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Interactions among species in a tri-trophic system: the influence of ants on the distribution of the Sinai Baton Blue butterfly

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ABSTRACT

Metapopulation dynamics is now so widely used to describe the distribution and abundance of species living in fragmented landscapes that other ecological factors (e.g. habitat quality) can be overlooked. To determine the precise habitat requirements of an endangered and narrowly endemic lycaenid butterfly, I studied its distribution within a patch of habitat, examining the effects of hostplant choice on larval survival. Ovipositing females were selective in the hostplants chosen: they selected a brief stage of flower-bud development, and preferred plants with many inflorescences. The distribution of surviving larvae was positively correlated to the presence of an attendant ant, suggesting that this ant caused their distribution. However, closer examination of the interactions occurring among species within the tri-trophic system revealed that another species of ant exerted a much stronger influence on larval survival and therefore the distribution of newly eclosed adults.

INTRODUCTION

Understanding why a species is absent from an area of apparently suitable habitat is a priority in ecology and conservation (Lawton & Woodroffe 1991; Hanski 1999). Over the past decade great advances have been made with the development of metapopulation theory (Hanski & Gilpin 1997), now the major hypothesis to explain extinction rates in fragmented landscapes (Hanski 1998, 1999) applied to a wide variety of taxa (e.g. Driscoll 1998; Esler 2000; Elmhagen & Angerbjörn 2001) and to many conservation strategies (Hanski & Thomas 1994; Gonzalez *et al*. 1998; Lopez & Pfister 2001; Harding & McNamara 2002). However, other ecological factors underpinning population persistence and patch occupancy can be overlooked due to the pervasiveness of the metapopulation paradigm (Harrison & Bruna 1999).

Habitat quality is just such a factor (Clarke *et al.* 1997; Caley *et al.* 2001). Thomas *et al.* (2001) recommended that conservation priorities be reorganised after empirically demonstrating the key importance of habitat quality (and site isolation) to population persistence. Thus, if conservation organisations are to be successful in halting decline of endangered species they need to be aware of the species' precise habitat requirements, as well as the spatial organisation of that habitat.

For reasons of practicality, most studies of habitat quality have involved only single species or pairs of species, despite evidence that suggests community dynamics and species persistence/abundance are affected by more than two interacting species (Begon *et al.* 1996; Holt & Polis 1997). This study focuses on a species in the less complex desert ecosystem, making it relatively easy to characterise four interacting species from three trophic levels. Within-site variation in vegetation structure (hostplant quality) and a previously overlooked factor (predation) determined distribution.

Predation has been suggested as a proximate factor threatening the survival of many endangered species (Schneider 2001) and has a major influence on animal behaviour, modifying foraging and reproductive strategies (Lima 1998; Dicke & Grostal 2001). Yet because actual predation is rarely observed in the field, its role is often underestimated and therefore ignored. This can lead to the implementation of benign (or even destructive) conservation policies: Caughley (1994) cites two contrasting examples to demonstrate the

importance of methodology in revealing why an endangered population is declining and/or absent from an area of apparently suitable habitat.

In non-myrmecophilous butterflies, ant predation can be a major source of mortality for larvae on ant visited plants (Freitas & Oliveira 1996). In myrmecophilous species (notably the family Lycaenidae) butterflies have been shown to benefit from living in proximity to ants. Most studies have reported that these benefits are either developmental (e.g. faster development, increased fecundity), or that the ants provide direct protection against natural enemies (e.g. parasitism, predation) (Pierce & Mead 1981; Pierce & Easteal 1986; Stadler *et al.* 2001); the positive effects of ants on larvae may also be species-specific (Fraser *et al.* 2001). Studies on spatial correlations between ants and lycaenids generally refer to obligate specific systems (e.g. Pierce & Elgar 1985; Seufert & Fiedler 1996). Spatial patterns in facultative myrmecophiles are more frequently either unpredictable with respect to ants (Peterson 1995), or are mediated by hostplant quality or diversity (Carey 1994).

This paper highlights the importance of correctly identifying, understanding, and incorporating all aspects of habitat quality into successful conservation policies and ecological theory. I studied oviposition and eclosion patterns in a monophagous ant-tended lycaenid butterfly, and discovered that these were positively correlated to an attendant ant: a pattern familiar in the literature and which suggested that the attendant ant directly determined the butterfly's distribution within the study patch. However, additional work demonstrated that other factors were important to the butterfly's survival. Thus my study also provides an example of how a priori assumptions can lead to subtle but nevertheless influential factors being ignored.

MATERIALS AND METHODS

Study species: The Sinai Baton Blue (*Pseudophilotes sinaicus* Nakamura) is endemic to the mountains of the St. Katherine Protectorate in South Sinai, Egypt (Nakamura, 1975), where its only known larval hostplant, the near-endemic Sinai Thyme (*Thymus decussatus* Benth.) is patchily distributed (James 2006a,c,d,e,f; James *et al.*, 2003; Hoyle & James, 2005). Eggs are laid singly and the developing larvae feed on buds and flowers; pupation and overwintering take place in the soil below a thyme plant (Nakamura, 1975; personal observation). When adults eclose the following spring, they crawl to the top of the thyme plant and remain there (often for several hours) until their wings have expanded and dried. Males usually find and mate with newly eclosed females before they have taken their first flight (James 2006f). There is a single generation with adults from mid-April to early-July (James 2006c). It is a tiny (forewing length 9.5 mm ± 0.04 [S.E.], n = 430), sedentary species (James 2006e).

Young larvae remain on the inflorescence on which they hatched; late instars are more mobile but have never been seen moving away from their natal thyme plant (personal observation). Habitat between thyme plants is extremely hostile, and is composed of bare, coarse sand that can reach very high temperatures during the day. Therefore, it is reasonable to assume that larvae are restricted to the plant on which they hatched.

Study site and distribution of butterflies: The study was carried out in 2002 in Farsh Shoeib – a patch of Sinai Thyme (13,600 m²) bordered on all sides by steep, bare cliffs, close to Gebel Safsafa on the Mt. Sinai massif. The study patch and thyme plants were accurately mapped relative to a GPS point (Garmin GPS 12 MAP, ± 5 m) using a tape measure and compass. Every day from dawn to sunset between 1st April and 13th July, two field workers continuously walked at a slow pace a pre-determined route that passed every thyme plant, examining each plant regularly (approximately every hour) throughout the day for new adults. Newly eclosed butterflies were always near the top of the plant, in pristine condition with particularly bright orange markings, and unable to fly. Adults never roost on thyme.

New adults were mapped, given an individual mark on the underwing using permanent marker pens, and returned to the same plant.

Some individuals took flight before capture and so from which plant they eclosed is uncertain; because of this they are excluded from analyses. My estimates from mark-release-recapture work indicate that these butterflies were caught at or close to their minimum possible age, and so would not have had time to move far from their point of emergence (James 2006c). Thus, these individuals will not significantly alter results because they represent only one-third of butterflies captured, and they were all captured in the same areas as butterflies emerging from known plants.

Between 10th June and 24th June (after the main adult flight period, but before inflorescences had become too dry), the number and position of eggs laid on each thyme plant was recorded. On small plants (<40 inflorescences) this was done by thoroughly searching each inflorescence for eggs, but on large plants it was estimated by counting the number of eggs on 40 randomly selected inflorescences and extrapolating. The presence of any Sinai Baton Blue caterpillars and/or occurrence of their characteristic feeding damage (James 2006f) was also noted. Twenty eggs laid on 30th May were marked, and of these 19 were still in place on the last day of the egg count: indicating that eggs remain in place for at least 3-4 weeks, thus eggs recorded during the egg count accurately reflect any oviposition onto the plant.

The lifecycle of the Sinai Baton Blue takes approximately one year to complete: adults eclosing in 2002 existed as eggs/larvae in 2001. Therefore, the pattern of egg laying in 2001 was assumed to be the same as that recorded in 2002 (weather conditions and population size were similar in 2001 and 2002: James *et al.* 2003, James 2006c; unpublished results). The presence or number of adults that eclosed from each thyme plant in 2002 when matched with egg distribution in 2002 (and considering the immobility of the larvae), was used to estimate larval survival on each plant. Only five out of 248 butterflies eclosed from three plants that did not have eggs laid on them in 2002; these were excluded from the analysis.

Hostplant quality: Thyme plants vary greatly in condition, so four different measurements were taken to describe 'hostplant quality'. These were plant height, condition (% green), green surface area (assuming hemi-spherical shape), and number of inflorescences. The phenology of each plant was measured weekly: five inflorescences were randomly selected from the most advanced area of the plant and their phenology scored on a 0-7 scale (0 = 100% pre-bud; 7 = >50% seed heads/flowers over). The average of these five scores represented the phenological state of the plant.

The phenology of inflorescences selected for oviposition was recorded during the egg-laying period. Gravid females were followed: an 'oviposition event' occurred when the female curled her abdomen and started to probe an inflorescence; such behaviour did not always result in the laying of an egg. After the female left the inflorescence, its phenology was scored (0-7) and the presence of an egg recorded.

The role of ants: In the last week of March, ant baits (sugar lump and piece of hard cheese) were left close to every plant for one hour immediately after dawn, one hour at midday and one hour before sunset. Samples of ants found on the baits were taken for identification. A plant was deemed to be within foraging range if an ant species was seen within 1 m of it. Eleven species of ant were identified from the baits, but only four (Table 1) were regularly seen foraging on thyme; only these species were included in the analysis.

To assess the effect of different ant species on larval survival, 28 larvae found in the study patch were transferred from their natal plant to different plants in the study patch (the sample size was small because of restrictions imposed when working on an endangered

species in a protected area). Larvae chosen were all of medium size (third and fourth instar) so they could easily be observed and would not pupate during the experiment. Half of the larvae were placed on plants within foraging range of the same species of ant as their natal plant (to control for the effects of handling); the other half were placed on plants within foraging range of a different ant species. To eliminate the effect that variation in hostplant quality might have on larval survival, the plants chosen were of similar size and had been used by ovipositing females in 2002 (suggesting they were of suitable quality). Each larva was monitored continuously for three hours immediately after transfer; after 24 hours the plant was searched thoroughly for the larva. If the larva was not found it was assumed not to have survived. At the time of this experiment one ant species was inactive so transfer of larvae had to be restricted to plants within foraging range of the remaining three species.

Replication: In 2003 the study was repeated in Farsh Shoeib, and also using a different patch of thyme (Farsh Il Loz). The 2003 study coincided with a severe drought in the area, and the population of butterflies was much smaller than in 2002 (James 2006c). This meant the pattern of egg laying could not be examined: the small number of females (and thus eggs) made searching for eggs too time-consuming and estimating the number of eggs per plant inaccurate. Similarly, manipulation experiments involving larvae could not be performed.

RESULTS

Distribution: One thousand twelve hundred and twelve thyme plants were distributed throughout the study patch in 2002 (Fig. 1). The distribution of newly eclosed adults was highly non-random: adults eclosed from only 102 plants (8%) in 2002, and these were concentrated in the narrow gullies to the north (52 plants) and northeast (27 plants) of the patch (Fig. 1a).

Plants selected for oviposition in 2002 were also non-random: 287 (24%) contained eggs, distributed throughout the patch (Fig. 1a). There is a correlation between the set of plants chosen for oviposition in 2002 and plants with newly eclosed adults in 2002 (i.e. plants which are assumed to have had eggs in 2001) ($r = 0.45$, $p < 0.001$, $n = 315$ plants), indicating that ovipositing females are selective in the plants they choose, and this choice is similar from one year to the next.

Butterflies were only recorded emerging from 26% ($n = 74$) of plants containing eggs in 2002. If egg distribution was similar in 2001, this implies that the pattern of emergence success from plants is determined by larval survival, rather than just egg distribution. To understand these patterns it is necessary to establish why ovipositing females accept some plants and reject others, and also the factors affecting larval survival.

Hostplant quality: The ovipositional niche of the Sinai Baton Blue is extremely narrow. One hundred and seventy-three (76%) eggs observed being laid in 2002 were on inflorescences just starting to bud. In addition to the phenology of the inflorescence as a whole, the position of the egg within the inflorescence followed the same pattern: 198 (87%) eggs were positioned on an early bud. Three hundred and ninety-five plants (33%) were excluded from analysis as they produced only vegetative growth in 2002 (no buds or flowers) and so were unavailable to ovipositing females.

When all the variables describing hostplant quality (plant height, condition, green surface area and number of inflorescences) were entered into a logistic regression to explain occurrence of eggs in 2002, only the number of inflorescences entered the model, accounting for 32% of the variation ($b = 0.02 \pm 0.002$, $p < 0.001$). Logic suggests that plants with more oviposition sites (inflorescences) should accumulate more eggs, but the mean number of eggs per inflorescence also increases with the number of inflorescences per plant ($r_s = 0.59$, p

<0.001, n = 817 plants). Thus females in 2002 appear to choose plants with many inflorescences when ovipositing.

Among the set of plants selected by ovipositing females in 2002, the number of inflorescences was the only hostplant quality variable which entered the logistic regression predicting whether a larva survived or not, accounting for 28% of the variation (b = 0.005 ± 0.001, p <0.001). There was a significant difference (independent samples t-test, t_{285} = 8.13, p <0.001) between the number of inflorescences on plants where a larva had survived (mean = 410 ± 64) and the number on plants where no larvae had survived (mean = 81 ± 9).

Survival rate was also measured by dividing the number of eclosing butterflies by the number of eggs laid on a plant. Where larvae survived, the expected detrimental effect of intraspecific competition (expressed as the number of eggs per plant) was significant in determining survival rate after the number of inflorescences on a plant (to control for the effect of this on egg number) was entered into the regression (b = -0.001 ± 0.001, one-tailed t-test, p <0.05).

The role of ants: Four species of ant were regularly seen foraging on thyme and therefore likely to come into contact with the caterpillars (Table 1, Fig. 1b). If within their ranges, larvae of all stages were tended by *Lepisiota* and (to a lesser extent) *Monomorium*. Seventeen different larvae were observed for a total of 87.5 hours: on average each larva was tended (by 1-6 ants) 71% of the time.

Eggs were found within the foraging range of all four species of ant (Table 1, Fig. 1). In logistic regression using presence of the different ant species and the number of inflorescences on a plant to explain occurrence of eggs, the number of inflorescences entered first (b = 0.020 ± 0.002, p <0.001), then presence of *Lepisiota* (b = 1.26 ± 0.18, p <0.001), and finally presence of *Crematogaster* (b = -1.15 ± 0.31, p <0.001). Together these variables explained 40% of the variation. The presence of these two species of ant was also correlated with hostplant quality: plants with lots of inflorescences were more likely to have *Lepisiota* (r = 0.16, p <0.001, n = 817 plants), and less likely to have *Crematogaster* (r = -0.08, p <0.05, n = 817 plants). These ants had a high degree of mutual exclusivity (χ^2_1 = 106.2, p <0.001): only 6 plants were in foraging range of both species.

Under natural conditions, butterflies only eclosed from plants within the foraging range of *Lepisiota* and/or *Monomorium*. Plants containing signs of larval presence were not randomly distributed among the sets of plants within foraging range of different ant species (χ^2_3 = 24.6, p <0.001) (Table 1). No newly eclosed butterflies were caught on plants within foraging range of *Crematogaster*, suggesting that if these plants had eggs laid on them in 2001, none of the larvae survived.

Table 1 The four species of ant most regularly seen foraging on thyme plants and the distribution of Sinai Baton Blue eggs, larvae, and newly eclosed adults, on plants within foraging range of these ants; larval survival rates are estimated as: (total number of adults / total number of eggs)*100

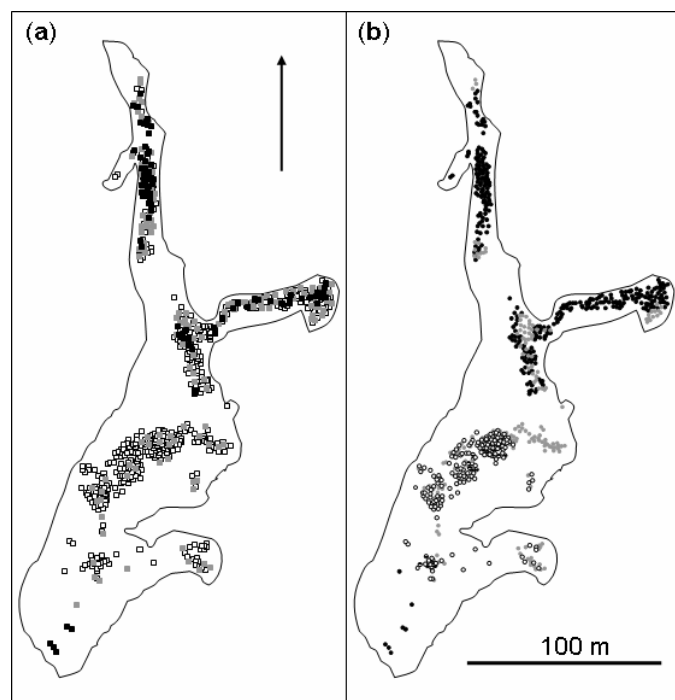| Ant species	Number of *Thymus* plants				Survival rate (%)
	Within foraging range	With eggs (total number of eggs)	With signs of larvae	With newly eclosed adults (total number of adults)	
Lepisiota obtusa (Emery)	443	214 (6282)	202	94 (239)	3.8
Monomorium niloticum (Emery)	261	68 (516)	39	8 (9)	1.7
Crematogaster (Cr.) aegyptiaca (Mayr)	186	26 (110)	5	0 (0)	0
Tapinoma simrothi (Krausse)	49	6 (34)	2	0 (0)	0

Fig. 1 Maps showing the study site in 2002 (squares and circles represent thyme plants). (a) Plants selected for oviposition (grey and black squares), and the distribution of newly eclosed adults (black squares); open squares are plants from which no adults emerged and on which no eggs were laid. (b) Species of ant predominant on each plant (black circles = *Lepisiota*; grey circles = *Monomorium*; open circles = *Crematogaster*; striped circles = *Tapinoma*); ranges are not always exclusive and up to 3 species may utilise the same plant

When larvae were transferred to different thyme plants, their survival (presence on the plant after 24 hours) was highly non-random (χ^2_2 = 15.3, p <0.001), being determined by the species of ant on their new hostplant (Table 2). Larvae survive at much higher rates on plants with *Lepisiota* and/or *Monomorium* than with *Crematogaster*. In five of the experiments in which a larva was transferred to a plant with *Crematogaster* the larva was seen being attacked and killed by this ant (see James 2006f).

Distribution in 2003: In Farsh Shoeib in 2003, only 28 newly eclosed butterflies were caught. As in 2002, all of these were on plants within foraging range of Lepisiota. In 2003, the distribution of ant species in Farsh Shoeib was the same as 2002 (see Fig. 1b).

In Farsh Il Loz, 21 newly eclosed butterflies were caught. Nineteen of these (90%) were on plants within foraging range of *Lepisiota*. The remaining two emerged from plants within foraging range of *Monomorium*. No adults eclosed from plants within foraging range of *Crematogaster* despite this group of plants containing 36% of all inflorescences in Farsh Il Loz in 2003.

Table 2   Summary of experiment in which larvae were transferred from their natal hostplant (in all cases these were within foraging range of *Lepisiota*) to different thyme plants within range of the same or a different species of ant, and their survival monitored. Survival of larvae is estimated as the proportion of larvae still found on the plant after 24 hours

Ant species within foraging range of plants on which larvae placed	Number of larvae moved	Number of larvae re-seen after 24 hours	Larval survival
Lepisiota obtusa	14	13	0.93
Monomorium niloticum	6	6	1.00
Crematogaster aegyptiaca	8	1	0.13

Competitive displacement ?

ANT #1 ←—————————————→ ANT #2

(*Lepisiota obtusa*)　　　　　　(*Crematogaster aegyptiaca*)

Appeasement　　　　　　　　　Predation

CATERPILLAR

(*Pseudophilotes sinaicus*)

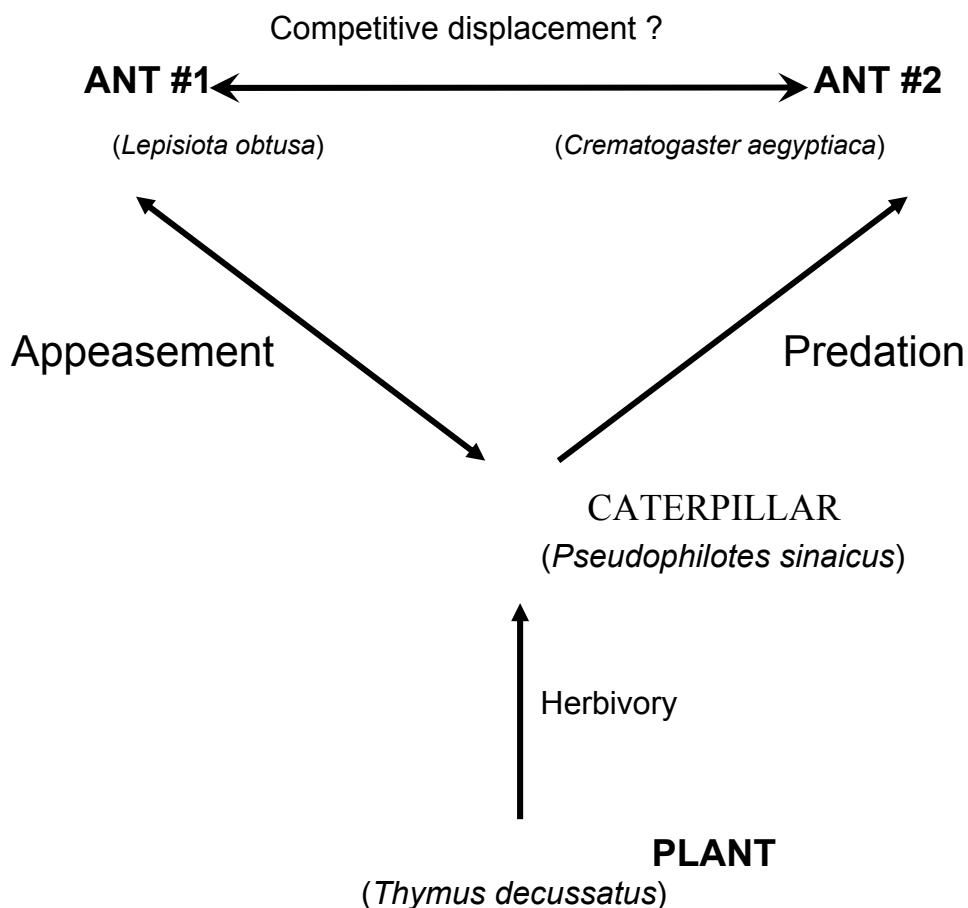Herbivory

PLANT

(*Thymus decussatus*)

Fig. 2 Direct and indirect effects of four interacting species from three trophic levels on each other's abundance. The figure is based on the results of this study: two ant species have a separate distribution within the study patch, which determines the pattern of Sinai Baton Blue larval survival within the patch, which determines herbivory. It is unknown what causes *Lepisiota* and *Crematogaster* to have mutually exclusive territories, but their distribution is likely to be the result of competitive displacement due to different micro-habitat requirements.

DISCUSSION

Female Sinai Baton Blues select a brief, phenologically determined stage of flower-bud development for oviposition and prefer plants with many inflorescences. Selecting the correct site for oviposition is critical as it allows larvae access to essential resources: first-instar larvae are absolutely tiny, cannot move far from where they hatched, and only feed on thyme buds; later instars feed on buds and flowers and are almost certainly restricted to the plant on which they hatched. It is therefore essential that adults eclose when thyme plants are coming into bud, and that females can distinguish buds. An attempt to re-establish *Maculinea arion* (a closely related butterfly which also oviposits on thyme buds) failed because the introduced population emerged two weeks later than the main flower-bud period of *Thymus* (Thomas & Elmes 2001).

Butterflies laid more eggs per inflorescence on plants with many inflorescences, suggesting that these plants are selected for reasons other than mere availability of oviposition sites. Plants with many inflorescences would presumably be more apparent to a searching butterfly and would provide more larval resource. Resource availability should be a function of the number of larvae utilising that resource, and my data provide some evidence of intraspecific competition among larval stages. The low numbers of adults eclosing in 2003 meant I was unable to develop this work further using egg estimates from 2002.

The analysis of hostplant quality revealed some important factors in decision making during oviposition, and explained almost a third of the variation in the distribution of eggs and surviving larvae. About 75% of the species of Lycaenidae associate with ants: lycaenid-ant interactions have been studied intensively (see Pierce *et al.* 2002), and in some cases lycaenids use attendant ants as oviposition cues (Henning 1983; Pierce & Elgar 1985;

Wagner & Kurina 1997). Thus it was essential to define the relationship between Baton Blue larvae and their attendant ants, and examine the consequence of this association with regard to hostplant choice. Eggs were most likely on plants within range of Lepisiota, an ant regularly seen attending larvae, and larval survival was restricted to plants within its foraging range. The Sinai Baton Blue is clearly a facultative myrmecophile, like other members of its genus, all of which Fiedler (1991) describes as 'moderately myrmecophilous'. Ant-dependent oviposition has been claimed in only one such facultative lycaenid (Wagner & Kurina 1997).

Under natural conditions some eggs were found on plants away from *Lepisiota*, and females never seemed to be able to detect this ant foraging. If the butterfly was not using ant cues when ovipositing, why was its distribution so closely linked to that of *Lepisiota*? My data (the distribution of newly eclosed adults and the experimental transfer of larvae) suggest that larvae survived on plants within foraging range of *Lepisiota*, but not of *Crematogaster*. Sinai Baton Blue larvae seem to have evolved the ability to appease *Lepisiota* (and *Monomorium*) but not *Crematogaster*, which instead prey upon it. This suggests that the distribution of newly eclosed adults was not a result of *Lepisiota* being there, but rather of *Crematogaster* being absent (Fig. 2). There are likely to be other costs and benefits to the butterfly resulting from its association with attendant ants, though further studies are needed (cf. Pierce & Mead 1981; Wagner 1993; Cushman *et al.* 1994; Fiedler & Saam 1994; Fraser *et al.* 2001; Stadler *et al.* 2001).

Some ant species 'mark' the larvae they tend with species-, or even colony-specific odour marks. For example, *Oecophylla smaragdina* weaver ants will attack larvae of their obligate mutualist *Anthene emolus* when these are directly transferred from one colony to another (Fiedler & Maschwitz 1989). All larvae used in my survival experiment were from plants within foraging range of *Lepisiota*, and so had presumably been tended by this ant prior to collection (this was not noted). However, there was usually a period of several hours between larvae being transferred from a plant containing *Lepisiota* and then subsequently being located by *Crematogaster*; this time delay is probably sufficient to allow any chemical marks on the larvae to evaporate. In addition, under natural conditions larvae were never observed surviving on plants within range of *Crematogaster*, also suggesting that aggressiveness of this ant against Baton Blue larvae is probably not elicited by chemical 'marks'.

One might expect ovipositing butterflies to avoid *Crematogaster*. However, this ant forages in the evening when butterflies are roosting, so to detect it the Sinai Baton Blue would have to rely on chemical cues (e.g. odour trails), and these are unlikely to last for long periods of time in the dry heat. Instead the distribution of surviving larvae probably dictates the distribution of eggs: adults are very sedentary (James 2006e) and so mainly oviposit on plants (with many inflorescences) near to where they eclosed. In another study, I suggested that dispersal of females might increase on reaching a certain age or condition (James 2006d). Eggs on thyme plants where no adults emerged could result from (older) ovipositing females moving away from where they eclosed. In the butterfly *Lopinga achine*, females move away from their natal site after laying two-thirds of their eggs (Bergman & Landin 2002).

In previous work on the Sinai Baton Blue, I described its optimum habitat as sheltered areas containing large thyme plants (James *et al.* 2003). This study confirms and explains this: *Lepisiota* nests in rock crevices at the base of cliffs (which provide shelter) and forages on thyme plants with many inflorescences; *Crematogaster* nests under plants in the middle of (exposed) wadi floors. The oviposition preference for many inflorescences thus increases larval survival. An important fact to consider in this case is the spatial dynamics of ant colonies over time (Peterson 1995). In this study, it would appear that (between two years at least) this pattern is static.

In this as in many insect species with immobile larvae, hostplant selection by ovipositing females is strongly influenced by variation among plants in suitability for growth, survival, and subsequent reproduction of the offspring (Jaenike 1990). Thus habitat quality is often defined by the requirements of the immature stages (Thomas 1991), a precise understanding of which is paramount for species conservation.

This study provided an opportunity to examine the effects of hostplant choice on larval survival and so precisely define habitat quality for an endangered and narrowly endemic species. It also provides a very clear example of the a priori danger of equating association and correlation with causality in a species facing very real conservation problems.

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