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Immigration and emigration in the Sinai Baton Blue butterfly: estimates from a single patch

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ABSTRACT

The movement of individuals among patches of suitable habitat is a key process in metapopulation biology, but is very difficult to observe under natural conditions. Thus, many estimates of rates of movement are indirect and incomplete, and there is little empirical knowledge of the factors affecting immigration and emigration. I studied intensively a local population of Sinai Baton Blue butterflies in a discrete habitat patch. The study lasted the entire adult flight period, and involved almost every individual in the local population. Using these data I attempted to estimate the number of immigrants and emigrants, and identified an important factor affecting inter-patch movement. Early in the season, individuals were resident in the study patch for only a very short time; I assumed this was because they were emigrating, and thus estimated that at least 14% of the population emerging in the study patch emigrated. I assumed that butterflies not caught until they were relatively old, had immigrated to the patch (rather than being missed at a young age), and thus estimated that 13% of the population caught in the patch was composed of immigrants, most of which were females. Individuals assumed to be immigrants arrived in the patch throughout the adult flight period, but older individuals generally arrived later in the season. Timing of migration was almost certainly linked to phenology of the butterfly's only hostplant, Sinai Thyme. Most butterflies remained in their natal patch. The degree of inter-patch movement estimated using this method was consistent with other metapopulation studies, and would suffice for this species to exist as a metapopulation.

INTRODUCTION

A metapopulation is a set of local populations, and typically each local population occupies a patch of suitable habitat (Moilanen & Hanski 1998). It is often easier and more practicable to delimit these local populations in terms of the discrete habitat patches they occupy. However, it is the degree of movement of individuals among patches that is fundamental in delimiting local populations (Ims & Yoccoz 1997). As well as helping to define local populations, the transfer of individuals among them also has important implications for their population biology and persistence (Hanski et al. 1995). Migration is therefore a key process in metapopulation biology, and to understand population-level processes in fragmented landscapes, it is vital to study both the spatial arrangement of the patches of suitable habitat and the movement of individuals among them .

An individual is expected to migrate whenever moving away is expected to increase individual, or inclusive fitness (Baker 1978). Many factors affect the costs and benefits of migration and these will fluctuate across space and through time. Examples of these factors include: inbreeding avoidance, competition for resources, conspecific attraction, bet hedging (an individual distributing its offspring widely will reduce the adverse impact of a poor year in the natal population), and migration mortality (only a fraction of individuals emigrating from local populations are expected to reach another patch of suitable habitat and successfully breed there) (Hanski 1999) .

Knowing which individuals migrate will help to determine why they migrate. A better understanding of these factors is critical for the successful conservation of metapopulations and networks of habitat patches (Kuussaari *et al.* 1996). Thus the evolution of migration rate is now an important topic in evolutionary ecology, particularly in today's increasingly fragmented landscapes (Hanski 1999; Thomas 2000; Thomas *et al.* 2001). The tendency, or ability of individuals to move away from their place of birth may be linked to environmental conditions (McPeek & Holt 1992; Kuussaari *et al.* 1996; Menéndez *et al.* 2002), or be to some extent heritable, in which case it is an important determinant of the genetic constitution of a population (Dingle 1996; Olivieri & Gouyon 1997) .

Emigration from habitat patches, the behaviour of migrating individuals, and colonisation of empty patches, are all very difficult to observe under natural conditions. This is particularly true when emigration rates are low (Kindvall 1999), and when several habitat patches need to be considered simultaneously, both of which are typical on the spatial scale of metapopulations. Because of these difficulties, we have little empirical knowledge of the factors affecting immigration and emigration (Hanski 1999) .

Studies involving butterflies, one of the most intensively studied groups of animals, highlight the problems of acquiring reliable empirical evidence of migration. Simple mark-release-recapture (MRR) studies suggested that many species were extremely sedentary with little or no inter-patch movement. However, when more intensive MRR work was carried out in several patches simultaneously, it became apparent that in some supposedly 'sedentary' species up to 30% of individuals emigrated from the population (Hanski *et al.* 1994; Nève *et al.* 1996; Thomas & Hanski 1997).

One of the main problems when examining MRR data is that it does not separate the components of transfer, making it difficult to distinguish between individuals that die or emigrate, and between individuals that immigrate or get recruited in situ. In this study, I attempt to separate these factors by studying in detail the short-term population changes occurring in just one discrete habitat patch, collecting data on virtually every adult (the mobile stage) appearing in the patch throughout the adult flight period. I use this 'patch-specific' approach to try and estimate migration rate, and to understand possible causal factors of emigration from the patch, and immigration to the patch. My system is particularly suitable because it concerns inter-patch movement in a rare species of butterfly living in a fragmented landscape that exhibits the characteristics of surviving as a true metapopulation (James *et al.*, 2003; James, 2006a,b,c,e,f; Hoyle & James, 2005) .

Using the information I determine / estimate: (1) the number of immigrants to the study patch; (2) the number of emigrants from the study patch; (3) how these numbers change over time; and (4) which individuals are most likely to migrate and possible reasons why. The study also provides an insight into whether the study patch is self-sustaining (i.e. whether it is a 'source' or a 'sink'), and investigates the level of exchange of individuals among patches, which will help define the spatial population structure of the species.

MATERIALS AND METHODS

Study species and habitat: The Sinai Baton Blue butterfly (*Pseudophilotes sinaicus* Nakamura: Lepidoptera, Lycaenidae) is endemic to the St. Katherine Protectorate in South Sinai, Egypt (Nakamura 1975), where its only known larval hostplant, the near-endemic Sinai Thyme (*Thymus decussatus* Benth.: Labiatae) is patchily distributed among the mountains (James *et al.*, 2003). It has an intimate association with this hostplant: eggs are laid singly on young thyme buds and the developing larvae feed on buds and flowers of the plant on which they hatched; pupation and overwintering take place in the soil below. 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 (personal observation). Adults almost always court and mate on the host inflorescences, and males usually mate with newly eclosed females before they have taken their first flight. Adults feed almost exclusively on Sinai Thyme when it is in flower, but have been recorded taking nectar from four other plant species (e.g. *Globularia arabica*), especially when thyme flowers are unavailable (James 2006f). Predation is probably the main source of adult mortality: spiders, praying mantids, birds, and particularly lizards (family Agamidae) have all been seen attacking Sinai Baton Blues (personal observation). During their main flight period, adults have a constant daily survival rate of approximately 0.8 (James 2006c). It is a tiny species and occurs in a single generation with adults from mid-April to early-July.

Development of Sinai Thyme: The stage of development of each individual thyme plant in the study patch was measured weekly: five inflorescences were randomly selected from the most advanced part of the plant and their development scored on a 0-7 scale (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 head; 7 = >50% flowers over/seed heads). The average of these five scores represented the stage of development of the plant, and the average score of all plants the overall stage of thyme development in the study patch.

Study site: The study was carried out in Farsh Shoeib, a patch of vegetation (13,600 m2) bordered on all sides by steep, bare cliffs and dominated by Sinai Thyme. Farsh Shoeib is close to Gebel Safsafa on the Mt. Sinai massif and is at an altitude of 1995 m; five other patches of thyme occur on the massif, separated from one another by at least 100 m, and ranging in altitude from 1,995 m to 2,030 m; Baton Blues are present in four of them (Fig. 1). The closest Baton Blue population not located on the Mt. Sinai massif is 2,200 m away from Farsh Shoeib. One thousand two hundred and twelve individual thyme plants were located and marked in Farsh Shoeib, distributed throughout the patch.

Weather conditions throughout the study period were fine and dry (no rain at all). Maximum daily temperature ranged from 17-28 °C in the early part of the flight period (mean 23 °C ± 0.5), and 19-35 °C in the main part of the flight period (mean 28 °C ± 0.4). At night the temperature rarely dropped below 10 °C.

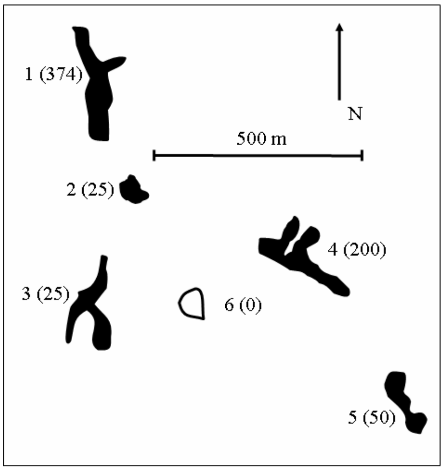

Fig. 1 The network of Sinai Baton Blue habitat patches on the Mt. Sinai massif. Filled shapes represent occupied patches, and open shapes vacant patches. Patch 1 is the study patch; numbers in brackets represent the estimated population of butterflies occurring in each patch.

Survey of butterflies: A mark-release-recapture (MRR) study was carried out over 97 consecutive days, from 8th April to 13th July 2002 in Farsh Shoeib. Every day from dawn to sunset, 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 newly eclosed butterflies. New adults were always near the top of the plant, in pristine condition with particularly bright orange markings, and unable to fly. New adults were caught and marked individually on the underwing using permanent marker pens, assigned a wing-wear score of 5, and returned to the same plant. Whilst walking this route any previously marked individuals were identified and noted. The butterflies never roosted on thyme, but chose other plants (mainly *Jasonia montana*) at the edge of the study patch and the tips of dead stalks/dry flower heads, and were very easy to find. Potential roosting sites were examined for Baton Blues every dawn and dusk, and the identity of roosting individuals recorded. When unmarked butterflies were seen flying in the patch or found whilst roosting, they were caught, marked, their wings scored for damage (1 = tatty to 4 = pristine) in order to estimate their age, and then released at the point of capture.

No butterfly was caught more than once: instead, close-focus binoculars were used to identify marked individuals (a 'recapture' was actually a 're-sighting'). Marking took place through the mesh of the butterfly net. This ensured that the effects of handling were kept to a minimum. The phenology of all butterflies caught for the first time was recorded as the number of days after the first butterfly eclosed in Farsh Shoeib (day 1). Butterflies eclosing before day 35 are classed as 'early', and butterflies eclosing on or after day 35 as 'main' (see Results).

Adult residence times were calculated by two methods: (1) the mean minimum lifespan of all individuals captured at least once (number of days between first and last sighting), and (2) using residence decay plots (following Watt *et al.* 1977). The first method bases residence on all marked animals and can be calculated for any stage of the sampling period; the second calculates residence using only those butterflies recaptured at least once on a subsequent sampling occasion.

Assumptions: My approach assumes all newly eclosing butterflies in the patch are located and marked on their day of emergence, ideally before they have taken their first flight, so that any unmarked individuals discovered flying in the patch must be immigrants. However, some butterflies emerging in the patch will start flying before they have been caught. To distinguish between these unmarked butterflies and immigrants, it was assumed that immigrants would be older and in worse condition at first capture than natal butterflies (due to age and/or their journey), and this would be indicated by their wing condition.

Because of the intensive marking effort, it is believed the majority of butterflies were marked at or close to their minimum possible age on entering Farsh Shoeib. I estimated population size in Farsh Shoeib in 2002 using the Jolly-Seber model (James, 2006c). My estimates indicated that 84% of the Sinai Baton Blue population in Farsh Shoeib was captured using the method described above, and on average only 15% of the estimated population was not recorded on a given day, but then observed on the next or subsequent days – i.e. were missed on a typical day's recording.

In 2002 change in wing wear of individuals was not monitored through time. However, in 2003 a similar MRR study was carried out on the Sinai Baton Blue, and every time an individual was re-sighted its wing wear was re-assessed. Wing wear in the 2003 study was negatively correlated with time since first capture (Fig. 2). If the rate of wing wear was the same in 2002, then butterflies first caught with a wing wear score of 4 were two days old or less, so it is possible they emerged in the patch but evaded capture for a day or two; they cannot be distinguished from butterflies known to have eclosed in the patch. Butterflies first caught with a wing wear score of less than 4 were at least three or four days old. If all individuals have the same chance (0.15) of being missed, then to evade being seen for three or four successive days is very unlikely (probability 0.003 and 0.0005 respectively). Given the low probability of not catching a butterfly present in the patch, the fact wing wear increases with age, and the likelihood that wing condition deteriorates during a migration event, it is reasonable to assume that butterflies first caught with a wing wear score of less than 4 were immigrants.

One way of assessing the accuracy of the wing wear score using butterflies caught in Farsh Shoeib in 2002, is to calculate residence of individuals of different wing wear score at first capture. This assumes that all individuals have the same life expectancy (in the patch), and if wing wear reflects age then individuals first caught with a high wing wear score will be present in the patch for longer than those with a low score. As expected (using residence estimates from either of the two methods of calculating it), residence time for both males and females with a wing wear at first capture of less than 4 was shorter than for individuals scoring 4 or more, though this difference was not significant (Table 1). Females with wing wear 4 had approximately the same mean expected residence time as females scoring 5 (as expected); males with wing wear 4 were resident for a slightly shorter period of time than males scoring 5, but this difference was not significant.

Using this information, I conclude that the data are sufficient to justify assumptions used in my estimation of immigration and emigration rates.

Table 1 Mean residence time (days) for butterflies of different wing wear score at first capture, as estimated by two separate methods. Results for individuals scoring less than 4 at first capture have been combined due to the small sample sizes

Wing wear score	Female: residency (days)			Male: residency (days)		
	n	Recapture decay plot	Mean minimum lifespan (± s.e.)	*n*	Recapture decay plot	Mean minimum lifespan (± s.e.)
5	118	3.73	4.5 ± 0.4	130	5.23	5.4 ± 0.5
4	65	3.73	4.6 ± 0.5	61	4.87	4.9 ± 0.6
1,2,3	36	3.03	3.6 ± 0.5	21	4.65	4.7 ± 1.0

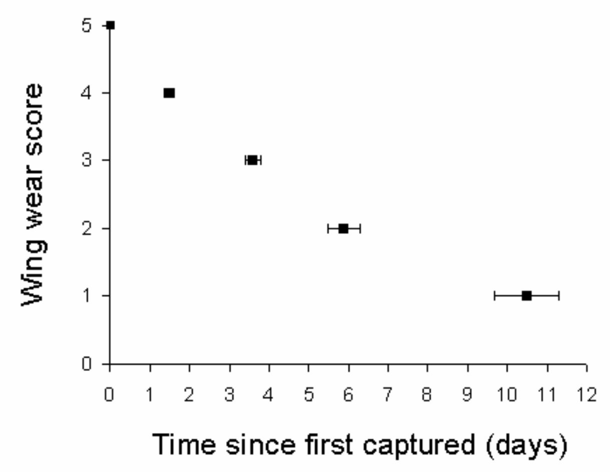

Fig. 2 Change in wing wear score with time since first capture, in an MRR experiment carried out in 2003. Mean number of days since first capture (± s.e.) are given for each of the 4 possible wing wear scores following release of newly emerged individual; there is a significant negative correlation between wing wear score and age (Spearman rank correlation, $r_s = -0.9$, $n = 114$, $p < 0.001$). Results for males and females are combined due to the small sample size (n = 42 butterflies)

RESULTS

Immigration: In total 431 butterflies (219 females, 212 males) were caught and marked in the study patch. The majority of these (58%) were caught before they had taken their first flight (wing wear 5) and so definitely eclosed from a known plant; a further 29% of all butterflies were first caught whilst still in pristine condition (wing wear 4), so it is reasonable to assume that these also eclosed in the patch although from which plant is uncertain. The other butterflies (n = 57) were first caught after their wings had deteriorated in condition (wing wear less than 4), indicating they were older. It is unlikely that these butterflies would have been overlooked had they eclosed in the patch (see Methods, above), and so these are all assumed to be immigrants: 40 butterflies had a wing wear of 3 and are classed as 'young' immigrants; 17 butterflies had a wing wear of less than 3 and are classed as 'old' immigrants (Table 2). In total, 13% of the adult Sinai Baton Blue population in the patch was estimated to be immigrants.

The number of males and females eclosing in the patch changed through the study period (Fig. 3). The study spanned the entire adult flight period and assuming this period was similar in other populations providing the patch's immigrants, those immigrants will to a certain extent reflect the number of eclosing adults. A correlation exists in both the sexes, between numbers eclosing on a given date and numbers immigrating on that date (females: $r_s = 0.361$, n = 97, $p < 0.001$; males: $r_s = 0.389$, n = 97, $p < 0.001$). This correlation is biased by the inclusion of data at the start and end of the season when adult numbers (and therefore potential immigrants) are extremely low. To remove this bias the correlation analysis can be restricted to the period between the first and last immigrant (females = days 26-78; males = days 24-70): the correlation between numbers immigrating and numbers eclosing disappears when this is done (females: $r_s = 0.095$, n = 53, ns; males: $r_s = 0.057$, n = 47, ns). Relative to adult females eclosing in the study patch, females believed to have immigrated were common around day 29 and again around day 64 (Fig. 3). The number of male immigrants is more constant throughout the study period than female immigrants, though relative to eclosing males they are also most common around day 64 (Fig. 3).

Although overall the sex ratio did not differ from 1:1 ($\chi^2_1 = 0.1$, ns), more females immigrated to the patch than males ($\chi^2_1 = 3.95$, $p < 0.05$). There were more old female immigrants than old male immigrants ($\chi^2_1 = 4.76$, $p < 0.05$), but the number of young immigrants did not differ significantly between the sexes ($\chi^2_1 = 0.90$, ns) (Table 2).

Old females immigrated to the patch later in the season than young immigrant females (Kruskal-Wallis test, KW = 4.59, $p < 0.05$). Old males also seemed to immigrate to the patch later than young males, but the sample size is very small (n = 4 old immigrant males) and the difference between these two groups is not significant (KW = 2.47, ns).

Table 2 The status and abundance of Sinai Baton Blue butterflies caught in the study patch during 2002. Numbers of immigrants and emigrants have been estimated using the methods outlined in the text. Numbers of emigrants are given before survival rates have been considered (see Results)

Sex	Status	Number	% Total population (*n* = 431)
Female	Resident (stay in patch)	154	35.7
	Emigrant (move away from patch)	29	6.7
	‘Young’ Immigrant (wing wear score 3 when enter patch)	23	5.3
	‘Old’ Immigrant (wing wear score <3 when enter patch)	13	3.0
Male	Resident (stay in patch)	142	32.9
	Emigrant (move away from patch)	49	11.4
	‘Young’ Immigrant (wing wear score 3 when enter patch)	17	3.9
	‘Old’ Immigrant (wing wear score <3 when enter patch)	4	1.0

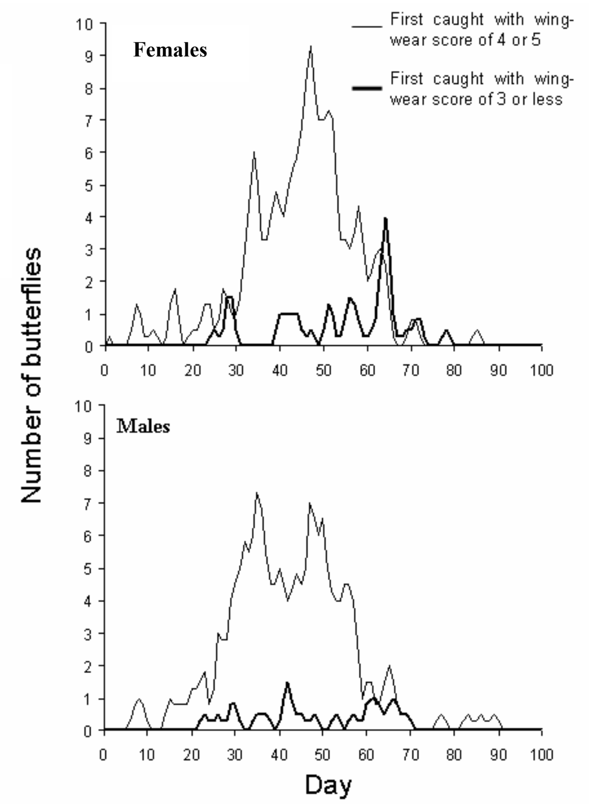

Fig. 3: Phenology of female (upper) and male (lower) butterflies caught for the first time (moving average of three successive days). Days are numbered from the day the first butterfly eclosed

Emigration: Among butterflies eclosing in the study patch, the number of days that both males and females were resident increased with thyme plant development (females: $r_s = 0.274$, $n = 183$, $p < 0.001$; males: $r_s = 0.396$, $n = 191$, $p < 0.001$). Figure 4 shows the phenology of the patch's thyme plants: thyme buds (i.e. oviposition resource) were only present in the patch for 41 days (days 32-72). If the length of time that a Sinai Baton Blue spends in an area is dependent on availability of this resource, one would expect butterflies to be present in this particular patch for considerably longer between days 32-72. In fact there is a marked change in residence time in males and females after day 34, just three days after the first thyme plants started coming into bud (Fig. 4). Because of these differences, butterflies eclosing before day 35 are classed as 'early', and those eclosing on or after day 35 as 'main'. There is an indication that butterflies eclosing in the patch after day 72 spent fewer days there than butterflies eclosing on days 35-72 (Fig. 4), but these estimates are based on just four males (mean days in patch = 3.75 ± 1.44) and one female (days in patch = 3).

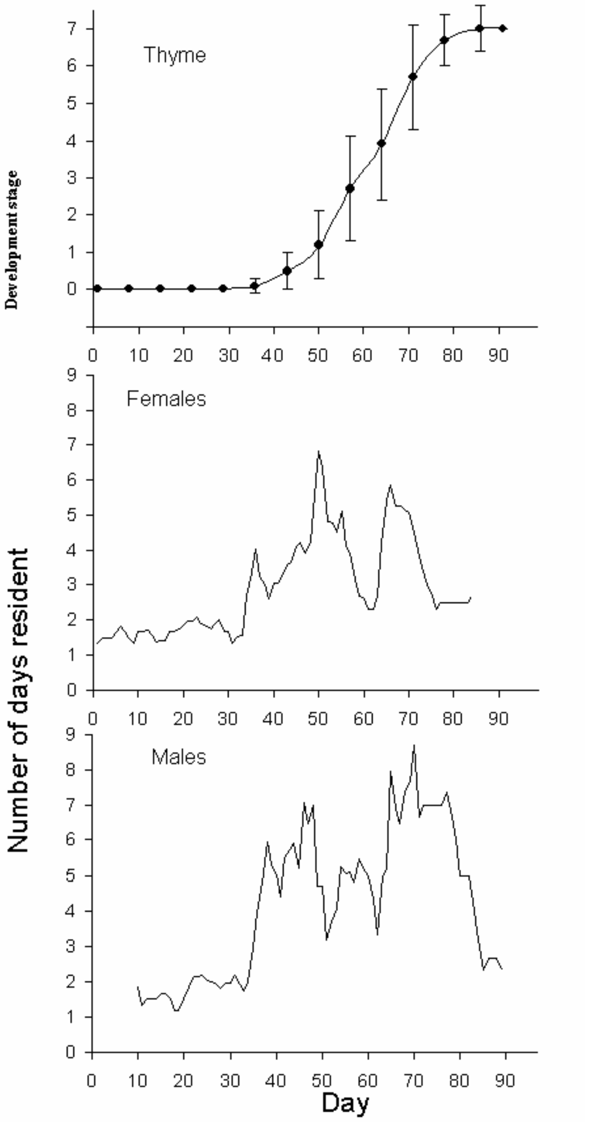

Fig. 4 Mean phenology (± s.e.) of thyme plants (upper) and residence time of female (middle) and male (lower) butterflies in the study patch (mean minimum lifespan: moving average of three successive days). Days are numbered from the day the first butterfly eclosed

Table 3 shows the residence time of individuals caught in Farsh Shoeib. Differences between time periods and between sexes are made by comparing mean minimum lifespans: among individuals eclosing in the study patch, 'main' females were resident for significantly longer periods of time than 'early' females (independent samples test, $t_{181} = 4.4$, $p < 0.001$); the same was true for males ($t_{189} = 5.6$, $p < 0.001$). There was no significant difference between the sexes in the number of days that 'early' butterflies eclosing in the patch spent there (independent samples test, $t_{76} = 0.9$, ns). Among 'main' butterflies eclosing in the patch, males were resident longer than females (independent samples test, $t_{294} = 2.5$, $p < 0.05$). Among young immigrants of both sexes, those arriving 'early' spent shorter amounts of time in the patch than those arriving in the 'main' period, but this difference was not significant in either case. Interestingly, during the 'main' period in both sexes, the mean minimum lifespan of young immigrants was approximately one day less than butterflies eclosing in the patch. Immigrants are older on entering the patch, so this is to be expected.

In total, 21% (n = 78) of Sinai Baton Blues eclosing in the study patch were classed as 'early'. There were more 'early' males than females ($\chi^2_1 = 5.12$, $p < 0.05$). Given the consistent difference in residence time between 'early' and 'main' butterflies (depending which method of calculation is used, the difference is 2-3 days in females, 2-4 days in males), early butterflies are assumed to be emigrants. However, some of these individuals will have died in the patch rather than have emigrated. Within-patch mortality can be accounted for using their survival rates (James, 2006c): daily female survival rate (0.78) applied over two days reduces the potential number of female emigrants to 18, and male survival rate (0.82) applied over two days reduces potential male emigrants to 33. Thus, I estimate that 14% (n = 51) of butterflies eclosing in Farsh Shoeib emigrated.

Table 3 Mean residence time (days) of butterflies entering the study patch during the 'early' (before day 35) or 'main' (on or after day 35) flight period, as estimated by two separate methods

Group and method of estimation	Females		Males	
	'Early' (< day 35)	'Main' (≥ day 35)	'Early' (< day 35)	'Main' (≥ day 35)
Eclosed in study patch (mean minimum lifespan)	1.8 ± 0.2 (range 1-10, *n* = 29)	5.0 ± 0.3 (range 1-18, *n* = 154)	2.1 ± 0.3 (range 1-10, *n* = 49)	6.3 ± 0.4 (range 1-24, *n* = 142)
Eclosed in study patch (residence decay plot)	1.36	3.23	2.35	4.63
'Young immigrants' (mean minimum lifespan)	1.8 ± 0.2 (range 1-2, *n* = 5)	4.1 ± 0.7 (range 1-12, *n* = 18)	2.0 ± 0.4 (range 1-3, *n* = 4)	5.1 ± 1.3 (range 1-13, *n* = 13)

DISCUSSION

The main objective of this study was to try and estimate the migration rate in the Sinai Baton Blue butterfly using data from an MRR study conducted in only one of its habitat patches.

The Sinai Baton Blue has an intimate association with Sinai Thyme, specialising on its ephemeral inflorescences. The butterfly is therefore likely to suffer increased mortality or decreased fecundity if the timing of its development does not match that of the thyme. Butterflies eclosing in a patch of thyme before the plants have come into bud, or when the thyme flowers are over, find themselves in unsuitable habitat. Confronted with little or no oviposition resource a butterfly can stay put in the hope that conditions improve, or migrate in search of favourable conditions. In a related butterfly (*Euphilotes enoptes*), Peterson

(1997) demonstrated that the hostplant's inflorescences influenced dispersal: females followed the hostplant phenology up an altitudinal gradient.

During the adult flight period, I estimated that 57 butterflies immigrated to the patch. This might be an overestimate because some butterflies could eclose in the patch but evade capture for several days, and so their wings would deteriorate in condition and they would be misclassified as immigrants. However, the data suggest this scenario was very unlikely because of the intensive survey method employed (James 2006c).

If an individual was not seen again after it had been caught and marked, it was assumed to have either died or emigrated. Thus the relatively short time that 'early' butterflies were resident in the study patch implies either that they had a much higher rate of mortality than butterflies in the 'main' period, or that their rate of emigration was higher. Nectar plants were available to Baton Blues before Sinai Thyme began flowering; indeed they were often seen feeding on *Globularia arabica* flowers which were abundant in the study patch before day 35 (James, 2006f), so it is reasonable to assume adults had sufficient food during this period. It is also unlikely that mortality due to predation caused the short residency time seen in 'early' butterflies: density of predators was not noticeably higher in the 'early' period. Weather conditions were stable throughout the study period and are unlikely to have had any adverse affect on survival. These observations, and the butterfly's dependence on thyme inflorescences, suggest the discrepancy in residency length between 'early' and 'main' butterflies is most likely to be a result of emigration. Emigration has been linked to resource availability in other butterfly studies, though the pattern is usually the reverse of that observed here, with emigration increasing over the course of the flight period matching a decrease in nectar abundance and/or declining quality of larval food (Kuussaari *et al.* 1996; Matter & Roland 2002; Schtickzelle *et al.* 2002).

The discrepancy in residency between 'early' and 'main' individuals could also result from 'early' individuals simply emigrating at a younger age. However, the mean number of days resident in 'main' butterflies (conservatively 3-6 days) is similar to the adult life-span recorded in other lycaenid butterflies (Scott 1973; Arnold 1983), which implies that these butterflies are probably dying in the study patch, and not emigrating.

Emigration from the study patch was estimated at 14% (51 individuals). In other specialist butterfly species, migration between patches varies from over 20% (e.g. *Melitaea cinxia*, Hanski *et al.* 1994; *Hesperia comma*, Hill *et al.* 1996; E. enoptes, Peterson 1997), to less than 3% (e.g. *Mellicta athalia*, Warren 1987; *Plebejus argus*, Lewis *et al.* 1997). In terms of the patch's overall health there is a balance between emigration and immigration: 51 individuals emigrated and 57 immigrated. However, emigration is likely to be slightly higher than indicated from my estimate because it is possible that some 'main' individuals also emigrated (see below).

I found the butterflies to be extremely sedentary within the patch, rarely moving more than 50 m between re-sightings; these data are part of a study on intra-patch movement (James, 2006e). These results emphasise how easy it would be for a less intensive survey to conclude that migration in the Sinai Baton Blue is negligible.

My estimates of immigration indicate that it was highest just before and just after the main period of eclosion. Butterflies emerging early in the season might find insufficient oviposition resource in their natal patch, and so be inclined to migrate. It is interesting that the pattern of residency length among young immigrants pre- and post-day 35 was similar to butterflies eclosing in the patch during those periods: 'early' immigrants discover inadequate oviposition resource in the study patch, and so are forced to migrate again. Individuals that were assumed to have immigrated during the main flight period were generally older and most were female. Much of this movement occurred before day 72 when thyme plants still provided oviposition resource, which suggests that in addition to migrating in search of these resources some females, perhaps on reaching a certain age or condition, might be inclined to migrate from one suitable habitat patch to another (Shreeve 1992; Warren 1998). This might explain the lower residence time of 'main' females compared with males, and is a very common strategy in many ovipositing insect species (e.g. Fitt 1986; Sadeghi & Gilbert 2000). In the butterfly *Lopinga achine*, females move away from their natal site after laying two-thirds of their eggs (Bergman & Landin 2002). When an individual moves between populations, the array of ecological conditions it experiences is modified, so migration can be viewed as an example of a bet-hedging strategy (McPeek & Holt 1992). In this study, emigration of 'main' individuals cannot be distinguished from mortality, but the low number of old immigrants and the match between residency lengths of 'main' individuals and their probable adult life-span, suggest this type of emigration is minimal. It would be interesting to know the level of mortality during migration, so the cost of migrating could be assessed.

The relatively reduced need for a phenological match with the hostplant in males, together with different costs and benefits associated with their migration, also helps to explain the differences observed between males and females that were assumed to have immigrated. A higher migration rate in females is common in many related species (e.g. Arnold 1983; Peterson 1997). The fact that more males were estimated to have emigrated from the study patch than females is to be expected using my method of estimation because more males eclosed before day 35 than females.

The approach used in this study provides no information as to where emigrants from the study patch go, or from which patch immigrants originate. I attempted to discover this in 2003 by increasing the MRR study to include patches 2-6 as well as Farsh Shoeib (Fig. 1). My study coincided with a severe drought in the area and population sizes in patches 1-5 were greatly reduced (James, 2006c). However, two females (aged 4 and 9 days old) did immigrate to Farsh Shoeib, one from patch 4 and one from patch 5 (via patch 4). Thus, whilst that study cannot confirm the levels of migration estimated using my patch-specific approach (because of the huge differences in population sizes between the years), it does confirm that individuals are able to move between even the most distant patches on the Mt. Sinai massif. It would be useful to repeat the 2003 study during a year of 'normal' butterfly numbers as this would provide an indication of the accuracy of the immigration and emigration rates estimated in this study. It would also be interesting to acquire additional information on the phenology of butterflies and plants in other patches. This would help to establish whether migration is an important means of finding resources before or after they are available in a butterfly's natal habitat patch.

Patches of thyme on the Mt. Sinai massif are close to one another (relative to other patches), and so it is reasonable to assume that the majority of immigrants originated from these patches (Harrison 1989; Kuussaari *et al.* 1996; Wahlberg *et al.* 2002). The timing of adult eclosion is likely to be more or less the same in these patches: there is very little difference in altitude (difference between lowest patch and highest patch is 35 m), and because of their proximity to one another environmental conditions are likely to be similar.

The patch-specific approach adopted in this study has been used to estimate the level of movement among patches of suitable habitat in a rare butterfly occupying a fragmented landscape. This approach has also enabled an apparently significant factor affecting immigration and emigration (oviposition resource) to be empirically quantified, and has suggested how and why migration changes through time and differs between the sexes. It has shown that the study patch delimits one local population of butterflies, with most butterflies remaining in their natal patch, but apparently with sufficient transfer of individuals among patches to enable their long-term persistence, a fact of fundamental importance to a species surviving in a metapopulation.

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