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# Thyme and isolation for the Sinai baton blue butterfly (*Pseudophilotes sinaicus*)

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**Abstract** The distribution of the narrowly endemic butterfly *Pseudophilotes sinaicus* (Lycaenidae) was studied. Potential habitat within its range was first located and then the quality of that habitat assessed. Degree of shelter, diversity of plant species, and resource area of an individual food plant (*Thymus decussatus*) all affected habitat quality and together were used to develop an index of habitat suitability applicable to each site. The butterfly's distribution was then studied within the identified network of suitable habitat patches: isolated patches with a small resource area were least likely to contain butterflies. Population size in a patch (as opposed merely to patch occupancy) was affected by resource area and the quality of habitat within that patch. Metapopulation processes and variation in habitat quality therefore appear to combine to describe the distribution of patches occupied by *P. sinaicus* and their population sizes. This finding provides insights into some of the processes operating on an endemic species throughout its geographical range and has important implications for the conservation of this rare butterfly.

**Keywords** Conservation · Endemic species · Fragmented landscape · Habitat quality · Metapopulation

## Introduction

When attempting to understand the distribution and dynamics of localised species in heterogeneous landscapes, both processes operating within populations (driven by habitat requirements, influencing extinction risks) and movement among populations (affecting immigration and emigration rates, influencing colonisation) must be studied simultaneously. Many species have highly specific habitat requirements combined with relatively limited dispersal abilities (e.g. Arnold 1983; Gall 1984; Thomas 1985; Thomas et al. 1992; New 1993; Baguette et al. 2000). As a result, areas of ostensibly suitable habitat may turn out to be unsuitable and some areas of suitable habitat will remain vacant (Thomas and Harrison 1992; Sutcliffe et al. 1997a; Dennis and Eales 1997, 1999; Thomas and Hanski 1997).

Metapopulation biology was developed and tested on the margins of the range of species with wide distributions, but as a model for possible processes in rare and endangered species. In this paper we show that the approach is applicable to a truly rare species throughout it range that has a total geographic distribution of <200 km$^2$. We also show that habitat quality is as important as metapopulation dynamics to the persistence of this highly vulnerable species.

A metapopulation approach has been applied to a wide range of species (e.g. Thomas and Jones 1993; Hanski et al. 1995; Lewis et al. 1997; Sutcliffe et al. 1997b): many habitat specialists that live in fragmented landscapes are most likely to occur in patches that are close to one another and relatively large. These patterns fit the theoretical effects of habitat isolation and patch size (Gilpin and Hanski 1991). The majority of this work has concentrated on species from the temperate zone, and has usually been restricted to one or more well-defined regions of their geographic range usually at or close to the northern limit; fragmentation of suitable habitat in these regions has almost always been exacerbated by Man (e.g. Thomas et al. 1986; Hanski et al. 1995; Marttila et al. 1997; Gutiérrez et al. 1999). As a factor influencing distribution, fragmentation is thus becoming increasingly important in the modern landscape and an understanding of its implications essential for effective long-term conservation.

In contrast, here we assess the distribution of a species living entirely within a fragmented ecosystem in the

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mountains of southern Sinai. By understanding its specific needs we characterise the network of patches of potential habitat in which the butterfly's distribution can be assessed throughout its known range and in which metapopulation processes might be operating. The Sinai Baton Blue represents a narrowly endemic and rare species with an extremely restricted range in a very arid environment, a quite different situation from virtually all other metapopulation studies. It is therefore subjected to climatic extremes very different from those experienced by temperate species at their northern limits but which nevertheless should result in the effects of habitat quality and fragmentation being amplified because relatively small fluctuations in weather are likely to have considerable effects on the amount and quality of habitat available (Thomas et al. 1999; C. D. Thomas et al. 2001).

We also quantify the quality of habitat at each site, since recent theory and empirical observations suggest that this is likely to be linked to metapopulation dynamics and is therefore important when trying to understand present distributions and for predicting future patterns (Thomas 1994; Dennis and Eales 1997; Gutiérrez et al. 1999; J. A. Thomas et al. 2001).

Knowledge of what constitutes suitable habitat and understanding the distribution of a species throughout its geographical range can provide important information with regard to processes acting at a much larger scale (e.g. climate warming) and are of considerable interest in ecology and conservation (Brown et al. 1996; Hill et al. 1999).

## Materials and methods

### Study species

The genus *Pseudophilotes* (Lepidoptera: Lycaenidae, Polyommatinae, Polyommatini) was established by Beuret (1958) for five Eurasian species all with peculiar male genitalia; several more rare, narrowly distributed species have now been described. Host plant records are available for seven species: all of these feed on Labiates, and six are restricted to or prefer different species of *Thymus* (Labiatae). The Sinai Baton Blue (*Pseudophilotes sinaicus* Nakamura) has only been recorded from the high mountains of southern Sinai, and probably only occurs above 1,500 m altitude; it is the most southerly of all *Pseudophilotes* species and is one of the smallest butterflies in the world (Larsen 1990). Despite Nakamura's (1975) speculation about a partial second brood, in this study the Sinai Baton Blue occurred only as a single generation with its main adult flight period from end-April to end-June. It is a relatively sedentary species: 93% of all detected movements in marked individuals were <50 m ($n$=176; unpublished observation). Its only known larval host plant is Sinai Thyme, *Thymus decussatus* Benth., an IUCN Red List endangered plant (Walter and Gillett 1998) endemic to Sinai and Saudi Arabia with a highly patchy distribution throughout the study area.

### Study area

The study was carried out between March and September 2001, in the St. Katherine Protectorate, around the town of St. Katherine. The area is characterised by jagged mountain peaks (up to 2,650 m) interspersed with dry valleys (wadis): a naturally fragmented landscape. It is in these wadis and above ca.1,500 m that Sinai Thyme grows. During winter the mountains are covered in snow; melt water from this seeps into the ground and provides the area with almost all of its water during the dry spring, summer and autumn. The area is classified as arid and in an average year receives <100 mm of precipitation (Greenwood 1997).

### Distribution

The mountains around the town of St. Katherine were searched intensively for Sinai Thyme, and thus potentially suitable habitat during March and April before the main flight period, and a map produced of all such sites (Fig. 1). Locations were established using a hand-held global positioning system (GPS 12 MAP; Garmin) accurate to ±10 m. Using this map, a survey for adults was conducted during the main adult flight period of May–June. Each thyme locality was re-visited at least twice between 1000 hours and 1600 hours (local time) when the adults were most active and thus easily spotted.

Sinai Baton Blues were found only in the vicinity of their food plant, and coupled with their lack of mobility this usually made discrete breeding populations very easy to define. Any area containing thyme and separated from any other area containing thyme by a distance of >100 m defined a patch. If two or more butterflies were seen in a patch on one or more occasions, then a breeding colony was defined as present. Initially any areas containing Sinai Thyme were deemed potential habitat sites. However as the butterflies began emerging, it became apparent that not all the area of every thyme patch was being utilised, with butterflies sometimes only ever being seen in restricted parts of patches. Thus each patch was revisited and divided into sub-sites based on the natural topography of the area (such as obvious changes in gradient or aspect) and on natural barriers (e.g. areas of rock-fall).

Seven habitat features were assessed at each sub-site (Table 1). The amount of thyme in each patch/sub-site was used to describe the "resource area" available to the Sinai Baton Blue. Using random numbers, 30 thyme plants were selected to represent each sub-site (in sites containing <30 plants, all plants were used). For each of these the height and two perpendicular widths were measured; plant condition (% green) was also assessed. From these measures the "resource area of a plant" was calculated. The average resource area of a plant in a sub-site multiplied by the total number of plants defined the "sub-site resource area".

Patch isolation was measured using Hanski's (1994) measure of patch connectivity. Distances were measured in kilometres using the GPS and were estimated between patch edges. Patch area was defined in terms of the amount of resource present (resource area) and was calculated in $m^2$. Insufficient mark-release-recapture (MRR) data meant that the species-specific parameter describing dispersal ability was estimated at 2 (Hanski 1994).

To ascertain the size of a breeding colony either transect counts or MRR experiments were carried out. MRR took place on a weekly basis from 26 April to 26 July in five localities. A predetermined route through each area was walked at a slow pace. Each time an adult was seen, its sex, position (using a GPS), time of day, behaviour, and condition (wing wear: scored subjectively between 1=tatty and 4=pristine) were recorded. Adults seen for the first time were caught, marked individually (using permanent pens), and immediately released at the point of capture. Population sizes were estimated using Eberhardt's geometric model (see Pollard 1977).

There was insufficient time to assess population sizes at all localities using the above method and therefore simple transect walks were conducted at other sites (see Pollard 1977; Thomas 1983a) 2 weeks either side of the day of peak adult emergence (as ascertained by the MRR study). The transect route zig-zagged through the site and included as many thyme plants as possible. Population size using this method was simply the mean total count of adults seen during at least five transect walks. In an attempt to reduce the inaccuracies associated with both methods, population

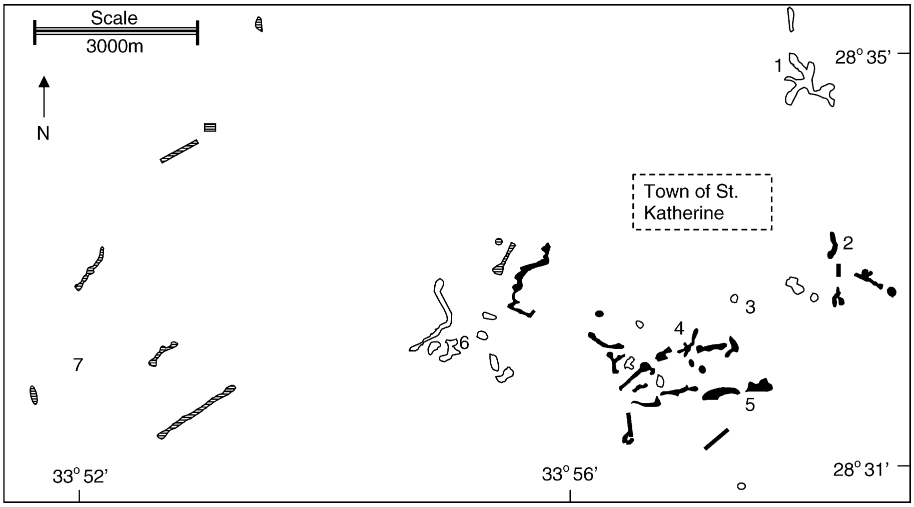


**Fig. 1** The known distribution of Sinai Thyme and the Sinai Baton Blue in the high mountain region, South Sinai, Egypt in 2001. *Open shapes* represent patches of thyme in which a Sinai Baton Blue colony was absent, and *filled shapes* patches in which a colony was present; *striped shapes* represent patches of thyme in which the status of the Sinai Baton Blue is uncertain. Patch size has been exaggerated slightly for clarity. Coordinates are latitude (north) and longitude (east) measured in degrees and minutes. *1* Gebel (Mt.) Sona, *2* Gebel Safsafa, *3* Wadi Arbaein, *4* Abu Hamen, *5* Wadi Ahmar, *6* Wadi Gibal, *7* Gebel Bab/Farsh Za'atar/Wadi Zuwei'tar region

**Table 1** Features of the habitat assessed at each sub-site

| Habitat feature | How measured |
|---|---|
| Slope | In degrees using a hand-held clinometer |
| Altitude | In metres using a hand-held GPS |
| Aspect | In degrees and then sorted into five categories (flat, NE, SE, SW, NW) |
| Shelter | Scored subjectively (*1* exposed on all sides, *2* good shelter on one side or partial shelter on two sides, *3* good shelter on two sides or partial shelter on three sides, *4* good shelter on three or more sides or partial shelter on all sides) |
| Plant diversity | Number and species of plants fully or partly within a circle (radius 2 m) centred around randomly selected thyme plants were recorded and diversity calculated using Simpson index of diversity (see Lande 1996) |
| Number of thyme plants | Two independent counts of all plants and an average taken |
| Boulders | Scored subjectively (*1* no large boulders present, *2* a few large boulders present, *3* lots of large boulders present, *4* area dominated by large boulders) |

estimates for every patch were lumped into seven broad categories: zero=0; 1=single sighting; 2=<25; 3=26–50; 4=51–100; 5=101–200; 6=>200.

### Statistical analysis

Logistic regressions were done using SPSS version 10.1 (SPSS 2000). Variables were added stepwise, using the forward likelihood ratio option. In stepwise multiple linear regression analyses with forward selection, variables were included in the model when $F$>3.84. We checked for linearity by visual inspection of residuals; there were no problems of collinearity (all $r^2$<0.6).

## Results

### Occurrence (presence/absence)

Past records are largely restricted to type specimens taken in 1974 (Nakamura 1975). Many of the paratypes were collected in the Gebel Bab/Farsh Za'atar/Wadi Zuwei'tar region in the west (see Fig. 1). This area was searched both at the beginning and end of the adult flying period and on both occasions very little Sinai Thyme was found. On the other hand, there are no previous records from the Gebel Safsafa region, which given that it forms part of Gebel Musa (Mount Sinai) must have been visited by lepidopterists in the past. The apparent discrepancy between what little is known of the butterfly's past distribution and its localities today, suggests that its food plant (and thus habitat) may be ephemeral, making inevitable a series of extinctions and colonisations within the changing network of patches.

Figure 1 shows the distribution of patches of Sinai Thyme and Sinai Baton Blues recorded during the study. Fifty-three patches of thyme were located throughout the study area during 2001. Complete records have been acquired for 34 of these (Fig. 1). Twenty-one patches were occupied and 13 apparently suitable patches were unoccupied. The areas containing Baton Blues are likely

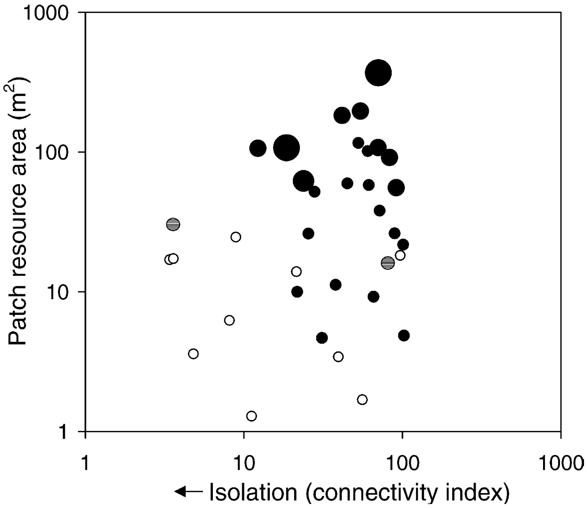


**Fig. 2** Distribution of occupied and vacant patches of Sinai Thyme and the population size of Sinai Baton Blues that they support. *Open circles* represent vacant patches, *solid circles* patches containing a Sinai Baton Blue colony; *size of the solid circle* indicates the estimated population size: smallest=2–25; 26–50; 101–200; >200=largest; *striped circles* are patches where only a single sighting of the butterfly occurred

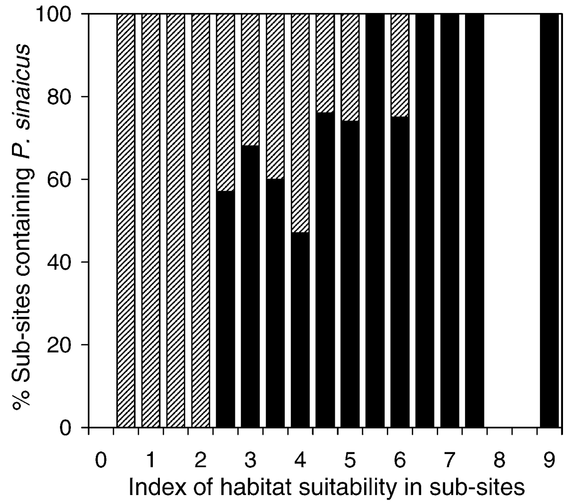


**Fig. 3** Index of habitat suitability in sub-sites, as derived from the equation: logit ($P$)=−1.75+0.9$S$+8.98$R$+13.19$D$, where −1.75=the constant (the actual fitted value is –5.34 but this was changed merely to shift the $x$-axis right until the index started at zero), $S$=degree of shelter, $R$=resource area of a thyme plant, and $D$=plant diversity. *Solid bars* represent sub-sites in which the Sinai Baton Blue is present, *hatched bars* sub-sites in which it is absent

to represent all, or a large proportion of its worldwide distribution.

## *Factors affecting occurrence*

At the patch level, when both the isolation of a patch and its resource area were entered into a logistic regression, both had a significant effect on patch occupancy (Table 2a).

At the sub-site level, when all measured macro-habitat variables (excluding measures of sub-site size or isolation) were entered into a logistic regression to explain the occurrence of Sinai Baton Blues, the sub-site's degree of shelter and plant diversity were the only characteristics to contribute significantly to the final model (Table 2b). This result remained the same when only those plant species from which the Baton Blue is known to take nectar (as opposed to all plant species) were used to represent plant diversity. Resource area of individual thyme plants within a sub-site is also an important determinant of habitat for the Sinai Baton Blue at that scale (Table 2c); the resource area of a plant was not correlated with plant diversity ($r$=–0.15, $n$=106, $P$ >0.05.). Thus occupied habitat at a sub-site scale for the Sinai Baton Blue can be described as containing relatively large, healthy thyme plants, which grow in sheltered conditions in amongst lots of other plant species (Table 2c).

Isolation, an important factor acting at the level of the patch, cannot be used at sub-site level since sub-sites are continuous within a patch. Sub-site resource area was not significant in explaining the occurrence of the Sinai Baton Blue after the significant habitat quality variables had been accounted for (Table 2c). Suitable habitat apparently has the potential to support a breeding colony of Sinai Baton Blues no matter how much of it there is. This result is supported by the fact that the butterfly seems capable of existing at very low population sizes (personal observation; Fig. 2).

## *An index of patch suitability*

Information on habitat requirements of the butterfly revealed by analysing sub-sites needs to be applied at the level of the patch in order to be able to predict patch suitability. The probability ($P$) that a sub-site of thyme will contain Sinai Baton Blues is described by the equation derived from logistic regression: logit ($P$)=−1.75+0.9$S$+8.98$R$+13.19$D$, where −1.75=the constant (the actual fitted value is –5.34 but this was changed merely to shift the $x$-axis right until the index started at zero), $S$=degree of shelter, $R$=resource area of a thyme plant, and $D$=plant diversity. When applying this index of habitat suitability to the level of the patch, the mean sub-site score per patch is the most useful summary statistic (Table 2d–f), and together with patch resource area accounts for 82% of the variation (Table 2f). Thus the quality and amount of habitat appear to be the best predictors of presence or absence of the Sinai Baton Blue. There is a significant positive correlation between patch quality and proximity ($r$=0.481, $n$=36, $P$<0.01), indicating that high-quality patches are clustered relatively close to one another within the study area. No significant correlation exists between patch quality and patch resource area ($r$=0.245, $n$=36, $P$>0.05).

**Table 2** Stepwise logistic regression analyses relating butterfly occupancy (presence/absence) in patches (*a*, *d–f*) and sub-sites (*b*, *c*), with measured variables

| | Variables available (independent) | Variables in final model (all terms significant at $P$<0.05) | *B* | Model | | | |
|---|---|---|---|---|---|---|---|
| | | | | $\chi^2$ | *df* | Significance (*P*) | % of variation |
| **a** | Connectivity index<br>Patch resource area | Connectivity index<br>Patch resource area | 0.032<br>0.056 | 20.1 | 2 | <0.001 | 59 |
| **b** | Boulders<br>Slope<br>Altitude<br>Aspect<br>Shelter<br>Plant diversity | Shelter<br>Plant diversity | 0.814<br>8.53 | 10.4 | 2 | <0.01 | 14 |
| **c** | Resource area of a plant<br>Shelter<br>Plant diversity<br>Sub-site resource area | Resource area of a plant<br>Shelter<br>Plant diversity | 8.981<br>0.900<br>13.188 | 27.0 | 3 | <0.001 | 33 |
| **d** | Max sub-site score/patch<br>Patch resource area<br>Connectivity index | Max. sub-site score/patch | 1.913 | 19.8 | 1 | <0.001 | 58 |
| **e** | Total sub-site score/patch<br>Patch resource area<br>Connectivity index | Total sub-site score/patch<br>Patch resource area | 2.240<br>0.233 | 31.6 | 2 | <0.001 | 80 |
| **f** | Mean sub-site score/patch<br>Patch resource area<br>Connectivity index | Mean sub-site score/patch<br>Patch resource area | 3.440<br>0.149 | 33.0 | 2 | <0.001 | 82 |

Baton Blues occurred in sub-sites scoring as little as 2.5 on the index of habitat suitability (Fig. 3). This would suggest that whilst sub-sites achieving scores of 4.5 or more represent *ideal* habitat, sub-sites scoring between 2.5 and 4.5 may also be *suitable* for the butterfly; the Sinai Baton Blue was at no time seen in sub-sites scoring <2.5. If only those sub-sites in each patch achieving >4.5 (ideal habitat) are included in a plot of resource area against isolation, without exception all patches containing ideal and occupied habitat score above 12 in the index of connectivity (isolation) and these patches are generally large (mean resource area=68.6m$^2$±19.2, $n$=20) (Fig. 4); vacant ideal habitat occurs in either isolated (connectivity index <12) and/or small patches (mean resource area=5.7m$^2$ ±2.2, $n$=5).

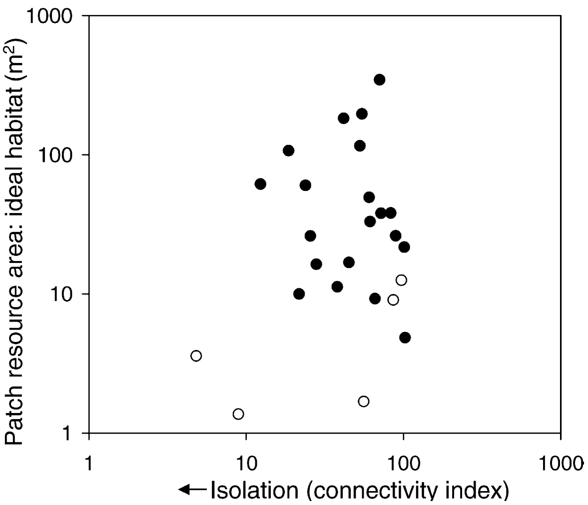


**Fig. 4** Distribution of the Sinai Baton Blue in patches containing apparently high-quality habitat (habitat score 4.5 or more). *Open circles* represent vacant patches, and *solid circles* patches containing a Sinai Baton Blue colony

## Population size

Once habitat requirements have been fulfilled, logic suggests that the amount of available resource must become a limiting factor to the population utilising that resource. Thus in addition to helping to predict mere presence or absence of the Sinai Baton Blue, it should also act as a predictor of the number of butterflies that are likely to be found in the suitable habitat.

If patch isolation is plotted against the resource area of suitable habitat using population number to distinguish individual patches (as opposed to presence/absence), all sizeable populations (>25 individuals) are in patches containing >50 m$^2$ of suitable habitat (cf. Fig. 2). As expected there is a significant positive correlation between resource area of suitable habitat and population size ($r$=0.690, $n$=32, $P$<0.01). Resource area appears to

**Table 3** Multiple regression analysis (stepwise) relating distribution of Sinai Baton Blue population sizes in patches, with resource area and habitat quality

| Variables available (independent) | Variables in final model (all terms significant at $P<0.05$) | $B$ | Model | | | |
|---|---|---|---|---|---|---|
| | | | $F$ | $df$ | Significance ($P$) | % of variation |
| Resource area | Resource area | 0.013 | 25.7 | 2 | <0.001 | 60 |
| Mean sub-site score/patch | Mean sub-site score/patch | 0.619 | | | | |

put a limit on the size a population of Sinai Baton Blues can attain.

In stepwise multiple regression with population size as the dependent variable, resource area (of suitable habitat) enters first, and then habitat quality (Table 3). Small but high-quality patches are able to support populations larger than would be expected from their resource area alone.

Thus once habitat quality has been assessed, the presence of the Sinai Baton Blue at a site can be largely explained by the amount of available resource present and the problems of physically getting to the site (its isolation). The resource area of the site and the quality of that resource further limits the size that a population of Sinai Baton Blues can achieve.

## Discussion

At the beginning of this study, the only known habitat criterion for the Sinai Baton Blue was the presence of its host plant, Sinai Thyme. In an attempt to understand the distribution of this butterfly, two general approaches were taken, namely habitat characterisation, and the spatial arrangement of that habitat in the landscape.

### Habitat requirements

Habitat specificity has been found in other species of butterfly (e.g. Thomas 1991; Thomas and Harrison 1992; Thomas and Jones 1993; Dennis and Eales 1997; Gutiérrez et al. 1999); indeed it has been suggested that such habitat selection restricts distribution. Therefore the first task was to try and ascertain whether those patches and sub-sites in which no butterflies were seen were vacant because they were unsuitable for the Sinai Baton Blue, or for some other reason.

High plant diversity, and thyme plants with a large resource area, were major factors in describing habitat for the Sinai Baton Blue. Both these factors may indicate areas in which the soil was more developed and/or fertile and the water content higher, presumably important to a butterfly living in a hot, arid environment and with limited powers of mobility. When studying *Melitaea cinxia* in Finland (where water is not limiting), Moilanen and Hanski (1998) found that immigration was increased and emigration reduced in areas containing high densities of flowers. Whilst lots of different species of plants (and abundance/diversity of potential nectar sources) might make the site attractive to a searching butterfly (Kuussaari et al. 1996; Hanski 1999), it is likely that the resource area of a host plant has a more subtle role. Baton Blue larvae were never observed moving from the plant on which they hatched, thus individual plants with a larger resource area would be more likely to contain enough resource for survival and growth. Myers (1985) showed that *Pieris rapae* preferentially oviposited on (greener) plants in good physiological condition and that this behaviour gave a fitness advantage to developing larvae. Soil moisture and/or temperature are likely to act as a cue for adult emergence; both of these factors will be altered by shade from the host plant (Thomas et al. 1999), which in turn is a function of its size, shape and condition.

The study of macro-habitat characteristics showed that the degree of shelter in a sub-site might also determine habitat suitability. Shelter is an important determinant of habitat in other mostly temperate species. It has been suggested this is because butterflies select a warm microclimate (Thomas 1983b; Thomas 1985; Thomas et al. 1986, 1999; Gutiérrez et al. 1999), though it is unlikely that the Sinai Baton Blue is limited by cold temperatures. The fact there was no preference for warmer (southerly) aspects, as in some northern hemisphere species at the coldest edge of their geographical range (e.g. Thomas 1985; Thomas et al. 1986, 1999; C. D. Thomas et al. 2001) also suggests sites are not being selected for their warmth. Indeed sheltered areas in this landscape are likely to be both cooler and damper than exposed areas as a result of reduced insolation, again suggesting that if the Sinai Baton Blue is selecting an area because of its microclimate, it is probably doing so for opposite reasons to temperate species at their northern range boundaries (Parmesan et al. 1999; Thomas et al. 1999).

The index of habitat suitability is useful in conservation as newly discovered habitat can quickly and easily be assessed for its likelihood to contain butterflies, or vacant habitat its appropriateness for (re)-introductions. A problem with this method is that habitat might be quantified as suitable not as a result of the quality of that habitat, but due to its proximity to truly high-quality habitat; in effect areas containing suitable habitat might be “sinks”, and ideal habitat “sources”. Unfortunately we do not have the data to test this.

Further studies, particularly involving oviposition behaviour, will help to refine further the characteristics of the habitat occupied by Sinai Baton Blues, and will also enable habitat requirements to be assessed at a third and finer resolution, that of the individual plant.

## Metapopulation structure

The Sinai Baton Blue inhabits a discontinuous patch network throughout its known range and this forms the habitat that is relevant for the butterfly's possible metapopulation dynamics. Measured distances between patches take no account of the inter-patch habitat, a factor hypothesised to be an important determinant of "real" inter-patch distance (Watt et al. 1977; Shreeve 1992; Åberg et al. 1995; Weins 1997; Moilanen and Hanski 1998). Patches of Sinai Thyme were usually separated from one another by ridges if not mountains, and the patch itself was often enclosed on one or more sides by steep (often bare) rock faces. In addition to the physical difficulties of moving across such terrain, "rule-of-thumb" searching patterns would presumably prevent the butterfly from straying too far from its suitable habitat. However, in another sedentary, patchily distributed lycaenid butterfly (*Euphilotes enoptes*), Peterson (1996) discovered a level of gene flow much greater than would be expected from a species with limited powers of dispersal. Thus, the Sinai Baton Blue may be able to move within its restricted patch network, despite the apparent difficulties, and this ability may be crucial to its long-term persistence.

Patch resource area helped in predicting presence/absence of Sinai Baton Blues and was also significant in determining the number of butterflies living there. This relationship helps predict local extinction in the patch network: small populations are more susceptible to demographic extinction, and small resource areas to environmental stochasticity (e.g. catastrophic destruction) (Thomas 1994; Hanski et al. 1995; Sutcliffe et al. 1997a; Thomas and Hanski 1997; Hanski 1999). The small population sizes and relatively low numbers of individuals in the entire system suggests that the absolute number of migrants from a patch is limited, and thus successful movement between patches a rare event (Lewis et al. 1997; Gutiérrez et al. 1999; Hanski et al. 2000; Roland et al. 2000).

Three patches of ideal habitat were vacant despite having a high degree of connectivity. These patches had a small resource area, with the potential to support only a small population with consequently a higher probability of extinction (demographic or stochastic). Due to their proximity to occupied patches, one would predict their successful (re)-colonisation in the near future; indeed in one of these patches a single butterfly was sighted in 2001. The index of habitat suitability includes information on plant diversity, and the degree of shelter. Large values of these two variables indicate additional resources which would help support larger populations and/or enhance population persistence (Sutcliffe et al. 1997a). Thus the quality of a patch can to some extent act as a substitute for patch area (Hanski and Ovaskainen 2000). In our study habitat quality, patch resource area and isolation were useful in helping to predict occupancy, and habitat quality remained important after patch resource area had been accounted for when describing the distribution of population sizes. We therefore agree with J. A. Thomas et al.'s (2001) claim that, "variation in habitat quality is the third missing parameter in metapopulation dynamics...'

The small size of almost all Sinai Baton Blue populations suggests that the species is liable to frequent local extinction. Even the largest populations numbered only several hundred individuals, and so these are also presumably at risk from extinction. Given the lack of data regarding the Sinai Baton Blue's past distribution, it is impossible to tell how patch occupancy has shifted through time. Future extinction and colonisation events will help clarify the dynamics of the species, and the degree to which its long-term persistence depends on metapopulation processes rather than on the long-term survival of local populations. The habitat patches themselves will alter in quality over time, and will be susceptible to extinctions and (re)-colonisations, thus shifting the patch network in space. It is presently impossible to assess the extent to which this occurs, though consultations with Bedouin experts suggest that patches of thyme can be temporary, appearing or vanishing within a lifetime (personal communication).

The distribution of the Sinai Baton Blue is highly localised, primarily because of its dependence on its host plant, Sinai Thyme. Features of the plant and the habitat in which it grows define its suitability (quality) for Sinai Baton Blues and this increases the restrictions placed on the butterfly's distribution. The ability of the butterfly to locate, reach, and persist in this restricted habitat network further determines its distribution at any given point in time. Thus, habitat quality and metapopulation dynamics combine to help us to understand why some patches of apparently suitable habitat are vacant, and to predict how the pattern of patch occupancy is likely to change through time (Harrison et al. 1988; Wahlberg et al. 1996; Dennis and Eales 1997; Moilanen and Hanski 1998; Gutiérrez et al. 1999). Knowledge of the health (size) of populations in occupied patches provides insights into the future distribution of the Sinai Baton Blue by revealing features of the habitat overlooked when assessing this distribution in terms of presence or absence only. All these factors are essential for conservation assessments of this rare and endemic species.

This study shows that a metapopulation approach is informative when applied to the entire known range of a narrow endemic species, provided that habitat quality is also considered.

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