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Food-plant niche selection rather than the presence of ant nests explains oviposition patterns in the myrmecophilous butterfly genus *Maculinea*

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It has been suggested that the socially parasitic butterfly *Maculinea alcon* detects ant odours before ovipositing on initial larval food plants near colonies of its obligate ant host *Myrmica ruginodis*. It has also been suggested that overcrowding on food plants near *M. ruginodis* is avoided by an ability to detect high egg loads, resulting in a switch to selecting plants near less suitable ant species. If confirmed, this hypothesis (H_1) would have serious implications for the application of current population models aimed at the conservation of endangered *Maculinea* species, which are based on the null hypothesis (H_0) that females randomly select food plants whose flower buds are at a precise phenological stage, making oviposition independent of ants. If H_1 were wrong, practical management based upon its assumptions could lead to the extinction of protected populations. We present data for the five European species of *Maculinea* which show that (i) each oviposits on a phenologically restricted flower-bud stage, which accounts for the apparent host-ant-mediated niche separation in sympatric populations of *Maculinea nausithous* and *Maculinea teleius*, (ii) there is no temporal shift in oviposition by *Maculinea arion* in relation to host ant distribution or egg density, and (iii) oviposition patterns in 13 populations of *M. alcon*'s closest relative, *Maculinea rebeli*, conform to H_0 not H_1 predictions. It is concluded that conservation measures should continue to be based on H_0.

Keywords: oviposition; social parasite; myrmecophily; conservation

1. INTRODUCTION

The closely coupled systems of interacting species centred around the parasitic caterpillars of the butterfly genus *Maculinea* provide useful models for studying evolutionary (Thomas *et al.* 1998*a*; Akino *et al.* 1999; Schönrogge *et al.* 2000), population (Hochberg *et al.* 1994, 1996) and community ecology (Clarke *et al.* 1997; Thomas *et al.* 1998*b*). In addition, all five European species of *Maculinea* are listed as globally threatened (IUCN 1990) and knowledge of their biology provides the rationale for successful conservation programmes (Thomas 1994; Wynhoff & Van der Made 1995). The distinctive biology of the *Maculinea* 'community module' has been reviewed by Thomas *et al.* (1998*b*). In brief, *Maculinea* caterpillars develop quickly through three instars on a specific food plant before being adopted into *Myrmica* ant nests, where they live as social parasites for ten to 23 months and obtain more than 98% of their ultimate biomass by feeding on the resources of the colony. Caterpillars of each *Maculinea* species are adopted with alacrity by any species of *Myrmica* that encounters them beneath the initial food plant, but survive almost exclusively in the colonies of a single and different 'host' species of *Myrmica* (*Maculinea alcon* uses a different host in parts of its European range) (Thomas *et al.* 1989; Elmes *et al.* 1994). On typical sites, the niche of the food plant encompasses that of three to five *Myrmica* species, each restricted to a subtly different microclimate; for a *Maculinea* population to persist, sufficient eggs must be laid within the foraging range of its host *Myrmica* colonies (Thomas *et al.* 1998*b*).

A few phytophagous species of lycaenid use ant cues for ovipositing near a preferred genus of ant with which they interact symbiotically (Pierce & Elgar 1985; Seufert & Fiedler 1996). An unresolved question affecting all *Maculinea* studies is to explain why many, in some species up to 90%, of the eggs in the populations of these obligate social parasites are laid near non-host species of *Myrmica* or near other genera of ants in whose respective nests the offspring have a very low or no chance of survival (Thomas & Elmes 1998). Van Dyck *et al.* (2000) presented field observations, made on two populations of *Maculinea alcon*, that females lay on food plants (*Gentiana pneumonanthe*) near to nests of the host ant *Myrmica ruginodis* during the early part of adult emergence but increasingly lay on gentians near unsuitable *Myrmica* species as the season progresses. They proposed two alternative explanations, which we present here as two (mutually exclusive) hypotheses.

(i) Hypothesis 0 (H_0). Any patterns in egg distribution on food plants that appear to reflect host-ant distributions are chance effects caused by variation in microhabitat within heterogeneous sites, which determines both the date on which a food plant flowers and the distribution of *Myrmica* species. More specifically, females restrict oviposition to a short-lived phenological stage of *G. pneumonanthe* flower production, using early-flowering plants early in the four-week breeding season and late-flowering plants at the end. This could result in most early eggs being placed near one species of *Myrmica* and most later eggs being laid near a second species.

(ii) Hypothesis 1 (H_1). Ovipositing females can detect ant odours and initially select food plants near their host ants' nests, but later reject these once the egg load exceeds a

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level at which density-dependent mortalities occur. Specifically, Van Dyck *et al.* (2000) hypothesized that *M. alcon* females can both detect the proximity of *M. ruginodis* colonies and assess the density of eggs already laid on a particular gentian: when all or most gentians near *M. ruginodis* nests have a high load, females switch behaviour, ignore ant odours and simply select gentians with low egg loads. This represents a trade-off between the high density-dependent mortalities that would occur if females continued to select plants near host ants and the low survival rates of larvae adopted by non-host *Myrmica* ants.

We have long considered the null hypothesis (H_0) to be the prosaic suggestion that oviposition patterns merely reflect local variation in microhabitat within sites, at least for *Maculinea alcon*, *Maculinea rebeli* and *Maculinea arion*. In the cases of *Maculinea teleius* and *Maculinea nausithous*, which share the same food plant but have different host ants, we speculated that the undoubted coincidence of egg and host ant distributions within sites is an indirect effect caused by female butterflies laying selectively on a growth form of the food plant that is expressed mainly in the vegetation structure preferred by the host ant of each (Thomas 1984*b*, 1991). Although we have published only part of our data describing the relationship between microclimate, oviposition choice and the narrow niches occupied by different *Myrmica* species (e.g. Thomas 1984*a*, 1991; Elmes *et al.* 1998; Thomas *et al.* 1998*b*,*c*), the assumption that H_0 explains preferential egg laying underpins our (largely validated) spatial models of *Maculinea* community modules (Hochberg *et al.* 1994; Elmes *et al.* 1996; Clarke *et al.* 1997; Thomas *et al.* 1997, 1998*b*) and our (largely successful) conservation projects (Thomas 1999).

In contrast, Van Dyck *et al.* (2000) concluded that their results 'provide evidence for ant-related oviposition patterns in *Maculinea alcon* in relation to the distribution of specific host-ant nests (i.e. *Myrmica ruginodis*)' (p. 861). In order to help resolve this difference, we present previously unpublished field data collected for all five European *Maculinea* species in 1972–2000 in order to test three specific predictions derived from each hypothesis, together with data establishing that the ovipositional niches of *Maculinea* are indeed closely tied to the phenological state of their food plants, a premise that was questioned by Van Dyck *et al.* (2000).

2. PREDICTIONS TESTED

(a) *Prediction 1: the distribution of* Maculinea *eggs on different dates during the egg-laying period*

(i) H_0. Throughout the season, oviposition occurs on any suitable food plant regardless of its proximity to host ants. This does not preclude the possibility that most eggs may be laid on plants close to a host-ant colony since *Maculinea* populations are only likely to persist on sites where phenologically suitable food plants and host ants coexist.

(ii) H_1. Initially, most eggs should be laid on plants growing near host-ant nests, with other food plants being favoured later in the season as the egg load increases on the plants near host ants.

(b) *Prediction 2: the distribution of eggs on sites supporting different densities of* Maculinea *and food plant*

(i) H_0. The proportion of the egg population laid per food plant close to host nests is independent of the number of *Maculinea* present.

(ii) H_1. By the end of the season, higher egg densities will be found on food plants growing near host ants than on plants near non-host ants on any site containing low densities of *Maculinea* per plant. This distinction will diminish at higher *Maculinea* densities.

(c) *Prediction 3: within-site variation in the clumping of eggs on food plants growing near host ant nests*

(i) H_0. By the end of the season eggs will have similarly clumped distributions on flowering spikes and flower buds, regardless of both *Maculinea* density and the species of ant foraging beneath those plants. This is because food plants vary in attractiveness to ovipositing butterflies according to the plant's phenological state, which varies broadly in the same way over the entire patch used by the butterflies.

(ii) H_1. On sites with low densities of *Maculinea*, a large proportion of eggs will be laid on plants near host ants. On sites with higher *Maculinea* densities, eggs will be more evenly distributed on the food plants near host ants as females 'fill up' any under-exploited plants before switching to lay on food plants near non-host-ant colonies.

3. METHODS

(a) *Phenology of plants chosen for egg laying by each species of* Maculinea

The phenology of the flower heads selected for oviposition was recorded for each species of *Maculinea* throughout their egg-laying periods, being scored as 1–6 (see legend to figure 1). Great care was taken to ensure that we scored genuine egg laying: most *Maculinea* conceal their eggs (Thomas *et al.* 1991) and may appear to be ovipositing when they are merely probing before rejecting unsuitable flower heads.

(b) *Niche segregation in* M. nausithous *and* M. teleius

In 1981–1988 we measured three parameters within four French and Polish sites, each supporting both *M. nausithous* and *M. teleius*, in order to determine whether the *Sanguisorba officinalis* flower heads selected for oviposition influenced the caterpillars' chances of adoption by their respective hosts *Myrmica rubra* and *Myrmica scabrinodis*. The three parameters were variation in the density of *S. officinalis* plants, the frequency of the flower-head types ($n = 427$) preferred by each butterfly in four classes of vegetation height, and the distribution of *Myrmica* species on 143 baits placed at optimum foraging times and conditions for *Myrmica* beneath *S. officinalis* in the same four classes of vegetation (Elmes *et al.* 1991); the proximity of ant nests to food plants was also recorded on one site.

(c) *The distribution of eggs on different dates during the egg-laying period of* M. arion

We recorded sequential oviposition only once. New eggs laid by *M. arion* on 48 marked plants were counted on 13 occasions between 28 June and 30 July 1973, encompassing the whole egg-laying period of a high-density population. The ants foraging

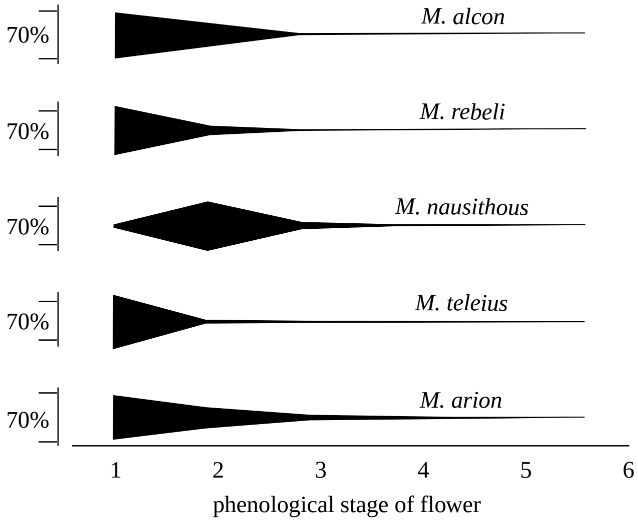

Figure 1. The developmental stages of flower buds selected for oviposition by the five European *Maculinea* species. 1, tight young buds with sepals apparent; 2, swollen buds with $<10\%$ flowers open; 3, 50–90% buds, 11–50% flowers open; 4, $<50\%$ buds, 50–100% flowers open; 5, 1–50% seed heads or pods; 6, $>50\%$ seed heads or pods. Percentage distributions are given for *M. arion* ($n = 136$), *M. teleius* ($n = 58$), *M. nausithous* ($n = 123$), *M. rebeli* ($n = 27$) and *M. alcon* ($n = 31$).

beneath each plant were identified. These data were used to test prediction 1.

(d) *Distribution of eggs within and between sites with high or low* M. rebeli *populations*

The numbers of eggs laid on all or a sample of 50 food plants (*Gentiana cruciata*) of *M. rebeli* were counted on eight sites supporting a wide range of butterfly and food-plant densities in 1984–1995 (Elmes *et al.* 1996). On a further site eggs on the same 50 gentians were assessed for five consecutive years (Thomas *et al.* 1997). The density of the 18 361 eggs recorded on each of 1753 flowering spikes (supporting 33 556 flower buds) of the 602 plants sampled could be expressed as density per spike or per flower bud per spike. The species of ant(s) foraging beneath each plant was identified. At egg densities less than 0.75 eggs per bud per spike, larval mortality on the plant is density independent and at densities greater than 0.75 eggs per bud per spike larval mortality becomes highly density dependent (Hochberg *et al.* 1994; J. A. Thomas and G. W. Elmes, unpublished data). These data were used to test predictions 2 and 3.

4. RESULTS

(a) *Do* Maculinea *oviposit in a narrow phenological niche during flower production?*

The data confirmed general accounts that the ovipositional niche of each *Maculinea* species is extremely narrow (figure 1). The youngest available stage of flower-bud production was selected in four species. *Maculinea nausithous* alone selects slightly older (figure 1) and also larger (Thomas 1984*b*; Figurny & Woyciechowski 1998) flower buds of *S. officinalis*, largely segregating its eggs from those of *M. teleius* which sometimes oviposits on the same plant.

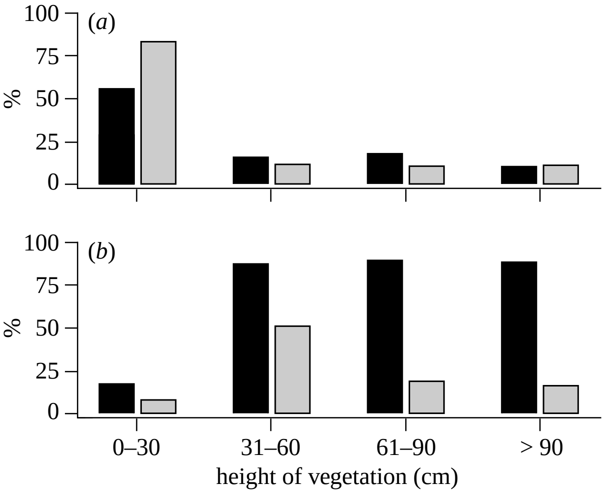

Figure 2. (*a*) The percentage of all stage-1 flower buds (the preferred type of *M. teleius*) (figure 1) in the *S. officinalis* populations (grey bars) classified according to the height of the vegetation (longer vegetation creates cooler soil temperatures) and the proportion of baits beneath *S. officinalis* plants (black bars) in the four vegetation categories which attracted its host ant *M. scabrinodis*. (*b*) The comparative distributions of the stage-2 buds preferred by *M. nausithous* (grey) and its host ant *M. rubra* (black).

(b) *Coincidence of food-plant niche and host ant in* M. nausithous *and* M. teleius

The separate egg-laying niches of *M. teleius* and *M. nausithous* (figure 1) had the additional effect of placing larvae of each species predominantly within the foraging ranges of their respective hosts. Both *M. teleius*' preferred flower buds and *M. scabrinodis* were most abundant in shorter (0–30 cm tall) vegetation (figure 2*a*), whereas *M. nausithous*' preferred flower buds and *M. rubra* predominated in taller patches (figure 2*b*). Thus, a *M. nausithous* female laying randomly on her preferred form of flower bud on these sites would place 82% of eggs near *M. rubra*; we observed 80% of eggs near *M. rubra* on the two sites sampled in detail ($n = 517$ eggs). *Maculinea teleius* eggs were inadequately sampled for a similar validation.

(c) *Prediction 1: the pattern of oviposition during the flight period of* M. arion

The *M. arion* site sampled in 1973 had exceptionally high egg numbers which caused a population crash in the next generation due to density-dependent mortalities (Thomas *et al.* 1998*b*); thus the behavioural switch of H_1 would apply. However, the proportions of sequential tranches (spanning the entire oviposition period) of 100 *M. arion* eggs laid on marked plants in *Myrmica sabuleti* host or non-host ant territories (figure 3) showed no trend nor any significant deviation ($p = 0.76$) from the overall 48:52 distribution predicted by H_0 from the proportion of host:non-host ants living on the site. The only trend was to lay increasingly within the territory of *M. ruginodis* as the season progressed. This can be explained by the fact that *M. ruginodis* is confined to scrubland on this site where *Thymus* is partially shaded and flowers later in the season. Every plant with a suitable phenology for oviposition ($n = 100$) at the onset of egg laying was growing in a *M. sabuleti* or *M. scabrinodis* territory on the same site in

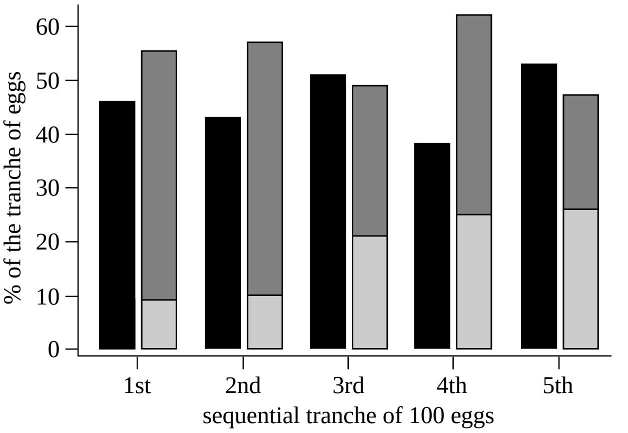

Figure 3. Time-series showing the proportion of 537 eggs laid by *M. arion* in 1973 on marked *Thymus praecox* growing in areas foraged by their host ants (*M. sabuleti*) (solid bars) and other *Myrmica* species (*M. scabrinodis* (dark grey bars) and *M. ruginodis* (light grey bars)). The first tranche of *ca.* 100 eggs was laid between days 1 and 8 of the egg-laying season and the next four tranches were laid on days 9–11, 12, 13 and 14–33, respectively. An estimated 48% of all *Myrmica* on the site were *M. sabuleti.*

2000. Thirty days later near the end of the flight period, significantly more (17 out of 75 plants) bearing suitable flower heads were in *M. ruginodis* territory ($\chi_1^2 = 23.5$ and $p = 0.0001$).

Other observations of *M. arion* support H_0.

(i) In the year preceding *M. arion*'s extinction in the Tidna Valley, Cornwall, 20% of the *ca.* 85 000 thyme plants grew near *M. sabuleti*, yet only three of the eight eggs seen laid by an estimated population of 13 females were laid near host ant colonies. Under H_1, the entire population should have selected these plants.

(ii) A recent attempt to re-establish *M. arion* in a Gloucestershire site failed after the introduced population emerged approximately two weeks later than the main flower-bud period of *Thymus*, thereby restricting the egg population to cool subareas where the host ant existed at its lowest densities (Thomas 1999).

(d) *Prediction 2: the distribution of the egg population on sites supporting different densities of* **M. rebeli**

On the average site ($n = 13$) only 28% of eggs were laid on flowering spikes near *M. rebeli*'s host ant *Myrmica schencki* (i.e. on schencki spikes). Intuitively, one would expect a higher proportion if egg laying were controlled by H_1. As predicted by H_0, there was no evidence for a correlation between the proportion of each egg population laid near *M. schencki* and the abundance of the butterfly in relation to the food-plant population, which was expressed as mean eggs per spike (Pearson's correlation coefficient, $r = 0.32$, d.f. $= 9$ and $p > 0.2$) (an almost identical result was obtained using mean eggs per flower bud per spike because these plant parameters are highly correlated) ($r = 0.99$, d.f. $= 11$ and $p < 0.0001$). Under H_1, there should be a negative correlation: at the very least, butterflies ovipositing on the nine sites with mean densities less than 0.75 eggs per flower bud should place a greater proportion of eggs near host ants compared to the four sites with densities greater than 0.75 eggs per flower. Yet there was no difference, the values being 0.271 ± 0.115 and 0.275 ± 0.100, respectively.

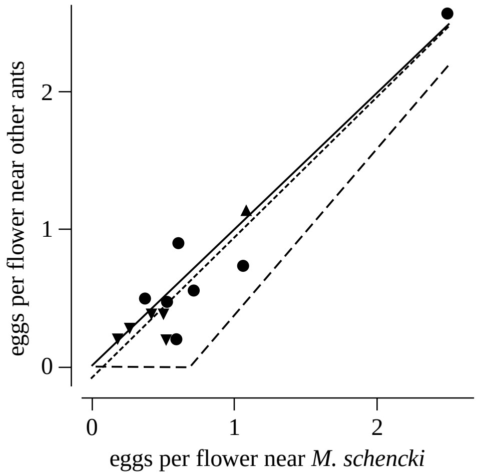

Figure 4. The density of *M. rebeli* eggs per flower bud on *G. cruciata* plants coexisting with non-host ant species plotted against the density on gentians near the host ant *M. schencki* (nine sites on 13 sampling occasions). Strong density-dependent mortality occurs at greater than 0.75 eggs per flower bud. Solid circles, French Alps (seven sites); triangles, Spanish Pyrenees (two sites). The same 50 gentians were sampled for five years at one of the Spanish sites (inverted triangles). The slope of the least-squares regression (dotted line) does not differ significantly from the 1:1 (solid) line expected from H_0 and the intercept is not significantly different from zero. The most probable relationship expected from H_1 is indicated as a dashed line: a regression derived from H_1 should have a significant negative intercept.

Our data also confirmed the H_0 prediction that the average density of eggs per flower bud on schencki spikes plotted against the average densities on other spikes should not differ from 1:1 (figure 4). This remained true even if the site with very high egg densities was discarded or if the data were log transformed. H_1 predicts that all eggs are laid on schencki spikes at low densities with an increasing proportion laid on other spikes as egg densities (competition for flower buds) increase. Although a precise relationship predicted by H_1 could not be deduced, it should be similar to the dashed line in figure 4, with a significant negative intercept estimated by linear regression. In fact, the intercept was not significantly different from zero.

(e) *Prediction 3: the pattern of clumping of* **M. rebeli** *eggs within sites on individual food plants growing near host-ant nests*

We next tested for within-site differences between the cumulative frequency (or shape) of the distributions of egg density per flower on schencki spikes and other spikes (Kolmogorov–Smirnov test, one-sided 5%). A statistically significant difference in shape between the two categories of spikes was recorded at only three sites (more eggs per flower on schencki spikes). The similarity in egg distributions on the two types of spike is illustrated (figure 5) for two Spanish sites, one having the lowest recorded average density of eggs per flower per spike

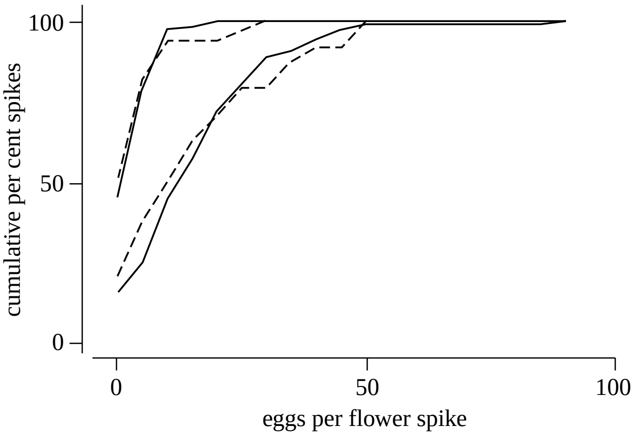

Figure 5. The cumulative frequency distribution of *M. rebeli* eggs on flowering spikes of *G. cruciata* at two Spanish sites supporting different densities of eggs per flower bud, one having the lowest recorded density of eggs (upper lines) and the other one of the highest densities of more than one egg per bud per spike (lower lines). Spikes foraged under by *M. schencki* (solid lines) were treated separately from those foraged by other ants (dashed lines). At neither site was a significant difference in the distribution of eggs on these two types of gentian.

(0.21) and the other a high density (1.13). As predicted by H_0, there was no difference between schencki spikes and other spikes. H_1 predicts that the shapes of the distributions should be very different at low egg densities with a much higher proportion of other spikes compared to schencki spikes having no eggs and with the distributions converging as egg densities increase. H_0 predicts that this ratio should be close to unity. Thus, H_1 predicts a negative correlation between the ratio of eggless other spikes:schencki spikes and the overall density of eggs per spike. No significant correlation existed in our data ($r = -0.19$, d.f. $= 11$ and $p > 0.5$): the average ratio over the 13 sites was 1.00, as predicted by H_0.

Finally, on the 12 sites where this was possible, we used nested analysis of variance in order to compare variation in the number of eggs on different flowering spikes of the same gentian with that between spikes on different gentians, taking account of the ant species foraging under the gentians. On average 31% (median) of the total variance could be attributed to variation between tillers on the same plant and 60% (median) was due to variations between plants, whereas the species of ant present had no effect whatsoever (median 0%). Given the large observed variation in the phenologies of the spikes on both the same and different plants (J. A. Thomas and G. W. Elmes, unpublished data), this is in accord with H_0 which predicts that butterflies should regard each spike as a separate food plant. H_1 predicts that ant species should explain a significant proportion of the overall variance.

5. DISCUSSION

The tests of all three predictions supported the null hypothesis (H_0) that spatial and temporal patterns in *Maculinea* oviposition can best be explained by variation in the phenology (or size) of the food plant and are random with respect to ants. In contrast, each result gave the opposite pattern to that predicted by H_1 which assumes that female *Maculinea* detect host ant pheromones before oviposition and also avoid plants with high egg loads.

The demonstration that females select a brief, phenologically determined stage of flower-bud development for oviposition (figure 1) coupled with the known microclimatic preferences of different *Myrmica* species (Elmes *et al.* 1998; Thomas *et al.* 1998*c*) provides a plausible mechanism for H_0 (see § 1). On typical sites, an individual flower head of the food plants of *M. arion*, *M. nausithous*, *M. teleius* and *M. rebeli* remains suitable for egg laying for two to five days and most individual plants contain a few suitable buds for five to 15 days. In contrast, the oviposition periods of typical *Maculinea* populations last 30–40 days. As we found with *M. arion* (figure 3), oviposition inevitably switches from early-flowering to late-flowering plants over the season, placing eggs laid on different dates in different microclimates inhabited by different species of *Myrmica*. By the same token, choosing different phenological stages and sizes of *S. officinalis* flower heads on the same dates not only segregates most larvae of *M. nausithous* and *M. teleius* on their food plants but also places the majority of each within the foraging territory of its host species of *Myrmica* (figure 2). We see no evidence to invoke ant odours in explaining the observed partial segregation of the two butterflies.

We also found Van Dyck *et al.*'s (2000) mechanism for explaining ant-induced oviposition (H_1) unconvincing for other reasons suggested in that paper.

(i) The short-lived trail odours of *Myrmica* are unlikely to exist near food plants during the warm sunny periods when most *Maculinea* eggs are laid, as *Myrmica* foragers stay underground during these conditions leaving ants of other genera with other odours to forage around food plants (Elmes *et al.* 1991). Moreover, *Myrmica* workers seldom ascend to the flower buds whereas other ant genera frequently do.

(ii) After watching all *Maculinea* species oviposit on many occasions, neither we nor others (Fiedler 1998; Figurny & Woyciechowski 1998) saw any obvious behaviour suggesting that females detect *Myrmica* nests first before dispersing to the nearest food plant. If they did, a touch pheromone would probably be involved because interspecific variation in *Myrmica* odours depends on subtle mixes of similar cocktails of mainly non-volatile hydrocarbons (Akino *et al.* 1999). In the few cases of lycaenid species for which ant-mediated oviposition has been demonstrated, the female butterflies exhibit very characteristic search behaviour in the pre- and post-alighting phases (Fiedler & Maschwitz 1989; Seufert & Fielder 1996; Fiedler 1998). Moreover, the specific ichneumonid parasitoid of *M. rebeli*, which can distinguish between host and non-host *Myrmica* odours, spends tens of seconds vibrating its long antennae inside a nest entrance before selecting *M. schencki* (Thomas & Elmes 1993). Female *Maculinea* exhibit none of these behaviours.

These results and reasons lead us to believe that H_0 is more likely to explain *Maculinea* oviposition patterns than H_1. Unfortunately, we have made few studies of oviposition in *M. alcon*, the species studied on two sites by Van Dyck *et al.* (2000). However, we consider it unlikely that *M. alcon* has evolved a radically different behaviour to

M. rebeli because, in other respects, the two species are so similar that many consider them to be subspecies. Moreover, if ant-induced oviposition or the avoidance of high egg loads did occur, we might expect to find both behaviours amplified in *M. arion* and *M. teleius* due to a theoretical shift in the trade-off for these species towards avoiding crowded plants near hosts in favour of other plants. These 'predacious' *Maculinea* species incur higher density-dependent mortalities when overcrowded in host ant nests due to their inefficient feeding behaviour and to scramble competition, but their survival in non-host nests is five times greater than that of the 'cuckoo' *Maculinea* species *M. alcon* and *M. rebeli* (Thomas & Elmes 1998; Thomas *et al.* 1998*b*). Our result for *M. arion* (figure 2) offers no support for such a trade-off.

The conundrum of why cuckoo species of *Maculinea* frequently lay 50–90% of their egg population in non-host *Myrmica* territories remains (Elmes *et al.* 1996). We suggest that a different trade-off exists, stemming from the fact that *Myrmica* workers seldom defend their foraging territories and, thus, the ranges of individual colonies overlap considerably. Our field observations showed that eggs placed on gentians near non-host ant colonies instead had a small but finite chance of being encountered by lone host workers from nests greater than 3 m (more than one ant colony away) from the gentian. Host nests greater than 3 m from a gentian are twice as large and twice as likely to survive 12 months compared to colonies near food plants because they avoid persistent infestation by *Maculinea* (Thomas *et al.* 1997). Thus, the small numbers of *M. rebeli* larvae adopted by such nests have a very high chance of surviving to maturity. There is no likely mechanism by which female *Maculinea* could assess the probability of their offspring being found by such a distant host nest. However, by laying eggs at random on any suitable gentian a trade-off is achieved between (i) the high probability of adoption into the weak, frequently infested host nests close to gentians where density-dependent mortalities are high, and (ii) the low probability of adoption by a host ant from gentians near other ants, but the high chance of survival among successful individuals.

Finally, for conservation we conclude that the assumptions of H_0 should be retained in models designed for selecting appropriate management for this endangered butterfly genus, at least pending firmer evidence for Van Dyck *et al.*'s (2000) attractive alternative. Under H_1, populations should persist on sites with lower host ant densities than the minimum recommended by H_0 (greater than 10% plant–ant coexistence for a cuckoo *Maculinea* species and greater than 50% for a predacious species) (Thomas *et al.* 1998*b*) due to the females' presumed ability to target ants. Empirical results have suggested that recommendations based on H_0 are valid and that lower host ant densities risk local extinction (Thomas 1994; Thomas & Elmes 1998).

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REFERENCES

Akino, T., Knapp, J. J., Thomas, J. A. & Elmes, G. W. 1999 Chemical mimicry and host specificity in the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *Proc. R. Soc. Lond.* B **266**, 1419–1426.

Clarke, R. T., Thomas, J. A., Elmes, G. W. & Hochberg, M. E. 1997 The effects of spatial patterns in habitat quality on community dynamics within a site. *Proc. R. Soc. Lond.* B **264**, 347–354.

Elmes, G. W., Thomas, J. A. & Wardlaw, J. C. 1991 Larvae of *Maculinea rebeli*, a large-blue butterfly and their *Myrmica* host ants: wild adoption and behaviour in ant nests. *J. Zool.* **223**, 447–460.

Elmes, G. W., Thomas, J. A., Hammarstedt, O., Munguira, M. C., Martin, J. & Van der Made, J. G. 1994 Differences in host-ant specificity between Spanish, Dutch and Swedish populations of the endangered butterfly *Maculinea alcon* (Schiff.) (Lepidoptera). *Zool. Mem.* **48**, 55–68.

Elmes, G. W., Clarke, R. T., Thomas, J. A. & Hochberg, M. E. 1996 Empirical tests of specific predictions made from a spatial model of the population dynamics of *Maculinea rebeli*, a parasitic butterfly of red ant colonies. *Acta Oecol.* **17**, 61–80.

Elmes, G. W., Thomas, J. A., Wardlaw, J. C., Hochberg, M. E., Clarke, R. T. & Simcox, D. J. 1998 The ecology of *Myrmica* ants in relation to the conservation of *Maculinea* butterflies. *J. Insect Conserv.* **2**, 67–78.

Fiedler, K. 1998 Lycaenid–ant interactions of the *Maculinea* type: tracing their historical roots in a comparative framework. *J. Insect Conserv.* **2**, 3–14.

Fiedler, K. & Maschwitz, U. 1989 The symbiosis between the weaver ant, *Oecophylla smaragdina*, and *Anthene emolus*, an obligate myrmecophilous lycaenid butterfly. *J. Nat. Hist.* **23**, 833–846.

Figurny, E. & Woyciechowski, M. 1998 Flowerhead selection for oviposition of the sympatric butterfly species *Maculinea teleius* and *M. nausithous* (Lepidoptera: Lycaenidae). *Entomol. Gener.* **23**, 215–222.

Hochberg, M. E., Clarke, R. T., Elmes, G. W. & Thomas, J. A. 1994 Population dynamic consequences of direct and indirect interactions involving a large blue butterfly and its plant and red ant hosts. *J. Anim. Ecol.* **63**, 375–391.

Hochberg, M. E., Elmes, G. W., Thomas, J. A. & Clarke, R. T. 1996 Mechanisms of local persistence in coupled host–parasitoid associations: the case model of *Maculinea rebeli* and *Ichneumon eumerus*. *Phil. Trans. R. Soc. Lond.* B **351**, 1713–1724.

IUCN 1990 *IUCN red list of threatened animals*. Gland, Switzerland: IUCN.

Pierce, N. E. & Elgar, M. A. 1985 The influence of ants on host plant selection by *Jalmenus evagoras*, a myrmecophilous lycaenid butterfly. *Behav. Ecol. Sociobiol.* **21**, 237–248.

Schönrogge, K., Wardlaw, J. C., Thomas, J. A. & Elmes, G. W. 2000 Polymorphic growth rates in myrmecophilous insects. *Proc. R. Soc. Lond.* B **267**, 771–777.

Seufert, P. & Fiedler, K. 1996 The influence of ants on patterns of colonization and establishment within a set of coexisting lycaenid butterflies in a South-East Asian tropical rain forest. *Oecologia* **106**, 127–136.

Thomas, J. A. 1984*a* The conservation of butterflies in temperate countries: past efforts and lessons for the future. In *Biology of butterflies* (ed. R. Vane-Wright & P. Ackery), pp. 333–353. London: Academic Press.

Thomas, J. A. 1984*b* The behaviour and habitat requirements of *Maculinea nausithous* (the dusky large blue butterfly) and *M. teleius* (the scarce large blue) in France. *Biol. Conserv.* **28**, 325–347.

Thomas, J. A. 1991 Rare species conservation: case studies of European butterflies. In *The scientific management of temperate communities for conservation* (ed. I. Spellerberg, B. Goldsmith & M. G. Morris), pp. 149–197. Oxford, UK: Blackwell.

Thomas, J. A. 1994 The ecology and conservation of *Maculinea arion* and other European species of large blue. In *Ecology and* *conservation of butterflies* (ed. A. Pullin), pp. 180–196. London: Chapman & Hall.

Thomas, J. A. 1999 The large blue butterfly—a decade of progress. *Br. Wildl.* **11**, 22–27.

Thomas, J. A. & Elmes, G. W. 1993 Specialised searching and the hostile use of allomones by a parasitoid whose host, the butterfly *Maculinea rebeli*, inhabits ant nests. *Anim. Behav.* **45**, 593–602.

Thomas, J. A. & Elmes, G. W. 1998 Higher productivity at the cost of increased host-specificity when *Maculinea* butterfly larvae exploit ant colonies through trophallaxis rather than by predation. *Ecol. Entomol.* **23**, 457–464.

Thomas, J. A., Elmes, G. W., Wardlaw, J. C. & Woyciechowski, M. 1989 Host specificity among *Maculinea* butterflies in *Myrmica* ant nests. *Oecologia* **79**, 452–457.

Thomas, J. A., Munguira, M. L., Martin, J. & Elmes, G. W. 1991 Basal hatching by *Maculinea* butterfly eggs: a consequence of advanced myrmecophily? *Biol. J. Linn. Soc.* **44**, 175–184.

Thomas, J. A., Elmes, G. W., Clarke, R. T., Kim, K. G., Munguira, M. L. & Hochberg, M. E. 1997 Field evidence and model predictions of butterfly-mediated apparent competition between gentian plants and red ants. *Acta Oecol.* **18**, 671–684.

Thomas, J. A., Elmes, G. W. & Wardlaw, J. C. 1998*a* Polymorphic growth in larvae of the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *Proc. R. Soc. Lond.* B **265**, 1895–1901.

Thomas, J. A., Clarke, R. T., Elmes, J. A. & Hochberg, M. E. 1998*b* Population dynamics in the genus *Maculinea* (Lepidoptera: Lycaenidae). In *Insect populations* (ed. J. P. Dempster & I. F. G. McLean), pp. 261–290. London: Chapman & Hall.

Thomas, J. A., Simcox, D. J., Wardlaw, J. C., Elmes, G. W., Hochberg, M. E. & Clarke, R. T. 1998*c* Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its *Myrmica* ant hosts. *J. Insect Conserv.* **2**, 39–46.

Van Dyck, H., Oostermeijer, J. G. B., Talloen, W., Feenstra, V., Van der Hidde, A. & Wynhoff, I. 2000 Does the presence of ant nests matter for oviposition to a specialized myrmecophilous *Maculinea* butterfly? *Proc. R. Soc. Lond.* B **267**, 861–866.

Wynhoff, I. & Van der Made, J. 1995 Reintroduction of *Maculinea teleius* and *Maculinea nausithous* in The Netherlands in 1990. *Proc. Exp. Appl. Entomol.* **6**, 79–80.

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