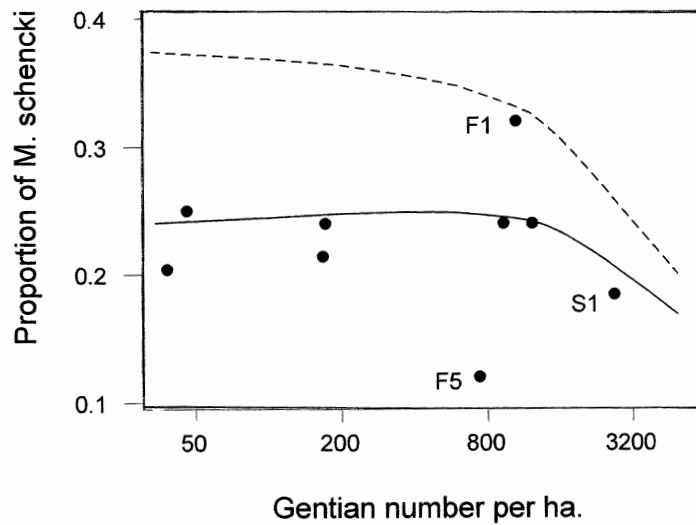


FIG. 5. – The observed proportions (●) of gentians under which *Myrmica schencki* were attracted to sugar baits on nine *Maculinea rebeli* sites. On sites occupied by the butterfly, HCET predicts that the proportion of gentians coexisting with *M. schencki* varies with gentian density (dashed line). The proportion of gentians coexisting with *M. schencki* nests large enough to find and adopt caterpillars is represented by the solid line.

by *M. schencki* and 52% by other *Myrmica*. The presence of *M. rebeli* is expected to reduce the proportion of *M. schencki* coexisting (sharing cells) with gentians in a non-linear manner according to gentian density (fig. 5, dashed curve). The proportion of *M. schencki* colonies coexisting with gentians and that are large enough to find and adopt *M. rebeli* caterpillars is predicted to be lower still (fig. 5, solid line).

On eight of the nine sites sampled for ants, the proportion of the sugar baits (which simulate caterpillars) beneath gentians that attracted *M. schencki* was close to or lower than the predicted value (fig. 5, solid line), and the other site (F1) was lower than the predicted proportion of gentians with a *M. schencki* nest of any size near it.

DISCUSSION

Although the data presented here do not provide a full test of all the HCET model predictions, we consider that the closeness with which observed data fitted predictions of egg densities on 13 other sites, and satisfied three key (non-intuitive) predictions, provides strong support for the validity and general applicability of the model.

The existence of a close relationship between gentian density and *M. rebeli* egg numbers (fig. 2) was among the least expected of the original HCET predictions, because the mortality of butterflies on gentians is comparatively insignificant (*see above*: "The model predictions tested"). However, the model highlighted the importance of the spatial distribution of gentians as the agent that transmits the infestation to the population of host ant colonies. It also led to the prediction that increasing gentians to very high densities would lead to low butterfly populations. It is unfortunate that we were unable to locate discrete sites supporting sufficiently high gentian densities to test this prediction, although the effect might be detected from future investigations of sub-areas within S1 and F12.

Nevertheless, it is reassuring that a model, constructed and parameterized from a site (S1) with a higher gentian density than that predicted for optimal exploitation of *M. schencki*, should predict the slope of the positive relationship found between butterfly egg and food plant densities on other sites (fig. 4), or indeed the range of gentian densities over which a linear relationship holds, as accurately as it does. For example, if we had accepted published accounts (SCHROTH & MASCHWITZ, 1984; HÖLDOBLER & WILSON, 1990) of caterpillar adoption rather than our own field measurements (ELMES *et al.*, 1991a; THOMAS, 1992a, b), our mechanistic model would predict that *M. rebeli* populations pass the peak after which increased food plant densities result in fewer ants and butterflies, at much lower densities of gentians than those shown in figure 2. The former suggest that *Maculinea* caterpillars actively seek their host nests by following ant trails, whereas we found that they wait passively within 6 cm of the food plant to be discovered by ants. Seeking nests would take caterpillars into the cells adjacent to their gentian host, rather than restrict them to an ant colony in the same cell, leading to the over-exploitation of *M. schencki* at low gentian densities.

Although the HCET model proved to be a more accurate predictor of population sizes and processes than might reasonably have been expected (table II, figs 3-5),

it is legitimate to query whether it has any practical importance given the equally close regression found between egg densities and just one of its 19 parameters, gentian density. We suggest that this empirical regression (equation 3, fig. 3) can be approximated by the equation $egg\ density = 40\ gentian\ density$, and applied as a useful rule of thumb that one adult *M. rebeli* will be supported by every two gentian plants per hectare on unknown sites. However it would be unwise to apply this indiscriminately, for three reasons:

(i) If HCET is correct, a positive linear relationship applies only to sites with gentian densities of < 1 200-1 600 gentians ha⁻¹.

(ii) HCET indicates that gentian distribution rather than abundance is the important factor. Although the clumping of gentians followed the same negative binomial on our 14 study sites (table I), the relationship between egg and gentian densities would break down on sites where the distribution of gentians was different or had been modified by management. For example, a conservationist hoping to increase a *M. rebeli* population by introducing additional gentians to a site would find this had the opposite effect at comparatively low food plant densities if he planted the new gentians to fill most gaps between existing plants (hence over-exploiting the *M. schencki* colonies) rather than followed the natural clumping described by equation (2).

(iii) On all our study sites, the gentians showed a nearly constant niche overlap with the *Myrmica* species present so that our assumption of a linear gradient with fixed proportions of habitat types 1-3 (see section Parameters measured) was reasonably consistent (see results). This almost certainly will not remain so, under the local climates further north and east in *M. rebeli*'s range (e.g. THOMAS, 1994), in which case, the empirical relationship (fig. 4) would no longer hold. By contrast, the mechanistic HCET model takes account of all three situations to some extent, besides giving insights into some mechanisms driving the underlying ecological processes. Furthermore, it should be relatively easy to alter the HCET model to realistically reflect the actual proportions of habitat types and associated gentian abundances, recorded at any site.

An unexpected result from this study was that the inclusion of all the site-specific parameters (table I) increased the explained proportion of between-site variance in egg density by only 4%, or 22% of the remaining variance not explained by gentian density (*i.e.* an increase from 82 to 86 percent, table II: S1.lo and Act.lo); whereas, substitution into the model, of between-site average parameters for gentian characteristics (table I) produced a better overall fit to the observed egg densities (table II: Avg.lo) explaining 89% of the variance, or 39% of the variance not explained by gentian density (table II: Act.lo). When this relationship was scaled using the higher values for R_{max} (see section The HCET Model), the model explains 91% of the between-site variance (table II: Avg.hi). This indicates that this set of average parameters should be used in any future practical applications of the HCET model.

One explanation for the superiority of the average rather than site-specific gentian parameters, is that probably, little between-site variation exists in gentian characteristics (e.g. tiller number, flower number) when averaged over the time span simulated by the model. In which case, the differences in parameter values measured at the different sites might owe more to temporal within-site variation than intrinsic between-site variation. Any increase in accuracy obtained by using

site-specific parameters would be outweighed by errors introduced by estimating them in only one. This, and the relationship between gentian density and clumping at the 3×3 m scale, suggest that the long-term population dynamics of *G. cruciata* would itself form an interesting study.

More generally, our work demonstrates that site to site differences in the populations of *Maculinea rebeli* and its associated community are dominated by relatively few, easily discriminated, ecological processes (e.g. BILLYCK & CASE, 1994; CHESSON, 1994); importantly, site-specific abiotic (e.g. climatic) variables are not necessary to explain the key population indices. This may appear surprising given the considerable variability shown by populations of other butterfly species, for which large fluctuations typically occur around site means (POLLARD & YATES, 1993; THOMAS *et al.*, 1994). We have shown that there was a low probability (< 5%) of detecting a relationship between site characteristics and *M. rebeli* populations recorded by single spot sampling if *M. rebeli* populations were as variable as even the least variable of UK phytophagous butterflies. In fact, it was the assumption that the same strong mechanisms that cause stability at S1 operate in all populations of *M. rebeli* that led us to investigate other populations in this way.

In our study the stability of egg-numbers of *M. rebeli* has been compared with the stability of adult populations in other species. Although gentian distribution and numbers are remarkably stable in space and time (see HCET) there is some variation in flowering characteristics (see table I and discussion above) but we have no evidence that this directly affects the number of eggs laid by individual females. Variation in flowering phenology, probably only affects the clumping of the distribution of eggs on plants. This was measured here and also, the model is not particularly sensitive to the egg-clumping parameter (HCET).

M. rebeli adult populations have low temporal variability most probably because ant nests provide a constant environment that is highly buffered against the variations in weather that directly affect populations of most phytophagous species. The strong density dependent survival in ant-nests, resulting from contest competition, ensures that a fairly constant resource is almost always fully exploited. Arguably, oviposition might be directly affected by weather even though adult numbers might be buffered, and it is possible that variation in adult populations is even less than observed for egg-numbers (in the model, each female produces a constant number of eggs so that egg-number is a surrogate measure of adult females). However, we predict that egg-numbers will be shown to be little more variable than adult numbers for several reasons. First, in a broad sense the phenology of the ants and hence the development of caterpillars, and the phenology of *G. cruciata* is closely correlated with average soil temperatures. In addition, the flowers on different tillers of *G. cruciata* develop at different times depending upon their position on the plant, and similarly flower development varies according to their position on a tiller (unpublished data). Thus, while butterfly emergence may vary by up to ± 14 days from year to year and from site to site, most gentians on a site will always have some flowers at the young-bud stage necessary for oviposition when the adults emerge. Secondly, in the mountain habitats studied, once a summer weather pattern is established it is relatively constant from year to year so that by the time adults emerge, the weather is suitable for oviposition throughout the adult flight period. Thirdly, the ant community would only change significantly if abiotic

factors, such as weather, showed long-term changes. In the context of the HCET model, these would alter the spatial distribution of R_{\max} for the host ant species.

This study illustrates how a handful of ecological axioms can serve as a basis for scrutinising both within-site and between-site population dynamics. Despite the complexities of the biology of *M. rebeli*, its life-cycle can be divided into a series of distinct phases (HOCHBERG *et al.*, 1992, HCET), each analyzable in isolation or in combinations for their importance to the population dynamics of the system. It provides strong support for the contention by HCET, that *M. rebeli* populations, unlike most butterflies are remarkably stable. In conclusion, the general concordance between predictions of egg numbers, butterfly population stability, host ant densities and the observed data at the 13 other sites reassures us that the HCET model is basically sound, and that it can be used with confidence to simulate the effects of various conservation options for *M. rebeli* and to investigate general issues in ecology concerning the spatial dynamics of interacting populations and the effects of habitat change.

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