

## Intra-patch movement in the Sinai Baton Blue butterfly: influence of micro-habitat and individual characteristics

Mike James

School of Biology, Nottingham University, Nottingham NG7 2RD

### ABSTRACT

Dispersal is a key process in metapopulation biology. The transfer of individuals among patches of suitable habitat has been widely studied, and rates of movement and the factors influencing these investigated. However, relatively few metapopulation studies have examined movement of individuals within a patch of habitat, and none of these have related intra-patch movement to inter-patch movement (dispersal). The intra-patch movement of a narrowly endemic butterfly *Pseudophilotes sinaicus* (Lycaenidae) that exists in a metapopulation structure was studied. It was found to be extremely sedentary, rarely moving more than 40 m in or between days, and occupying a very small area during its residency of the study patch. Its level of movement (distance between sightings) and the factors affecting this depended on its sex, and was primarily determined by the density of conspecifics in its immediate vicinity. Other factors also influenced movement, notably the phenology and size of hostplants in an individual's immediate vicinity. Responding to these variables in a predictable way can be regarded as strategies enabling the butterfly to locate mates, food, and oviposition sites, and to escape resource depletion, and intraspecific competitors. These behavioural patterns are similar to mechanisms involved in dispersal of individuals among patches of habitat in fragmented landscapes.

### INTRODUCTION

Ongoing habitat destruction means that for many species, areas of suitable habitat are becoming more and more fragmented, and consequently local populations of animals are becoming small and isolated. Thus, in addition to a healthy balance of births over deaths (within-patch processes), the role of movement is also considered to be a vital component in the persistence of species occupying fragmented landscapes (Hanski & Gilpin 1997). Migration into populations may postpone their extinction – the rescue effect (Brown & Kodric-Brown 1977; Hanski *et al.* 1995), and patches of empty habitat may be (re)-colonised. Conversely, if emigration is too high from a small population this may increase the risk of extinction (Thomas & Hanski 1997). Hence, dispersal plays a crucial role in metapopulation studies (Ims & Yoccoz 1997), and so it is important to understand the mechanisms of dispersal so the specific factors influencing immigration to and emigration from particular sites can be determined (Petit *et al.* 2001; Schneider *et al.* 2003).

In most metapopulation models, the movement of individuals is assumed to be random, and so colonisation of patches is assumed to depend on variables such as patch size and isolation (Hanski 1998). These models have proved useful in explaining the occurrence and abundance of species and predicting future patterns of distribution (e.g. Wahlberg *et al.* 1996). Empirical studies have demonstrated that the number of dispersers reaching new habitats declines with distance from the source patch (Harrison 1989; Kuussaari *et al.* 1996; Wahlberg *et al.* 2002), and that individuals emigrate disproportionately often from small areas (Hill *et al.* 1996; Kindvall 1999; Baguette *et al.* 2000; Roland *et al.* 2000). However, in reality little is known about the factors affecting an animal's dispersal, or the strategy it uses to locate suitable habitat (Conradt *et al.* 2000), and dispersal behaviour of individual animals is likely to be complex. For example, patch boundary and matrix conditions (Stamps *et al.* 1987; Roland *et al.* 2000; Schtickzelle & Baguette 2003; Keyghobadi *et al.* 2003), abundance of nectar flowers (Kuussaari *et al.* 1996; Brommer & Fred 1999), mating opportunities (Baguette *et al.* 1998), presence of conspecifics ('social attraction': Ray *et al.* 1991; Stamps 1991), number of conspecifics (Serrano *et al.* 2001), population density (Denno & Peterson

1995; Baguette *et al.* 1996; Loxdale & Lushai 1999), and intraspecific competition (Dobson & Jones 1985) all might affect the occurrence and magnitude of movement.

Butterflies are excellent model organisms for the study of dispersal, and a great deal of information has been gathered on their movement among patches of suitable habitat (e.g. Harrison *et al.* 1988; Hanski & Kuussaari 1995; Petit *et al.* 2001; Wahlberg *et al.* 2002). A number of studies have examined how butterflies locate patches of suitable habitat (Conradt *et al.* 2000, 2001; Schultz & Crone 2001), and how they maintain their position within these patches (Odendaal *et al.* 1989; Schultz 1998). Recently, and in contrast to the assumptions of many metapopulation models, the way some species search for patches of suitable habitat has been shown to be non-random (Seymour *et al.* 2003), and to involve a kind of systematic search strategy (Conradt *et al.* 2000, 2001). Indeed, one could imagine a process whereby an individual discovers it has left a patch and therefore initiates a special kind of search for a patch. Or, it decides in the patch itself that it is going to disperse. However, detailed information about how individual animals disperse is limited because of the difficulty of keeping track of dispersing individuals in the field, especially 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.

Here, I focus on the movements of a rare and narrowly-endemic butterfly, the Sinai Baton Blue (*Pseudophilotes sinaicus* Nakamura). Habitat for the butterfly is distinctly structured at two spatial scales: (1) its hostplant Sinai Thyme (*Thymus decussatus* Benth.) which grows in discrete units (individual plants) and, (2) the well-defined habitat patches in which the thyme plants occur.

In a previous study, I investigated Baton Blue dispersal among patches of habitat, estimated its immigration and emigration rates, and observed an individual move approximately 1 km in 3 days (James, 2006d). Here, I study movement within one of its well-defined habitat patches, whose quality varies both spatially and temporally. Many insect species survive in patchy habitats that are subject to large environmental fluctuations of patch quality (Hanski 1998); under these conditions dispersal is crucial for long-term survival of populations. Most butterfly studies use the (mean or maximum) distance moved between sightings / recaptures to determine the mobility of a species and evaluate its dispersal ability (e.g. Schultz 1998; Ide 2003; Schneider *et al.* 2003), and it is now apparent that the size of the study area has an important influence on these estimations (Schneider 2003).

I test here the impact of habitat quality (density and suitability of oviposition sites, larval food plants, and adult nectar sources, and the density of conspecifics) on distances moved at a very local scale, among plants within a patch. I also investigate whether an individual's characteristics (size, age, and sex) affect its movement within the patch. I do not attempt to estimate the dispersal ability of the species, but rather identify the factors affecting its day-to-day movement within a patch of habitat. Having done this, I am in a position to ask whether factors determining how far individuals move within a patch, are related to factors influencing dispersal among patches. By only addressing intra-patch movement, the influence of spatial scale on quantifying movement becomes irrelevant. However, I also investigate the area utilised by individuals during their residency of the patch. This enables me to determine the actual degree of movement in the Sinai Baton Blue more precisely.

Studies involving intra-patch movement in insects have usually concentrated on foraging (e.g. Goulson *et al.* 1997; Weiss 1997) or ovipositing behaviour (e.g. Withers & Harris 1996; Cronin *et al.* 2001), and have rarely been conducted in a metapopulation context. This paper will therefore advance our knowledge of some of the mechanisms involved in small-scale movements, and increase our understanding of how and why these might affect larger (inter-patch) movements. My findings have implications for studies of metapopulations.

## MATERIALS AND METHODS

**Study species:** The Sinai Baton Blue is endemic to the St. Katherine Protectorate in South Sinai, Egypt (Nakamura 1975), where its only known larval hostplant, the near-endemic Sinai Thyme is patchily distributed among the mountains (James *et al.*, 2003; James, 2006a,b,c,d,f; Hoyle & James, 2005). 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 the nectar of Sinai Thyme when it is in flower (James, 2006f).

**Study site:** In 2002 I studied intensively a local population of butterflies in Farsh Shoeib, a 13,600 m<sup>2</sup> patch of thyme bordered on all sides by steep, bare cliffs, close to Gebel Safsafa on the Mt. Sinai massif. The study patch contained 1,212 thyme plants, which were accurately mapped relative to a GPS point (Garmin GPS 12 MAP, + 5 m) using a tape measure and compass. The phenology of each thyme plant was measured weekly: five inflorescences were randomly selected from the most advanced area of the plant and their phenology scored on a 0-7 scale (0 = 100% pre-bud; 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 scores represented the phenological state of the plant. Between 10th June and 24th June (after the main adult flight period but whilst inflorescences were still readily observable), the number of inflorescences on each thyme plant was recorded. On small plants (<200-300 inflorescences) this was done by counting each individual inflorescence, but on large plants it was estimated by taking the average number of inflorescences counted in four randomly placed 10 cm x 10 cm quadrats and extrapolating.

**Survey of butterflies:** A mark-release-recapture (MRR) study was carried out over 97 consecutive days, from 8th April (the date the first adult was seen) to 13th July (the date the last adult was seen) in Farsh Shoeib. Every day from dawn to sunset, two field workers actively searched for butterflies whilst continuously walking at a slow pace a pre-determined route that passed every thyme plant and covered the area of the thyme patch. When unmarked butterflies were seen, their location (closest thyme plant), sex, and behaviour were recorded. They were then caught using a butterfly net, given an individual mark on the underwing(s) using permanent marker pens, measured (length of forewing from base to apex), and then released at the point of capture. Newly eclosed adults were easy to identify as they were always near the top of a thyme plant, in pristine condition with particularly bright orange markings, and unable to fly. To reduce the effects of handling no butterfly was caught more than once: when previously marked individuals were seen they were identified using close-focus binoculars (i.e. a 'recapture' was actually a 're-sighting'), and their location (closest thyme plant) and behaviour noted. There were no detectable effects of handling (James, 2006c).

To describe movement of butterflies within the patch, the straight-line distance moved between each consecutive sighting was measured. Every time a butterfly was sighted, four features describing its location were calculated (Table 1). These variables and the individual's size and age were used to examine the variability of distances moved between sightings (the within-subjects nature of the data was allowed for in the analysis by including individual as a factor). This method provides information on the flight capabilities of the

species and factors affecting its movement, but it gives no indication of the actual area that individuals utilise. To understand this, the location of an individual was plotted each time it was seen and a line connecting the peripheral points drawn to form a polygon. The area of this polygon described the home range of the butterfly. This method could only be used for individuals seen on at least three occasions. The ‘core area’ utilised by a butterfly was the area of the polygon that enclosed ~90% of the locations in which it was observed.

## RESULTS

Four hundred and thirty-one individuals were marked during the adult flight period. Of these 155 males and 168 females were seen at least once after initial marking, and 130 of these males and 145 of the females were first caught on the day they eclosed and so were of known age (James, 2006c). Males were re-sighted a total of 979 times and females 1,122 times.

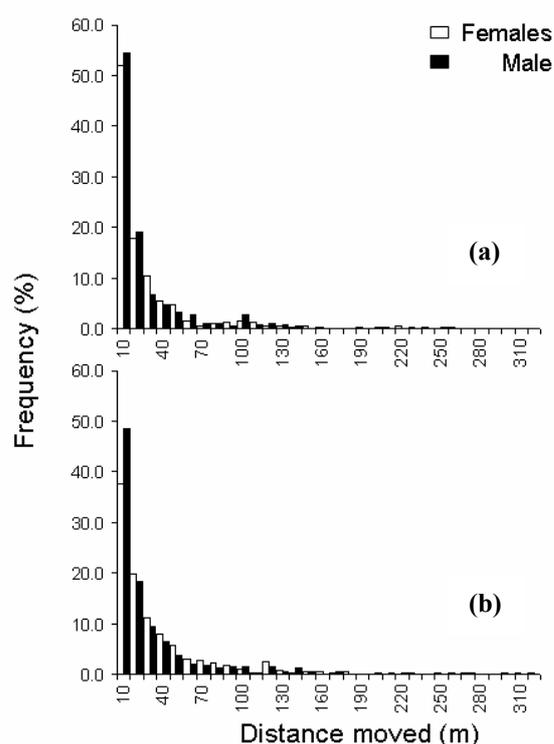
Males were seen flying more often than females ( $\chi^2_1 = 31.3$ ,  $p < 0.001$ ) (James, 2006f), presumably because in addition to locating thyme flowers from which to take nectar, males also actively searched for newly eclosed females. The maximum-recorded distance moved between two successive sightings within a day was 253 m for a female (in 24 minutes) and 243 m for a male (in 56 minutes). Thus butterflies are certainly capable of travelling relatively long distances relatively quickly. There was no significant difference between males and females in terms of the distance they moved between successive sightings on the same day (independent samples test,  $t_{920} = 1.03$ , ns) (Table 2). Individuals were extremely sedentary within the study patch, rarely moving more than 40 m between successive sightings within a day (Fig 1a), or between their first sighting on consecutive days (Fig. 1b). The maximum-recorded distance moved between the first sighting on consecutive days was 313 m for a female and 266 m for a male. Females moved significantly further than males between consecutive days (independent samples test,  $t_{847} = 2.66$ ,  $p < 0.05$ ) (Table 2).

**Table 1** Features describing the location of an individual each time it was sighted

Variable	How measured
Female density	Number of female Baton Blues seen within 5 metres of the plant nearest to where the butterfly was seen and during the period of the day (before or after midday) in which it was seen
Male density	Number of male Baton Blues seen within 5 metres of the plant nearest to where the butterfly was seen and during the period of the day (before or after midday) in which it was seen
Number of inflorescences	Total number of inflorescences on all the thyme plants within 5 metres of the plant nearest to where the butterfly was seen. The number of inflorescences on each thyme plant in the study site was counted once, in the second half of the adult flight period
Phenology of thyme	Average phenology of all the thyme plants within 5 metres of the plant nearest to where the butterfly was seen. The phenology of every thyme plant in the study site was measured weekly and on a scale of 0 (pre-bud) to 7 (flowers over/seed heads) (see methods)

Table 2 Distances moved by butterflies between successive sightings that were made varying lengths of time apart

	Mean distance moved between consecutive days (metres)	Mean distance moved between successive sightings in one day (metres)	Mean distance moved between successive sightings in one day (metres)			
			<2 hours between sightings	<4 hours between sightings	<6 hours between sightings	>6 hours between sightings
Female	31.6 ± 2.3 (n = 404)	22.1 ± 1.5 (n = 559)	21.4 ± 2.0 (n = 320)	21.7 ± 3.1 (n = 136)	17.1 ± 2.0 (n = 121)	33.0 ± 8.0 (n = 30)
Male	24.0 ± 1.7 (n = 445)	19.8 ± 1.6 (n = 363)	19.7 ± 2.7 (n = 168)	19.5 ± 2.9 (n = 103)	20.8 ± 2.8 (n = 89)	23.2 ± 7.6 (n = 24)



**Fig. 1** Frequency of movements of the Sinai Baton Blue (a) between consecutive sightings within a day, and (b) between the first sighting made on consecutive days

The time gap between successive sightings of the same individual varied greatly (range 1 minute to 14 days); as expected there was a positive correlation between this time gap and the distance moved (males  $r_s = 0.219$ ,  $n = 979$ ,  $p < 0.001$ ; females  $r_s = 0.285$ ,  $n = 1122$ ,  $p < 0.001$ ). To control for the effect of the time interval on recorded distances moved, analyses have been restricted to data from consecutive sightings separated by between 20 and 300 minutes. This time interval was chosen to ensure all pairs of sightings were made on the same day, and to minimise the likelihood of duplicated records (i.e. an individual recorded by field worker #1 in the same location and within a few minutes of being recorded by field worker #2). In this restricted data set, the correlation between the time interval and distance moved disappears. Scatter plots show the relationship between the distance moved and individual environmental variables (Figs 2-7). To describe the shape of the curve that best fits each of the plots, multiple regression analyses were performed with distance moved as the dependent variable and the independent variable entered in linear, quadratic, and cubic forms to test for curvature (Table 3). If at least one of the terms of the independent variable was significant (or near significance) in the multiple regression then the linear, quadratic, and cubic models were fitted to the data to estimate the curve, which was then plotted (Figs 2-7; Table 3).

Age was not significant in determining the distance moved between sightings in females. However, the linear term in the regression was positive and close to significance, indicating that older females may have moved further between sightings than young females (Fig. 2). The size of a female did not determine how far she moved between sightings (Fig. 3). As the density of females increased, the distance a female moved between sightings decreased; there is an indication that females moved further as female density increased above 6, though this is not significant (Fig. 4). Male density affected female movement in a similar way: the distance moved between sightings initially decreased as male density increased, and then the distance moved increased (Fig. 5). There is a negative correlation between the distance females moved and the number of inflorescences in the area, but there was a slight increase in this distance when inflorescences numbered over 6,000 (Fig. 6). Distance moved by females was inversely related to the phenology of thyme plants (Fig. 7).

In males, age was not significant in determining the distance moved between sightings (Fig. 2). Both small and large males moved further between sightings than medium-sized males (Fig. 3). As the density of females increased, the distance a male moved between sightings decreased until a female density of 4, at which point it showed signs of increasing, though this was not significant (Fig. 4). The distance moved by males was negatively correlated with male density, and levelled off at a density of 4 males and above (Fig. 5). As the number of inflorescences increased, the distance males moved between sightings decreased until inflorescences numbered about 4,000; above this there is an indication that they moved further, but this is not significant (Fig. 6). The phenology of thyme plants did not determine how far males moved between sightings (Fig. 7).

There was a reasonable degree of correlation among measured variables (Table 4), so to ascertain which variables had the strongest independent effect on the distance moved between sightings, a general linear model was constructed. The starting model contained all the significant variables identified from the multiple regressions (Table 3), and then the non-significant term with the lowest F-value was removed and the adjusted model re-run until all variables remaining in the model were significant (the minimum-sufficient model: Table 5). To control for potential non-independence of observations (different males in the data set were seen on between 1 and 20 occasions, and different females on between 1 and 23 occasions) the identity of each butterfly was always entered as a factor in the model (Table 5). Three variables were in the minimum-sufficient model to explain the distance females moved from an area: the local density of males and females, and the phenology of nearby thyme plants (Figs 4, 5, 7; Tables 3, 5). The only factor in the minimum-sufficient model influencing how far a male moved was the number of other males in his vicinity (Fig. 5; Tables 3, 5).

Individuals did not utilise the entire patch during their life and most had a home range that consisted of one small, well-delimited 'core area'; sightings outside the core area usually occurred (males = 75%, females = 82%) on their first or last day of residency in the patch (Table 6, Fig. 8). Among individuals with one core area, there was no significant difference between males and females in the size of that core area (mean core area: males =  $241 \pm 20$  m<sup>2</sup>, n = 87, females =  $231 \pm 18$  m<sup>2</sup>, n = 104;  $t_{189} = 0.35$ , ns). Among males with identifiable core areas, bigger individuals had significantly larger core areas (Spearman rank correlation,  $r_s = 0.23$ ,  $p < 0.05$ , n = 94 males). However, among females there was no correlation between core area and female size. Males with two core areas were bigger (mean forewing length  $9.86 \pm 0.30$  mm, n = 7) than males with one core area (mean forewing length  $9.43 \pm 0.09$  mm, n = 87), though this difference was not significant.

**Table 3** Results of multiple regression analyses relating distance moved between consecutive sightings (separated by between 20-300 minutes) with individual (a, b) and environmental (c-f) variables; the linear, quadratic, and cubic terms of the variable were entered together. The results of the regressions were used to predict the distance moved for each variable, and the curve fitted to the data (Figs 2 - 7). ns = not significant ( $p > 0.05$ )

Variables available (independent)	<i>Females</i>				Males			
	<b>B</b>	Significance ( <i>p</i> )	<i>Model</i>		<b>B</b>	Significance ( <i>p</i> )	<i>Model</i>	
			<b>F</b>	Significance ( <i>p</i> )			<b>F</b>	Significance ( <i>p</i> )
<b>a</b> Constant	16.32	<0.001	2.01	ns	19.76	<0.001	0.41	ns
Age	6.76	ns (0.06)			0.59	ns (0.83)		
(Age) <sup>2</sup>	-1.32	ns (0.09)			-0.09	ns (0.81)		
(Age) <sup>3</sup>	0.06	ns (0.20)			0.00	ns (0.90)		
<b>b</b> Constant	53.59	ns (0.31)	5.15	<0.05	243.26	ns (0.06)	4.68	<0.05
Size	-7.3	ns (0.37)			-38.49	ns (0.06)		
(Size) <sup>3</sup>	0.04	ns (0.15)			0.16	<0.05		
<b>c</b> Constant	34.28	<0.001	16.69	<0.001	37.89	<0.001	8.06	<0.001
Male density	-25.36	<0.001			-15.31	<0.001		
(Male density) <sup>2</sup>	7.92	<0.01			2.67	<0.05		
(Male density) <sup>3</sup>	-0.73	<0.05			-0.15	ns (0.12)		
<b>d</b> Constant	42.93	<0.001	16.97	<0.001	25.72	<0.001	3.6	<0.05
Female density	-13.59	<0.001			-9.63	<0.01		
(Female density) <sup>2</sup>	1.78	<0.05			1.86	<0.05		
(Female density) <sup>3</sup>	-0.07	ns (0.07)			-0.09	ns (0.09)		
<b>e</b> Constant	42.19	<0.001	10.16	<0.001	34.12	<0.001	6.92	<0.001
No. inflorescences	-0.02	<0.001			-0.02	<0.001		
(No. inflorescences) <sup>2</sup>	0.00	<0.001			0.00	<0.01		
(No. inflorescences) <sup>3</sup>	-0.00	<0.01			-0.00	ns (0.09)		
<b>f</b> Constant	37.06	<0.001	4.92	<0.01	22.86	<0.001	1.40	ns
Phenology	-19.67	<0.01			1.49	ns (0.83)		
(Phenology) <sup>2</sup>	5.68	ns (0.06)			-1.80	ns (0.54)		
(Phenology) <sup>3</sup>	-0.49	ns (0.12)			0.21	ns (0.51)		

**Table 4** Correlation (Spearman rank) matrix of variables entered into a general linear model to describe movement of males and females. \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ ; ns = not significant ( $p > 0.05$ )

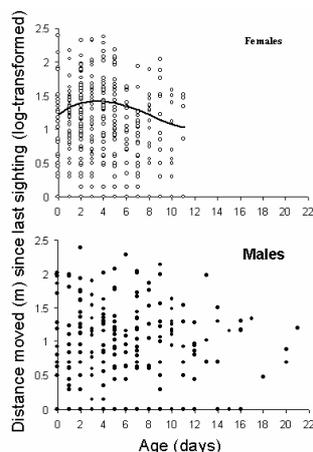
	Females ( $n = 482$ )				Males ( $n = 286$ )				
		Male density	Female density	Number inflorescences	Thyme phenology	Male density	Female density	Number inflorescences	Thyme phenology
Male density	Coefficient ( $r_s$ )		0.58 ***	0.38 ***	0.14 **		0.52 ***	0.38 ***	0.16 *
Female density	Coefficient ( $r_s$ )	0.58 ***		0.48 ***	0.07 ns	0.52 ***		0.50 ***	0.01 ns
Number inflorescences	Coefficient ( $r_s$ )	0.38 ***	0.48 ***		0.27 ***	0.38 ***	0.50 ***		0.37 ***
Thyme phenology	Coefficient ( $r_s$ )	0.14 **	0.07 ns	0.27 ***		0.16 *	0.01 ns	0.37 ***	

**Table 5** Significant (bold) and near-significant terms remaining in the minimum-sufficient model of the general linear model to explain distance moved by males and females. The error term of the intercept (females, df = 452; males, df =265) was different to the error term used for the others sources (females, df = 368; males, df = 208).

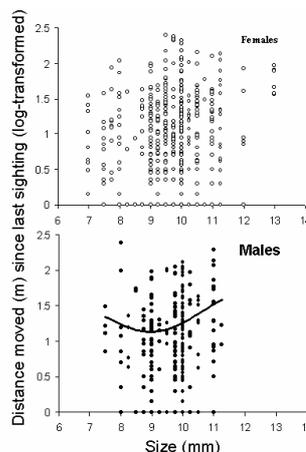
Sex	Source	Parameter estimate (B)	Standard error	df	Test (F)	Significance ( <i>p</i> )
Female	Intercept			1	86.29	<0.001
	Butterfly ID			109	1.35	<0.05
	Male density	-2.17	1.24	1	3.07	ns (0.08)
	Female density	-6.50	1.82	1	12.73	<0.001
	(Female density) <sup>2</sup>	0.42	0.16	1	6.94	<0.01
	Phenology of thyme	-4.00	2.02	1	3.93	<0.05
Male	Intercept			1	53.54	<0.001
	Butterfly ID			73	2.05	<0.001
	Male density	-10.61	3.77	1	7.91	<0.01
	(Male density) <sup>2</sup>	1.31	0.61	1	4.67	<0.05
	No. Inflorescences	-0.01	0.00	1	2.94	ns (0.09)
	(No. Inflorescences) <sup>2</sup>	-0.00	0.00	1	3.50	ns (0.06)

**Table 6** Numbers of butterflies conforming to each recognised pattern of patch utilisation. The core area is the area of a polygon that enclosed ~90% of the locations in which the butterfly was observed; an outlier is a sighting of a butterfly away from its core area

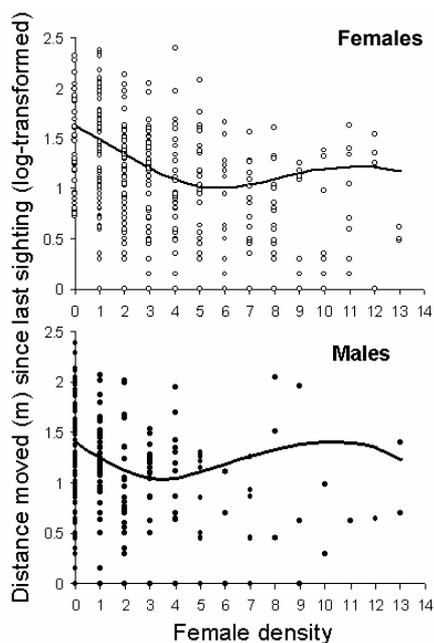
	Number of core areas: females			Number of core areas: males		
	0	1	2	0	1	2
Outlier at start	0	13	2	0	10	0
Outlier in middle	0	6	0	0	6	0
Outlier at end	0	13	0	0	7	1
Outlier absent	8	72	9	16	64	6



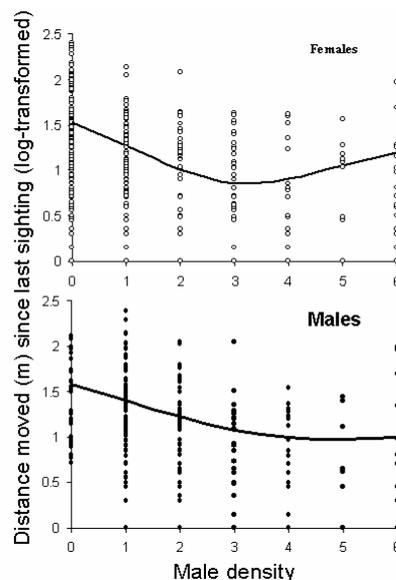
**Fig. 2** Relationship between the distance an individual moved between consecutive sightings and its age. The curve was fitted if its age was significant as a linear, quadratic, and/or cubic term in multiple regression, with distance moved as the dependent variable (see Table 3)



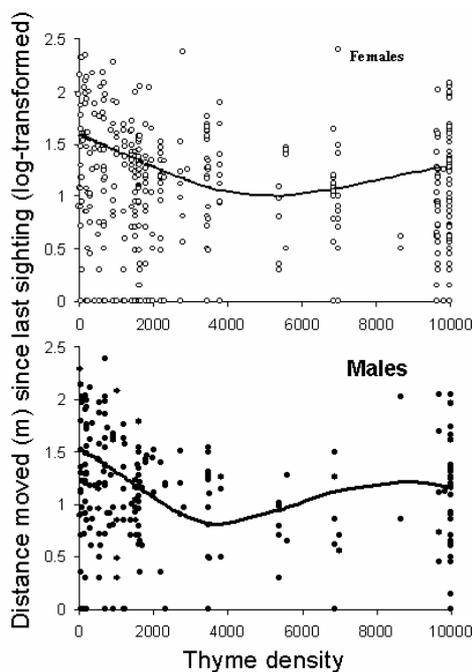
**Fig. 3** Relationship between the distance an individual moved between consecutive sightings and its size (forewing length). The curve was fitted if its size was significant as a linear, quadratic, and/or cubic term in multiple regression, with distance moved as the dependent variable (see Table 3)



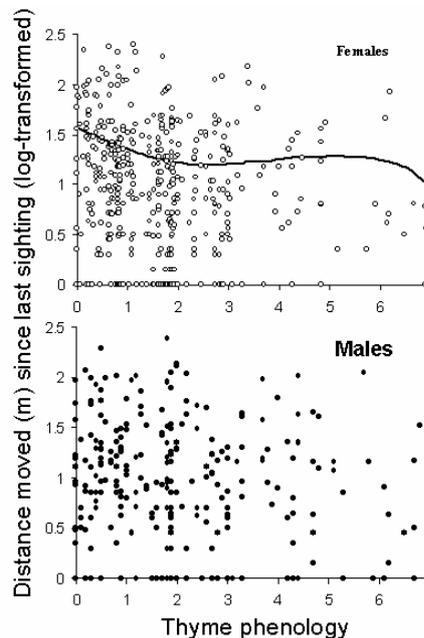
**Fig. 4** Relationship between the distance an individual moved between consecutive sightings and the number of females in the vicinity of where it was last seen. The curves were fitted because female density was significant as a linear, quadratic, and/or cubic term in multiple regression, with distance moved as the dependent variable (see Table 3)



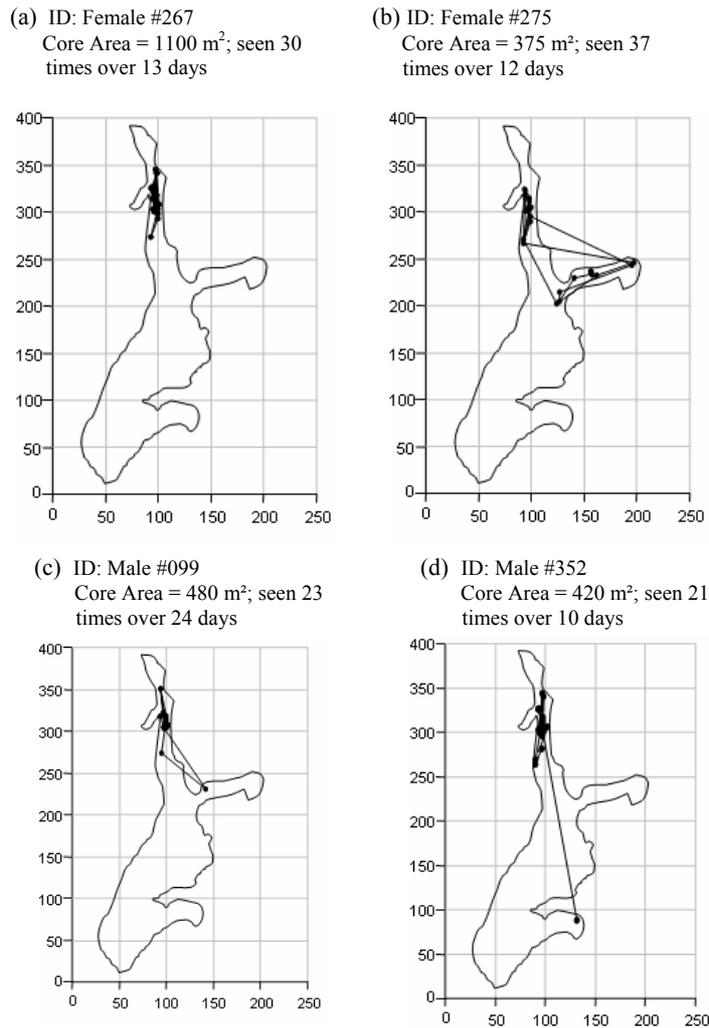
**Fig. 5** Relationship between the distance an individual moved between consecutive sightings and the number of males in the vicinity of where it was last seen. The curves were fitted because male density was significant as a linear, quadratic, and/or cubic term in multiple regression, with distance moved as the dependent variable (see Table 3)



**Fig. 6** Relationship between the distance an individual moved between consecutive sightings and the number of thyme inflorescences in the vicinity of where it was last seen. The curves were fitted because thyme density was significant as a linear, quadratic, and/or cubic term in multiple regression, with distance moved as the dependent variable (see Table 3)



**Fig. 7** Relationship between the distance an individual moved between consecutive sightings and the phenology of thyme plants in the vicinity of where it was last seen. The curve was fitted if thyme phenology was significant as a linear, quadratic, and/or cubic term in multiple regression, with distance moved as the dependent variable (see Table 3)



**Fig. 8** Typical patterns of patch utilisation by individual butterflies. (a) Individual with one core area; (b) individual with two core areas; (c) individual with one core area, but with one movement away from and then back to that area during the middle of its residency in the patch; (d) individual with one core area, but with movement away from that core area at the end of its residency in the patch

## DISCUSSION

Distances moved by individuals were recorded on different days throughout the flight season, but observed differences can be attributed to the effect of the measured variables and not to differences in the butterfly's behaviour from day to day: the weather was consistent (sunny and warm) on all days of the study, and so would not have dramatically affected butterfly activity (cf. Kingsolver 1983; Shreeve 1992). The use of close-focus binoculars meant that butterflies were identified and observed from several metres away, ensuring that disturbance to their behaviour was kept to a minimum. In addition, unlike similar studies on butterfly movement in which individuals are continuously followed (e.g. Odendaal *et al.* 1989; Schtickzelle & Baguette 2003), the method employed in this study meant that problems of field workers inadvertently chasing butterflies or preventing them settling, were minimised. Each time an individual was sighted, its location was described using features of its habitat in a circle of radius 5 m with the butterfly in the centre. This method was chosen because it was assumed that the butterflies, given their mobility, would be aware of habitat in their immediate (5 m) vicinity as well as the actual plant they were on; it also gave a more realistic representation of the number of conspecifics likely to be encountered. However, it is not known at what scale the Sinai Baton Blue can detect features of its landscape, or the extent to which visual and / or chemical cues are used. At the range of a few centimetres, females of *Battus philenor* use leaf shape to select oviposition sites (Rausher 1978), and female butterflies may also be attracted to the colour of oviposition substrates (Rutowski 2003).

Male butterflies typically locate females by looking for them, but their visual acuity means they can only detect females from a distance of a few metres (Rutowski 2003); experiments have shown that some species use visual cues to detect more conspicuous objects associated with the presence of females (Dennis & Shreeve 1988; Wickman *et al.* 1995). There is also a suggestion that males of smaller species have a lower overall acuity than larger species, and so can only detect females at a relatively close range (Rutowski 2003); this appears to be true in the Sinai Baton Blue (James, 2006f). Chemical and visual cues, at both long and close range, are probably used to locate and recognise nectar sources (Prokopy & Owens 1983).

My results indicate that the Baton Blue is a sedentary species: less than 20% of individuals emigrate from the natal patch, and lifetime movements were between 10-200 m; they were capable of moving relatively long distances, but apparently rarely did so (Pollard & Yates 1993; James, 2006d). It is possible that butterflies temporarily emigrate from the patch, leaving it for a few hours / days before returning (James, 2006c). However, the high number of re-sightings for many individuals (e.g. Fig. 8), and the mean residency of the butterfly in the patch (James, 2006c,d) suggest that the area they were recorded to utilise and the distances they were observed moving between sightings, accurately reflected their utilisation of the patch. Individuals moved different distances within a patch depending on their individual characteristics (age, or size), the presence of nearby conspecifics, and the abundance and condition of nearby hostplants; males and females responded differently to these variables.

In general, females moved further between sightings within a patch than males, and this may correspond to greater dispersal in females. A higher migration rate in females is common in many species (e.g. Arnold 1983; Väisänen *et al.* 1994; Peterson 1997; Albrechtsen & Nachman 2001; Yáber & Rabenold 2002). When studying inter-patch movement in the Baton Blue (James, 2006d), I discovered that most immigrants to the patch during the main flight period were generally older and most were female. Much of this movement occurred when thyme plants still provided oviposition resource, which suggested that in addition to migrating in search of these resources some females, perhaps on reaching a certain age or condition, might be inclined to move further (within a patch); this might increase their chance of crossing the patch boundary and so migrating from one suitable habitat patch to another (Shreeve 1992). This might explain the lower residence time of females compared with males (James, 2006d), 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).

It has been demonstrated for a number of insect species that individuals with long forewings are more prone to dispersal (e.g. Taylor & Merriam 1995; Conrad *et al.* 2002), and are fitter (suffered less stress in their larval stages: Nylin & Gotthard 1998) than smaller individuals. Furthermore, changes in a butterfly's flight morphology may be an evolutionary response to fragmentation (Thomas *et al.* 1998; Hill *et al.* 1999a,b). Within the patch, big Baton Blue males occupied larger core areas than small males. I did not collect any quantitative data on territoriality, so it is impossible to know whether these males were actually defending their core areas. However, if forewing length was related to flight capability, then one would expect larger males to have larger territories and this would also explain why they had a tendency to move further between sightings. However, distances moved between sightings in very small individuals was similar to those recorded in very large individuals, and small males did not have large core areas. Thus, it may be that small males are unable to defend a territory of any size, their size making them inferior to larger individuals who chase them away, causing them to move further. The potential effects of territoriality in the Sinai Baton Blue are extremely interesting and require further study since they have consequences for its dispersal behaviour and individual fitness. Males of two very

closely related species, *P. baton* (Väisänen *et al.* 1994) and *P. panoptes* (Morris 1995), have been observed defending territories.

The distance moved by an individual of either sex was influenced by the number of conspecifics in its vicinity prior to movement: individuals moved further from areas containing few conspecifics. Conspecific attraction has the potential to influence metapopulation dynamics (Kuussaari *et al.* 1996; Serrano & Tella 2003; Välimäki & Itämiä 2003). The number of conspecifics (specifically, the number of male conspecifics in determining male movement, and the number of females in determining female movement) was the most important factor affecting distance moved in the general linear models. This indicates that butterflies cue on the number of conspecifics and not on other confounding factors: high numbers of conspecifics in a given area presumably provide information about habitat quality and suitability (Roland *et al.* 2000). To a certain extent these results concur with the suggested negative relationship between dispersal rate and local population size (McPeck & Holt 1992); for example the butterfly *Parnassius smintheus* leaves meadows with few butterflies (Roland *et al.* 2000). However, it is interesting that females also tended to move further once the density of males or (to a lesser extent) females increased above a certain number. This is probably because at very high female densities there is competition for resources (e.g. oviposition sites), and so some females are forced to move in search of resources that are available to them. A female-density effect on movement of females has been demonstrated in two species of tephritid fly: in one species (*Rhagoletis pomonella*) there is a greater propensity for long-distance flight at high female density, in the other (*Paroxyna plantaginis*) dispersal increases with female density (Albrechtsen & Nachman 2001). Female Baton Blues also respond to high male densities by moving further, perhaps because of resource competition (for nectar), but a much more likely explanation is that males are harassing females, and this motivates them to move to an area of the patch containing fewer males. In the solitary bee *Anthophora plumipes*, females changed their flight behaviour and foraged on different parts of plants in response to sexual harassment (Stone 1995). Male harassment has also been shown to influence the movement behaviour of the butterflies *Euphydryas anicia* (Odendaal *et al.* 1989) and *Proclissiana eunomia* (Baguette *et al.* 1998).

Unlike females, distances moved by males did not increase at very high male densities and instead remained low; at high female densities the distance moved increased, but this may be an artefact of the sparse data ( $n = 6$  observations at female density of more than 9). As well as the number of conspecifics, male movement is also likely to be influenced by territoriality. Observations suggest that at low male densities, males were territorial, whereas at high male densities this territoriality seemed to disappear, with males continuously patrolling areas in search of virgin females. This behaviour would make sense given the high density per unit area of males during the main flight period – otherwise they would constantly be defending their territory, leaving little time to search and mate with females, or to feed. A density effect on territoriality has been suggested in other insect studies (e.g. Alcock & O'Neill 1986; Albrechtsen & Nachman 2001). In both sexes, the negative linear relationship between distance moved and density of conspecifics changed at a density of 4 or 5 individuals (male or female), indicating that they are unable to differentiate conspecific density above this.

Females select a brief, phenologically determined stage of thyme flower-bud development for oviposition and prefer plants with many inflorescences (James, 2006b,f). It is crucial that they oviposit on thyme plants coming into bud, and so it is unsurprising that the phenology of thyme plants was a significant independent variable in the general linear model for females. The generally negative relationship between the distance females moved from an area and the phenology of thyme plants in that area was therefore expected. When flowering has almost finished ( $>6$  on my scale), there will be very few unopened buds, most of the

flowers will have gone over and the seed-heads will have started to develop. Thus, one might have expected the distances moved by females at these late stages to be similar to those observed at very early stages (<1 on my scale) (when availability of oviposition resource was also low because only a few buds had developed). However, distances moved by females actually decreased at late phenological stages, but the data were very sparse (n = 9 observations). In a related butterfly *Euphilotes enoptes*, movement of females among hostplant patches was influenced by patch phenology (Peterson 1997); and in an earlier study I proposed that migration in the Baton Blue was linked to the phenology of Sinai Thyme (James, 2006d). The relatively reduced need for a phenological match with the hostplant in males explains the absence of any relationship between this variable and the distances they moved.

As expected in both males and females, movement decreased as inflorescence number increased (because of more nectar, more oviposition resource, and consequently a greater likelihood that unmated females would either eclose in, or move to the area). However, the distances moved by both sexes began to level off and then increase slightly at very high numbers of inflorescences. This is a strange result and might be because they are unable to differentiate between very high numbers of inflorescences (5,000 to 10,000), or it could be explained by other covarying factors (e.g. high densities of conspecifics at high thyme densities). Baton Blues take nectar almost exclusively from thyme flowers (James, 2006f), so as well as describing the potential density of oviposition sites, the number of inflorescences also describes the potential density of the nectar source. Kuussaari *et al.* (1996) observed that emigration rate in *Melitaea cinxia* decreased with high flower density in patches, and a similar observation has been made by Schneider *et al.* (2003) for the scarce copper, *Lycaena virgaureae*. However, in the lycaenid *Plebejus argus*, nectar source density was not a cue for habitat selection (Seymour *et al.* 2003).

Thus I have demonstrated that within a patch of habitat, the Sinai Baton Blue is capable of surviving in a very small area. However, environmental variables (habitat quality) and individual characteristics affect its movement in predictable ways and this can be regarded as a strategy enabling butterflies to locate mates, food, and oviposition sites, and to escape resource depletion and intraspecific competitors. These behavioural patterns would require flight behaviours that tend to retain butterflies in good-quality habitat, and result in dispersal from low quality or non-habitat. Odendaal *et al.* (1989) found that female *Euphydryas anicia* make tighter, more frequent turns in hostplant habitat, thus concentrating their flight in their preferred habitat. Similarly, females of the Fender's Blue *Icaricia icarioides fenderi* moved further and covered more ground in unfavourable habitat (Schultz 1998). In areas of the patch perceived as suitable, the Sinai Baton Blue flies relatively short distances, thereby maintaining its position. In less suitable areas it is forced to move longer distances in search of favourable habitat and this might increase its chances of ending up in unsuitable habitat (and dispersing). The several factors affecting movement within a patch of habitat are therefore to a large extent similar to the factors important in dispersing between habitat patches.

## REFERENCES

- Albrechtsen B & Nachman G (2001) Female-biased density-dependent dispersal of a tephritid fly in a fragmented habitat and its implications for population regulation. *Oikos* 94: 263-272.
- Alcock J & O'Neill RM (1986) Density-dependent mating tactics in the grey hairstreak, *Strymon melinus* (Lepidoptera: Lycaenidae). *Journal of Zoology* 209: 105-113.
- Arnold RA (1983) Ecological studies of six endangered butterflies (Lepidoptera: Lycaenidae): island biogeography, patch dynamics, and the design of habitat preserves. *University of California Publications in Entomology* 99

- Baguette M, Convi I & Nève G (1996) Male density affects female spatial behaviour in the butterfly *Proclissiana eunomia*. *Acta Oecologia*, 17: 235-232.
- Baguette M, Vansteenwegen C, Convi I & Nève G (1998) Sex-biased density dependent migration in a metapopulation of the butterfly *Proclissiana eunomia*. *Acta Oecologia*, 19: 17-24.
- Baguette M, Petit S & Queva F (2000) Population structure and migration of three butterfly species within the same habitat network: consequences for conservation. *Journal of applied Ecology* 37: 100-108.
- Bergman KO & Landin J (2002) Population structure and movements of a threatened butterfly (*Lopinga achine*) in a fragmented landscape in Sweden. *Biological Conservation* 108: 361-369.
- Brommer JE & Fred MS (1999) Movement of the Apollo butterfly *Parnassius apollo* related to host plant and nectar plant patches. *Ecological Entomology* 24: 125-131.
- Brown JH & Kodric-Brown A (1977) Turnover rates in insular biogeography: effects of immigration on extinction. *Ecology* 58: 445-449.
- Conrad KF, Willson KH, Whitfield K, Harvey IF, Thomas CJ & Sherratt TN (2002) Characteristics of dispersing *Ischnura elegans* and *Coenagrion puella* (Odonata): age, sex, size, morph and ectoparasitism. *Ecography* 25: 439-445.
- Conradt L, Bodsworth EJ, Roper TJ & Thomas CD (2000) Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. *Proceedings of the Royal Society of London* 267(B): 1505-1510.
- Conradt L, Roper TJ & Thomas CD (2001) Dispersal behaviour of individuals in metapopulations of two British butterflies. *Oikos*, 95: 416-424.
- Cronin JT, Hyland K & Abrahamson WG (2001) The pattern, rate, and range of within-patch movement of a stem-galling fly. *Ecological Entomology* 26: 16-24.
- Dennis RLH & Shreeve TG (1988) Hostplant-habitat structure and the evolution of mate-locating behaviour. *Zoological Journal of the Linnean Society* 94: 301-318.
- Denno RF & Peterson MA (1995) Density dependent dispersal and its consequences for population dynamics. pp. 113-125 in N Cappuccino & PW Price (eds). *Population dynamics: New approaches and synthesis*. Academic Press, London.
- Dobson FS & Jones WT (1985) Multiple causes of dispersal. *American Naturalist* 126: 855-858.
- Fitt GP (1986) The influence of a shortage of hosts on the specificity of oviposition behaviour in species of *Dacus* (Diptera, Tephritidae). *Physiological Entomology* 11: 133-143.
- Goulson D, Ollerton J & Sluman C (1997) Foraging strategies in the small skipper butterfly, *Thymelicus flavus*: when to switch? *Animal Behaviour* 53: 1009-1016.
- Hanski I (1998) Metapopulation dynamics. *Nature* 396: 41-49.
- Hanski I & Kuussaari M (1995) Butterfly metapopulation dynamics. pp. 149-171 in N Cappuccino & PW Price (eds). *Population dynamics: New approaches and synthesis*. Academic Press, London.
- Hanski I & Gilpin ME (1997) *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, London.
- Hanski I, Pakkala T, Kuussaari M & Lei G (1995) Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos* 72: 21-28.
- Harrison S (1989) Long-distance dispersal in the bay checkerspot butterfly. *Ecology* 70: 1236-1243.
- Harrison S, Murphy DD & Ehrlich PR (1988) Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis* – evidence for a metapopulation model. *Am. Nat.*, 132: 360-382.
- Hill JK, Thomas CD & Lewis OT (1996) Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *J. Anim. Ecol.*, 65: 725-735.
- Hill JK, Thomas CD & Lewis OT (1999a) Flight morphology in fragmented populations of a rare British butterfly, *Hesperia comma*. *Biological Conservation* 87: 277-283.
- Hill JK, Thomas CD & Blakeley DS (1999b) Evolution of flight morphology in a butterfly that has recently expanded its geographic range. *Oecologia* 121: 165-170.
- Hoyle, M. & James M. (2005) Global warming, human population pressure and viability of the world's smallest butterfly. *Conservation Biology* 19(4): 1113-1124.
- Ide JY (2003) Mating behaviour and light conditions cause seasonal changes in the dispersal pattern of the satyrine butterfly *Lethe diana*. *Ecological Entomology* 27: 33-40.
- Ims RA & Yoccoz NG (1997) Studying transfer processes in metapopulations: emigration, migration and colonization. pp. 247-265 in I Hanski & M E Gilpin (eds). *Metapopulation Biology: Ecology, Genetics and Evolution*. Academic Press, London.
- James, M. (2006a) Metapopulations and the Sinai Baton Blue (*Pseudophilotes sinaicus* Nakamura): an introduction. *Egyptian Journal of Biology* 8: 7-16
- James, M. (2006b) Interactions among species in a tri-trophic system: the influence of ants on the distribution of the Sinai Baton Blue butterfly. *Egyptian Journal of Biology* 8: 17-26

- James, M. (2006c) Demographic processes in a local population: seasonal dynamics of the Sinai Baton Blue butterfly. *Egyptian Journal of Biology* 8: 27-38
- James, M. (2006d) Immigration and emigration in the Sinai Baton Blue butterfly: estimates from a single patch. *Egyptian Journal of Biology* 8: 39-50
- James, M. (2006e) Intra-patch movement in the Sinai Baton Blue butterfly: influence of micro-habitat and individual characteristics. *Egyptian Journal of Biology* 8: 51-66
- James, M. (2006f) The natural history of the Sinai Baton Blue: the smallest butterfly in the world. *Egyptian Journal of Biology* 8: 67-85
- James, M., Gilbert, F. & Zalat, S. (2003) Thyme and isolation for the Sinai Baton Blue butterfly (*Pseudophilotes sinaicus*). *Oecologia*, 134, 445-453.
- Keyghobadi N, Roland J, Fownes S & Strobeck C (2003) Ink marks and molecular markers: examining the effects of landscape on dispersal using both mark-recapture and molecular methods. pp. 169-183 in CL Boggs, WB Watt & PR Ehrlich (eds). *Butterflies: ecology and evolution taking flight*. University of Chicago Press, Chicago.
- Kindvall O (1999) Dispersal in a metapopulation of the bush cricket, *Metrioptera bicolor* (Orthoptera: Tettigoniidae). *Journal of animal Ecology* 68: 172-185.
- Kingsolver J G (1983) Thermoregulation and flight in *Colias* butterflies: elevational patterns and mechanistic limitations. *Ecology* 64: 534-545.
- Kuussaari M, Nieminen M & Hanski I (1996) An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of animal Ecology* 65: 791-801.
- Loxdale, H.D. & Lushai, G. (1999) Slaves of the environment: the movement of herbivorous insects in relation to their ecology and genotype. *Philosophical Transactions of the Royal Society* 354(B): 1479-1495.
- McPeck MA & Holt RD (1992) The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* 140: 1010-1027.
- Morris R J (1995) Observations on the behaviour of the panoptes blue butterfly, *Pseudophilotes panoptes* (Hubner) (Lep.: Lycaenidae). *Entomologist's Record and Journal of Variation*, 107: 245-247.
- Nakamura I (1975) Descriptions of two new species of butterflies (Lepidoptera, Lycaenidae) from the South Sinai. *Journal of Entomology* 44(B): 283-295.
- Nylin S & Gotthard K (1998) Plasticity in life-history traits. *Annual Review of Entomology* 43: 63-83.
- Odendaal FJ, Turchin P & Stermitz FR (1989) Influence of host-plant density and male harassment on the distribution of female *Euphydryas anicia* (Nymphalidae). *Oecologia* 78: 283-288.
- Peterson M (1997) Host-plant phenology and butterfly dispersal: causes and consequences of uphill movement. *Ecology* 78: 167-180.
- Petit S, Moilanen A, Hanski I & Baguette M (2001) Metapopulation dynamics of the bog fritillary butterfly: movements between patches. *Oikos* 92: 491-500.
- Pollard E & Yates TJ (1993) *Monitoring butterflies for ecology and conservation: the British butterfly monitoring scheme*. Chapman & Hall, London.
- Prokopy RJ & Owens ED (1983) Visual detection of plants by herbivorous insects. *Annual Review of Entomology* 28: 337-364.
- Ray C, Gilpin M & Smith AT (1991) The effect of conspecific attraction on metapopulation dynamics. *Biological Journal of the Linnean Society* 42: 123-134.
- Rausher MD (1978) Search image for leaf shape in a butterfly. *Science* 200: 1071-1073.
- Roland J, Keyghobadi N & Fownes S (2000) *Alpine Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology* 81: 1642-1653.
- Rutowski RL (2003) Visual ecology of adult butterflies. pp 9-25 in CL Boggs, WB Watt & P R Ehrlich (eds) *Butterflies: Ecology and Evolution taking Flight*. University of Chicago Press, Chicago.
- Sadeghi H & Gilbert F (2000) Oviposition preferences of aphidophagous hoverflies. *Ecological Entomology* 25: 91-100.
- Schneider C (2003) the influence of spatial scale on quantifying insect dispersal: an analysis of butterfly data. *Ecological Entomology* 28: 252-256.
- Schneider C, Dover J & Fry GL (2003) Movement of two grassland butterflies in the same habitat network: the role of adult resources and size of the study area. *Ecological Entomology* 28: 219-227.
- Schtickzelle N & Baguette M (2003) Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. *Journal of animal Ecology* 72: 533-545.
- Schultz CB (1998) Dispersal behaviour and its implications for reserve design in a rare Oregon butterfly. *Conservation Biology* 12: 284-292.
- Schultz CB & Crone EE (2001) Edge-mediated dispersal behaviour in a prairie butterfly. *Ecology* 82: 1879-1892.

- Serrano D & Tella JL (2003) Dispersal within a spatially structured population of lesser kestrels: the role of spatial isolation and conspecific attraction. *Journal of animal Ecology* 72: 400-410.
- Serrano D, Tella JL, Forero MG & Donázar JA (2001) factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *Journal of animal Ecology* 70: 568-578.
- Seymour AS, Gutiérrez D & Jordano D (2003) Dispersal of the lycaenid *Plebejus argus* in response to patches of its mutualist ant *Lasius niger*. *Oikos* 103: 162-174.
- Shreeve TG (1992) Monitoring butterfly movements. pp 120-138 in RLH Dennis (ed). *The Ecology of Butterflies in Britain*. Oxford University Press, Oxford.
- Stamps JA (1991) The effect of conspecifics on habitat selection in territorial species. *Behavioral Ecology & Sociobiology* 28: 29-36.
- Stamps JA, Buechner MB & Krishnan VV (1987) The effects of edge permeability and habitat geometry on emigration from patches of habitat. *American Naturalist* 129: 533-552.
- Stone GN (1995) Female foraging responses to sexual harassment in the solitary bee *Anthophora plumipes*. *Animal Behaviour* 50: 405-412.
- Taylor PD & Merriam G (1995) Wing morphology of a forest damselfly is related to landscape structure. *Oikos* 73: 43-48.
- Thomas CD & Hanski I (1997) Butterfly metapopulations. pp 359-386 in I Hanski & ME Gilpin (eds). *Metapopulation biology: ecology, genetics and evolution*. Academic Press, London.
- Thomas CD, Hill JK & Lewis OT (1998) Evolutionary consequences of habitat fragmentation in a localized butterfly. *Journal of animal Ecology* 67: 485-497.
- Väisänen R, Kuussaari M, Nieminen M & Somerma P (1994) Biology and conservation of *Pseudophilotes baton* in Finland (Lepidoptera, Lycaenidae). *Annales Zoologici Fennici* 31: 145-156.
- Välimäki P & Itämies J (2003) Migration of the clouded Apollo butterfly *Parnassius mnemosyne* in a network of suitable habitat – effects of patch characteristics. *Ecography* 26: 679-691.
- Wahlberg N, Moilanen A & Hanski I (1996) Predicting the occurrence of endangered species in fragmented landscapes. *Science* 273: 1536-1538.
- Wahlberg N, Klemetti T, Selonen V & Hanski I (2002) Metapopulation structure and movements in five species of checkerspot butterflies. *Oecologia* 130: 33-43.
- Weiss MR (1997) Innate colour preferences and flexible learning in the pipevine swallowtail. *Animal Behaviour* 53: 1043-1052.
- Wickman PO, García Barros E & Rappe George C (1995) the location of leks in the small heath butterfly *Coenonympha pamphilus*: support for the female preference model. *Behavioral Ecology* 6: 39-45.
- Withers TM & Harris MO (1996) Foraging for oviposition sites in the Hessian fly: random and non-random aspects of movement. *Ecological Entomology* 21: 382-395.
- Yáber MC & Rabenold KN (2002) Effects of sociality on short-distance, female-biased dispersal in tropical wrens. *Journal of animal Ecology* 71: 1042-1055.