

Demographic processes in a local population: seasonal dynamics of the Sinai Baton Blue butterfly

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ABSTRACT

Quantifying abundance and determining the factors affecting it are critical to understanding and conserving small animal populations. The seasonal dynamics of a local population of butterflies *Pseudophilotes sinaicus* (Lycaenidae) occupying a discrete patch of habitat were investigated using data from a capture-recapture study that sampled the local population every day during the adult flight season in 2002 and 2003. Throughout the study (re)capture rates were extremely high, meaning that intra-seasonal changes in demographic parameters could be accurately assessed. 'Survival' rates were not related to the age of adult butterflies, but were lower early in the season compared with later on. This is probably due to emigration of butterflies early in the season, rather than within-patch mortality. Lower survival rates in females compared with males were probably because females have both higher within-patch mortality and a higher emigration rate. This confirms results from another study (see James 2007d) that suggested migration in the Sinai Baton Blue was linked to the phenology of its hostplant, *Thymus decussatus*. Daily variation in the sex ratio is a consequence of between-sex differences in daily recruitment and within-patch survival rates. Males were most abundant relative to females early in the season, indicating protandry. Total adult population size was small and showed dramatic variation between the two years, indicating how vulnerable the local population is to demographic extinction.

INTRODUCTION

Animal populations fluctuate across space and through time, and in open populations this is because of the addition of individuals by recruitment and immigration and the loss of individuals through mortality and emigration. These parameters are important when studying population dynamics and determining population structure, and their estimation is informative to animal population biology, evolutionary ecology, and conservation biology (Lebreton *et al.* 1993; Murdoch 1994; Colbert 1995; Thomas 2000).

Habitat fragmentation now threatens many species and is thought significantly to affect population dynamics (Saunders *et al.* 1992; Henle *et al.* 2004). Consequently, there is a need to understand the ecology of species living in fragmented landscapes, particularly since the advent of metapopulation theory (Hanski 1994, 1999). In fragmented landscapes, information on local demographic processes (births and deaths), and the transfer of individuals among the network of habitat patches, is required when studying metapopulation dynamics (Hill *et al.* 1996; Hanski 1999; Thomas & Kunin 1999). Much work has been devoted to determining the level of inter-patch movement (migration) in a species, and this has increased understanding on metapopulation spatial structure and dynamics (e.g. Harrison 1989; Kuussaari *et al.* 1996; Hill *et al.* 1996; Thomas & Hanski 1997; Menéndez *et al.* 2002). Variation in survival and recruitment within a local population will also influence metapopulation dynamics, but these factors can be difficult to study in natural populations, especially when emigration cannot be separated from mortality, and immigration from recruitment.

A number of butterfly studies have compared population parameter estimates between years (e.g. Warren *et al.* 1986; Thomas 1991), but surprisingly few have compared estimates within a year (season). This is probably because parameter estimation is difficult at the beginning and end of the adult flight period when sample sizes are often unavoidably small.

This is especially so when population size is small (a common feature of local butterfly populations in fragmented landscapes) and recapture rates low. Unpredictable weather and limited time also prevent sampling throughout the season, and make intra-season comparisons difficult. However, behaviour of individuals might be very different at different times of the adult flight period (Kuussaari *et al.* 1996; Matter & Roland 2002), so determining how population parameters change through the season is potentially informative in predicting the persistence of small populations, and their conservation .

Here, I study seasonal dynamics in one of the largest local populations of a narrow endemic, rare species of butterfly (the Sinai Baton Blue) living in a fragmented landscape (James, 2006a,b,d,e,f; James *et al.* 2003; Hoyle & James 2005), using the Jolly-Seber model (Jolly 1965; Seber 1965) to estimate population parameters. Previous work has suggested that the species is a weak flier, easy to catch/observe (Nakamura 1975; James *et al.* 2003; James 2006f), and that sampling during the study period will not be interrupted or biased by weather (personal observation). These are important considerations if changes in population parameters are to be accurately assessed within a season. In a different study (James, 2006d), I attempted to estimate immigration and emigration in the same local population of Baton Blues as I have used here; parameter estimates in the present study are discussed with reference to those findings. This work provides important information on factors affecting the butterfly's migration, survival and recruitment, and how these vary during its flight period; knowledge that is essential for the conservation of a specialist species confined to living in a network of small, discrete patches of habitat. It also provides a practical example of how the Jolly-Seber model can be used with data representing virtually every individual present at any given sampling period.

MATERIALS AND METHODS

Study Species: The Sinai Baton Blue butterfly (*Pseudophilotes sinaicus* Nakamura: Lycaenidae) is univoltine, living in fragmented populations in the high mountains around the town of St. Katherine, South Sinai, Egypt. It is restricted to areas where its only larval hostplant, Sinai Thyme (*Thymus decussatus* Benth.: Labiatae) grows. The butterfly's main flight period is in May and June. Females lay eggs on thyme buds, and larvae are fully developed in a few weeks; they then crawl to the base of the thyme plant, overwintering as pupae in the soil below. Individuals are absolutely tiny and are relatively sedentary within a patch. Most butterflies remain in their natal patch, but are capable of migrating between patches and exhibit characteristics of surviving as a metapopulation (James *et al.* 2003; James 2006d,e; Hoyle & James 2005). Predation is probably the main source of within-patch adult mortality, the most apparent predator being lizards (family Agamidae).

Study area and data collection: The study was carried out in Farsh Shoeib, an area of thyme (13,600 m²) bordered on all sides by steep, bare cliffs, close to Gebel Safsafa on the Mt. Sinai massif. Five other areas of thyme occur on the massif, separated from one another by at least 100 m: in 2002 Baton Blues were present in four of them. Weather conditions throughout the study period were fine and dry (0 mm of rain). 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 temperatures rarely dropped below 10 °C.

A mark-release-recapture (MRR) study was carried out over 97 consecutive days, from 8th April to 13th July 2002 in Farsh Shoeib; the actual study period extended 7 days either side of this period to make sure that no butterflies were present in the study patch before or after these dates. 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 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. Mature Sinai Baton Blues never roost on thyme. New adults were caught, given an individual mark on the underwing(s) using permanent marker pens, and returned to the same plant. Whilst walking this route any previously marked individuals were identified and noted. Baton Blues roosted on plants (mainly *Jasonia montana*) at the edge of the study site and on the tips of dead stalks/dry flower heads, and were easy to find. Potential roosting sites were examined every dawn and dusk, and the identity of roosting individuals recorded. To assess the level of disturbance/mortality occurring at night, on 5 separate evenings the exact location of 20 roosting butterflies was noted and these individuals were searched for the following dawn. Because of the intensive marking effort, it is believed that the majority of butterflies were marked at or close to their minimum possible age. When unmarked butterflies were seen flying in the site or found whilst roosting, these were caught, marked, and then released at the point of capture. To reduce the effects of handling, no butterfly was caught more than once: close-focus binoculars were used to identify marked individuals (a 'recapture' was actually a 're-sighting').

Capture histories of individual butterflies were used as an input to the Jolly-Seber model for open populations (here adapted from Pollock *et al.* 1990). This enabled daily estimation of survival rate, capture rate, recruitment, and population size. Accuracy was assessed following the method developed by Robson & Regier (as cited in Begon 1979), which compares the population size estimate (N) with the sample sizes used to derive it. Jolly-Seber model assumptions were justified by reference to the known biology of the butterfly, and their validity checked using goodness-of-fit tests using RELEASE software (Burnham *et al.* 1987). To determine whether males and females were equally catchable, the capture sex ratio vs. estimated sex ratio test was used (following Tabashnik 1980); this method disentangles catchability and residence.

Where possible I used capture-recapture data collected throughout the study period. However, because of the unavoidably small sample sizes at the beginning and end of emergence, not every day yielded enough data to provide meaningful output using the Jolly-Seber method. Estimates from days in which data are too sparse are excluded in analyses. I have split the sampling period into two sections based on hostplant phenology: 'early' (before day 35) and 'main' (on or after day 35) (see James, 2006d). Unless stated otherwise, all analyses consider males and females separately.

The MRR study was repeated in 2003, simultaneously in Farsh Shoeib and its five neighbouring patches of thyme. The 2003 study coincided with a severe drought in the area, and the population of butterflies was much smaller than in 2002, leading to very small sample sizes and many days with no (re)captures. This meant that estimation from these data is not possible and so I have included the results only as a between-year comparison in Farsh Shoeib.

Accuracy: Robson & Regier considered that an accuracy of 0.1 (95% probability that the true population size is in the range $0.9N - 1.1N$) was necessary when investigating population dynamics. Here, to assess accuracy I have only used the 32 days when the total population size estimate (N) was >25 individuals (males + females). On the majority of these days ($n = 20$), sample sizes (number of butterflies caught) gave a population size estimate accurate at the 0.1 level (Begon 1979); eleven days had an accuracy of <0.25 , and just one day had an accuracy of <0.5 . Thus, the precision of the estimators is high and adequate for investigating population dynamics. Indeed, the butterfly's survival rate was high (see results) meaning that the required sample size for a given accuracy is probably lower than that set out by Robson and Regier, and so the accuracy calculated here is likely to be an underestimation.

Review of assumptions: The two most important Jolly-Seber model assumptions are that (1) every marked individual in the population has the same survival probability between two successive samples; and (2) the probability of capture is the same for all individuals in the population. Results of the full goodness-of-fit test suggested the Jolly-Seber model did not fit the data adequately (tests 2 and 3 in RELEASE: males $\chi^2_{123} = 173.9$, $p < 0.001$; females $\chi^2_{101} = 173.8$, $p < 0.001$). In other words one or more of the model assumptions were violated, indicating that parameters are heterogeneous within each sex.

Examining why the goodness-of-fit test failed is potentially informative, and close inspection showed the primary reason for lack of fit was due to heterogeneity in capture probability.

There was no evidence over all occasions for which there were enough data that survival differed between newly marked and previously marked individuals. Among butterflies seen again, there was no evidence over all occasions for which there were enough data, that when a butterfly was seen again was conditional on when it was seen for the first time. Thus, the first assumption of constant survival rates is not violated (Test 3.Sr + Test 3.Sm: males $\chi^2_{73} = 54.2$, $p = 0.97$; females $\chi^2_{64} = 32.0$, $p = 1.00$). However, only a few χ^2 -tests could be calculated at the beginning of the study due to data being unavoidably sparse. Survival rate during this period was much lower than subsequently (see Fig. 1; Table 1).

The result of the test for equal catchability among marked individuals suggests that the probability of being seen on occasion (i+1) is a function of whether or not the individual was seen on occasion (i) (males $\chi^2_{50} = 119.7$, $p < 0.001$; females $\chi^2_{37} = 141.9$, $p < 0.001$). In both sexes, there was the same systematic difference between observed and expected results, with butterflies seen on occasion (i) being more likely than expected to be seen again the next day (i+1), and butterflies not seen on (i) (but which were definitely alive at i) less likely than expected to be seen the next day (i+1). Unmarked individuals were searched for with equal effort by ensuring that the sampling method was equally employed over all areas of the site, and with equal intensity on each day of the study.

Within the bounds of experimental error, the other Jolly-Seber model assumptions are justified: (3) All marks are permanent and are noted correctly on recapture: marks could not be lost, except by the loss of all or part of the marked wing(s). Loss of an entire wing never happened, and in the very rare event that the mark was incomplete, careful checking of individual attributes (e.g. sex, wing wear, other marks etc.), made mark reading errors very uncommon. A recapture was only classed as such if a positive identification of the individual could be made. (4) Emigration is permanent, and so is indistinguishable from death: In 2003 the MRR study was extended to include Farsh Shoeib and its five closest patches. Although total numbers were much lower (133 individuals caught in all patches), no individual was observed moving from one patch to another patch and then returning to its original patch, not between days (285 recaptures) nor within days (960 recaptures). This suggests that temporary emigration to other patches is highly unlikely.

Thus the only assumption to be violated is assumption 2 – that of equal catchability. However, Carothers (1979) demonstrated that Jolly-Seber estimates of survival are robust in the face of unequal catchability. If all individuals are not equally catchable, population size estimators will generally be negatively biased (Begon 1979; Pollock *et al.* 1990). However, Gilbert (1973) and later Hwang & Chao (1995) both used simulation tests to demonstrate that heterogeneous capture probabilities are relatively unimportant with respect to population size estimators when all animals have high capture probabilities, e.g. > 0.5 . In this study, daily capture probabilities were more than 0.5 on 82% (males) and 86% (females) of the days on which they could be calculated (Table 1).

I conclude that the Jolly-Seber output was both accurate and reliable enough to estimate demographic parameters of the Sinai Baton Blue butterfly.

RESULTS

Numbers marked and recaptured: In total in 2002, 431 butterflies were marked. The sex ratio of these individuals did not differ significantly from an expected ratio of 1:1 (212 males:219 females; $\chi^2_1 = 0.1$, ns). Another method of calculating the population sex ratio divides the estimated total male population size by the estimated total female population size; again there was no significant difference from a 1:1 sex ratio (261 males:253 females; $\chi^2_1 = 0.1$, ns). Three hundred and eight individuals (71%) were recaptured at least once, with neither males nor females more likely to be recaptured ($\chi^2_1 = 0.01$, ns). The maximum number of times an individual was recaptured was 17 (a male) and the same individual had the longest time between its first and last captures (24 days). There were 1557 releases after (re)capture, meaning that each individual was (re)captured on average 3.61 times, females being (re)captured significantly less often (mean 3.3 times) than males (mean 3.9 times) ($\chi^2_1 = 9.3$, $p < 0.01$).

Overall, 84% of the estimated Sinai Baton Blue population was captured, and on average only 14% of the estimated female population and 16% of the estimated male population were not recorded on a given day, but then observed on the next or subsequent days.

Survival and catchability: Survival rate was not related to the age of the butterfly in either sex, but mean daily survival rate in ‘early’ butterflies was significantly lower than mean survival rate in ‘main’ butterflies (independent samples test: males $t_{71} = 3.9$, $p < 0.001$; females $t_{65} = 4.8$, $p < 0.001$) (Fig. 1; Table 1). Daily survival rate was always lower in females than males, but this difference was not significant at any stage in the flight period (independent samples test: ‘early’: $t_{37} = 1.6$, ns; ‘main’: $t_{99} = 0.97$, ns). In the experiment to assess survival at night, only one roosting butterfly on the 100 occasions (20 individuals x 5 nights) failed to be seen again in exactly the same location the following morning.

Table 1 Survival rate and catchability of butterflies caught in Farsh Shoeib at different stages of the adult flight period in 2002. Estimates are Jolly-Seber means \pm s.e

Period	Survival rate (per day)		Capture probability (per day)	
	Males	Females	Males	Females
‘Early’ flight period (< day 35)	0.59 \pm 0.07	0.42 \pm 0.08	0.69 \pm 0.09	0.92 \pm 0.08
‘Main’ flight period (\geq day 35)	0.82 \pm 0.03	0.78 \pm 0.03	0.69 \pm 0.03	0.67 \pm 0.03
Entire flight period (days 1- 97)	0.76 \pm 0.03	0.67 \pm 0.04	0.69 \pm 0.03	0.72 \pm 0.03

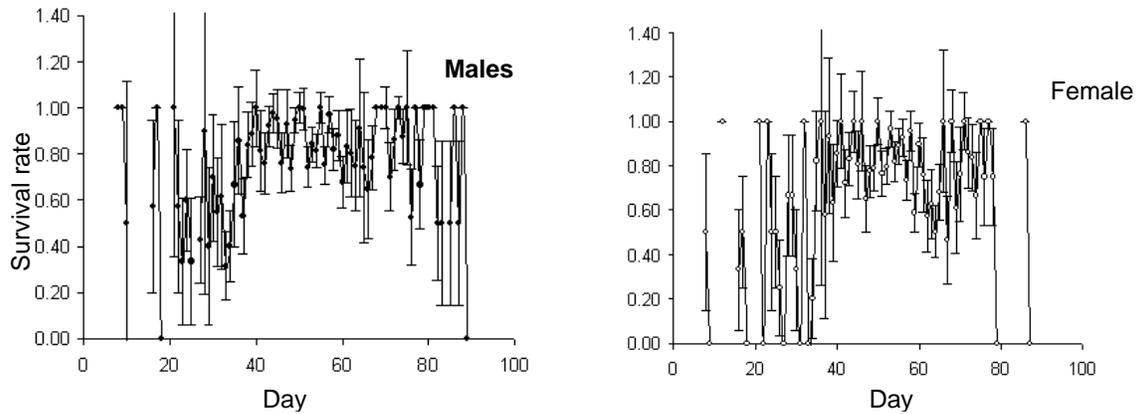


Fig. 1 Change in daily survival rate during the flight period in 2002. Estimates are calculated using the Jolly-Seber model and are plotted as means \pm s.e. Gaps in the plot represent days on which insufficient data meant reliable estimates could not be calculated

Daily capture rate at different stages of the flight period did not differ significantly in males, but ‘early’ females had a higher mean daily capture rate than both ‘main’ females (independent samples test: $t_{57} = 3.71$, $p < 0.001$), and ‘early’ males (independent samples test: $t_{29} = 2.1$, $p < 0.05$) (Table 1). However, the number of females during the early period was low, meaning catchability estimates may be inaccurate. There was no significant difference in daily capture rate between ‘main’ males and females (when estimates were much more reliable) (independent samples test: $t_{98} = 0.4$, ns). In both ‘early’ and ‘main’ butterflies, the capture sex ratio did not differ significantly from the estimated sex ratio, indicating that males were equally as catchable as females in both periods (paired samples test: ‘early’, $t_{11} = 2.14$, ns; ‘main’, $t_{45} = 0.21$, ns).

Population size: Figure 2 shows the change in daily population size estimates during the 2002 flight period. The general pattern fits a normal distribution in both sexes, with a peak in numbers of 67 males (day 51) and 61 females (day 47) occurring in the middle of the flight period. The total population peaked at 120 butterflies on day 51. The flight period in both sexes lasted 88 days, males and females beginning and ending their flight periods at approximately the same time (males day 9 to 96; females day 1 to 88).

There is an indication of protandry: significantly more males were recruited during the early flight period than females (88 males, 39 females: $\chi^2_1 = 18.9$, $p < 0.001$) (Fig. 3). Peak recruitment of males (day 35) occurred four days before female peak recruitment, at a time when the female population size started to rapidly increase (Figs 2, 3). A secondary, slightly smaller male recruitment peak (around day 50), coincided with the middle of the plateau in female population size (days 46 to 60) (Figs 2, 3). More ‘main’ females than males were recruited to the population, though the difference is not significant (177 males, 215 females: $\chi^2_1 = 3.7$, ns). The operational population sex ratio changed during the flight season from being strongly male biased at the beginning, balanced in the middle, and male biased once again at the end (Fig. 4).

Inter-year differences: Despite a similar capture effort in 2002 and 2003, only 60 butterflies were marked in Farsh Shoeib in 2003 (14% of the number marked in 2002). In terms of actual numbers caught there were significantly more females than males (19 males : 41 females; $\chi^2_1 = 8.1$, $p < 0.001$). Insufficient data in 2003 prevented use of the Jolly-Seber model for males and females separately, but limited output was achieved by pooling data collected for both sexes and this could be compared with similarly pooled data from 2002. The highest estimated total daily population size in 2003 was 14 butterflies, 12% of the peak in daily numbers estimated in 2002; the flight period in 2003 started later and finished earlier

than in 2002, lasting 51 days (Fig. 5). Survival rate (over all occasions for which there were enough data) seemed to follow a similar pattern in 2003 to 2002: ‘early’ butterflies had a significantly lower mean survival rate than ‘main’ butterflies (‘early’ = 0.37 ± 0.13 ; ‘main’ = 0.73 ± 0.04 ; independent samples test: $t_{42} = 2.5$, $p < 0.05$). There was no significant difference between the years in either ‘early’ or ‘main’ survival rates.

Fig. 2: Change in daily population size of males (upper) and females (lower) during the flight period in 2002. Estimates are calculated using the Jolly-Seber model and are means \pm s.e. Gaps in the plot represent days on which insufficient data meant reliable estimates could not be calculated

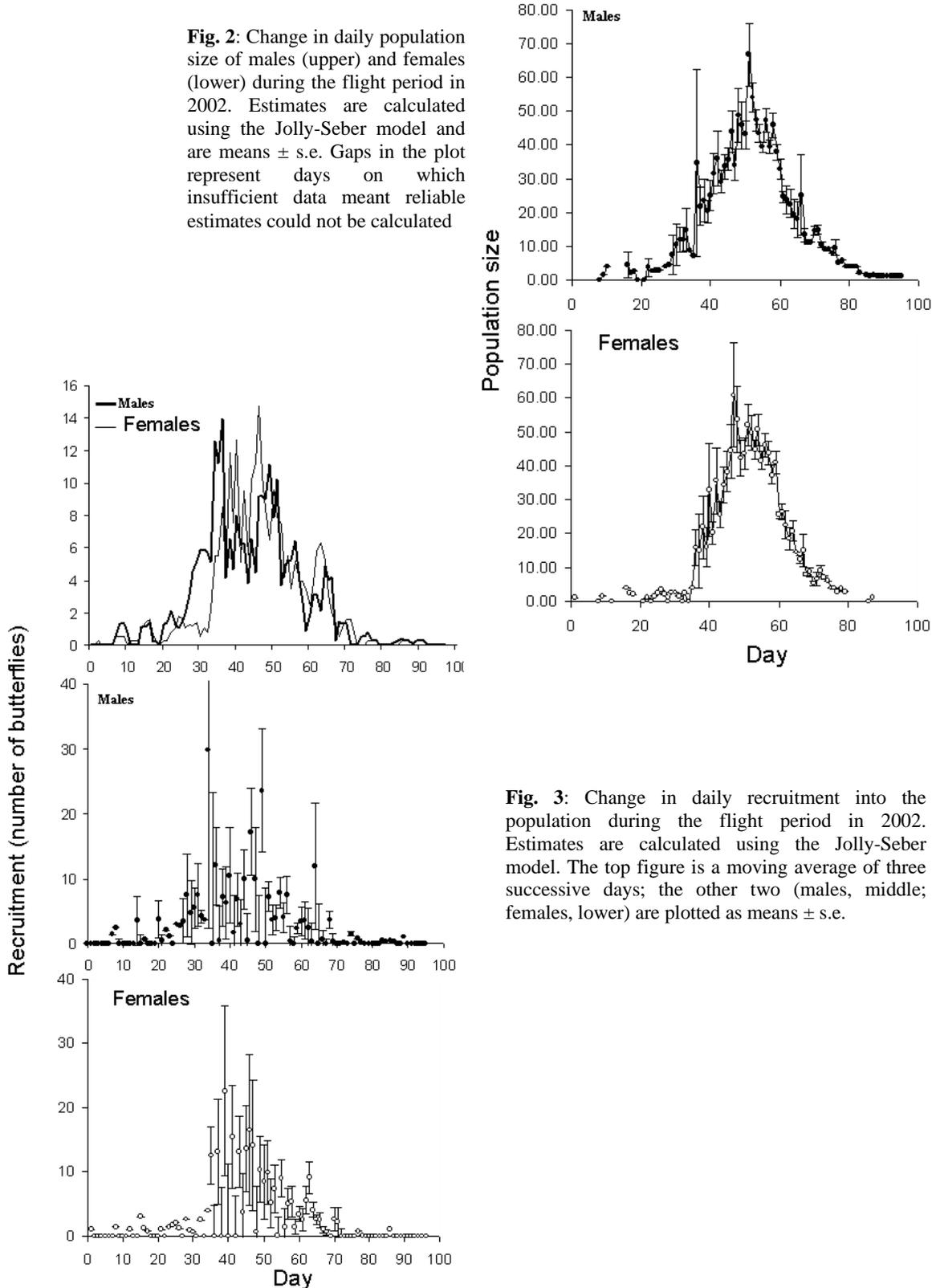
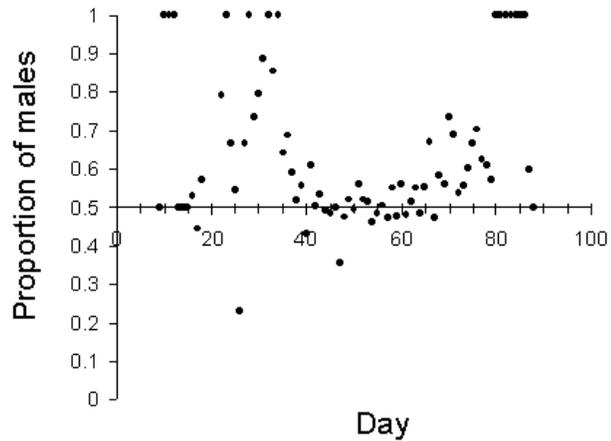


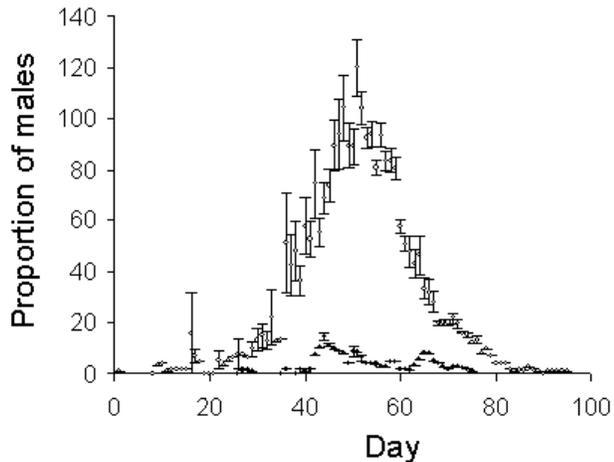
Fig. 3: Change in daily recruitment into the population during the flight period in 2002. Estimates are calculated using the Jolly-Seber model. The top figure is a moving average of three successive days; the other two (males, middle; females, lower) are plotted as means \pm s.e.

Fig. 4: Sex ratio (proportion of males in the population) during the flight period in 2002, based on Jolly-Seber population size estimates. The same number of males and females in the population on any given day would equal 0.5



In 2003, no butterflies were recorded moving from Farsh Shoeib to any of its four neighbouring patches. Two individuals immigrated to Farsh Shoeib. They were both female (aged 4 and 9 days old) and both arrived on day 44, coinciding with the highest estimated daily population size in Farsh Shoeib.

Fig. 5: Total adult (males + females) population size during the flight period in 2002 (upper) and 2003 (lower). Estimates are calculated using the Jolly-Seber model and are means \pm s.e.



DISCUSSION

Despite data being unavoidably sparse, particularly at the beginning and end of the season, high capture rates indicate that this was a true reflection of the real situation, meaning comparisons between different stages of the flight period within a season, and between the two seasons, are informative.

Survival rate and catchability: Throughout the paper the term survival has been used. However, emigration cannot be separated from death in the Jolly-Seber method. Does the lower survival rate in ‘early’ butterflies compared with ‘main’ butterflies, reflect a higher rate of mortality at this time, or a higher rate of emigration? In another study (James, 2006d), I observed that adult nectar plants were available in sufficient quantity throughout the butterfly’s flight period, and the composition/abundance of predators was the same between the ‘early’ and ‘main’ flight periods. I proposed that emigration was likely to be higher early in the flight period because butterflies moved out of the study site in search of resources (Sinai Thyme). Thus, the low survival rate estimates for ‘early’ butterflies in the present study probably resulted from emigration, as opposed to within-patch mortality.

‘Early’ butterflies eclosed in Farsh Shoeib when hostplant resource was unavailable (James 2006d), and they occurred at low density within the study patch. Both factors might

alter their behaviour, making them more likely to emigrate than butterflies eclosing in the 'main' period. In males, a lower number of interactions (e.g. male-male chasing and courtship), might mean the probability of performing directed flights leading to emigration is increased (Odendaal *et al.* 1988; Kuussaari *et al.* 1996; Petit *et al.* 2001), and searching for females itself could lead to emigration (Baguette *et al.* 1998). In the Fender's Blue butterfly (*Icaricia icarioides fenderi*), females alter their dispersal behaviour depending on habitat type, flying further and over more ground when hostplants are absent (Schultz 1998). In the Sinai Baton Blue, females mate shortly after eclosion, so 'early' females will either emigrate after mating (in search of suitable oviposition sites), or they might emigrate before mating, in response to a lack of male encounters.

To confirm that 'early' butterflies were emigrating and not dying in the study patch, the MRR study in 2003 took place simultaneously in Farsh Shoeib and its five neighbouring patches. However, no butterflies from Farsh Shoeib were recaptured in a different patch. The number of butterflies seen that year were extremely low, particularly early in the season (6 individuals caught in Farsh Shoeib before day 35), meaning recapture of surviving emigrants would be unlikely. The 2003 study needs to be repeated during a year of high Baton Blue numbers, and in as many patches as possible because it is likely that early emigrants are forced to travel further in search of suitable resources.

Although not significant, the difference in daily survival rate between males and females is of interest. In many butterfly species, males take a few days to reach sexual maturity and are not usually ready to mate when they emerge (Scott 1973a; Petit *et al.* 2001). Higher survival in 'early' males compared with 'early' females might result from this delay: 'early' females emigrate almost immediately (before or after mating), while 'early' males spend a day or two after eclosion foraging in the patch before they are able to mate with (and actively search for) females. In the butterfly *Proclossiana eunomia*, Schtickzelle *et al.* (2002) suggested that higher within-patch mortality in males occurred because they 'patrolled' for females, making them more prone to predation. Sinai Baton Blue males are 'patrollers' but this is likely to assist them in avoiding their main predator (lizards), as these animals hunt by 'sitting-and-waiting' next to a flowering thyme plant (personal observation). Females tend to spend more time on a plant, selecting a site for oviposition and laying eggs, so lower survival seen in 'main' females compared with males could be due to slightly higher rates of within-patch mortality. Mortality at night is negligible. 'Main' females may be slightly more predisposed to emigrating than 'main' males. This could be a strategy of spreading the risk i.e. distributing offspring among several habitat patches to avoid parasitism (e.g. Brown & Ehlich 1980; Petit *et al.* 2001), or to avoid the stochastic chance of extinction, which is presumably high in a small, fragile patch of habitat like Farsh Shoeib. Females might also be motivated to emigrate because of male harassment (Odendaal *et al.* 1989; Baguette *et al.* 1998).

Survival rate estimates for 'main' butterflies were similar to those from other butterfly MRR studies (e.g. 0.78 in *Lycaena arota*, 0.79 in *Polyommatus icarus*, Scott 1973b; 0.8 in *Plebejus argus*, Lewis *et al.* 1997; 0.86 in *P. eunomia*, Schtickzelle *et al.* 2002). In studies where within-patch mortality has been separated from emigration, within-patch survival rates are usually slightly higher e.g. 0.84 in *Lysandra coridon* and 0.88 in *Lysandra bellargus* (Scott 1973b), 0.93 in *P. eunomia* (Petit *et al.* 2001), and 0.88 to 1.0 in five species of Melitaeini (Wahlberg *et al.* 2002), suggesting that some 'mortality' observed in 'main' Sinai Baton Blues was a result of emigration. However, with the exception of *L. coridon*, the species in these studies are longer-lived than the Sinai Baton Blue, making comparisons difficult.

Recapture rates were much higher in this study (71%), than in other butterfly studies, e.g. *P. argus* = 31% (Lewis *et al.* 1997); *Danaus plexippus* = 56% (Knight *et al.* 1999); 5 species of Melitaeini butterflies = 22-49% (Wahlberg *et al.* 2002). This is due to the intensive

sampling method employed. Additional sampling at dawn and dusk when the butterflies were roosting, enabled individuals to be recorded without the difficulties of trying to capture them or wait for them to land and be identified.

The Sinai Baton Blue is relatively sedentary within a patch, with individuals rarely moving more than 50 m between sightings (James 2006e). The unequal catchability indicated by the goodness-of-fit tests might be because field workers learnt the approximate location of butterflies from one day to the next, due to the intensive sampling method. However, high daily recapture rates suggest that rather than simply being missed, some individuals perhaps whilst trying to emigrate, leave the patch and spend a day or two in matrix habitat before returning.

Sex Ratio: The population sex ratio ($\approx 1:1$) and the general lack of difference in recapture probabilities between the sexes, indicate males and females were sampled equally, and throughout their flight period (higher overall number of male recaptures is a function of higher survival in males compared with females). Thus, the biased sex ratios observed are unlikely to be an artefact of differences in recapture probabilities between the sexes (Stoks 2001) and the true pattern of male and female population sizes can be examined throughout the season.

Recruitment includes birth and immigration. In another study (James 2006d), I estimated 13% of the Farsh Shoeib population in 2002 was composed of immigrants, and that these arrived in low numbers throughout the main flight period. This low level of immigration is unlikely to dramatically alter the results reported here.

In protandrous species, the operational sex ratio usually changes from being strongly male biased early in the flight season to strongly female biased at the end (Schtickzelle *et al.* 2002). Here, estimated recruitment rates indicate males are eclosing before females. However, male bias is exaggerated in 'early' daily population estimates (Fig. 4) because of low female 'survival' rates at this time. This bias decreases after day 35, reaching a balance shortly after, due to female recruitment being greater than or equal to male recruitment, and the disparity in survival rates between the sexes being reduced. Thus, daily variation in the population sex ratio is a consequence of the combination of between-sex differences in daily recruitment, and daily survival rate. The male bias in daily population estimates towards the end of the season might be due to Sinai Thyme once again becoming unavailable (end of its flowering period) leading to reduced female survival (probably increased emigration) in the patch (James, 2006d), though this is hard to interpret due to the small sample sizes.

Population size: Population size varied dramatically between 2002 and 2003. In other butterfly species, population size differences among years have been attributed to the impact of parasitoids (e.g. Schtickzelle *et al.* 2002; Joyce & Pullin 2003). In 2002, approximately 7,000 eggs were laid in Farsh Shoeib and I devoted much time observing larvae that hatched from them (James, 2006f). These observations suggested that larval infection by parasitoids was extremely low. Indeed, the incidence of parasitoids in arid montane environments is likely to be low. This evidence and the severe drought during the 2002-2003 winter period (when most precipitation falls), suggest either that pupal mortality was very high, or that adults suspended their emergence. The latter hypothesis is a reasonably common strategy among eremic butterfly species, some of which are able to postpone eclosion for several years while waiting for conditions to improve (Larsen 1990; Benyamini 1999). To discover if the Sinai Baton Blue had prolonged pupal diapause, a search was carried out for 'healthy' pupae at the end of the 2003 flight period. Although one healthy pupa was located, the results are inconclusive because (1) pupae are tiny (length ca. 6 mm), buried in soil under thyme plants, cryptically coloured, and so very inconspicuous, and (2) Sinai Thyme is an

endangered plant and the study site is in a protected area, so only three thyme plants could be destroyed in the search for pupae.

The low estimated population size of the Sinai Baton Blue, indicates that the species is susceptible to demographic extinction, even in one of its largest local populations, and the dramatic reduction in its population size in a drought year illustrates just how vulnerable it is.

The high capture rates make this study almost unique among butterfly MRR work. This has not only enabled a detailed picture to be built-up concerning seasonal dynamics in the Sinai Baton Blue, but also provides a practical example of how the Jolly-Seber model can be used when almost every individual in the population is sampled at any given sampling period.

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