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ORIGINAL PAPER

Plant quality and the presence of beneficiaries govern the larval distribution of the critically endangered Sinai Baton Blue butterfly (*Pseudophilotes sinaicus*)

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Abstract The larval distribution of herbivorous insects play an important role in their development and hence future fitness. Here we study larval distribution of the critically endangered Sinai Baton Blue butterfly, *Pseudophilotes sinaicus*, which feeds exclusively on the buds and flowers of a single host plant, also endangered, the near-endemic Sinai thyme, *Thymus decussatus*. We studied the larval distribution over 131 plants, recording the size, quality and phenological stage of the plants along with the presence of beneficiaries. Larvae were found on plants with a high number of flowers, a relatively advanced flowering phenology and tending ants. This highlights the importance of the vitality and quality of the host plant to the spatial distribution of the Sinai Baton Blue. Future conservation plans might concentrate on improving the quality and quantity of the host plant in order to increase resources for this narrowly endemic species.

Keywords Larval niche · Habitat quality · Arid environment · Resource level · Egypt · *Thymus decussatus*

Introduction

In the struggle to conserve rare species, the metapopulation paradigm has become dominant almost the the exclusion of other older ideas about the importance of habitat area and quality (Hodgson et al. 2009, 2011; Fronhofer et al. 2012). A review of the published evidence (Hodgson et al. 2011) suggested that habitat area and quality have larger effects on populations than the spatial arrangement of patches, or the nature of the interstitial matrix. Coupled with the conclusion that true metapopulations, where spatial configuration effects dominate, are relatively rare in nature (Fronhofer et al. 2012), perhaps too much emphasis has been placed on fragmentation and connectivity in conservation.

The system we study here involves a butterfly in a hyper-arid environment, where resource availability is primarily governed by water (Pueyo et al. 2008) and spatial variation in rainfall and the subsequent soil moisture plays a large role in determining plant quality and abundance (Reynolds et al. 2004). Abiotic and biotic conditions can vary across the local spatial scale, impacting the realised niche of associated herbivores (Anthes et al. 2008): the population density of many butterfly species is known primarily to be determined by the quality and condition of the host plant (Thomas et al. 2011). Insect herbivores utilise different host plant characteristics depending upon their developmental stage, and the availability of resources in turn influences survivorship (Hellmann 2002). A critical driver for population size and persistence is the availability of suitable sites for larval development, as mortality at this stage can govern population dynamics, with explosive growth when resources are abundant or potential extinction if mortality rates are too high (Ehrlich and Hanski 2004; Thomas et al. 2011). Adequate feeding at the larval stage is essential for future fitness. Starvation, even just over a short period, affects larval growth and development; small larvae develop into small adults with lower fecundity and reduced survival (Boggs and Freeman 2005; Bauerfeind and Fischer 2009).

Many butterfly species are constrained to a single genus or species of host plant (Dennis et al. 2004) and variation in host plant quality can leave some plants unsuitable for

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larval development (Singer and Lee 2000). This will result in spatial variation in respect to occupied larval host plants (Roy and Thomas 2003) with varying conditions enhancing larval development (Davies et al. 2006). Larvae frequently have a narrower habitat range than the adult stage (Warren 1987) and often it is essential to identify suitable habitat in order to successfully conserve rare and endangered butterflies, such as the heath fritillary (*Melitaea athalia*: Nymphalidae) (Warren 1987; Thomas et al. 2011).

Due to the vital role of larval habitats, we look at the larval distribution of the critically endangered Sinai Baton Blue butterfly, *Pseudophilotes sinaicus*, to see which host plant and other characteristics govern its spatial distribution. As a lycaenid, interaction with ants are probably an important factor: the larvae of many lycaenids avoid ant predators by being myrmecophiles, with other further possible benefits of increased survival, lower incidences of parasitism and shorter development times (e.g. Fiedler 1995; Fiedler et al. 1996). Previous work (James 2006a–f) suggested this species occurred in a metapopulation (James et al. 2003; James 2006a) and studied its movements within (James 2006e) and between patches (James 2006d) in some detail. An occupancy metapopulation model estimated its likely risk of extinction to be low under various scenarios including climate change (Hoyle and James 2005). The sketchy data hint at a regular 3-year population cycle (Gilbert et al. 2010), potentially driven by host plant quality (e.g. Quiring and McKinnon 1999). We therefore carried out this study at the patch level to determine the conditions necessary for larval development.

Materials and methods

The study system

The Sinai Baton Blue butterfly (*P. sinaicus* Nakamura 1975) has a narrowly endemic distribution localised to just 7 km^2 within the St Katherine Protectorate in South Sinai. It is critically endangered and it is considered a flagship species in the area (Thompson and Gilbert 2013). Because of its status as one of only three animal species endemic to Egypt, and one of two endemic to the St Katherine Protectorate (the other is the Sinai Hairstreak *Satyrium jebelia* Nakamura 1975), it is not possible to obtain permission for manipulative experiments and we have had to rely only on observational data.

The Sinai Baton Blue is monophagous: the near-endemic Sinai thyme (*Thymus decussatus*, Bentham, 1834) is the sole host plant for the larval stage, and the adults also primarily feed on nectar from its flowers. Plants vary greatly in size and condition, and this should result in strong preferences for the selection of suitable plants (James 2006f). The eggs hatch approximately 4 days after oviposition. The green larvae are immobile, remaining on their natal host plant during the approximately 1 month of their development and pupating in the soil beneath the host plant. Adults only leave their natal plant in the following summer upon eclosion. The larval survival rate is slightly, yet significantly, reduced by an increased density of larvae on the plant, potentially because of higher intraspecific competition (James 2006b). The larvae have a facultative relationship with the ants *Lepisiota obtusa* (Emery, 1901) and *L. hirtusa* (Santschi, 1914) (James 2006a; Shepherd 2010), appeasing them with sugar secretion and in return gaining protection (James 2006a). It was recently discovered (Shepherd 2010) that another species of *Lepisiota*, *L. hirsuta* (Santschi 1914), cohabits the same range and also tends the larvae. Natural enemies include the ant *Crematogaster antaris* (Forel, 1894) (previously referred to as *Crematogaster aegyptiaca* in James 2006a), which preys on the larvae; in fact, within the foraging range of *C. antaris*, apparently no larvae survive to emerge as adults (James 2006b). We therefore test here the larval distribution to see whether it is influenced by the beneficial ant, avoiding plants without them (James 2006f; cf. Berenbaum and Feeny 2008). This test was in an area lacking any nests of the predatory ant.

Fig. 1 Map of Farsh Shoeib upon the Mount Sinai massif

The study site was Farsh Shoeib (Fig. 1), a flat open area within the arid rocky mountains where a patch of thyme plants had one of the largest populations of Sinai Baton Blues in 2001 (James et al. 2003). Farsh Shoeib is near the summit of Gebel Safsafa on the Mt. Sinai massif, close to the town of St Katherine in South Sinai, at an altitude of approximately 1,950 m. It has an area of 14,000 m^2, containing 669 thyme plants in 2010. The majority of the patch has been fenced off as a conservation effort to prevent public access, grazing and any damage to the plants, with only a few plants of the patch found outside the enclosure. The fieldwork was carried out from March until late June 2010. The main flight period typically lasts from the start of May to mid-June.

Fieldwork

Detailed larval counts were made on thyme plants in Farsh Shoeib. The majority of butterfly sightings in the patch were within the main gulley (Fig. 1) outside the foraging range of colonies of the predatory *C. antaris*, which only forage in wide open spaces. It is a section of the site containing 148 thyme plants, 131 of which were searched thoroughly once a week. For each plant, the number of Sinai Baton Blue larvae, flowering phenology and the number of flowers present were recorded weekly. Flowering phenology was recorded weekly according to a 0–7 scale (Table 1). Five randomly selected inflorescences from the most advanced flowering area of the plant were scored and averaged to get the phenological status for each plant at that time. The height (m), two perpendicular widths (m) and condition (percentage green) of each plant were recorded in the field once before the beginning of the adult flight season, and later the resource area (m^2, assuming an ellipsoidal shape for the plant) calculated from these measurements (i.e. surface area × proportion green). We used surface area because thyme is basically a hemispherical cushion plant with the flowers on the outside; thus visually to the adult females and nutritionally for the larvae, it is surface area rather than volume that should matter. We also measured the distance to the nearest neighbouring plant to view the effects of isolation.

Table 1 The way flowering phenology was scored (from James 2006b)

Phenological score	Appearance of plant
0	100 % Pre bud
1	Sepals visible, buds not yet visible
2	Sepals apparent, buds starting to develop
3	Large buds <2 flowers open
4	50–90 % Buds, 10–50 % flowers open
5	1–50 % Buds, 50–100 % flowers open
6	1–50 % Flowers over/seed heads
7	>50 % Flowers over/seed heads

During plant searches, any ants found on the plants were recorded: it was impossible to differentiate in the field between the two *Lepisiota* species, *L. obtusa* and *L. hirsuta*, and so these were lumped together. For each of 27 Sinai Baton Blue larvae found in the presence of a tending ant, an ant sample was taken for identification to confirm which species tended the larvae.

The foraging range of *Lepisiota* was determined by pitfall traps (Shepherd 2010) during the first 3 weeks of surveys, during the peak flight season but before the first Sinai Baton Blue larvae was found. *C. antaris* were not found inside the gulley at any point during the 6 weeks of surveys. The ant distribution in Farsh Shoeib remained identical between 2002 and 2010, with no variation in foraging range of either species (Shepherd 2010).

Analysis of data

ArcGIS 9.3 was used to map plants and observations from detailed field measurements of plant locations; nearest-neighbour distances were estimated from these data. All analysis used the statistical package R 2.14.1 (R Development Core Team 2012) to assess the predictability of larval distribution from weekly characteristics of the thyme plants. Note the number of flowers was previously found to be independent of plant size (i.e. surface area: Thompson 2013). Models were simplified in accordance to Zuur et al. (2009). We ran generalized linear mixed models (*glmer* from the *lme4* package) in order to account for the repeated-measures nature of the data, using the random factor of individual plant identity. There were two response variables: the presence/absence of larvae (binomially distributed), and larval counts for plants in the gulley (Poisson distributed). We simplified the full model based on the AIC criterion using stepwise backwards deletion of model terms: significance was assessed with a χ^2 test. Repeated surveys of individual plants allowed estimates of occupancy and detectability of larvae using the program Presence 6.2 (MacKenzie et al. 2005).

Results

In the main gulley a total of 64 Sinai Baton Blue larvae were found, but on just 35 plants, i.e. only 27 % of those available. On plants with larvae, there were an average of 1.6 larvae found per visit, with no more than six on a plant at one time. The distribution of larvae was scattered across the gulley, with few larvae found in the southern and northern sections and the majority located in the central plant cluster (Fig. 2), on plants with a high numbers of flowers and with *Lepisiota* spp. *Lepisiota* species were not found in the southern section of the gulley which may have

Fig. 2 The distribution of the Sinai Baton Blue larvae in the main gulley. *Black circles* indicate thyme plants without larvae; *grey circles* indicate plants where larvae were found

influenced the lack of larvae in that plant cluster. From samples of tending ants, clearly both *L. obtusa* and *L. hirsuta* tend the larvae (n = 27; 4 samples of *L. hirsuta* & 23 *L. obtusa*).

Plants with larvae had on average more flowers ($\chi^2 = 14.8$, $df = 1$, $p < 0.001$) (Fig. 3a), a higher phenological score ($\chi^2 = 18.1$, $df = 1$, $p < 0.001$; Fig. 3b) and were more likely to have *Lepisiota* ants ($\chi^2 = 16.2$, $df = 1$, $p < 0.001$), compared with plants with no larvae detected. The phenological state of the plants was the most influential predictor of presence/absence of larvae (i.e. it had the greatest change in deviance upon deletion from the model); plants with larvae were more advanced in seasonal development than those that did not have larvae. The presence of a tending ant species and the number of flowers on the thyme plant were both strongly significant predictors of larval distribution. No larvae were ever found on a thyme plant without either of the *Lepisiota* species. There was no evidence that resource area, condition, greenness and distance to the nearest neighbouring plant affected whether a plant had *Pseudophilotes* larvae.

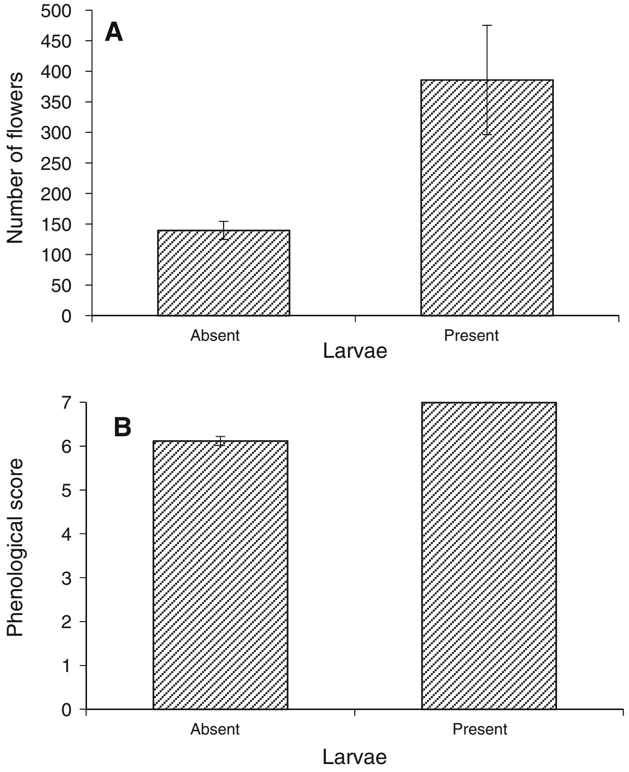

Fig. 3 Differences between **a** the number of flowers and **b** the phenological scores of thyme plants (n = 131) where Sinai Baton Blue larvae were present or absent. Mean values ± SE. Please note there was no standard error in the phenology of the plants with larvae

The 'naive' estimate of the proportion of plants occupied by larvae was simply the proportion of plants where larvae were ever detected (0.267). From the repeat surveys of individual plants, detectability was low (0.154 ± 0.055) and the true occupancy was estimated at 0.676 ± 0.225.

Phenology was again the most significant predictor of the number of larvae, with more larvae on plants with an advanced phenological score ($\chi^2 = 18.7$, $df = 1$, $p < 0.001$). The number of flowers ($\chi^2 = 30.4$, $df = 1$, $p < 0.001$) (Fig. 4), and *Lepisiota* presence ($\chi^2 = 17.7$, $df = 1$, $p < 0.001$) were again significant predictors. The resource area, condition, greenness and isolation again had no significant effect on how many larvae were on the plant.

Discussion

This study highlights the importance of the vitality of the host plant for the Sinai Baton Blue larvae, as the number of

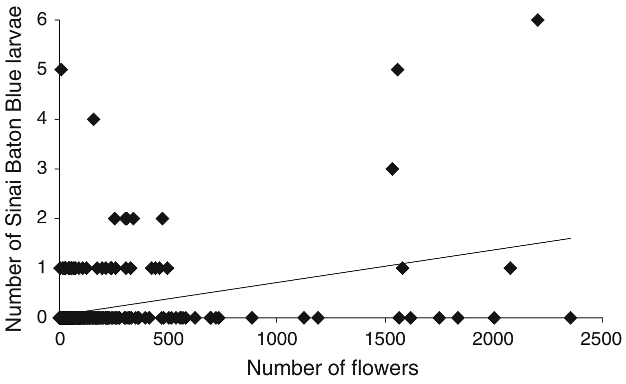

Fig. 4 The relationship between the number of Sinai Baton Blue larvae and the number of flowers for the plants (n = 131) in the main gulley

flowers and hence resource level influences larval spatial distribution. Despite the low detectability of larvae, there was evidence of more larvae on plants with a high number of flowers, an advanced phenological stage and with tending ant species, *L. obtusa* and *L. hirsuta*. The distribution is consistent with the maximisation of fitness, since there would be an expected lower larval mortality rate where there more resources (Boggs and Freeman 2005) and the presence of beneficiaries (Berenbaum and Feeny 2008). The first two instars feed exclusively upon the buds, with the later stages feeding upon the flowers (James 2006a); thus it makes sense that the number of flowers influences the larval distribution (James 2006c; Berenbaum and Feeny 2008). It is interesting that plants with larvae were predominantly in the seeding stage of flower phenology (Fig. 3b). This is unexpected for the larvae of a bud- and flower-feeding species, but probably was a consequence of the peculiar weather and flowering of 2010 that advanced flowering phenology greatly relative to 'normal years' (Thompson 2013).

The average number of larvae found on a plant was just below two, very similar to that found previously by James (2006d) in 2001. Intraspecific competition reduces food resources, leading to longer development and reduced survivorship. Higher densities can lead to density-dependent mortality from threats such as predators or parasitoids (Gibbs et al. 2004; Sato et al. 2004; Strausz et al. 2012). Thus this dispersed spatial distribution may increase offspring survival (Fig. 2).

The Sinai Baton Blue distribution could be due to larval mortality, with increased survival on plants with more flowers and the presence of beneficiaries. However it could be an example of the preference performance hypothesis, which evolves where it is advantageous for females to discriminate amongst plants in selecting oviposition sites for optimum offspring performance (Berenbaum and Feeny 2008; Wise et al. 2008; Gripenberg et al. 2010; Mphosi and Foster 2010). The larvae are immobile, barely able to move among inflorescences, let alone amongst plants (James 2006f); therefore they were always found on the same plant that the female selected for oviposition, placing stronger selective pressures on females to pick superior plants (Craig and Itami 2008). The eggs hatch approximately 4 days after oviposition and so presumably the plants would be in a similar state as when selected by the female (James 2006f).

The Sinai Baton Blue larvae were only found within the foraging range of the attendant ant; either the larvae only survived in the presence of *Lepisiota* spp. due to the protection provided, or potentially the ants were used as an oviposition cue. The larvae are certainly able to survive outside the foraging range of *Lepisiota* because their relationship is facultative (James 2006b), making it unlikely that all larvae from eggs laid outside their foraging range died before being recorded. The predatory *C. antaris* was not recorded at all from the gulley area of the site whence these data come. Larvae in the presence of tending ants have a higher survival rate than in the presence of other ant species (James 2006b), probably due to the protection from predators and parasitoids afforded in return for larval secretions of amino acid and sugars (James 2006b; Trager and Daniels 2009).

Facultative ant species could be used as oviposition cues because they can signal the presence of enemy-free space. This would be the situation here since the attendant ant *Lepisiota* spp. has a mutually exclusive distribution in relation to the predatory *Crematogaster* (James 2006b). Therefore the presence of *Lepisiota* would signal to a gravid female the absence of *Crematogaster*, and therefore enemy-free space. For ants to be good cues they need to have a consistent foraging range and consistently to occupy the same individual plants. *Lepisiota* spp appeared to consistently forage on the same plants, with the surveys noting similar foraging patterns across multiple weeks (indeed, across many years too: Shepherd 2010). Despite being an obvious prediction, studies of both obligate (Musche et al. 2006; Fürst and Nash 2010) and facultative (Collier 2007) relationships have generally failed to find evidence of the use of host ants as oviposition cues by lycaenid butterflies.

A key challenge for conserving the Sinai Baton Blue is therefore to manage the thyme patches in order to promote plant growth and flowering, and to encourage the presence of the tending ants. Sinai thyme is an extremely slow-growing plant, and we do not yet understand the main modes of its reproduction: regeneration from seed is not at all obvious. The ages of individual plants are almost certainly counted in decades, and could be in hundreds of years. The role of grazing in maintaining plant vigour is not yet clear, although a short-term experiment found no effects (Thompson and Gilbert 2013). A fence was erected to surround Farsh Shoeib in 2003 on the assumption that grazing was the main threat to the plants, but there are few indications of any effects of its prevention. As yet we know nothing about the survival and reproduction of the tending ants, although they clearly prefer narrow rocky gorges (Shepherd 2010).

Overall, this study has highlighted the importance of the density of flowers and hence the quality of host plant in determining the Sinai Baton Blue's larval distribution in this arid environment. The thyme is already a limited resource, currently in relatively poor condition across the entire range of the butterfly due to a long period of relative drought, recently broken (Thompson and Gilbert 2013). It will be important to understand how to improve the quantity and quality of the host plants, and thus the number of inflorescences, to try to augment butterfly numbers in the future. Occupancy modelling suggests the butterfly is in no immediate danger of extinction unless climate change effects increase dramatically (Hoyle and James 2005), but other types of model are not so sanguine (Thompson 2013).

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