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Assessing the conservation status of the Sinai

Baton Blue butterfly (*Pseudophilotes sinaicus*)

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Abstract

Arid environments are resource-limited, with scarcity of water the key limiting factor for plants and their associated fauna. Consequentially bottom-up forces often control food webs, influencing the whole system through high levels of competition. The Sinai Baton Blue butterfly, *Pseudophilotes sinaicus*, is Critically Endangered, with a tiny endemic distribution in the St Katherine Protectorate, South Sinai, an arid environment. Its range is restricted to that of its sole host plant, the near-endemic endangered Sinai Thyme, *Thymus decussatus,* leaving the butterfly in a highly fragmented distribution. This study looks into the spatio-temporal variations in quality and abundance of the host plant and its implications for the Sinai Baton Blue. Over the past decade the butterfly has exhibited severe population cycles, with the causes still unclear; it could be due to the fluctuating resource levels with large temporal variation in the quality of thyme and density of inflorescences. The number of flowers significantly influences the larval distribution, indicating that resources play a key role in offspring survivorship. Population viability analysis has also highlighted the importance of management techniques aimed at increasing the butterfly's survivorship. The butterfly population sizes are positively correlated with the total resource area and the number of host plants but not the distance between habitat patches. Population viability analysis also suggests that habitat area is more influential than connectivity in this system driving current dynamics. Overall this project has highlighted the urgent need for conservation focused on improving plant quality within patches in order to save this fragile species.

Acknowledgments

Contents

Chapter 1.

General introduction; a brief overview of the Sinai Baton Blue

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The Sinai Baton Blue (*Pseudophilotes sinaicus* Nakumara, 1975: Lycaenidae) is the World's smallest butterfly; the smallest recorded wingspan is 6.25 mm and the average is just 9.5 mm (James, 2006b). The butterfly is Critically Endangered, with an Extent of Occurrence less than 7 km^2 and an estimated total population below 3000 in 2001 (Thompson & Gilbert, 2012). Its narrowly endemic distribution is localised to the St Katherine Protectorate, South Sinai, Egypt and it is one of two endemic butterfly species to the area, the other being the Sinai Hairstreak (*Satyrium jebelia:* Lycaenidae*)*. The larvae feed exclusively upon the host plant, Sinai Thyme (*Thymus decussatus* Bentham, 1834: Lamiaceae), restricting the distribution to a patchy formation on mountaintops at altitudes above 1800 m (James, 2006a). The population can crash dramatically between years with a crash in 2003 reducing the peak butterfly population in one patch (Farsh Shoeib) to 12% of its size in 2002 (James, 2006c). Consequentially it is considered a top conservation priority for the local Protectorate and a flagship species for the area (Hoyle & James, 2005). Figure 1.1 is a timeline demonstrating the significant events over the past decade for the Sinai Baton Blue.

The adult is univoltine with the main flight period starting at the beginning of May and finishing mid-June (James et al., 2003). Adults live for 3-6 days and females mate almost immediately, with 47% mating before their first flight (James, 2006f). Females lay approximately 26 eggs, distributed singly on inflorescences across multiple thyme plants, possibly as a bet-hedging strategy to spread the risk (Bergstrom et al., 2006, James, 2006f). Larvae hatch approximately four days after oviposition and are immobile, remaining on the inflorescences on which the eggs were laid. Little is known about the larval development, but it is presumed to take approximately 21 days with four or five instars; the first two instars feed exclusively on the buds of the Sinai Thyme, whilst later instars can also feed upon the flowers (James, 2006d,f). The larvae are myrmecophilous with facultative associations with *Lepisiota obtusa* and *Lepisiota hirsuta* ants (Shepherd, 2010); the larvae were tended 71% of the time by *Lepisiota* species (James 2006f) with lesser associations with *Monomorium niloticum* ants. The larvae produce volatile secretions to attract and alert attendant ants; in return for protection, the larvae secrete simple sugars

and amino acids from their dorsal nectary organs (James, 2006f). *Crematogaster antaris* ants prey upon the larvae, reflected by the fact that no adult butterflies emerged within the foraging range of *C. antaris* (James, 2006f). The foraging ranges of *C. antaris* and *Lepisiota* spp. are mutually exclusive, and the distributions of the two species do not overlap (Shepherd, 2010).

The larvae pupate in the soil below the plant where they remain over winter, eclosing the following year. It is unknown whether the pupae can delay emergence for multiple years if conditions are sub-optimal, a tactic known in other desert Lycaenidae (Larsen, 1990). If this occurs then it might explain the low number of adults seen during the 2003 drought, otherwise attributed to mortality (James, 2006c,f). The tactic is used by *Pseudalmenus chlorinda* (Lycaenidae), which can remain in its pupal state for an additional year, whilst *Cupha prosopa (*Nymphalidae) can delay emergence for seven months. The extension of the pupal diapause in *C. prosopa* has been associated with unsuitable conditions, such as low rainfall (Sands & New, 2008). *Pseudophilotes jordanicus* (Lycaenidae) is closely related to the Sinai Baton Blue, and can enter a long-term pupal diapause; one individual remained in its pupal stage for three years (Benyamini, 2008).

If butterflies eclose before the thyme is flowering they feed upon the nectar of four other plant species, including *Globularia arabica* (Globulariaceae), but they preferentially feed upon the Sinai Thyme (James, 2006d). *Thymus decussatus* has a limited and fragmented distribution (Nakamura, 1975; Hoyle & James, 2005) in the St Katherine Protectorate, only at altitudes above 1500 m, growing best in well-defined soils at the base of cliffs and wadis. According to local Bedouin knowledge the steepness of the slope also influences growth; if it is too steep the surface run-off is too fast for water to infiltrate the soil (Nasr Mansour, 2011, pers. comm.). Elsewhere thyme is often an emblematic species for degraded landscapes, particularly arid environments with long-standing grazing pressures; the characteristically small leaves and flowers limit the effects of drought and grazing (Navarro et al., 2006).

The patchy habitat structure and the butterfly's detectable but limited movement make this system ideal for the metapopulation studies carried

out by Mike James during 2001-2003. By modelling the system, Hoyle & James (2005) identified two patches as critical in sustaining the metapopulation, both located in Gebel Ahmar in the centre of the butterfly's distribution (Fig. 1.2). Critical patches within metapopulations are often centrally located, enhancing connectivity and dispersal (Hanski, 1999; Drechsler et al., 2003; Rozenfeld et al., 2008). The theoretical removal of these patches reduced occupancy of neighbouring patches, increasing the probability of metapopulation extinction (Hoyle & James, 2005). Figure 1.2 shows the published distribution of the thyme and Sinai Baton Blue, whilst Figure 1.3 incorporates additional thyme patches found during the present study with the help of local Bedouin knowledge. Classical metapopulations consists of similar-sized populations, but as in most real-life examples this is not observed in the Sinai Baton Blue, which has a couple of large patches surrounded by many small patch populations, suggesting it exists in a mainland – island formation (Driscoll et al., 2010; Fronhofer et al., 2012).

The butterfly's fitness and survival is dependent upon the quality and quantity of the endangered host plant. Current threats are probably now predominately environmental, with anthropogenic climate change and global warming increasing the occurrence of droughts, directly impacting the quality and condition of the thyme (Hoyle & James, 2005; Allen et al., 2010). A severe drought in 2003 caused a 40% reduction in the number of inflorescences, which may have increased mortality from egg to adult by 6.6%, elevating the mortality rate to 99.1% and resulting in an 86% decline in population numbers within one patch (Hoyle & James, 2005; James, 2006f). The butterfly is unable to respond to rising temperatures through migration as it is a mountainous species, limited by a fragmented host plant distribution, with no other patches of host plants on nearby cooler, moister locations (Hoyle & James, 2005; Wilson et al., 2005; Thomas, 2010). Increasing temperatures could result in a further loss of habitat and increasing fragmentation amongst patches, reducing dispersal (Vandewoestijne et al., 2008; Habel et al., 2009). Dispersal is already low in this species due to its relatively sedentary nature; the majority of movements appear to be less than 50 metres, although the emigration rate into one patch was a fairly high estimate at 14% (James, 2006d,f). Dispersal plays an important role in population viability (Hodgson et al., 2011), acting synergistically with the initial population size to maintain

genetic diversity (Vandewoestijne et al., 2008; Habel et al., 2009). Loss of genetic diversity has been linked to a sharp decline in the adult life expectancy of *Polyommatus coridon* (Lycaenidae), a major constituent of fitness (Vandewoestijne et al., 2008).

Thyme has a high medicinal value in the area and until recently it was threatened by over-collection, mainly a problem of outsiders rather than of local Bedouin collectors (Murphee et al., 2008). In the past overgrazing by goats of local Bedu was considered to cause habitat loss and destruction (Gilbert, 2013). As a result, with Bedouin agreement, grazing was removed from some patches and the collection of thyme was banned with enforced penalties. How realistic this threat is uncertain, discussed further in Chapter Six.

This study looks into the endangered Sinai Thyme and the impact of environmental fluctuations in this arid environment, whilst also evaluating the latest conservation efforts. Chapter Two focuses on one patch of thyme, Farsh Shoeib, found to have one of the largest Sinai Baton Blue populations in 2001. Fluctuations in the quality and quantity of thyme are studied in relation to the large temporal variations in rainfall, comparing the thyme to the only other survey in 2002. Spatio-temporal variation in the thyme will have fitness implications for associated herbivores, such as the Sinai Baton Blue, and therefore it is important to identify the key drivers of patch quality (Weiss et al., 1988).

Chapter Three studies how climate impacts the phenology of the system. Not all such interacting species respond at the same rate, potentially resulting in temporal mismatches and varying degrees of asynchrony (Visser & Holleman, 2001).

Chapter Four investigates spatial-temporal variation in ten neighbouring patches upon the Mt. Sinai massif. It compares the quality and flowering in the thyme and butterfly relative abundance to try to understand what influences population size. It looks at the importance of habitat quality and resource area influencing the occupancy, population turnover and local abundance (Thomas et al., 2001; Lawson et al., 2012).

Chapter Five studies larval distribution, comparing that of the Sinai Baton Blue to the larval distribution of a migratory generalist moth species. I look for at the key role of resources for the juvenile stages to yield into habitat quality and drivers of populations dynamics (Thomas et al., 2011).

Chapter Six studies the latest conservation actions to preserve the butterfly using an experimental approach. It tests whether current management actions (the banning of grazing via enclosure) have been successful; the local Bedouin think that grazing is needed by the plants to maintain plant vitality. I experimentally manipulated the thyme through artificial grazing, fertiliser and water treatments to test whether grazing has beneficial effects on flowering and growth. Conservation interventions and outcomes need to be monitored, particularly with respect to social sensitivities (Sutherland et al., 2004).

Chapter Seven uses population viability analysis using the software Vortex to predict the butterfly's future, using sensitivity analysis to vary life history parameters to see which influence the dynamics the most. Population viability analyses are an important tool for directing conservation and future research goals (Brook, 2000; Hoyle & James, 2005)

Chapter Eight summarizes the principal conclusions from the work for the principal stake-holder - the St Katherine's Protectorate. It re-evaluates current threats to the Sinai Baton Blue butterfly and potential conservation techniques, and offers suggested ways forward in order to save this flagship species.

2001 Entire population survey; ~2000 individuals & 24 known populations	2002 Survey on butterflies & thyme quality/ phenology in Farsh Shoeib	2003 No rain for 12 months. Butterfly population cashed to 86% of previous year

		2003 Two dams built in Farsh Shoeib and fence erected around perimeter

2001				2012

2002-2003 Mike James MRR	2004-2009 Protectorate surveyed butterfly; 3-14 days per year

2010 Heavy rain in spring & summer	2011 Heavy rain in spring	2012 No rain for 12 months

2002-2009
8 years of very little rainfall

Figure 1.1 Timeline of significant events for the Sinai Baton Blue between 2001 & 2012.
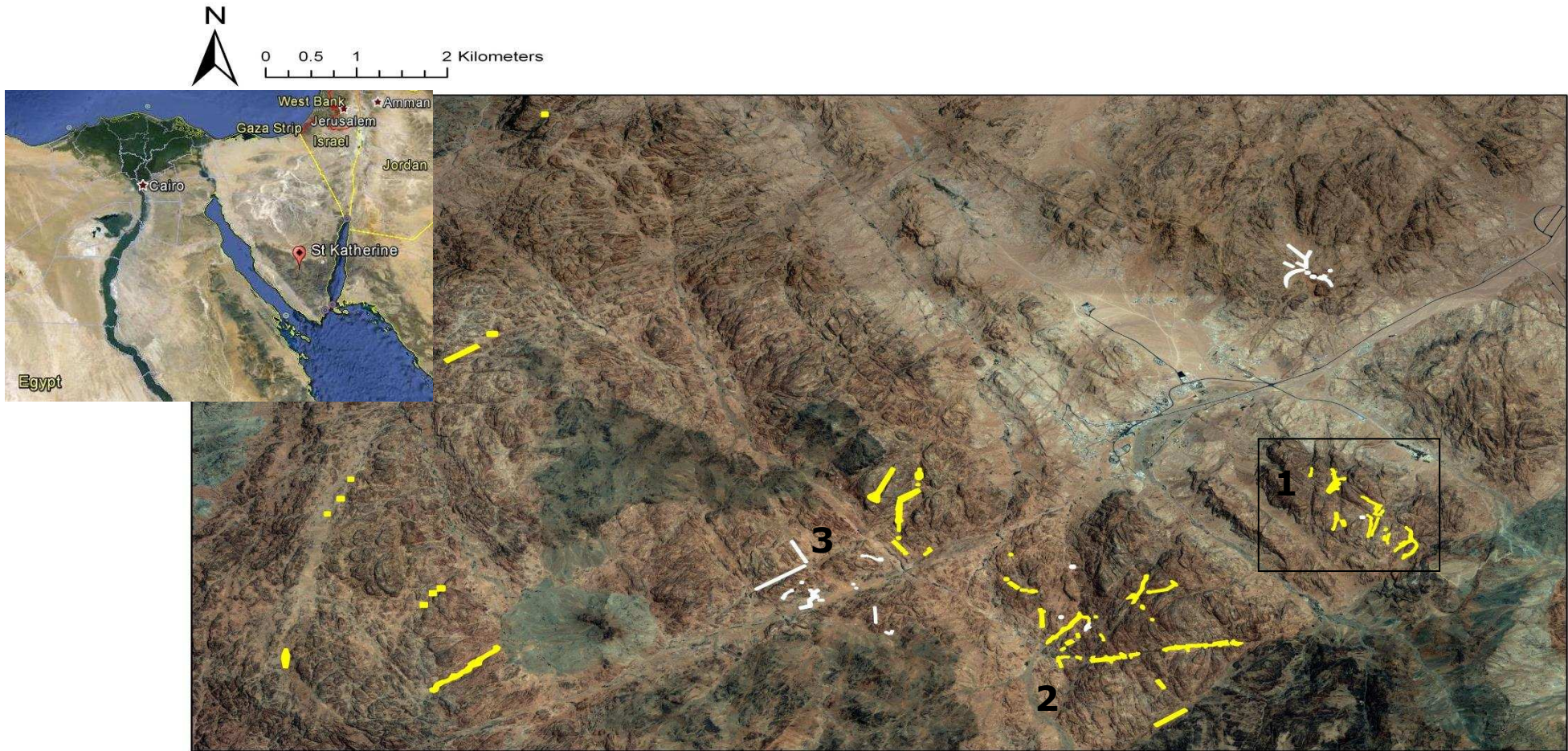
Figure 1.2. The published global distribution of the Sinai Baton Blue. The yellow indicates a thyme patch with a colony and the white indicates uncertain populations, with no sightings in the 2001 survey. There are three sets of patches; (1) Gebel Safsafa; the location of Farsh Shoeib and the main focus of this study (2) Gebel Ahmar & (3) Wadi Gebel. Adapted from James (2003).
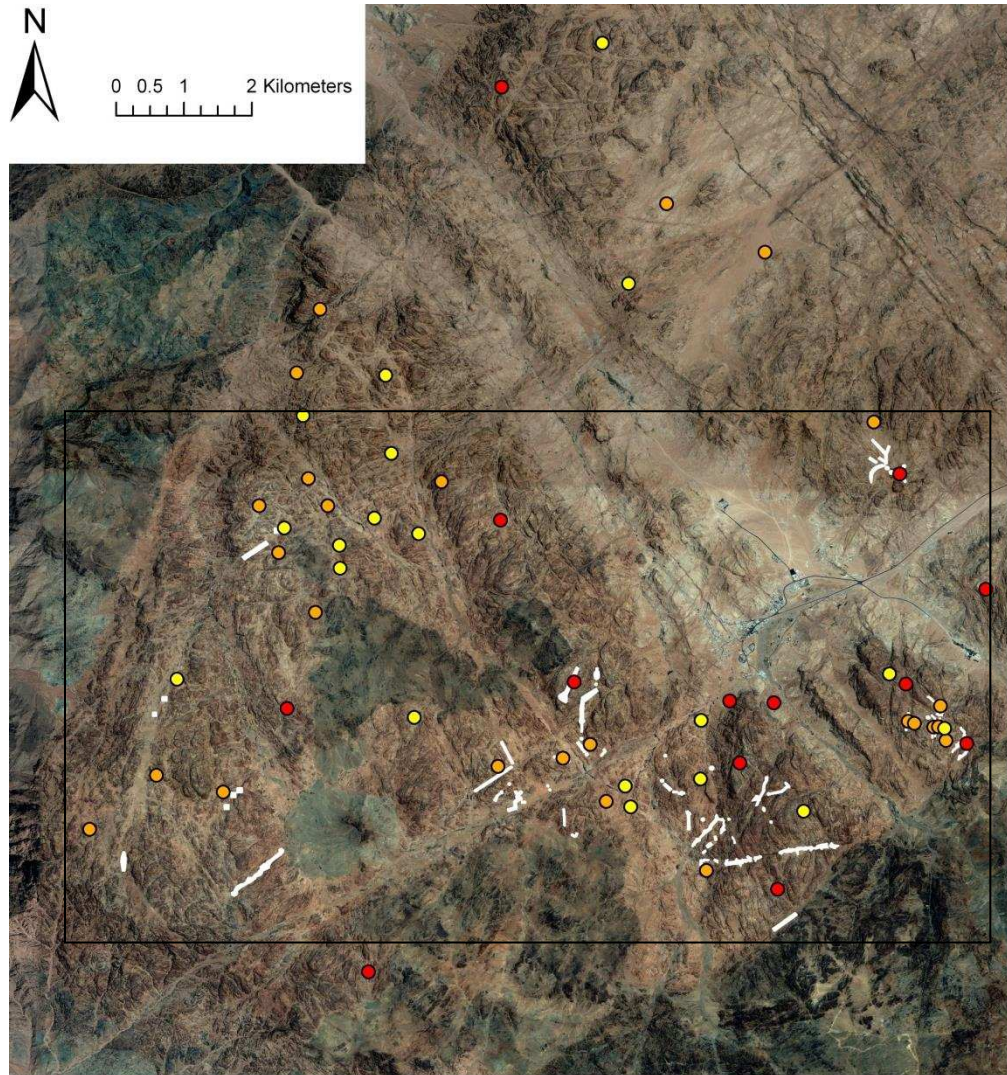
Figure 1.3. Locations of published (shapes) and new (dots) patches of thyme and therefore the potential distribution of the butterfly. Dot colour indicates patch size as large (red), medium (orange) and small (yellow). Patches were not visited so the size is according to local knowledge and the presence of the butterfly within these patches is currently unknown. The box highlights the known distribution shown in Figure 1.3.

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Chapter 2.

The response of the endangered *Thymus decussatus* to eight years of low rainfall in an already arid environment
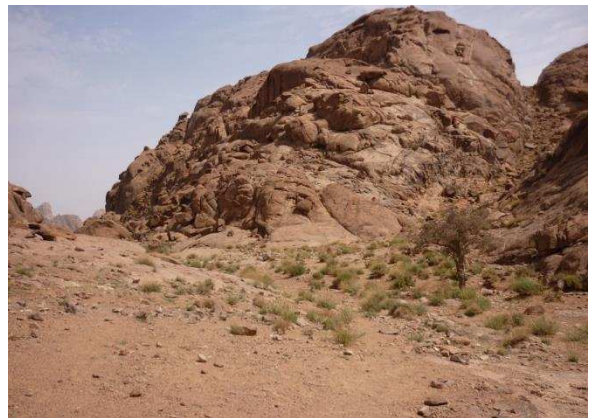
Farsh Shoeib

The response of the endangered *Thymus decussatus* to eight years of low rainfall in an already arid environment

Abstract

Arid environments are resource-limited, with scarcity of water the key limiting factor. Irregular rainfall generates resource pulses, increasing primary productivity. Sinai Thyme (*Thymus decussatus*) is endangered and exists as a set of patches on mountaintops within the St Katherine Protectorate, South Sinai, an arid environment. This study focuses on one population of thyme over the past decade where I found a 45% mortality rate over eight years of little or no rainfall, with a loss of 30 m² of green thyme, reducing the population's resource area to 45 m² in 2010. The remaining individuals were in significantly worse condition but larger in size, indicating both growth and size-dependent mortality. Between 2010 and 2011 there was heavy rainfall, but there were further plant deaths within the patch with no evidence of any recruitment despite a 130% increase in flower production. There was no rainfall in 2012, and the proportion of flowering plants dropped sharply, coupled with a 61% decrease in the number of flowers on plants that did flower. Droughts are expected to become increasingly frequent due to climate change and this may have important consequences for the thyme and its associated herbivores, particularly the Critically Endangered Sinai Baton Blue (*Pseudophilotes sinaicus*) whose larval stage feeds exclusively upon this plant.

Introduction

Inter-annual variation in plant performance is predominantly explained by environmental and climatic variation, with water availability frequently cited as the limiting factor in arid areas (Boyer, 1982). In drier systems the variability of precipitation has a stronger influence on productivity than absolute quantities, and arid areas usually show a high degree of inter-year variability (Di Bella et al., 2009; Fabricante et al., 2009). There is often a time lag, with increased rainfall enhancing productivity the following year. The length of the time lag varies amongst systems; for example, annual

variation in the condition of Patagonian flora is correlated with the accumulated rainfall in the autumn months prior to the growing season, with no relationship with the current or previous year's rainfall (Fabricante et al., 2009).

Variation in primary productivity cannot be explained by any single factor; temperature, soil characteristics and precipitation all influence plant quality (Bai et al., 2008). Often there are complex interactions between abiotic and biotic components in the growth and condition of plants, including many spatial effects (Bai et al., 2008), and hence no single variable can predict the increase in biomass via growth: cues such as the timing of precipitation, soil nutrients and temperature all have varying impacts (Robertson et al., 2009). Climate variation can affect co-existing species in different ways; increased precipitation one year can alter community structure, with different functional groups dominating depending upon their optimal conditions. For example, in wetter years forbs can be outcompeted by grasses, and vice versa in drier years (Westoby et al., 1989; Vazquez-de-Aldana et al., 2008; Lue & Han, 2010).

The 'pulse-reserve' model of arid plant communities focuses on the idea that rainfall leads to a pulse of plant growth (Reynolds et al., 2004). Water stress can reduce available soil resources by lowering the abundance and activity of micro-organisms, with knock-on effects on the levels of available nitrogen (Aguilera et al., 1999). It has a negative impact on nutrient uptake from the soil, and impairs acropetal translocation (Hu & Schmidhalter, 2005). Lower soil moisture reduces overall plant condition, i.e. leaf nitrogen content, photosynthetic ability, turgor pressure, etc., all with consequences for associated herbivores (Ostfeld & Keesing, 2000; Harrison, 2001). The key regulator of the pulsed response is the initial soil condition which is itself influenced by numerous factors such as topography, soil texture, atmospheric conditions, plant cover and biomass (Reynolds et al., 2004). Ecosystems can store water and nutrients from previous pulses, and the size of these reserves then influences sensitivity to further pulses - sometimes called the 'memory effect' (Schwinning et al., 2004). If there are consecutive dry years, the influence of prior levels of soil moisture, if low, can exaggerate the effects of diminished water resources on plant condition and performance, or, if high, can act as a buffer (Reynolds et al., 2004). In such marginal conditions, the trade-off

between reproduction and survival may be even more important than usual, with reproduction sacrificed until rain occurs (Allen et al., 2010). Global climate change is increasing the frequency and duration of adverse environmental conditions such as droughts (Giannakopoulos et al., 2009), increasing detrimental impacts on plant populations and thereby increasing extinction risks (Verboom et al., 2010).

Life history strategies change depending upon environmental conditions; one stress response could be for the plant to become dormant, reducing growth and fecundity to enhance survival until conditions improve. This tactic is often seen in long-living clonal species existing in harsh conditions (Forbis, 2003; Thompson et al., 2007). Flowering entails a high water cost, so flowering and leaf production is often reduced until there are more available resources (Harrison, 2001). The inevitably fluctuating resource level influences herbivore competition and controls the food web through bottom-up forces. The population dynamics of primary consumers in arid regions are particularly sensitive to rain-driven bursts in primary productivity, with cascading effects in the ecosystem to higher trophic levels (Schwinning et al., 2004; Letnic & Dickman, 2010). Herbivore population explosions are observed with the renewal of rain after drought, observed in multiple lepidopteran species (Harrison, 2001). After a resource pulse, when primary resources are no longer the limiting factor and after a corresponding boom in herbivores, the system often switches to be controlled by top-down forces, with predators and parasitoids controlling the dynamics (Letnic & Dickman, 2010).

Here I study one patch of a rare plant growing in the arid mountains of the St Katherine Protectorate in South Sinai in Egypt, the most arid country in the world (FAO, 2012). Because this plant is the host of an endemic butterfly, the flagship conservation target of the Protectorate, the health of its populations is a vital concern of the park management. Thus long-term changes in plant condition, and the way the plant responds to rainfall, are important components of a long-term strategy to conserve both plant and butterfly. I study the inter-annual and localised spatial variation in this plant to see how its vitality varies in time and space in response to environmental variation.

Materials & Methods

The study system

The Sinai Thyme (*Thymus decussatus* Bentham, 1834) is an endangered species, only occurring above 1500 m altitude within the St Katherine Protectorate (and recorded once from an adjacent area in Saudi Arabia) (James, 2006a). It grows best in well-defined soil at the base of cliffs and wadis, resulting in a naturally patchy distribution (Nakamura, 1975). According to local Bedouin the topography also influences growth because if the slope is too steep the surface run-off is too fast for water to infiltrate the soil (Nasr Mansour, 2011, pers. comm.). The genus *Thymus* contains species regarded as indicators for degraded landscapes in arid environments with long-standing grazing pressures because of characteristics that resist the impact of disturbance: the small leaves help limit the effects of drought and grazing (Navarro et al., 2006).

The fieldwork was carried out from March until the end of June in 2010 and 2011, and from April until mid-July in 2012, in Farsh Shoeib (see Fig. 2.1) near the summit of Gebel Safsafa on the Mt. Sinai massif, close to the town of St Katherine in South Sinai. The farsh (an open, exposed area) sits at an altitude of approximately 1950 m, with an area of 14,000 m^2 that contained 652 thyme plants in 2012. In 2001 Farsh Shoeib held one of the largest populations of the Critically Endangered Sinai Baton Blue butterfly (*Pseudophilotes sinaicus* Nakamura 1975), whose larval stages are monophagous on the flower buds of Sinai Thyme (James et al., 2003). As a conservation effort to protect both plant and butterfly, the majority of the patch was fenced off in 2003 to prevent public access, grazing and any damage to the plants: only a few plants are found outside the enclosure in this patch. Two large dams were built specifically for conservation purposes in the main farsh in 2003 to hold more water in the soil after flash floods.

There have been severe fluctuations in the weather over the past decade. There has been meteorological data collected in the area over the past year so we frequently are dependent on local Bedouin knowledge. In 2002 the highest recorded temperature was 35˚C with no rainfall. Since 2002, when the first and only other thyme survey was carried out, there has been severe drought in the area, with very little (<50 mm) or no rain every year

until March 2010. In 2010 temperatures of 40˚C were recorded, and in May there was heavy rainfall which left parts of Farsh Shoeib submerged for over a week. 2011 was an extraordinarily wet year, with heavy rainfall and snow in the winter and spring, whilst 2012 had very little rainfall and was colder than normal. The extent to which these variations are normal for the area is uncertain because of incomplete meteorological records. Undoubtedly, however, the long period of little or no rain will have had effects on the thyme.

Mapping of Farsh Shoeib

In order to map the plants of Farsh Shoeib accurately, in 2010 each individual thyme plant was recorded relative to one of 12 landmarks, measuring the distance and the bearing of each plant from the nearest landmark. The coordinates of each landmark were repeatedly recorded during March and April at varying times of day using a hand-held GPS unit (Garmin etrex Venture HC), a single reading of which was found to be accurate to about ± 10 metres; repeat measurements were averaged to gain much greater precision in the location of the landmarks. The distances and bearings were converted to get an accurate location for each plant in Farsh Shoeib relative to the landmark features, and then plotted using ArcGIS 9.3 to create a map. This map was compared to one created in 2002 by James (2006b).

In order to compare the number and quality of thyme plants in Farsh Shoeib to the data collected in 2002, in 2010 and 2011 each plant was identified and labelled, and its height, two perpendicular widths and condition (% green) measured, the same variables that James (2006b) recorded in 2002. I did not record the size in 2012 due to the slow growth rate and the relatively large measurement error involved in determining the widest part of the plant. The 'resource area' for each plant was then calculated from the surface area (assuming each plant was a hemi-ellipsoid) multiplied by the condition (as a proportion). The numbers of flowers on 50 randomly chosen plants from an area particularly dense with plants (the Gulley: see Fig. 2.1) were counted during the first six weeks of flowering in 2010, 2011 and 2012. The proportion of flowering plants were compared by weekly inspections of 642 individuals in 2010, and of 100 randomly selected plants in 2011 and 2012.

Analysis of data

The 2010 mapping was much more detailed than in 2002, when James (2006b) did not map all of the plants individually within Farsh Shoeib; instead he mapped particular individuals and attributed the surrounding set of close neighbours to that location. This made it impossible to re-identify his individuals to monitor the changes over time directly. He did, however, divide the site into five sections, and I could therefore compare all individuals within each of these sections.

All analyses used the statistical package R 2.14.1 (R Development Core Team, 2012) and models were simplified in accordance to Zuur et al. (2009). I carried out generalised linear models, using the R routine *glm*, to compare sets of plants in 2002, 2010 and 2011 in number and quality. I used the condition and size (assuming the hemi-ellipsoidal shape) as response variables, and year (2002, 2010 & 2011) and section as the factors. I simplified the full model based on the Akaike Information Criterion (AIC) criterion using stepwise backwards deletion of model terms. Condition was normally distributed, whilst the size was logarithmically transformed to have a normal distribution: significance was assessed for both with an F-ratio. A GLM with a binomial distribution compared the mortality amongst sections between 2002 and 2010, tested with a χ^2 test.

I compared the size per plant in 2010 with 2011, to check for temporal and spatial variation in performance. I again split the patch into five sections, but because it was possible to identify the same individuals I ran a linear mixed model (*lmer* from the *lme4* package) using section and year as factors and the individual plant identity as the random factor. I again simplified the full model based on the AIC criterion using stepwise backwards deletion of model terms. I compared the condition in 2010-2012 using this analysis. In 2011 I artificially manipulated 120 plants in Farsh Shoeib for experimental work (see Chapter 6), and hence these were excluded from this analysis. A GLM compared the proportion of flowering plants in 2002, 2003 and 2010 – 2012, using the R routine *glm* with a binomial distribution. All these analyses were again tested with a χ^2 value.

To see if there was a significant difference in the characteristics of the plants which have died since 2010, I ran a t-test to compare the size and condition of all individuals in 2010 to those which subsequently died.

Results

Between 2002 and 2010 the number of thyme plants in Farsh Shoeib notably reduced from 1208 to 669 i.e. 44.6% of the plants disappeared, and are assumed to have died. The locations of thyme plants appear to be similar in 2002 to 2010 (Fig. 2.1), except that the majority of plants in the southern part of the patch appear to have died: more than 60% of the plants seem to have disappeared from Farsh II and the Southern area. The mortality rate varies considerably across Farsh Shoeib among the five sections (χ^2=136, df=4, p <0.001), with the lowest proportion (21%) of plants dying in the Side arm (Table 2.1). The frequency distribution of plant size showed that the vast majority of plants lost during the eight years were the smaller individuals. This has been accompanied with growth, shown by a higher frequency of larger individuals (Fig. 2.2). Because it was impossible to identify individual plants between 2002 and 2010, I cannot tell if any plants were recruited into the population. The death rate between 2010 and 2011 was 1.6% with the loss of 10 individuals, whilst between 2011 and 2012 it was 1.1% with 7 losses. No recruits to the population were observed in either year. Table 2.2 describes the locations and measured traits of individuals in 2010 that subsequently died in either 2011 or 2012. The plants which have died since 2010 are significantly smaller in size than survivors (t=2.04, df=1, p<0.05). However the condition was not significantly different (t=0.87, df=16, p=0.40), despite the plants which died having, on average, a lower preceding condition (Fig. 2.3).

Plant condition had significant temporal (F=774, df=3,3035, p<0.001) and spatial (F=22.4, df=4,3035, p<0.001) differences, and also an interaction (F=73.7, df=12,3035 p<0.001). Between 2002 and 2010 plants of every section markedly, except those in the side arm; those of Farsh II declined sharply to below 15% green, whilst those of the Side arm decreased by a small amount to 29% green. Overall, plant condition decreased from 53% to 25%, a huge difference; one third of the surviving plants were less than

10% green (Fig. 2.4). With individual plants identifiable (2010–2012), plant condition showed significant spatial (χ^2= 64.3, df = 4, p<0.001) and temporal variation (χ^2= 15.6, df = 2, p<0.001), but in this case there was no interaction between these factors (χ^2= 5.02, df=8, p=0.28). Average plant condition rose from 25.2% to 29.3% in 2011, before dropping to 28.6% in 2012. Between 2010 and 2011, average plant condition increased in every section except for the Side arm, but this was the only section which increased in 2012. The plants in Farsh II consistently had the poorest condition, and this was the location of more than half of the mortalities (Table 2.2).

Plant size (not measured in 2012) varied significantly both temporally (F=783, df=2,2470, p<0.001) and spatially (F=135, df=4,2470, p<0.001), with an interaction also present (F=5.34, df=8,2470, p<0.001). With individual plants identifiable (2010-2011), plant size again showed significant temporal (χ^2 = 4.13, df=1, p<0.05) and spatial variation (χ^2 =96.9, df=4, p<0.001), this time with no significant interaction between these two factors (χ^2=1.48, df=4, p=0.83). Between 2002 and 2010, average plant size increased in every section of the study site, with the largest increase observed in the Gulley. In contrast, there was a slight decrease in average size across the patch between 2010 and 2011. In all years, plants in the Gulley were considerably larger (Fig. 2.5b).

Between 2002 and 2010 there was an overall increase in resource area of 28 cm^2 per plant, but the change was inconsistent across the patch; plants in the Gulley gained 189 cm^2 resource area per plant, whilst those of Farsh II lost 254 cm^2 (Fig. 2.5a). Although the average resource area per plant remained similar in 2002 and 2010, the loss of individuals meant that the total resource area reduced dramatically from 76 m² in 2002 to 45 m^2 in 2010. Overall the plants were slightly smaller in 2011 than 2010 (Fig. 2.5b), but an increase in condition resulted in a 165 cm^2 increase in resource area per plant, increasing the total patch resource area by 9.7 m^2 to 55 m^2, despite the loss of ten individuals (Fig. 2.5a). Plant size was not measured in 2012 because of the extremely low apparent growth rates between 2010 and 2011: if plant size was the same between 2011 and 2012, then the total resource area would have decreased by 2.9 m^2 to 52 m^2, while remaining 15% greater than in 2010.

The proportion of plants that flowered varied significantly amongst years (χ^2=759, df= 4, p< 0.001). In 2002, 91% flowered (n=851), but this dropped to 48% in the following year. In 2010 there were 96% of plants flowering (n=637), remaining similar in 2011 at 98% (n=100) before dropping to 83% in 2012 (n=100). The total number of flowers on 50 plants across 6 weeks of flowering more than doubled between years, from 27,730 in 2010 to 63,704 in 2011, before falling to 24,712 in 2012.

Discussion

Nearly half of the plants died between 2002 and 2010, with fewer than 700 individuals remaining in 2010. The loss is likely to be due to mortality because the patch was fenced off to prevent collection or grazing. The changes in quality between 2002 and 2010 are probably primarily environmental in origin, caused by the adverse conditions over the eight years, with many of those years experiencing no or little rainfall. The changes in size and condition are in the same direction across the whole patch, suggesting this is a stress response to reduced rainfall in an already arid environment. The average thyme plant increased significantly in size since 2002. The death of smaller individuals since 2010 suggests that there has been differential survival over the past decade, with the loss of smaller individuals. There is also evidence of growth with a higher frequency of larger plants, but it is impossible to disentangle the two because we cannot compare individual plants. The deaths could be an example of size-dependent survival with the death of smaller individuals that lacked necessary resources to survive. Smaller plants and juveniles are often more susceptible to drought-based mortality in arid environments (Hamerlynck & McAuliffe, 2008). Larger shrubs may have more reserve nutrients, such as carbohydrates, essential for survival during adverse years (Reynolds et al., 1999). A large biomass also increases the surface area for water uptake. All of these factors would favour survival of larger individuals during drought years in an already arid environment (Gilad et al., 2004). Drought can also reduce recruitment, an essential process in maintaining populations; however recruitment is already an irregular event in arid environments due to sporadic rainfall (Wiegand et al., 2004; Andersen & Krzywinski, 2007).

Since 2002 the average condition of the plants decreased, with the percentage green dropping from 53% to 25%; the overall figures mask substantial spatial variation, with the biggest reductions in the Gulley and Farsh II. Although surviving plants were larger, they were also in a poorer condition despite two periods of heavy rainfall in 2010. This shows that short but heavy rain is insufficient to produce immediate recovery; perhaps more than one year with good rain is needed to improve plant condition and prevent further deaths. The decline in condition and numbers may be due to extraordinarily good conditions in 2002 with a peak year and a recruitment boom, but it is more likely to be from the subsequent years with little or no rainfall. Soil moisture is critical in nutrient uptake and translocation (Hu & Schmidhalter, 2005). One mechanism of drought tolerance could be for the plant to become dormant, seen in other thyme species and perhaps responsible for the decline in average condition measured here (Thompson et al., 2007).

The mortalities since 2010 were not random, significantly affecting smaller plants and those generally in a poorer condition. This suggests that to survive plants need sufficient resources. Individuals in good condition only die if they are small with too few resources or inadequate rooting systems, generating the size-dependent component of mortality between years. The majority of deaths were of plants in poor condition, i.e. low-quality plants (Reynolds et al., 1999), in Farsh I, Farsh II and the Side arm, but none in the Gulley. The plants in the Gulley have the largest resource area per plant; since the Gulley drains the rest of the Farsh, it is probable that it has better and more reliable water than elsewhere in the site, perhaps explaining the higher vitality of plants there.

The lack of new individuals or seedlings suggests that recruitment rate is very low despite the apparent return of good conditions. *Thymus decussatus* can produce daughter plants by the rooting of branches via asexual propagation, and hence potentially does not rely much on sexual reproduction via seed set. Other thyme species such as *Thymus loscosii*, a rare endemic in arid Spain, reproduce sexually via seeds or asexually through above-ground vegetative stolons which grow horizontally before rooting (Matesanz et al., 2009). However, the apparent absence of recruitment from seed in Sinai Thyme is surprising given its high flowering output, particularly in 2011 when soil conditions were presumably good.

Recruitment in arid environments is often a rare event. The harsh conditions decrease the likelihood of successful seedling establishment, with water being the main limiting factor. The high variability in the intensity and timing of precipitation can result in sporadic recruitment events (Wiegand et al., 2004). For example, tree recruitment in the arid Eastern desert of Egypt is very low; annual recruitment is, on average, between 0.31 and 0.60% with high seedling mortality rates being the foremost problem in establishment (Andersen & Krzywinski, 2007). Recruitment in many arid environments can be too low for long-term population survival. This is a concern for acacia trees in the Negev desert of Israel (Wiegand et al., 2004), where substantial recruitment happens only episodically with rainfall events and the corresponding resource pulse. However, acacias lack smaller more continuous recruitment events, partially attributed to insufficient rainfall, and this threatens long-term population persistence. Reliance on episodic recruitment is only viable for larger populations which can survive long periods without new individuals; small yet continuous recruitment is required to buffer against long periods between pulse events to ensure population survival (Wiegand et al., 2004).

Arid environments often have high degrees of spatial and temporal variation in soil quality, with nitrogen levels in the soil varying spatially across a few centimetres (Jackson & Caldwell, 1993). Nitrogen levels are often higher under shrub canopies than inter-shrub spaces, whilst highly localised variation in rainfall also influences soil nutrient levels, leading to fitness differences and differential survival. Varying amounts of shade will also influence plant fitness, with light levels affecting photosynthesis and evaporation (Peek & Forseth, 2003). Farsh Shoeib shows significant spatial variation in resource area across the patch. Between 2002 and 2010 there were contrasting responses in thyme resource area among sections, but overall the average resource area per plant has remained similar. However, the drastic reduction in the number of plants has resulted in a loss of nearly 30 m^2 of thyme. Fluctuations in resource area will ultimately affect the number and abundance of associated herbivores, and the Sinai Baton Blue butterfly in particular. The large decline in resources between years supports previous studies that climatic fluctuations could be responsible for a large decline in butterflies observed between 2002 and 2003 (James, 2006c). Reduced resources increase competition, affecting the growth,

performance and population dynamics of insects (Boggs & Freeman, 2005; Kay et al., 2010), particularly in short-lived herbivores with highly specific interactions (Ostfeld & Keesing, 2000).

A high proportion of plants flowered in 2010 and 2011, but this was followed by a large decline in 2012, perhaps the result of heavy rainfall during 2010 and early in 2011, followed by a year of no rainfall. Superimposed on the incidence of flowering, there were very large fluctuations in the density of flowers per plant, more than doubling in 2011, followed by a big decline. Flowering entails a high cost in water usage, and during drought years plants with fewer reserves may be unable to bear this cost (Galen et al., 1999; Harrison, 2001). Drought stress in other plant species has a negative effect on flowering, but production typically increases again after renewed rainfall (Galen et al., 1999; Carroll et al., 2001; Harrison, 2001). The number of flowers per plant is the resource base for the Sinai Baton Blue butterfly, with a higher density of flowers supporting larger larval populations because of the increased carrying capacity.

The productivity of vegetation in arid Africa responds to rainfall of the previous and current years. If there are successive years of low rainfall, populations become caught in a downward spiral of less flowering, reduced population size and longer recovery period. After particularly wet years, often a one-year time lag is observed with the vegetation flourishing the subsequent year (Schwinning et al., 2004). This may be the case here; the 2010 rains may have caused the flowering surge in 2011. This is perhaps an example of the memory effect, the soil retaining the effects of excess rainfall and impacting plant productivity (Schwinning et al., 2004, Martiny et al., 2005). However, the subsequent decline in flowering in 2012 suggests that rainfall in the previous winter or the current year is very influential, since rainfall in late 2011 was absent and hence perhaps insufficient to maintain the flowering.

Over the past decade there has apparently been a severe drop in the quantity and quality of the Sinai Thyme. To conserve both the plant and its dependent herbivore, the Sinai Baton Blue butterfly, it is essential to understand the causes of the high mortality and loss of condition, and to

learn more of the recruitment dynamics of the plant. Without such knowledge it is not possible to design effective management plans.

Table 2.1. Distribution of plants in sections of Farsh Shoeib in 2002, 2010, 2011 & 2012.

	Number of individuals				disappearing 2002 to 2010		disappearing 2010 to 2011		disappearing 2011 to 2012	
	'02	'10	'11	'12	number	%	number	%	number	%
Gulley	242	148	148	148	94	39	0	0	0	0
Farsh I	244	136	134	133	108	44	2	1.5	1	0.7
Farsh II	366	136	132	127	230	63	4	2.9	5	3.8
Side arm	283	224	221	221	59	21	3	1.3	0	0
South	73	25	24	23	48	66	1	4	1	4.2
Overall	1208	669	659	652	539	45	10	1.5	7	1.1

Table 2.2. The condition, height, width and location of the plants which died between 2010 and 2012. The plants are split into two categories; those with a preceding condition below average condition (< 25% green) and those with a higher condition (≥ 25% green). It also shows the average measurements across the entire patch in 2010.

	Condition (% green)	Height (cm)	Width (cm)	Location	Year of death
i) Lower preceding condition	1	9	38.5	Farsh II	10/11
	1	14	20	Side arm	10/11
	2	25	56.5	Farsh I	10/11
	2	18	51.5	Farsh II	11/12
	3	25	18.5	Farsh II	11/12
	7	17	58	Farsh II	11/12
	7	22	23.5	Farsh II	11/12
	10	20	51.5	Side arm	10/11
	10	11	28.5	Farsh I	11/12
	10	20	28	Outer	11/12
	15	26	83.5	Side arm	10/11
Average:	6.2	18.8	41.6		
ii) Higher preceding condition	25	18	35.5	Farsh II	10/11
	30	13	21.5	Farsh I	10/11
	30	7	9	Farsh II	10/11
	50	10	14	Farsh II	11/12
	60	9	17.5	Farsh II	10/11
	80	16	32	South	10/11
Average:	45.8	12.2	21.5		
Overall patch average	25	19.2	40.0		

Figure 2.1. A map of the thyme plants in Farsh Shoeib in 2002 (red dots) and 2010 (blue). The pink illustrates the location of two dams, which were built in 2002 for conservation purposes.
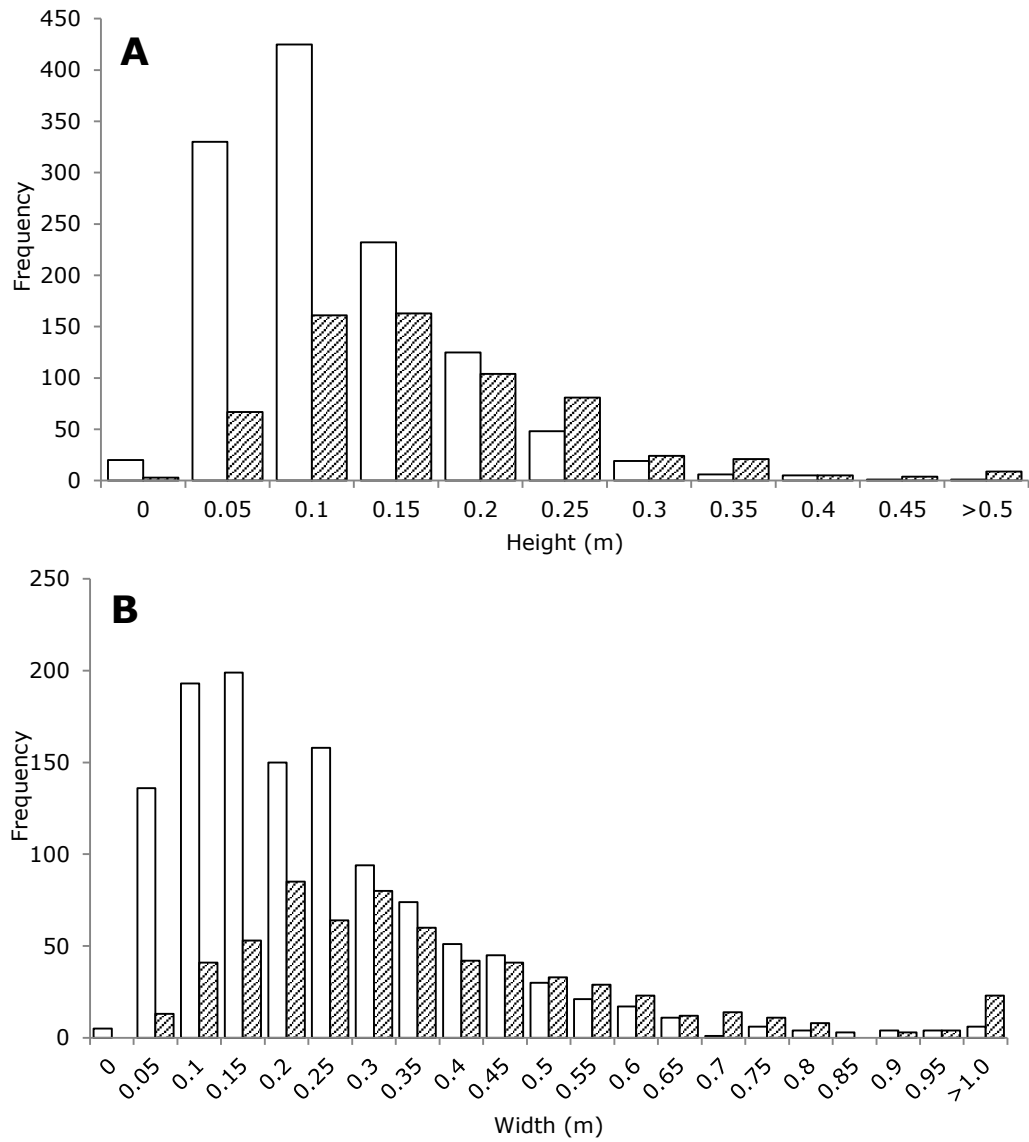
Figure 2.2. Frequency distribution of a) the height and b) width of the thyme plants in Farsh Shoeib in 2002 (white bars) and 2010 (striped), n= 1208 in 2002 & 642 in 2010.
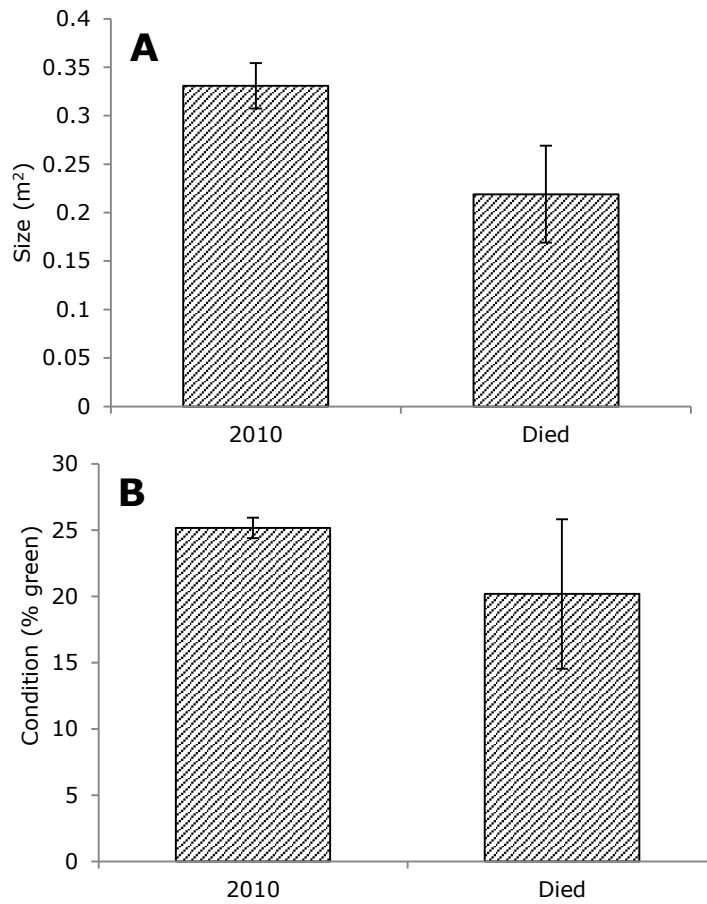
Figure 2.3. Comparison of the a) size and b) condition in 2010 and of those which subsequently died. Mean values ± SE.
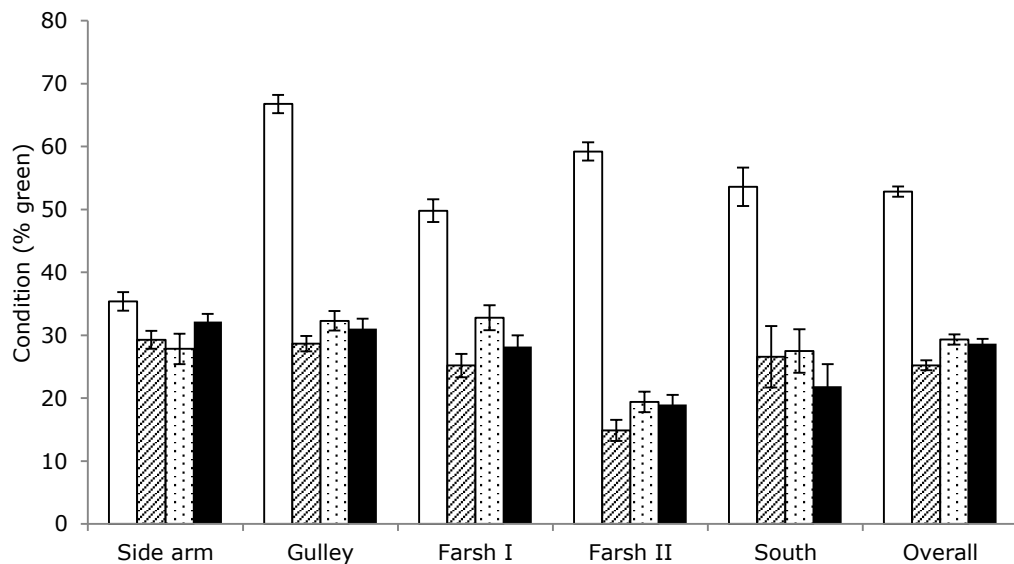
Figure 2.4. Condition per plant amongst sections in Farsh Shoeib in 2002 (white bars), 2010 (striped), 2011 (spotted) & 2012 (black). Mean values ± SE, n= 1208, 642, 632 & 532 respectively.
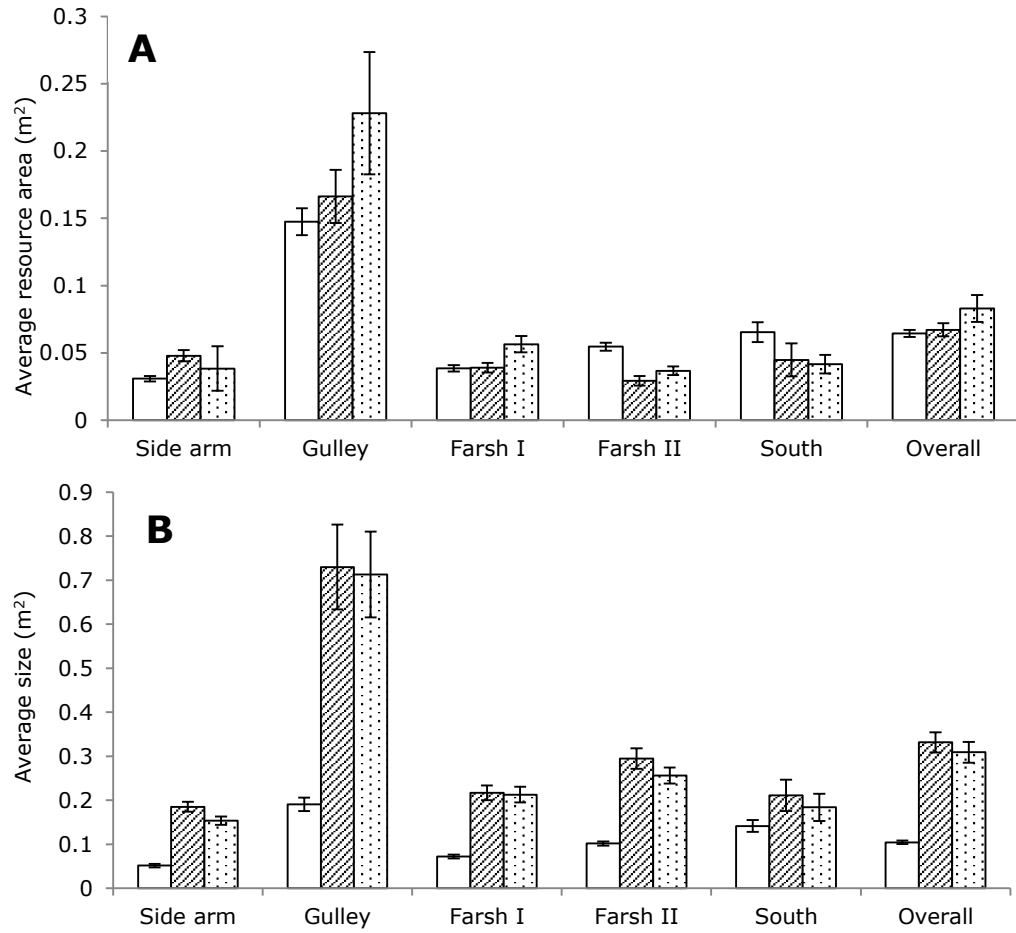
Figure 2.5. Comparisons of a) the average resource area and b) size per plant amongst sections in Farsh Shoeib in 2002 (white bars), 2010 (striped) and 2011 (spotted). Mean values (± SE), n= 1208, 642, 632 respectively.

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Chapter 3.

Synchronous shifts in the flowering of *Thymus decussatus* and the flight period of the associated Sinai Baton Blue butterfly, *Pseudophilotes sinaicus*

Synchronous shifts in the flowering of *Thymus decussatus* and the flight period of the associated Sinai Baton Blue butterfly, *Pseudophilotes sinaicus*

Abstract

Climate change is globally altering the phenology of species, with implications for interacting species. If species use different cues or respond at different rates, this could result in asynchrony between hosts and herbivores. The larval stage of the Critically Endangered Sinai Baton Blue butterfly (*Pseudophilotes sinaicus*) feeds exclusively on the buds and flowers of an endangered plant, the Sinai Thyme (*Thymus decussatus*), with a narrow window in time when both larvae and flowers are present. This study focuses on one patch of thyme, comparing the phenology of thyme and butterfly over the past three years with that of a decade ago, and estimating population numbers over the eleven years of monitoring. Sinai Thyme has a very variable flowering phenology, two weeks different in one year from other years, whilst variation in the flight period of the butterfly is seemingly correlated, it was advanced in the same years as that of the host plant. This is optimistic for the future, however I also observed large shifts in resource level which may have contributed to the dramatic cycles observed over the past decade. Other potential drivers are discussed.

Introduction

Climate change and global warming pose a serious threat to many species, with habitats expected to become drier accompanied with a rise in average temperatures (Giannakopoulos et al., 2009). Species dependent on environmental cues face problems if climatic patterns change, especially for herbivorous insects where ecological success is correlated to synchrony with host plants (Powell & Logan, 2005). Some interacting species will use the same cues and show similar levels of plasticity, but not all species will respond in the same way (Phillimore et al., 2012). Such differences in cues could result in increasing levels of asynchrony between interacting species, with the potential for a complete mismatch (Visser & Holleman, 2001). Short-lived species are particularly vulnerable to asynchrony since

consecutive years of sub-optimal resources could lead to rapid declines in numbers and the possibility of extinction. Synchrony can have consequences for the whole set of interacting species, affecting their population dynamics through bottom-up forces (Miller-Rushing et al., 2010). For example, the abundance and fitness of the winter moth (*Operophthera brumata*: Geometridae) is dependent upon precise synchrony between egg hatching and the bud burst of the host oak tree (*Quercus robur*: Fagaceae). Development of the egg uses environmental cues to maintain synchrony, and over the past 25 years, rising spring temperatures have caused mis-timings between host and herbivore, resulting in higher mortality and large fluctuations in moth populations (Visser & Holleman, 2001).

Spring temperatures play a dominant role in determining plant phenology, with advancing phenologies associated with rising spring temperatures (Cook et al., 2012). The phenology of many, but by no means all, plants in the Northern hemisphere is affected (Doi & Katano, 2008), since flowering can be influenced by other abiotic cues, particularly photoperiod, but also soil moisture and winter temperatures. Frost events can affect phenological timings, and some temperate species require cool autumns and winters for vernalization, for example, in the flowering of Drummond's rockcress (*Boechera stricta*: Brassicaeae) in the Rocky Mountains (Anderson et al., 2012; Cook et al., 2012). A study of 500 plant taxa in Concord (Massachusetts, USA) since 1852 shows that flowering is 3.3 days earlier in the year per $1\degree$C rise in mean monthly temperatures for January, April and May (the last two being the two months preceding flowering)(Miller-Rushing & Primack, 2008). There have been many plant extinctions observed in Concord over the past 150 years, and their pattern indicates that susceptibility is linked to climate response since species whose phenology did not follow the rising temperatures were much more likely to become locally extinct (Willis et al., 2008).

Phenological timings of the host plants of the Bay Checkerspot butterfly (*Euphydryas editha bayensis*: Nymphalidae) are dependent upon precipitation. Increased fluctuations in precipitation reduce the temporal overlap between larvae and host, increasing larval mortality, amplifying population fluctuations and creating local extinctions (McLaughlin et al., 2002). Host plants of this butterfly also demonstrate significant micro-

climatic variation, within a scale of tens of meters, with significant implications for the fitness of the butterfly (Weiss et al., 1988). Current climatic variation combined with habitat loss and fragmentation has increased the extinction risk for this species, and perhaps many others, particularly those with limited dispersal (McLaughlin et al., 2002).

Insect herbivores also respond to rising average temperatures, usually by a shift in the flight season: diapause induction and termination, and thus adult emergence, in many insect species varies with temperature and other environmental cues (van Asch & Visser, 2007; Robinet & Roques, 2010). As with plant responses, since climate change is likely to alter temperature but not daylength, a maladaptive response between interacting species may result (Hodgson et al., 2011). In general, insect phenologies seem to be changing at a steeper rate than plant phenology, which could lead to the adult insects appearing when there are fewer resources, reducing survival and reproduction (Gordo & Sanz, 2005; Mattila et al., 2006). For example, the flowering of the glacier lily (*Erythronium grandiflorum*: Liliaceae) is determined by the date of snowmelt, with up to a month's difference observed amongst years. The plant is now suffering from pollination limitation, particularly at the start of the flowering period, indicating a temporal mismatch between the phenologies of plant and pollinator (Thomson, 2010). Climate change seems also to be altering population cycles, disrupting mutually beneficial ecological interactions, particularly in insects whose life cycles contain climate-dependent stages. (Ims et al., 2008; Memmott et al., 2007). In general we expect climate change to shift the flight period of many insect species to be earlier in the year due to the rising temperatures initiating pupal termination and eclosion (van Asch et al., 2007; Robinet & Roques, 2010).

There is a lack of long-term observational data in this field to establish the extent of asynchrony and mismatches across multiple systems (Miller-Rushing et al., 2010). Where there have been long-term studies, such as the phenological timings of the plants in Concord, there are no recordings of their interactions with insects (e.g. pollinators), so it is impossible to investigate changing levels of synchrony (Miller-Rushing & Primack, 2008; Singer & Parmesan, 2010). In most cases we do not know what the 'normal' levels of asynchrony are, making it impossible to say whether detrimental effects of asynchrony are being exaggerated (Singer &

Parmesan, 2010). A review by Visser & Both (2005) of the available literature found only 11 studies of phenological changes in interacting species. The majority of these studies involved increasing asynchrony with detrimental effects.

Here I study the phenology of the Critically Endangered Sinai Baton Blue butterfly and its exclusive larval host plant, the Sinai Thyme. There is a narrow window when the host plant is flowering and the larvae are present, so any degree of asynchrony will dramatically reduce available resources.

Materials and Methods

The study system

The Sinai Baton Blue butterfly (*Pseudophilotes sinaicus* Nakamura, 1975: Lycaenidae) is the World's smallest butterfly, studied in detail in 2000-2003 (James, 2006a-f), but not subsequently. It is Critically Endangered (Thompson & Gilbert, 2012), one of two endemic butterfly species in the St Katherine Protectorate and a flagship species for the area (Hoyle & James, 2005). The larval stage is entirely dependent on the also-endangered Sinai Thyme (*Thymus decussatus* Bentham, 1834: Lamiaceae), with the first instars feeding exclusively upon the buds and later stages also on the flowers. Adults preferentially feed on thyme, choosing these flowers over alternatives (James, 2006a,f). Climate change is a serious threat for the Sinai Baton Blue due to its limited dispersal and restricted habitat. The butterfly is constrained to the distribution of its host plant, whose patches only occur at elevations above 1500 m. Climate change could decrease the area with suitable conditions for the thyme, reducing it to smaller, increasingly fragmented patches at higher elevations; such reduced patches may be insufficient to sustain the butterfly's metapopulation (Hoyle & James, 2005). There is only a narrow window in time when the plant is flowering and larvae are present, increasing the seriousness of mismatches and hence making the butterfly very sensitive to any shift in the thyme's phenology or changes to its own flight season (James, 2006f).

There have been strong weather fluctuations over the past decade. In the 2002 season the highest recorded temperature was 35˚C with no rainfall.

Between 2002 and 2010 there was little rain in the area, with very little or no rain every year until March 2010. In 2010, temperatures of 40˚C were recorded, and in May there was heavy rainfall which left some patches submerged for over a week. The extent to which these are normal for the area is uncertain because of the scanty and incomplete meteorological records and we have to rely upon local Bedouin knowledge. In contrast, 2011 was an extraordinarily wet year, with heavy rainfall and snow in the winter and spring, whilst 2012 had very little rainfall in spring, although a great deal in the autumn: both these years were said to be colder than normal (local Bedouin knowledge).

Since 2004 the rangers of the St Katherine Protectorate have monitored the Sinai Baton Blues in a key patch of thyme, Farsh Shoeib (see below), albeit time limitations have meant that surveys could not be as intense as desired: for example, only three days of surveys were carried out in 2006. The survey data that exist indicate that the population undergoes cycles (Gilbert et al., 2010), with an apparent three-year period involving large fluctuations in population size and crashes to very low numbers. The underlying drivers of this cycle are unknown. They could involve fluctuations in the resource base (i.e. the thyme flowers) caused by factors such as plant pathogens (Morris et al., 2007; Gotelli, 2008) or possibly sporadic rainfall: the 2003 crash in numbers from those of 2002 was attributed to drought (Hoyle & James, 2005). Other causes could be natural enemies, an induced plant defence response or feedback on plant reproduction via herbivore density (Agrawal, 1999; Boggs & Freeman, 2005; Veldtman et al., 2007). These interactions may not be mutually exclusive explanations, and could drive the Sinai Baton Blue cycle synergistically.

Field work was based in Farsh Shoeib (see Chapter 2, Fig. 2.1), a patch of thyme previously found to harbour one of the largest populations (James et al., 2003). Farsh Shoeib is found near the summit of Gebel Safsafa on the Mt. Sinai massif, close to the town of St Katherine in South Sinai in Egypt, the most arid country in the world (FAO, 2012). It sits at an altitude of approximately 1950 m with an area of 14,000 m^2 that contained 652 thyme plants in 2012. The majority of the patch has been fenced off since 2003 as a conservation measure to prevent public access, grazing and any damage to the plants: only a few plants of this patch are found outside the

enclosure. The field work was carried out from March until the end of June in 2010 and 2011, and from April until mid-July in 2012.

Monitoring phenological timings in Farsh Shoeib

To compare the flowering phenology of the thyme with 2002, each plant was scored according to the same phenological scale created by James (2006e). Once a week, from the first weekend in April, five inflorescences were randomly selected from the most advanced area of flowering on the plant and scored phenologically on a scale of 0-7 (Table 3.1): the average of the five scores represented the phenological state of plant. In 2010, 642 plants were surveyed every week, while in 2011 and 2012 100 plants were randomly selected and scored every week.

Monitoring the status of the Sinai Baton Blue

In Farsh Shoeib, a fixed transect was walked twice a week to count the numbers of Sinai Baton Blues seen, from mid-April until the end of June (Thomas, 1983). One walk was missed in the peak season in 2012 so I incorporated an estimate by averaging the counts from the preceding and subsequent transect. Since the lifespan of an adult was estimated by James (2006d) to be 3-6 days, I assumed that butterflies seen on any one transect had not been seen on any previous transect, and also that each individual was only seen once during the transect and the butterflies are extremely sedentary: see James (2006c). The majority of butterfly sightings were within the main Gulley, a section containing 148 thyme plants. In 2010 131 of these plants were searched thoroughly once a week. For each thyme plant the number of larvae and phenology were recorded weekly.

The number of adults recorded in 2010-2012 were compared to previous survey data collected between 29th April and the 21st July in 2002 and 2003 by James (2006a-e) and data from 2004 to 2009 by rangers of the St Katherine Protectorate (Gilbert et al., 2010). Because butterflies were only sometimes individually marked in the period between 2003 and 2010, I had to make some assumptions about the 2004-2012 data in order to make comparisons. I assumed that these visits did not record the same individual more than once, so that the number of sightings was equal to

the number of individuals. In 2002-2003 each individual was marked and there were daily observations, enabling both sightings and individuals to be separated. The data were also compared amongst years in a different way by matching the number of butterflies counted in 2004-2012 to the numbers seen on the same survey days in 2002. This 'adjusted number of sightings' was expressed as a percentage of the number seen in 2002 to get comparisons of the annual population size in relation to that of 2002.

Analysis of data

All analysis used the statistical package R 2.14.1 (R Development Core Team, 2012) and models were simplified in accordance to Zuur et al. (2009). The phenology was compared amongst years using three summary indices for each plant: i) the average phenological score for 11 weeks commencing the 1st April; ii) the week when the first flower was seen; and iii) the week of peak flowering. Weeks were counted from the 1st April. A one-way ANOVA was used to compare the phenology amongst years, using the R routine *glm*, with the three summary indices as response variables and the year as a factor. I simplified the full model based on the Akaike Information Criterion (AIC) criterion using stepwise backwards deletion of model terms. The average phenological score had a normal distribution and significance was assessed with an F-ratio whilst the other two indices had a Poisson error structure and were assessed using a χ^2 test. Non-flowering plants were excluded from analysis. A Kruskal Wallis test compared the flight season of the butterfly amongst years, comparing the weekly numbers from the end of April.

Results

In 2010 the flowering season began two weeks earlier than 2002. In the middle of June 2010 the majority of the flowers had finished, whereas at the same time in 2002 the plants were approaching their flowering peak. In 2011 the phenology had shifted back to be similar to 2002, with the peak flowering in the middle of June. 2012 was again similar to 2002 and 2011 (Fig. 3.1). When comparing the phenology amongst years, there were highly significant differences in the average score (F=43.8, df=3,1534, p <0.001), the week of first flower (χ^2=165, df=3, p<0.001) and week of

peak flowering (χ^2=96.2, df=3, p<0.001 in each case). 2010 was clearly more advanced than the other years, whilst the other three years all had similar phenological timing. 2011 was the latest phenology, with the lowest average score and week of peak flowering, whilst 2012 was slightly earlier than 2002 and 2011 (Fig. 3.2). The week of the first flower and peak flowering does not suggest much difference between 2002, 2011 and 2012, but the mean phenology score indicates a larger difference, perhaps an artefact of the methodology used to score the phenology.

The adult flight period significantly varied amongst years (χ^2=0.05, df=4, p=0.006): 2010 had the earliest flight period over the years with the first peak mid May whilst the remaining patches peaked consistently towards the end of May/beginning of June. Overall 2011 had the latest flight period (Fig. 3.3 & Fig. 3.4). In 2010, larvae appeared on the plants towards the end of the main flight season, when butterfly numbers were decreasing. Larvae were first seen when plants were at their flowering peak, with the majority of buds open. However, flowering was finishing in the weeks when the majority of larvae were counted: inflorescences were dying and plants were beginning to produce seeds (Fig. 3.5).

A summary of the butterfly data from 2002 onwards is shown in Table 3.2 (see also Figures 3.6). The data from 2010-11 appeared to confirm the cyclical pattern of regular crashes that leave the population close to extinction, followed by recovery. However, 2012 was an unexpected peak year with the highest number of sightings per day since 2002. The number of individuals relative to the 2002 survey days shows three severe crash years and an overall decline in numbers, with the population not recovering from the 2003 crash, but this assumes that since 2004 there have been multiple sightings of the same individuals (Table 3.2). If there have been no re-sightings in the surveys since 2004, then the average number of individuals per day shows a pattern of alarming crashes. However it shows a slight rise in population numbers (Fig. 3.6).

Discussion

Phenotypic plasticity in plants is induced by environmental factors such as air temperature, and the resulting changes in phenotype enable plants to respond to stress in a way that maximises fitness, e.g. via altering their

flowering phenology (Crepinsek et al., 2006, Matesanz et al., 2010). It is an important life-history strategy under fluctuating climatic conditions; plants with increased plasticity will have higher fitness if flowering phenology can match temporal climatic variation (Anderson et al., 2012). A two-week shift is notably large considering the flowers are only present for approximately 6 weeks; the phenology could have been induced by air temperature: 2010 had an uncharacteristically warm period in March which may have advanced development. Other plants in the area, such as the Sinai milkweed (*Asclepias sinaica*: Asclepiadaceae) also had advanced flowering in 2010 when compared to 2011 (Stine Simensen, 2011, pers. comm). The 2012 phenology is similar to 2002 and 2011, and hence is more likely to be closer to the long-term norm, with 2010 uncharacteristically early. The maximum temperature recorded in 2010 was 5°C higher than that recorded in 2002, and may be responsible for the shift observed here (Anderson et al., 2012; van Asch & Visser, 2007; Cook et al., 2012).

Plant species which can track climatic fluctuations are more likely to have a higher relative abundance than those with a non-responsive phenology (Willis et al., 2008; Johansson et al., 2013). Plants are, in general, moving their phenologies earlier into the year (Doi & Katano, 2008; Miller-Rushing & Primack, 2008), but inter-annual variation can be large; the onset and duration of flowering in apricot cultivars (*Prunus armeniaca*: Rosaceae) in Siberia can vary up to 34 days between years and is strongly correlated to air temperature (Ruml et al., 2011). This can potentially cause problems for interacting herbivores that rely on synchronous timings (Ims et al., 2008), such as the Sinai Baton Blue whose larval stage feeds exclusively upon the buds.

The butterfly's main flight period appears to have also shifted amongst years; with the flowering and flight period occurring earlier in 2010. This suggests that both the butterfly and plant are responsive to the climatic fluctuations, which is optimistic for the future. If the butterfly phenology remained relatively unchanging in the face of large changes in thyme phenology, annual abundance would be more and more affected by bottom-up forces. Asynchrony could still be a problem if the phenology of the host and herbivore respond by different magnitudes between years; if they respond to the same cue at different rates then long-term

synchronisation is possible, but the outlook is less optimistic if the two species use different environmental cues, or have different levels of sensitivity if using the same climatic cues (van Asch et al., 2007; Robinet & Roques, 2010).

Population dynamics in arid environments are commonly controlled by bottom-up forces, with primary productivity predominantly governed by rainfall and the corresponding resource pulse (Schwinning et al., 2004; Letnic & Dickman, 2010). When resources become abundant, primary consumers undergo a population boom due to alleviated competition (Ostfeld & Keesing, 2000; Letnic & Dickman, 2010). Insect populations have a large instantaneous rate of increase and as a consequence are sensitive to changes in carrying capacity (Gotelli, 2008) which may explain the population cycles here. There was a large increase in the resources available to the butterfly between 2010 and 2011: in Farsh Shoeib there was a 10 m^2 increase in thyme greenery and flower production doubled, probably caused by the heavy rainfall of 2010 and 2011 (Chapter 2), and in the following year (2012) there were the highest number of individual butterflies per day since records began in 2002. It would be interesting to model this two-year response to unpredictable rainfall to see whether in principle this can lead to three-year population cycles: it seems unlikely.

Resource level may therefore play a key role in generating the population cycles of the Sinai Baton Blue; the first two instars feed exclusively on buds, and subsequent instars on the flowers (James, 2006f). The majority of larvae were found at the end of the 2010 flowering season, when resources were quickly diminishing and the proportion of dead flowers was dramatically increasing, suggesting that this cohort may have run short of food, causing the population to decline in 2011 (cf. Fig. 3.5). The regularity of the apparent peaks and troughs in abundance suggest that the cycle cannot be driven by the effects of stochastic forces such as weather on the carrying capacity.

An alternative possible cause of population cycles is temporal variation in plant defence, including biochemical changes to deter or reduce herbivore fitness, or re-allocation of resources to reduce larval survival (Boggs & Freeman, 2005; Miler & Straile, 2010). Plants can induce secondary metabolites flexibly, only investing when necessary (Zangerl, 2003; Metlen

et al., 2009). In principle the alternation of induction of defence chemicals followed by their suppression as herbivore density rises and falls could generate population cycles, although it is not clear why thyme plants would do this synchronously. An alternative herbivore-induced defence is the shifting of flowering to minimise damage from insect herbivores (Ohgushi, 2005). Depending on the extent of herbivore damage, the white spruce (*Picea glauca*: Pinaceae) can adjust bud burst to reduce damage the subsequent year (Quiring & McKinnon, 1999). Herbivory-induced shifts in flowering have a direct impact on the abundance and distribution of folivorous insects, and thus could cause population cycles as well as explaining the dramatic shifts in thyme phenology (Quiring & McKinnon, 1999).

Overall, the relatively large population of Sinai Baton Blues in Farsh Shoeib appears to undergo substantial fluctuations, apparently with a three-year cycle, potentially facing extinction when the population drops to its low points. If extinction occurred it would be an important event for the butterfly metapopulation (James, 2006d), although modelling suggests that two other patch populations are more critical to its long-term survival (Hoyle & James, 2005). The causes of the population crashes are unknown, but undoubtedly the large shifts in thyme phenology affect the available resources, especially if the magnitude in shift is not matched by the butterfly. Although the cycles seem fairly large, and hence the status of the Sinai Baton Blue seems precarious, the species has survived many thousands of years so far successfully. It is possible that dispersal from neighbouring patches is vital in rescuing this population from extinction (see James 2006d). This highlights the importance of neighbouring patches and the need for conservation across multiple patches, not just in Farsh Shoeib.

Table 3.1. Scoring of flowering phenology (from James, 2006e).

Phenological score	Appearance of plant
0	100% pre-bud
1	sepals visible, buds not yet visible
2	sepals apparent, buds starting to develop
3	large buds with fewer than 2 flowers open
4	50-90% buds, 10-50% flowers open
5	1-50% buds, 50-100% flowers open
6	1-50% flowers over/seed heads
7	more than 50% flowers over/seed heads
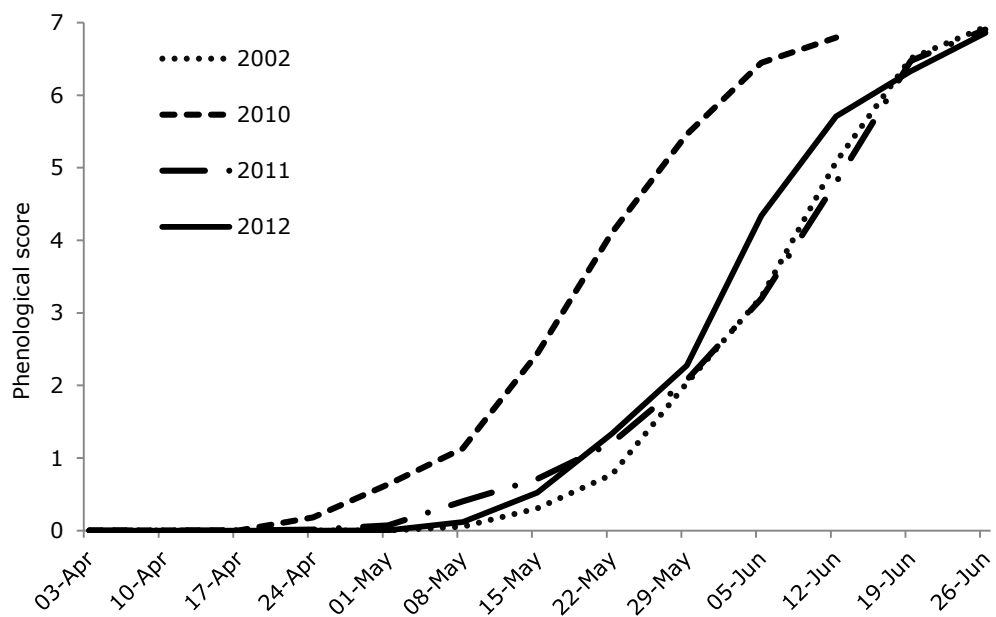
Figure 3.1. The flowering season of *Thymus decussatus* as recorded by the mean phenological score (see Methods) in 2002, 2010, 2011 and 2012, n = 760, 594, 98 & 83 respectively.

Table 3.2. Comparison of surveys of the Sinai Baton Blue butterfly among years (data from years 2002 - 2009 from Gilbert et al 2010, with slight modifications). Line 6 of the table ("number seen on same survey days in 2002") is the number of butterflies spotted in 2002 on the survey days of the subsequent years, in order to compare with lines 1 and 2. Line 7 of the table ("Adjusted number of sightings") is the number of sightings in any particular year relative to the number seen on the same survey days in 2002, expressed as a percentage.

	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
Number of butterflies seen	1496	181	56	60	0	113	54	9	91	107	222
Number of individuals seen	431	60	56	60	0	113	54	9	91	107	222
Days surveyed	74	51	7	11	3	13	14	11	11	18	18
Number of sightings per day	20.2	3.5	8.0	5.5	0.0	8.7	3.9	0.8	8.3	5.9	12.3
Number of individuals per day	5.8	1.2	8.0	5.5	0.0	8.7	3.9	0.8	8.3	5.9	12.3
Number seen on same survey days in 2002	1496	1496	132	209	10	194	350	150	381	418	417
Adjusted number of sightings	100	12.1	42.4	28.7	0.0	58.2	15.4	6.0	23.9	25.6	53.0
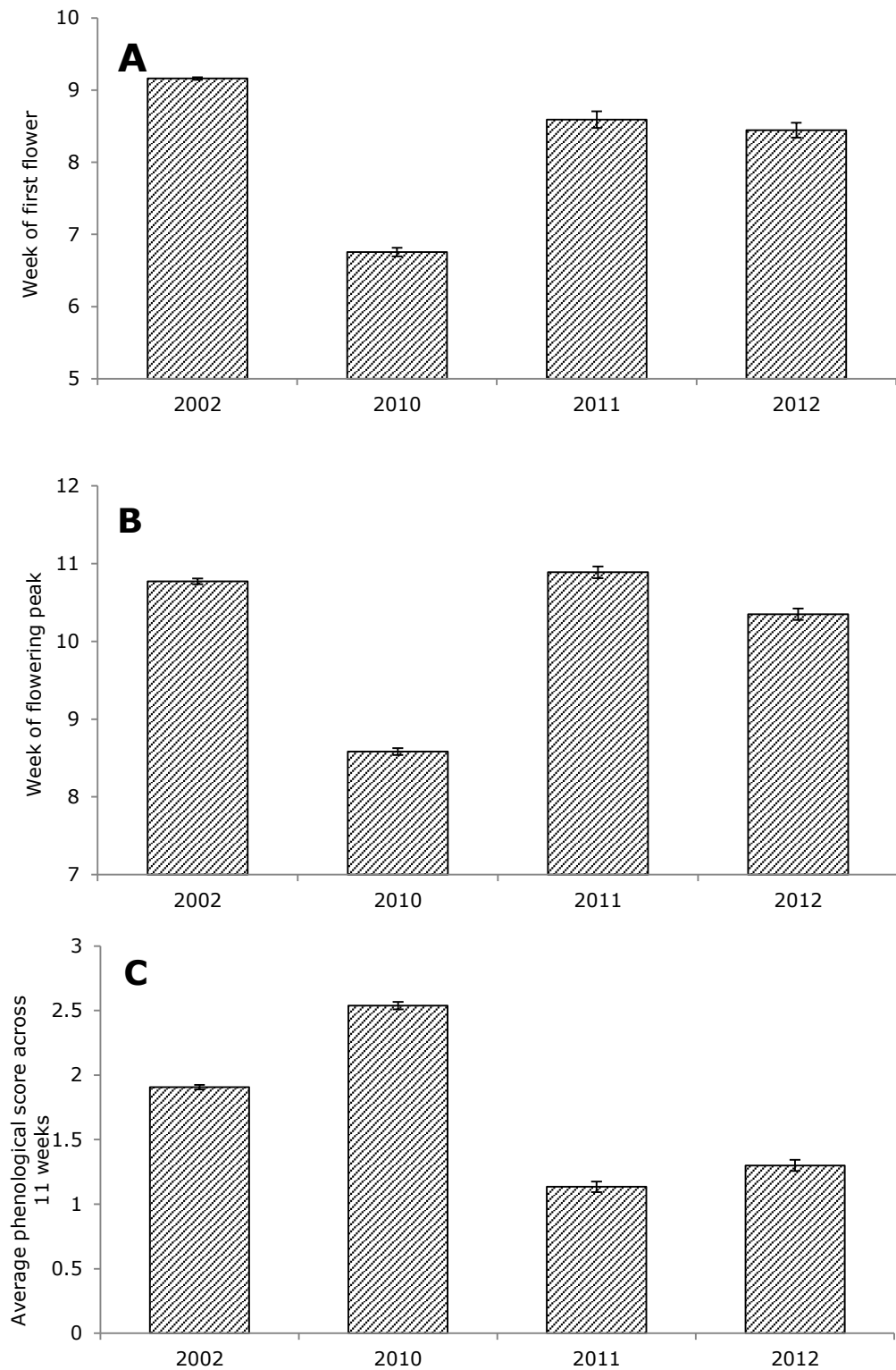
Figure 3.2. Comparisons of the phenology of *Thymus decussatus* in Farsh Shoeib showing a) the week of first flower b) week of peak flowers and c) the average across 11 weeks (start of April until mid June) in 2002, 2010, 2011 & 2012. Mean values ± SE, n = 760, 594, 98 & 83 respectively.
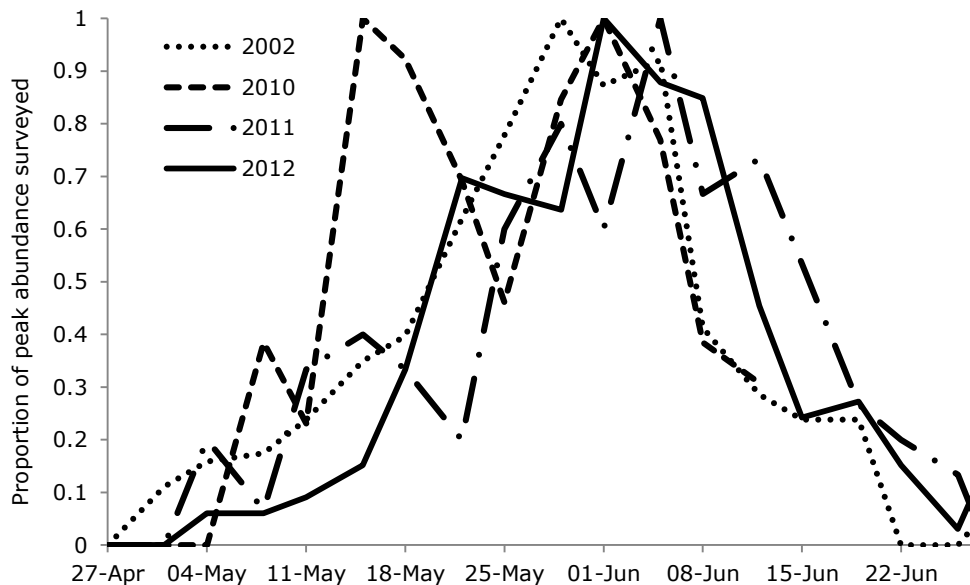
Figure 3.3. The butterfly flight period, expressed as a proportion of peak abundance, in 2002, 2010, 2011 and 2012.
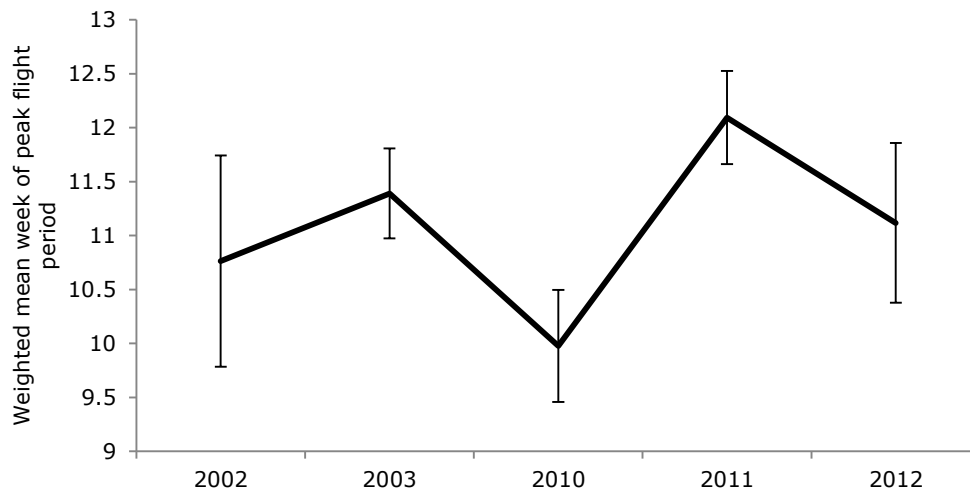
Figure 3.4 The weighted average peak flight period in 2002, 2003 & 2010-2012. Week count commencing the first weekend in April.
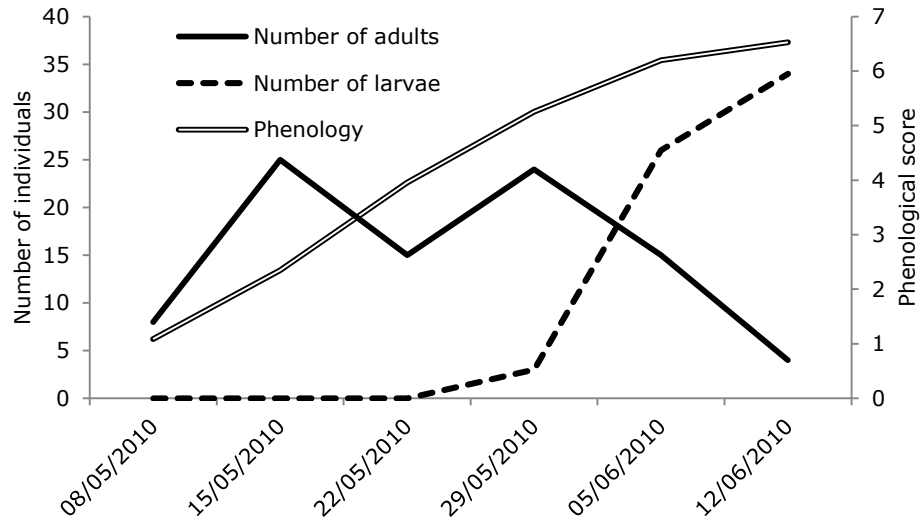
Figure 3.5. Number of Sinai Baton Blue larvae and adults compared to the flowering phenology of the host plant seen in Farsh Shoeib in 2010.
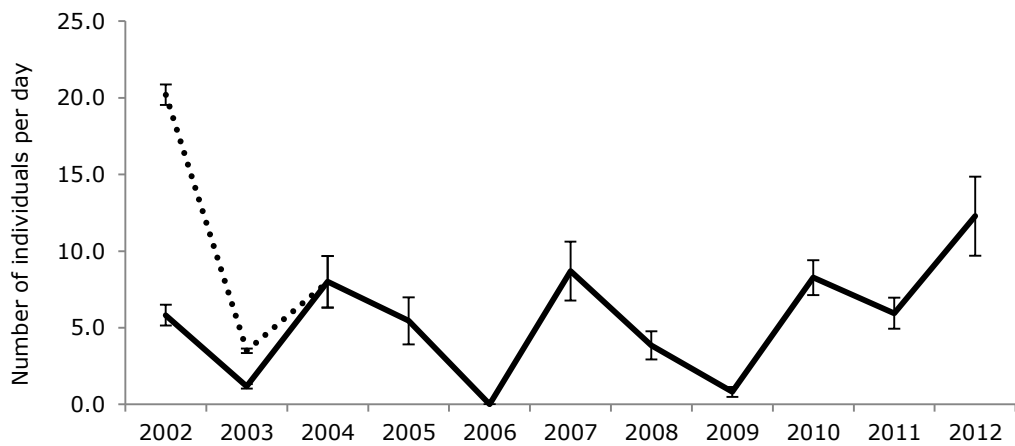
Figure 3.6. The number of butterflies seen per day (mean ± SE). The solid line shows the number of separate individuals, known by marking in 2002-3, but the data for 2004-2012 assume that individuals were not seen more than once because the line records the number of sightings; the dashed line indicates the total number of sightings in 2002-3.

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Chapter 4.

Spatio-temporal variation in a herbaceous shrub, *Thymus decussatus*, and the associated butterfly populations of *Pseudophilotes sinaicus*

Mt. Sinai massif

Spatio-temporal variation in a perennial herbaceous shrub, *Thymus decussatus*, and the associated butterfly populations of P*seudophilotes sinaicus*

Abstract

Arid environments are resource-limited, with scarcity of water the key limiting factor for plants and their associated fauna and consequentially are often controlled by bottom-up forces. Environmental variation can act synergistically with spatial features to create habitat heterogeneity, effecting floral life history traits, such as growth and flowering. The Sinai Baton Blue, *Pseudophilotes sinaicus,* lives in a highly fragmented metapopulation dependent upon the patches of its sole host plant, Sinai Thyme, *Thymus decussatus*. I study here spatial differences in thyme quality across ten patches within the St Katherine Protectorate, South Sinai. The findings show significant variation in the size, condition and flowering phenology amongst thyme populations, indicating that the plant is responding to micro-variation amongst patches. There were also temporal fluctuations in the flowering timings and abundance, with a uniform decline across the whole massif. I also found that the butterfly population sizes are positively correlated with the total resource area and the number of host plants, so the observed decline in flowers will have negative implications for the species, highlighting the importance of future conservation work to be focused on improving plant quality within patches.

Introduction

Resource availability in arid environments is primarily governed by water (Pueyo et al., 2008) and spatial variation in rainfall and the subsequent soil moisture plays a large role in determining resource levels and hence plant quality and abundance (Reynolds et al., 2004). Environmental variation may act synergistically with geomorphological and edaphic features to cause spatial variation in distribution (Bestelmeyer et al., 2006; Ju et al., 2008), abundance (Reynolds et al., 2004), productivity (Popp et al., 2009) and mortality (Hamerlynck & McAuliffe, 2008). This habitat heterogeneity also influences plant life history traits, such as growth and phenology (Gaston et al., 2004; Montesinos-Navarro et al., 2010). For example,

populations of *Arabidopsis thaliana* (Brassicaceae) have different biomass allocation, fecundity and phenology depending upon the altitude of the home site; these traits have a genetic basis indicating previous selection to adapt to the environment (Montesinos-Navarro et al., 2010). The timing of growth and bud burst in Norway spruce (*Picea abies:* Pinacaeae) varies amongst populations, showing local adaptation with both latitude and altitude influencing phenological traits (Chmura, 2006). Spatial variation in the phenology of host plants leads to pressure for their associated herbivores to be phenologically synchronized appropriately. Otherwise there will be detrimental consequences for their population dynamics and abundance (Phillimore et al., 2012).

Many herbivores have a naturally fragmented distribution, but it is common for their population dynamics to be governed by habitat quality and local resource levels, rather than connectivity and isolation. Both Driscoll et al. (2010) and Fronhofer et al. (2012) argue that metapopulation structure is in fact rather rare in nature. Resource quality and abundance are key determinants underlying the distribution and abundance of many species of butterflies and day-flying moths (Bruckmann et al., 2010; Sanford et al., 2011; Williams, 2011). Isolation and inter-patch connectivity can affect the distribution of insect herbivores, but its effect size on insect abundance is currently in debate. Hodgson et al. (2011) argue that patch area and quality have more significance than connectivity and isolation in regulating the relative abundance of insect herbivores. For 54 butterfly species occupying calcareous grasslands in Germany, species richness was positively correlated with habitat area, whilst isolation had no apparent effects (Krauss et al., 2003). Patch aggregation and connectivity can have positive effects on species richness, especially for specialist butterflies and plants, but habitat area still had a larger effect (Bruckmann et al., 2010). This is also true for patch occupancy in individual species. A good example is the Carson Valley silverspot butterfly (*Speyeria nokomis carsonensis*: Nymphalidae), which exists in a narrowly endemic metapopulation, but environmental variation is important for patch occupancy; habitat quality explained more disparities in occupancy than patch area and isolation (Sanford et al., 2011). It is usually the quality of the larval habitat that plays a critical role in population size and persistence; increased larval resources reduce extinction risk and attract more emigrants, explaining more variation in site occupancy than isolation (Thomas et al., 2011).

Here I study the Critically Endangered Sinai Baton Blue butterfly and its exclusive larval host plant, the Sinai Thyme, a rare plant growing in the arid mountains of the St Katherine Protectorate in South Sinai in Egypt, the most arid country in the world. I study the spatial variation in plant quality and phenology among ten patches, together with the associated populations of the Sinai Baton Blue.

Materials & Methods

The study system

The Sinai Baton Blue butterfly (*Pseudophilotes sinaicus* Nakamura, 1975) is Critically Endangered, occupying a total area of less than 7 km^2 (Thompson & Gilbert, 2012). It is considered a flagship species for the region (Hoyle & James, 2005), and its long-term conservation is a top priority of the Protectorate management team (StKP, 2003). Because of its status, and as one of only three animal species currently known to be endemic to Egypt, two of which are endemic to the St Katherine Protectorate (the other is the Sinai Hairstreak, *Satyrium jebelia* Nakamura, 1975), it is not possible to obtain permission for manipulative experiments, and hence I have had to rely on observational data alone.

The Sinai Baton Blue lives in an arid environment, marooned by Pleistocene climate change on the top of mountains in a fragmented landscape: in 2001 it was recorded as occupying 24 of 39 patches of the host plant (James et al., 2003). The larval stage is entirely dependent on an endangered near-endemic plant, Sinai Thyme (*Thymus decussatus* Bentham, 1834). Since the plant only occurs above an altitude of 1500 m within the St Katherine Protectorate (and recorded once from an adjacent area in Saudi Arabia), the distribution of the butterfly is severely restricted (James, 2006a). The plant grows best in well-defined soil at the base of cliffs and wadis, resulting in a natural patchy distribution (Nakamura, 1975).

Ants play an important role in larval survival and thus probably influence population size. *Crematogaster antaris* (called *Crematogaster aegyptiaca* by James) is a predator: no adult butterflies emerged within its foraging

range in 2002 (James, 2006b). In contrast, Sinai Baton Blue larvae have a facultative relationship with *Lepisiota obtusa* (Emery, 1901) ants, appeasing them with sugar and in return gaining protection (James, 2006b). It was recently discovered (Shepherd, 2010) that another species of *Lepisiota*, *L. hirsuta* (Santschi, 1914), cohabits the same range and also tends the larvae along with *Monomorium* sp., which tends to a lesser extent. The largest butterfly population in Farsh Shoeib was surveyed for ant species in 2002 and 2010, and both *Crematogaster antaris* and *Lepisiota* spp were detected. The foraging ranges of these species were mutually exclusive, with *C. antaris* occupying the farsh section of the site (a wide, open area) and *Lepisiota* the gulley section (a narrow area with steep rocky sides). It is not completely understood why these two species have mutually exclusive distributions; the current most likely explanation is different habitat choices, with *Crematogaster antaris* preferring the open farshes and *Lepisiota* the more sheltered gullies (Shepherd, 2010). The ant distribution in Farsh Shoeib remained identical between 2002 and 2010, with no variation in foraging range of either species (Shepherd, 2010).

The field work was carried out upon the Mount Sinai massif above the town of St Katherine in two four-month periods from March 2011 and April 2012. There are ten patches upon the massif: Farsh Shoeib - a patch containing one of the largest butterfly populations in 2001, Farsh Loza, Farsh El Hammar (Lower and Upper), Farsh Elia, Elia Garden, Elia Circle, Farsh Safsafa, Gulley Zahtuna and Gulley Sharr (Fig. 4.1). The first five patches had previously been recorded as potential habitat, but the latter patches were only discovered in 2011 from extensive explorations at the start of the field season. Therefore butterfly populations in these patches were previously unrecorded. 2011 was an extraordinarily wet year, with heavy rainfall and snow in the winter and spring, whilst 2012 had very little rainfall until the autumn (when it was heavy and prolonged) and was also colder than normal.

Evaluating the quality of thyme amongst patches

The average quality per patch was calculated in 2011 by measuring the height, two perpendicular widths and the condition (the proportion of the plant that was green). The resource area was calculated using the assumption that the plant had a hemi-ellipsoidal shape so it was possible to

calculate the surface area. This was then multiplied by the condition to get the resource area per plant. This was measured for every plant in Farsh Shoeib, and for 100 or all plants in the remaining patches, whichever was the smaller number. The condition of 50 randomly selected plants per patch (apart from Safsafa which had fewer than 50 individuals) was recorded in 2012. I did not record plant size in 2012 due to the obviously slow growth rate and the relatively large human error involved in determining the widest part of the plant. Another measurement of plant quality was the density of inflorescences: these were counted towards the end of the flowering season in a randomly placed 10 x 10 cm quadrat for 50 random plants per patch, regardless of whether they were flowering or not. I also recorded the proportion of plants flowering amongst patches using the same plants from which I counted the density of inflorescences. The density of inflorescences and proportion of flowering plants were re-surveyed in 2012.

Monitoring phenology

In order to compare the phenological synchrony amongst patches, 100 plants in Farsh Shoeib and 50 plants from the remaining patches were randomly selected and scored according to the phenological scale created by James (2006e). Once a week, from the start of April in 2011 and from mid-April in 2012, five inflorescences were randomly selected from the most advanced area of flowering on the plant and scored phenologically on a scale of 0-7 (Table 4.1): the average of the five scores represented the phenological state of each plant.

Mapping of patches upon the Mt. Sinai massif

The boundary of each patch upon the Mt. Sinai massif was mapped by walking around the perimeter and recording a track using a hand-held GPS unit (Garmin etrex Venture HC, found to be accurate to ± 10 metres) and the waymarks from the tracks were then imported into ArcGIS. Each plant situated outside a patch was individually labelled and its position recorded using the GPS unit. I decided whether plants formed a discrete patch if there were more than 30 plants closely situated, separated from another patch by either 100 m or a natural barrier (which was often the situation on the Mt. Sinai massif). The plants located outside the patches were

sparsely distributed with considerable distances between them and took considerably longer to locate. To calculate connectivity amongst patches, I measured the distance to the nearest occupied patch. Prugh (2009) describes this as the NS_i value and found this measurement of connectivity to be as effective as an Incidence Function Model in explaining patch occupancy.

Monitoring the status of the Sinai Baton Blue

In order to monitor the synchrony of the flight season and the relative population abundance, a transect of each patch was walked twice a week between 10 am and 2 pm – the peak time of butterfly activity - to count the numbers. Transects started in mid-April and finished at the end of June: there were 22 transects carried out per patch in 2011 and 21 in 2012. Since the lifespan of an adult was estimated by James (2006d) to be 3-6 days, I assumed that butterflies seen on any one transect had not been seen on any previous transect, and also that each individual was only seen once during the transect and the butterflies are extremely sedentary: see James (2006c).

Ant sampling

In order to see which ants were present in the patches, 30 pitfall traps were placed under randomly selected thyme plants in 2011. The traps were left for 24 hours and the catch collected. This was repeated three times in all patches except Farsh Shoeib, which had been sampled extensively in 2010 (Shepherd, 2010). The pitfalls were only placed after the plants had started to flower in order to obtain the species which forage upon the thyme inflorescences. It is impossible to differentiate between *Lepisiota obtusa* and *Lepisiota hirsuta* in the field, so these two species were lumped together: since both species tend the larvae, this should not affect the interpretation of the results.

Analysis of data

All analyses used the statistical package R 2.14.1 (R Development Core Team, 2012) and models were simplified in accordance to Zuur et al. (2009). A GLM was run to compare the size (assuming the hemi-ellipsoidal

shape) amongst patches in 2011. The size was logarithmically transformed (normalising it) and analysed using the R routine *glm*, with significance assessed with an F-ratio. The condition, density of inflorescences and proportion of plants that flowered were compared in turn using a two-way GLM to test for differences between years (2011 and 2012) and among patches. I simplified the full model based on the Akaike Information Criterion (AIC) criterion using stepwise backwards deletion of model terms. Condition and density of inflorescences per 10 cm^2 were over-dispersed and so the GLM had a quasi-poisson error structure with significance tested with an F-ratio; the proportion of flowering plants had a binomial distribution, tested with a χ^2 test. A Pearson correlation was run to test the association between the proportion of flowering plants and the density of inflorescences across 2011 and 2012.

Plant flowering phenology was compared among patches and between years using three summary indices of each plant as response variables: i) the week of first flower; ii) the week of peak flowering; and iii) the average phenological score across 13 weeks of sampling. Weeks were counted from the 1st April. A two-way GLM was run with patch and year as factors. I simplified the full model based on the Akaike Information Criterion (AIC) criterion using stepwise backwards deletion of model terms. The average phenological score had a normal distribution whilst the other two indices had a quasi-poisson structure due to over-dispersion. Significance was assessed with an F-ratio. Non-flowering plants were excluded from analysis.

A further GLM compared the butterfly flight season amongst years, with the proportion of total butterflies seen as the response variable and the year, patch and week as factors. A quasi-poisson error structure was used. I again simplified the full model based on the AIC criterion using stepwise backwards deletion of model terms and significance assessed with an F-ratio. A Pearson correlation was run to test the association between the relative butterfly abundance and peak flowering across all patches in 2011 and 2012. I also assessed the predictability of butterfly abundance among patches. I ran a GLM using the number of butterflies per patch in 2011 as the response variable (using Poisson errors) and patch characteristics as the predictors, tested with a χ^2 test. The characteristics used were presence/absence of *Crematogaster antaris* and *Lepisiota* spp., total

resource area, number of plants, number of inflorescences per patch (estimated by density of inflorescences multiplied by total resource area) and connectivity (distance to nearest occupied patch).

Results

Plants

There were ten patches of thyme upon the Mt Sinai massif with 206 'corridor' plants located amongst the patches in seven clusters (Fig. 4.1). There were a total of 2471 plants in ten patches, with a combined resource area within the patches of 174 m^2. Farsh Shoeib held the largest amount of resource, with 54.8 m^2 of green thyme (32% of the massif total) in 2011 (Table 4.2). Plant size (only measured in 2011) showed significant spatial differences (F=9.82, df=9,1460, p<0.001) with Farsh Loza having the largest individuals (Fig. 4.2a). There was also significant spatial variation in condition (F=6.05, df=9,2426, p<0.001), but no differences between years (F=0.82, df=1,2426, p=0.36), nor any evidence of an interaction (F=1.82, df=9, 2426, p=0.06). In 2011 there was a 15.1% difference between the healthiest (largest average condition) and unhealthiest patches (Loza and Elia Garden) and 10.4% difference in 2012 (Gulley Zahtuna and Farsh Elia)(Fig. 4.4a). Overall the average condition decreased by 0.7% between 2011 and 2012, from 28.1 to 27.3%. If plant size remained constant this would have caused a loss of 5.6 m^2 of green thyme across the massif.

The density of inflorescences varied significantly between years (F=193, df=1,953, p<0.001) and amongst patches (F=3.89, df=9,953, p<0.001), with a significant interaction between these two factors (F=3.8, df=9,953, p<0.01). The average density of inflorescences across the massif decreased by 22.3 per 10 cm^2, from 47.2 in 2011 to 24.9 in 2012. The largest decline (of 33.2 per 10 cm^2, n=50) was seen in Elia Garden, the patch that had flowered most prolifically in 2011 (Fig. 4.4b). The proportion of flowering plants also varied significantly between years (χ^2=41.8, df=2, p<0.001), but there was no evidence of any spatial variation (χ^2=9.64, df=9, p=0.38), nor of any interaction (χ^2=14.5, df=9, p=0.11). The overall proportion of flowering plants decreased from 98% to 89% in 2012, varying from a 20% decrease in Farsh Elia to a 4% increase in Farsh Loza (Fig. 4.4c). There was a significant positive correlation

between the densities of inflorescences and the proportion of flowering plants in 2011 and 2012 (r=0.882, df=18, p<0.001)(Fig. 4.3).

There were significant differences in the week of first flowering amongst patches (F=25.3, df=9,984, p<0.001) and between years (F=18.3, df=1,984, p<0.001), but no evidence of any interaction (F=1.88, df=9,984, p=0.051). The week of peak flowering was also significantly different between years (F=138, df=1,984, p<0.001) and amongst patches (F=41.1, df=9,984, p<0.001), again with no evidence of any interaction (F=1.41, df=1,984, p=0.18). In 2012 the first flower was later than in 2011 in every patch (except Farsh Shoeib), but peak flowering was earlier (Fig. 4.5). When comparing the phenologies in detail, the 2012 flowering commenced later but the flowering season was more condensed, with peak flowering occurring slightly earlier (Fig. 4.6). Comparing the average phenological score achieved across 13 weeks of flowering, the scores were significantly different between years (F=20.4, df=1,984, p<0.001), amongst patches (F=45.1, df=9,984, p<0.001) and with a significant interaction (F=2.69, df=9,984, p<0.01). The average phenology was earlier in 2012 than 2011 in every patch except Lower Hammar. Lower Hammar remained the earliest-flowering patch, flowering first in both years, whilst Farsh Safsafa was the last to flower; there was approximately a 2-3 week difference in flowering between these two patches in 2011 (Fig. 4.5).

Butterflies

The majority of butterflies were seen in Farsh Shoeib, with 56.3% of all sightings in 2011 and 87.7% in 2012 (Table 4.3). Butterflies were seen in every patch except Farsh Safsafa. Farsh Elia and Farsh Loza had the second and third largest populations, with butterflies present on half of the transects, suggesting relatively large populations. There was a maximum of only two transects with sightings in Upper Hammar, Gulley Sharr and Elia Circle, suggesting very low population numbers, or perhaps just dispersing individuals from other patches. 2012 was a peak year for butterflies in Farsh Shoeib, with the numbers almost doubling over the previous year, but numbers in the other patches of the massif appeared to have crashed. Farsh Elia and Farsh Loza remained the second and third largest populations, despite their numbers halving; together with Farsh Shoeib the

three patches contained 96% of all the butterflies seen on the massif (Table 4.3). Gulley Zahtuna was the only other population with more than two transects with sightings in 2012 (Table 4.3).

There were no significant differences in the flight period amongst patches (F=0.089, df=9,56, p=0.731) or between years (F=0.216, df=1,56, p=0.213), nor was there any evidence of any interaction (F=0.043, df=9,56, p=0.862). 2011 showed a wider spread of flight periods across the massif (Fig. 4.7). When comparing the flight periods there was no correlation between the week of peak flowering and peak butterfly abundance (r=0.36, df=18, p=0.12)(Fig. 4.8). Farsh Shoeib, Farsh Elia and Farsh Loza consistently had the highest numbers of butterfly sightings in 2011, with the majority of transects containing sightings. The timings of the adult flight season within these patches again appear to be correlated to host plant phenology in space but not across years; butterflies peaked in Farsh Loza and Farsh Elia when buds were starting to form, whilst numbers peaked in Farsh Shoeib slightly later, when the plants had large buds but on average fewer than two flowers. The number of butterflies in Farsh Loza and Farsh Elia appeared to have a second peak towards the end of the flowering period, but Farsh Shoeib did not have this second peak (Fig. 4.9).

Butterfly numbers varied amongst patches. The presence of the attendant *Lepisiota* spp. (χ^2 =15.9, df=9, p<0.001), total resource area (χ^2= 22.6, df=9, p<0.001) and number of plants (χ^2=149, df=9, p<0.001) all influenced butterfly numbers recorded from a patch. The presence of the attendant ant had a positive effect on the abundance of Sinai Baton Blues; the five patches containing *Lepisiota* species had the five largest populations on the Mt. Sinai massif (Fig. 4.10). There were positive correlations between butterfly numbers and both the total resource area per patch and the number of plants (Fig. 4.11). Farsh Shoeib, Farsh Loza and Farsh Elia had the three highest number of sightings with nearly 80%, and these patches also had the three largest total resource areas - combined more than 60% of the thyme – and number of plants. Safsafa, which had no sightings, had the lowest total resource area (less than 4 m^2 of thyme) and only 37 thyme plants. The number of inflorescences per patch, presence of the predatory *Crematogaster antaris* and distance to nearest occupied patch did not affect the numbers of butterfly sightings.

Ants

The diversity of ant species varied amongst patches, with Farsh Elia having the largest number of species (seven) whilst Elia Circle had only two (Table 4.2). *Monomorium* was found in every patch on the massif: it does tend the Sinai Baton Blue larvae, but to a lesser extent than *Lepisiota* species. The predatory *Crematogaster antaris* was found in the farsh of three patches; Farsh Loza, Upper Hammar and Farsh Elia. The attendant *Lepisiota* spp. were found in just four patches: Farsh Loza, Farsh Elia, Gulley Zahtuna and Lower Hammar. *Lepisiota* inhabited the gullies of two patches, Gulley Zahtuna (which had no farsh) and Lower Hammar (where they also occupied the adjacent farsh). In the other two patches, *Lepisiota* occupied the farsh. *Crematogaster* and *Lepisiota* co-existed in three patches (Farsh Loza, Farsh Elia and Farsh Shoeib), but were present in separate sections - thus co-existence was more apparent than real. In the 810 pitfalls placed under 270 plants, there were no cases of both ant species being caught: the ants were mutually exclusive. The foraging ranges of the ant species are shown in Figure 4.12.

Discussion

Here, I have found significant temporal differences in the phenology, density of flowers and proportion of flowering plants in the Sinai Thyme. The changes in the flowering were in the same direction across the massif, suggesting that the plant is responding to macro-variation in the climate. Between 2011 and 2012 there was a large decline in resources, which will have negative implications for the associated Sinai Baton Blue larvae. The flowering has also demonstrated significant spatial variation amongst populations, indicating that it also responds to micro-variation between patches.

Spatio-temporal variation

Water is the primary driver of productivity in arid environments with soil moisture having a direct impact on plant growth and establishment. Water levels are influenced by many variables, such as soil permeability, incline or uneven rainfall distribution. These variables interact to alter infiltration

and surface run-off, which in turn affect the vegetation, such as canopy density and proportion of bare ground (Davies et al., 2007; Pueyo et al., 2008). The patches on the massif are not uniform; they certainly vary in altitude, gradient and shelter and hence probably also climatically, with different temperatures, soil moistures or nutrient levels. These factors may act synergistically to influence plant quality, condition and phenology, and such spatial differences could potentially lead to the evolution of different life history traits, such as flowering period or growth rate (Montesinos-Navarro et al., 2010), in the absence of gene flow (about which we know nothing for Sinai Thyme) or simply plasticity. Increasing fragmentation has almost certainly occurred over the long term from climate change over the last 5000 years, and in the short term due to habitat loss and damage from over-collection and possibly also over-grazing. These will have resulted in smaller patch sizes and increased isolation (Hanski, 1991; Hoyle & James, 2005), reducing or limiting dispersal and gene flow amongst patches, and possibly increasing trait differentiation. There are significant spatial differences in size, resource area and condition across the massif, with Farsh Loza and Farsh Safsafa consistently having the largest, healthiest individuals. The density of inflorescences also showed spatial variation, with Farsh Loza having high densities in both years. Evolved differences seem unlikely, however, given the small distances between patches.

Plant condition did not change significantly between years but there was inter-annual variation in the density of inflorescences and proportion of flowering plants. The severity of decline in the density of inflorescences varied amongst patches; some appear to be more affected by the dry period. The proportion of flowering plants also declined between years, but it did not significantly differ amongst patches. The inter-annual variation in flowering but not condition suggests that flowering has more plasticity to adapt to the climate, with the thyme reducing flowering in response to a dry winter. Flowering has a high water cost to the plant so during sub-optimal years plants with fewer reserves may conserve them by not flowering, or may simply be unable to bear the costs of flowering (Galen et al., 1999). Drought stress in other plant species negatively affects flowering but this typically increases again after renewed rainfall (Galen et al., 1999; Carroll et al., 2001; Harrison, 2001). There were spatial differences in flowering phenology across the Mt. Sinai massif, with up to 2-3 weeks difference amongst patches in 2011. The order of flowering

amongst patches was similar between years, suggesting that the spatial variation is controlled by localised topographic differences acting through microvariation in climate; for example aspect influences exposure to the sun, and hence the length of time available for photosynthesis (Gaston et al., 2004).

There is also evidence that the flowering here responds to macro-variation in the climate as the temporal variation is consistent in every patch across the massif. The 2012 flowering onset was later, but the flowering peak and culmination was earlier, condensing the flowering season; this is a response seen in other plants exposed to experimental warming (Sherry et al., 2007). Such temporal plasticity is predominately induced by temperature but can also be affected by other environmental factors such precipitation (Nord & Lynch, 2009; Matesanz et al., 2010; Cook et al., 2012). Plants show diverse responses to climatic variability, but generally in arid environments at high elevations flowering correlates with spring temperatures; cooler springs and drier conditions commonly delay flowering (Crimmins et al., 2010). A shorter flowering season accompanied with a lower density of inflorescences is a problem for associated herbivores such as the Sinai Baton Blue: 2012 had significantly fewer larval resources, and the shorter flowering period on an already narrow time frame when larvae and flowers are present could result in a population decline in 2013. If this window shrinks further, there will be increased chances of a phenological mismatch, especially as the butterfly flight season appears to be almost static between years (Chapter 3). The detrimental consequences of greater mortality and higher levels of competition for limited resources could easily increase the extinction risk (Visser & Holleman, 2001; Powell & Logan, 2005).

The butterfly's flight period did not show spatial or temporal variation, but the small population numbers in the majority of the patches coupled with low detectability may increase the relative error in the timings of the flight period. When comparing the three largest patches (Farsh Loza, Farsh Elia & Farsh Shoeib) the flight season appears to coincide with the flowering phenology of the plants; butterfly numbers peaked at a similar stage in flowering phenology, when the buds were large and flowers were starting to appear. One explanation could be that similar cues are used for eclosion and flowering, which would ensure synchrony. Eclosion cues are unknown

but presumably involve environmental variables such as soil moisture, temperature or photoperiod, which would also indicate the presence of buds and flowers (James, 2006f). However this seems unlikely due to the apparent asynchrony observed in Farsh Shoeib in 2010 (Chapter 3). The adult butterflies prefer to take nectar from thyme flowers, but if they eclose before the thyme flowers then they can forage from alternative species (James, 2006f). The search for alternative floral nectar sources might easily lead them out of the patches of thyme and into neighbouring patches or the surrounding matrix. Butterflies might then migrate into the patches once the thyme was flowering, explaining the apparent synchrony. The buds and flowers are the sole larval food, and there could be a higher rate of movement into patches once buds are present for oviposition (James, 2006d).

Ant community composition

The foraging range of *Lepisiota* spp. and *Crematogaster antaris* were mutually exclusive inside Farsh Shoeib in 2002 and 2010 with similar distributions in both years; *C. antaris* occupied the farsh (a wide open space) and *Lepisiota* spp. the gully (Shepherd, 2010). The cause of the separation is unclear: James (2006b) suggested competitive displacement whilst Shepherd (2010) suggested that differences in habitat preference were a more likely explanation. When looking at the foraging ranges across the massif, including the data collected from Farsh Shoeib by Shepherd (2010), it is possible to get a clearer picture of the distribution. *Crematogaster antaris* and *Lepisiota* species remain mutually exclusive, with absolutely no overlap in foraging ranges. In the three patches with both *Crematogaster* and *Lepisiota* (Loza, Elia and Shoeib), the ants foraged in separate sections of each site with considerable distance between their ranges. *Crematogaster antaris* was present in four of the ten patches on the massif, in all of which they only occupied the farsh. *Lepisiota* spp. were found in five patches including the gulley of three: within Shoeib, where the farsh was occupied by *C. antaris*; in Gulley Zahtuna, which did not contain a farsh; and in Lower Hammar, where they also occupied the adjacent farsh. In the two remaining patches *Lepisiota* foraged within the farsh. The presence of *Lepisiota* spp. within the farsh suggests that exclusivity may not be due to habitat preference differences: the lack of overlap indicates that ant distributions may be controlled by dominance

relationships. *Crematogaster* may competitively exclude *Lepisiota* from farshes, and only where *Crematogaster* is absent can *Lepisiota* forage there. A further possibility is the coloniser effect, where the first species to arrive colonises the area and becomes dominant, excluding other species; a founder-controlled community (Campos et al., 2007).

Sinai Baton Blue distribution across the Mt. Sinai massif

In 2012 the numbers of butterflies nearly doubled inside Farsh Shoeib, but numbers in other patches crashed, with fewer than a third of individuals in the remaining patches compared to 2011. This suggests that the Sinai Baton Blue might exist as separate populations on the massif with asynchronous cycles. The butterfly population in Farsh Shoeib appears to have crashed to very low numbers repeatedly over the past decade (Chapter 2). If these are more-or-less separate populations existing as a metapopulation, then asynchrony will help limit simultaneous extinctions via dispersal from neighbouring patches, extending the longevity of the metapopulation (Pandit et al., 2013). Despite the apparent crashes in numbers, butterflies in Farsh Elia and Farsh Loza remained the second- and third-largest on the massif.

Here I assessed the butterfly's habitat requirements and modelled its relative abundance using variables expressing the metapopulation structure (i.e. connectivity), habitat quality and resource area (i.e. number of inflorescences) and I found that the total resource area, the abundance of the host plant and the presence of beneficial ants all positively influenced the abundance of the Sinai Baton Blue. The resource area within the patch was identified by James et al. (2003) as a critical factor for occupancy, with other contributing factors including isolation and the quantity of alternative adult food sources. James et al. (2003) suggested that shelter may be another important feature of patch occupancy, perhaps because of the butterfly's low mobility and the frequent strong winds in the area. However, there were very few individuals in the very sheltered Gulley Zahtuna or Gulley Sharr patches, suggesting that shelter may not be an important factor.

In 2011 more than half of the butterflies were observed in Farsh Shoeib, and nearly 80% in the three patches with the largest resource areas on the

massif. None were seen in Farsh Safsafa, the smallest patch. There may be a minimum resource area required to support a population. Furthermore, there is a positive correlation between the numbers of thyme plants and butterfly sightings. Females apparently lay about 26 eggs singly upon inflorescences across multiple thyme plants, choosing plants with fewer than six larvae to reduce intraspecific competition (James, 2006f). This implies that females need a large number of plants to avoid larval over-crowding and to enhance reproductive success. The quantity of larval host plants has been found to play a significant role in other butterfly species too (Thomas et al., 2011).

Connectivity does not appear to affect numbers. This is perhaps unsurprising in such a relatively sedentary species: the best estimate from earlier work was that a maximum of 13-14% of butterflies move among patches in any one year, based on work in just one patch, Farsh Shoeib (James, 2006e). Movers appear to be concentrated in early and late-appearing individuals (James, 2006e). Thus probably only a few butterflies move around patches on the massif: very few butterflies were seen around plants in the connecting 'corridors'. The major role of plant condition and numbers in influencing butterfly numbers, coupled with lack of evidence that promoting movements would be useful, suggests that conservation should be focused on enhancing the quality and condition of the host plants. We cannot rule out the effect of patch isolation on metapopulation dynamics, because this study only examines abundances on a local scale, within a 1-km radius in some but by no means all the patches where the butterfly exists. Isolation may play a greater role on a larger scale, but equally well all patches on the massif could really constitute a single population. However, this seems unlikely because I observed a boom in one large patch (Farsh Shoeib) whilst the remaining patch populations apparently crashed. Other butterfly studies have found that habitat quality and condition are key determinants of population size (Krauss et al., 2003; Sanford et al., 2011; Williams, 2011), with connectivity a less important factor. Isolation often plays a significant role in population persistence, but its effect on populations is frequently less than that of habitat area and quality (Thomas et al., 2001; Hodgson et al., 2011). Habitat area, quality and connectivity are not mutually exclusive; increasing patch area would decrease inter-patch distance, increasing connectivity; by enhancing

populations through increased habitat quality and area, the number of dispersers and connectivity would also increase.

It is essential to understand what drives changes in the abundance of the Sinai Baton Blue. This study suggests that the number and quality of host plants are paramount. The strength of the associations between habitat quality, patch isolation and population dynamics varies amongst species, but my results indicate that conserving the Sinai Baton Blue should focus on enhancing the quantity and vitality of the thyme within patches.

Table 4.1. Scoring of flowering phenology scale (from James, 2006e).

Phenological score	Appearance of plant
0	100% pre-bud
1	sepals visible, buds not yet visible
2	sepals apparent, buds starting to develop
3	large buds but fewer than 2 flowers open
4	50-90% buds, 10-50% flowers open
5	1-50% buds, 50-100% flowers open
6	1-50% flowers over/seed heads
7	more than 50% flowers over/seed heads

Table 4.2. Patch characteristics across the Mt Sinai massif, indicating the number of thyme plants, total resource area per patch, distance to nearest source patch and number of different ant species per patch in 2011. *The ant data in Farsh Shoeib are from Shepherd (2010).

Patch	Number of thyme plants	Total resource area (m²)	Distance to nearest source patch (NS$_i$)	Number of ant species
Farsh Shoeib	659	54.8	350	6*
Farsh Loza	263	31.7	38	6
Gulley Zahtuna	203	18.9	38	4
Farsh Elia	558	20.1	38	7
Elia Garden	218	17.0	67	3
Gulley Sharr	151	9.5	38	5
Upper Hammar	144	6.9	39	4
Lower Hammar	163	6.8	39	5
Elia Circle	74	4.2	67	2
Safsafa	37	3.9	203	6

Table 4.3. Number of transects with sightings of Sinai Baton Blues and total number of butterflies seen in each of the named patches of Sinai Thyme on Safsafa over an 11-week period. 22 transects were carried out in 2011 and 21 in 2012.

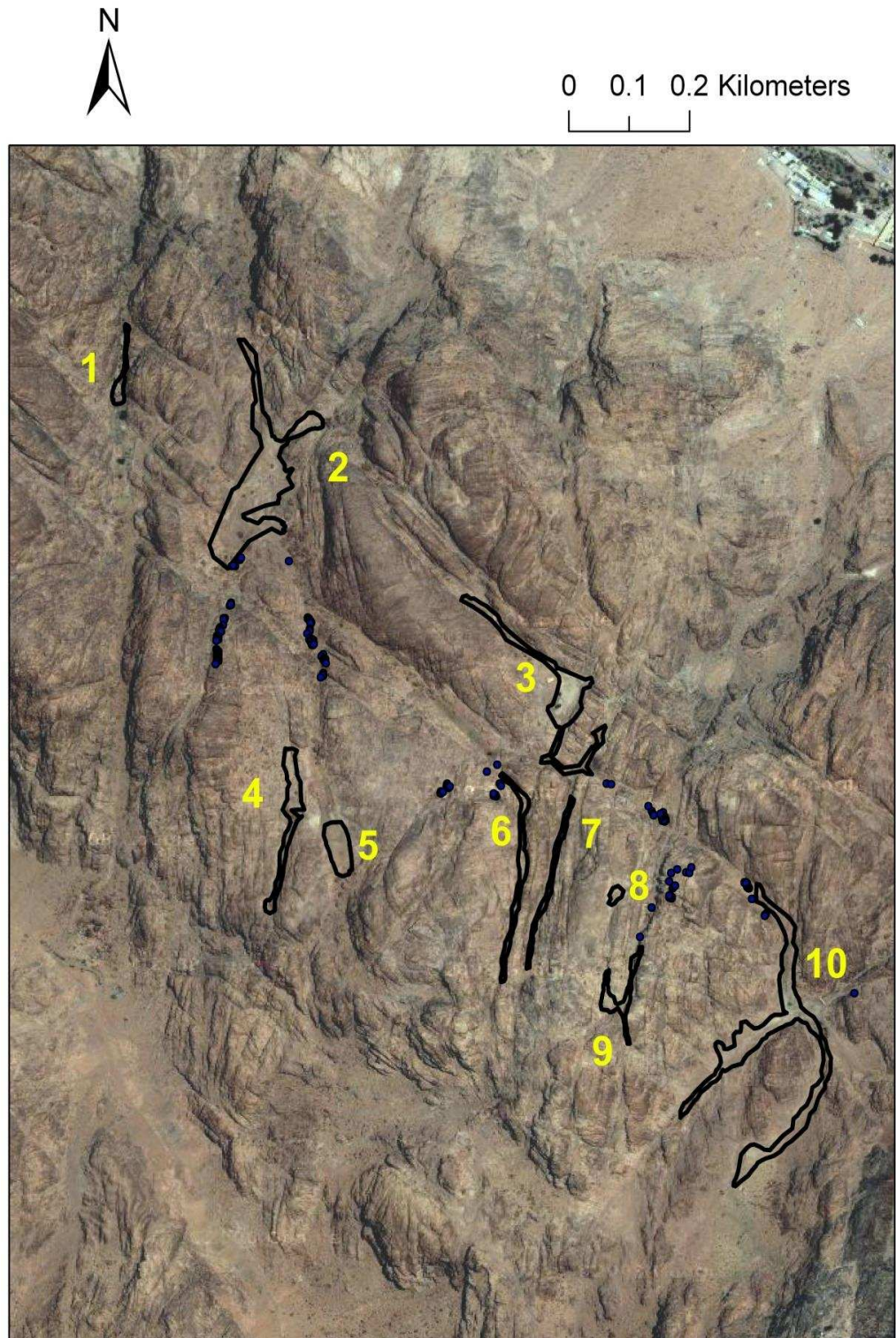| Patch	Transects with butterflies		Total number of butterflies	
	2011	2012	2011	2012
Farsh Shoeib	21	18	112	200
Farsh Loza	11	6	21	8
Gulley Zahtuna	6	3	16	3
Farsh Elia	11	6	23	9
Elia Garden	5	2	8	2
Gulley Sharr	2	0	5	0
Upper Hammar	2	2	2	2
Lower Hammar	4	2	9	2
Elia Garden	5	2	8	2
Elia Circle	1	0	1	0
Safsafa	0	0	0	0

Figure 4.1. Map of the perimeter of the Sinai thyme (*Thymus decussatus*) patches upon the Mount Sinai massif, with the blue dots indicating isolated individuals outside patches. 1) Farsh Safsafa 2) Farsh Shoeib 3) Farsh Loza 4) Lower Hammar 5) Upper Hammar 6) Gulley Zahtuna 7) Gulley Sharr 8) Elia Circle 9) Elia Garden 10) Farsh Elia. The Monastery of St Katherine is seen in the top right of the map.
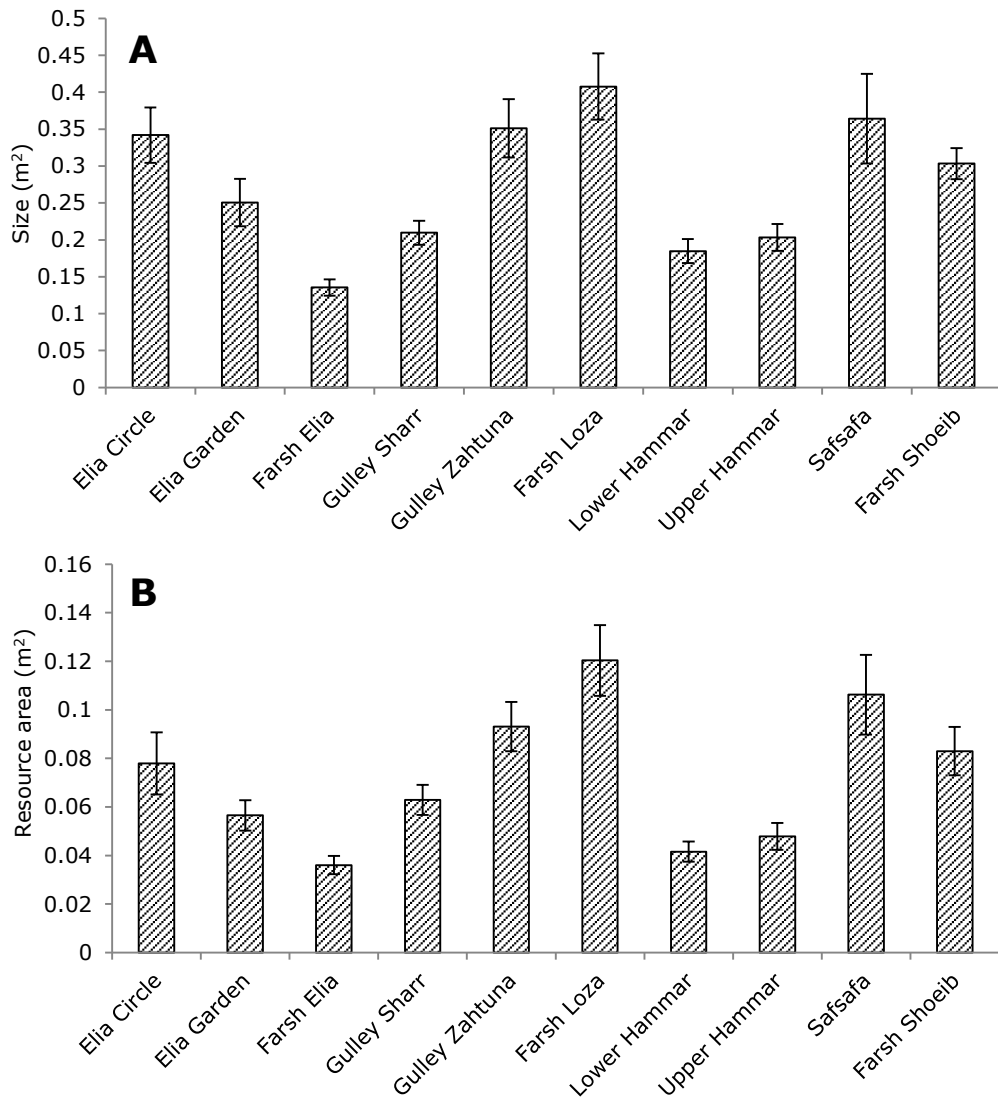
Figure 4.2. Comparisons of a) the size and b) resource area per plant in the patches of Sinai Thyme (*Thymus decussatus*) on the Mt Sinai massif in 2011. Mean values ± SE.

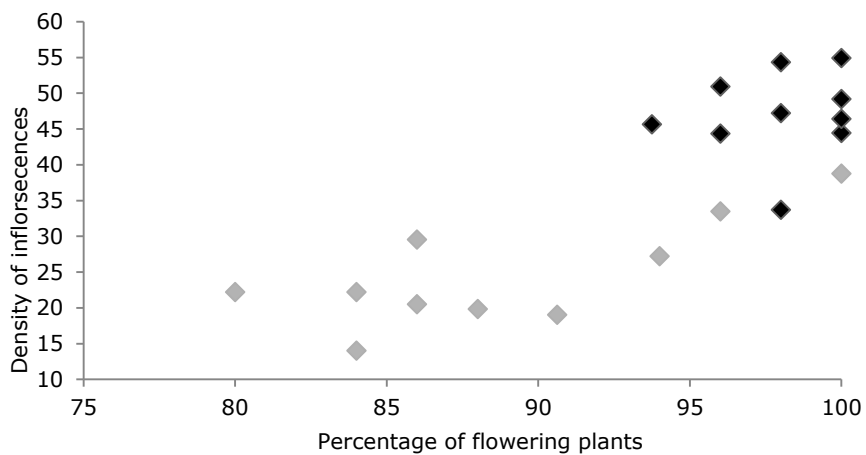**Figure 4.3.** Scatterplot of the proportion of plants flowering in a patch and the average density of inflorescences (per 10 cm^2) in 2011 (black) and 2012 (grey).
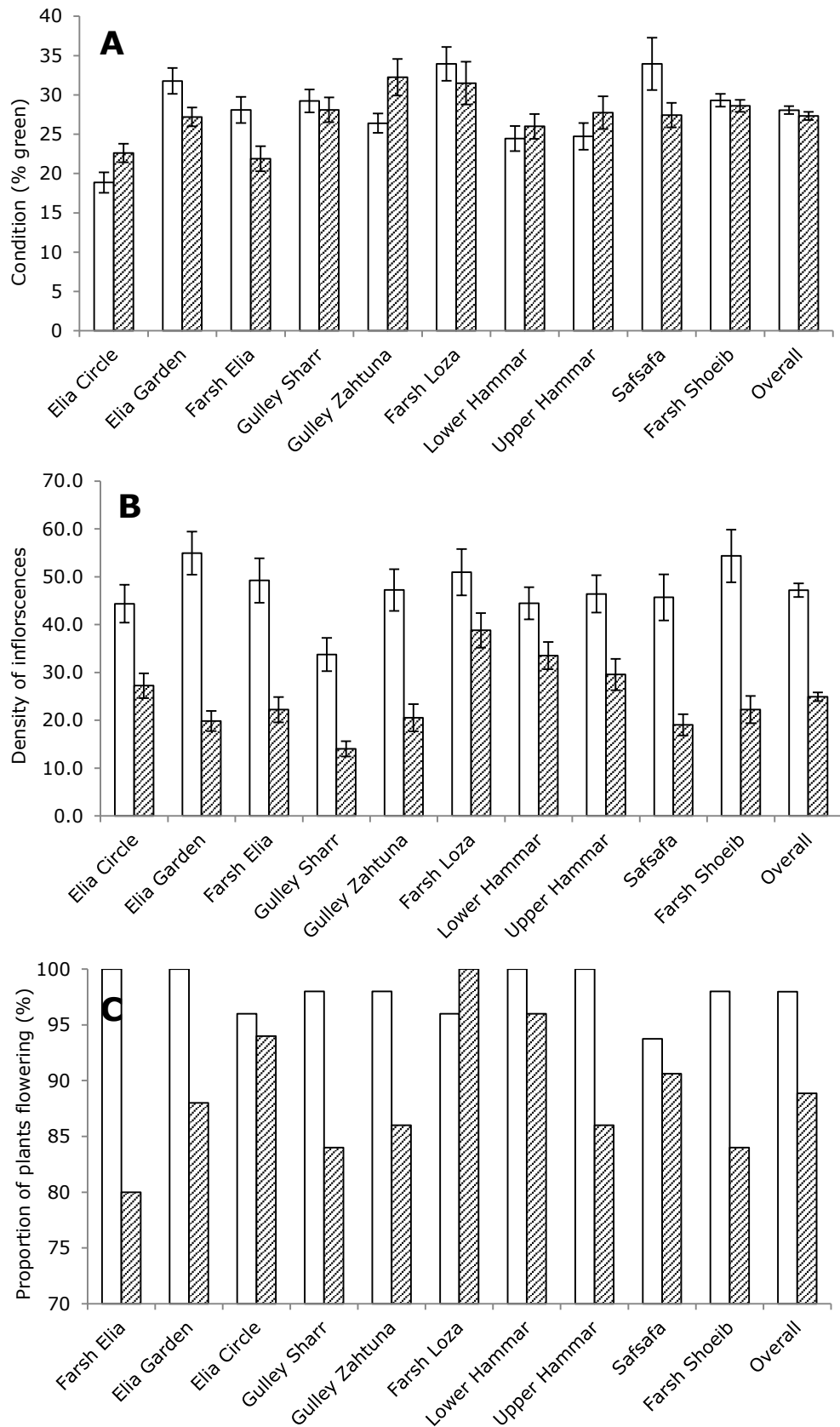
Figure 4.4. Comparison of measured aspects of plant quality in *Thymus decussatus* on the Mt. Sinai massif in 2011 (white bars) and 2012 (striped bars): a) condition b) density of inflorescences c) proportion of flowering plants. Mean values ± SE.
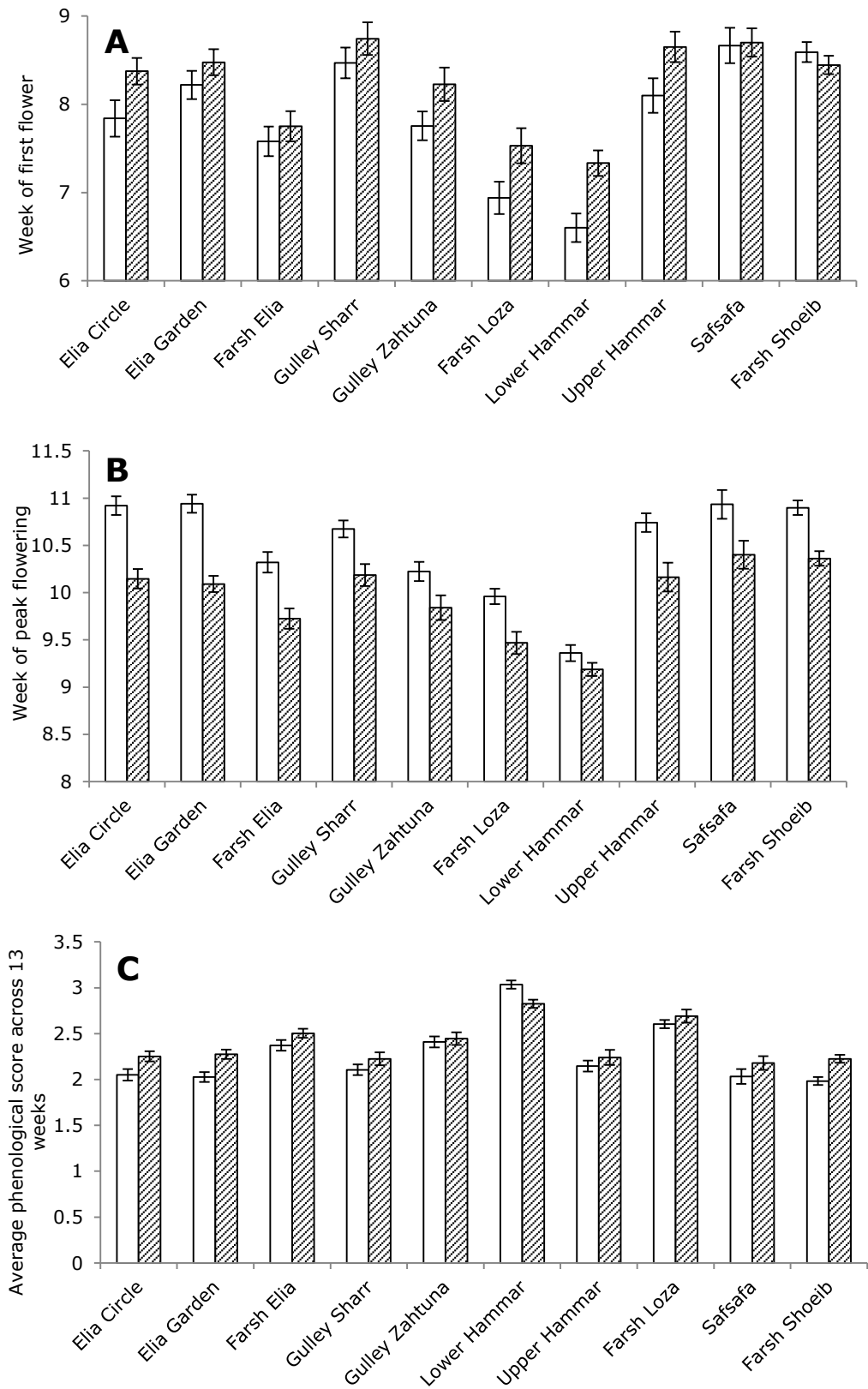
Figure 4.5. Comparisons of the phenology of *Thymus decussatus* on the Mt. Sinai massif showing the a) week of first flower b) week of peak flowers and c) average score across 13 weeks (start of April until end of June) in 2011 (white bars) and 2012 (striped) . Mean ± SE.
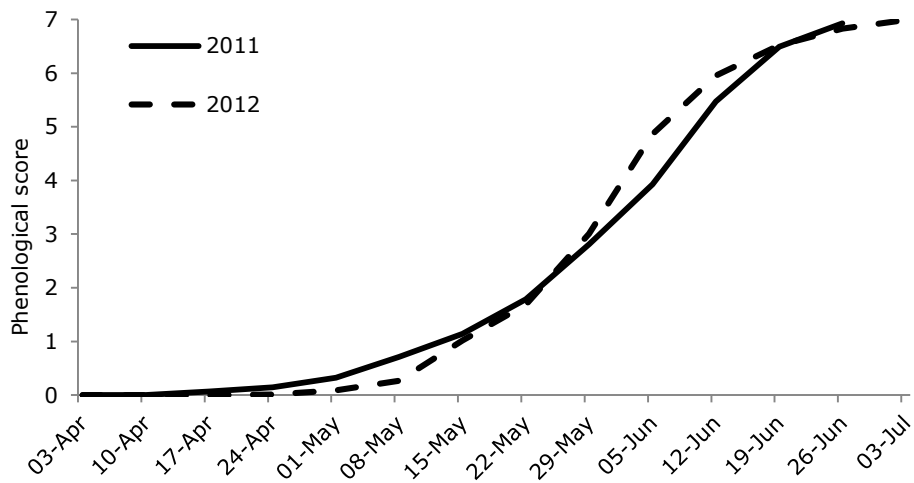
Figure 4.6. Average phenology scores on the Mt. Sinai massif in 2011 (solid line) and 2012 (dashed line).
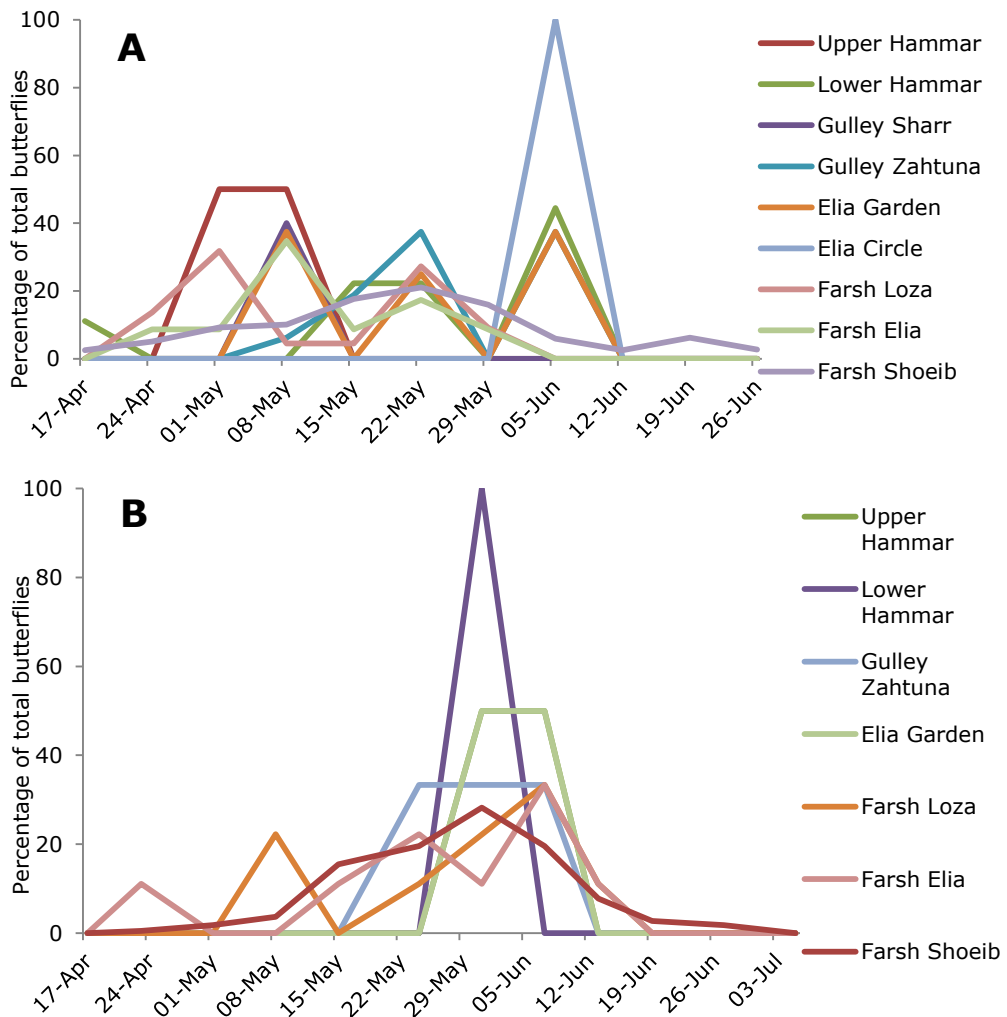
Figure 4.7. The flight seasons of the Sinai Baton Blue in a) 2011 & b) 2012. It shows the percentage of butterflies seen per week in comparison to the total patch sightings. *Excluding the patches without sightings.
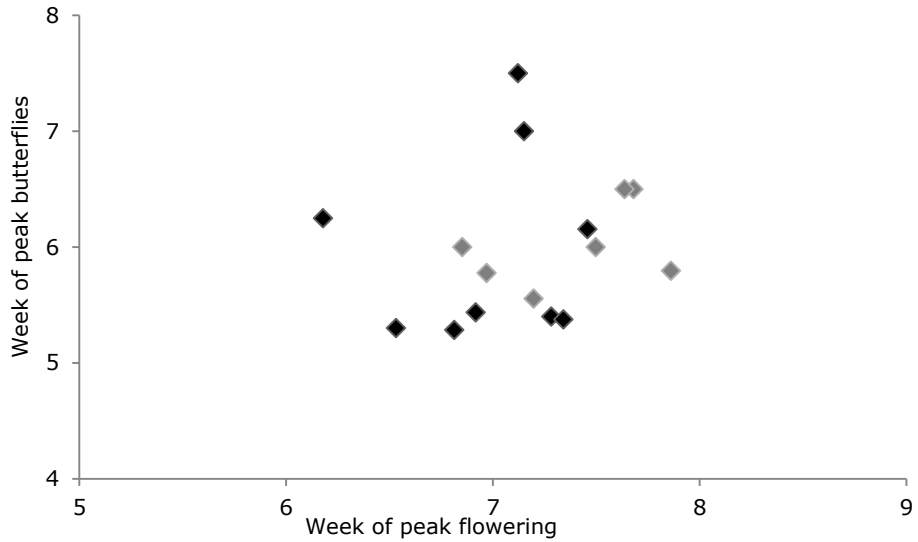
Figure 4.8. Weighted averages of the week of peak flowering and peak butterfly sightings in 2011 (black) and 2012 (grey). *Excluding patches without any butterfly sightings.
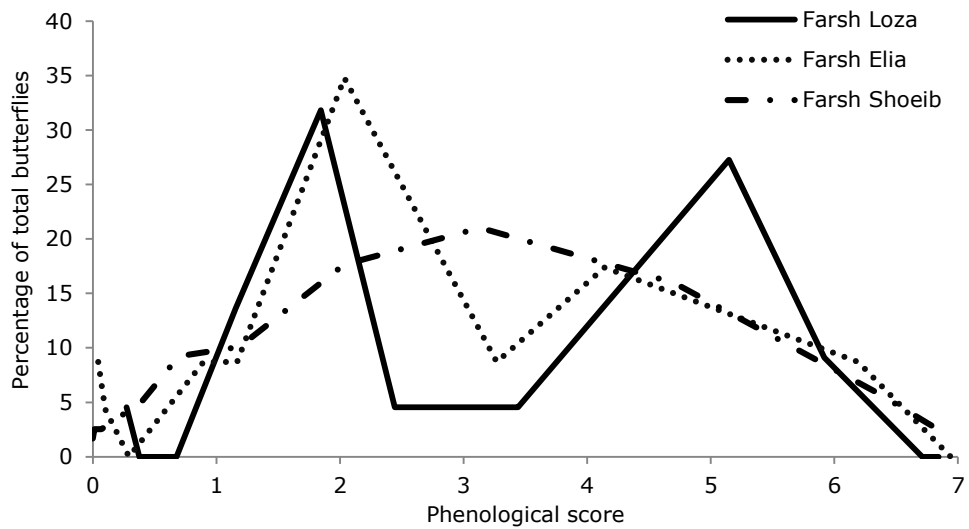
Figure 4.9. The weekly number (expressed as a percentage of the total seen in each site) of Sinai Baton Blues in Farsh Loza, Elia and Shoeib in 2011 compared to the average weekly phenological score in each patch.
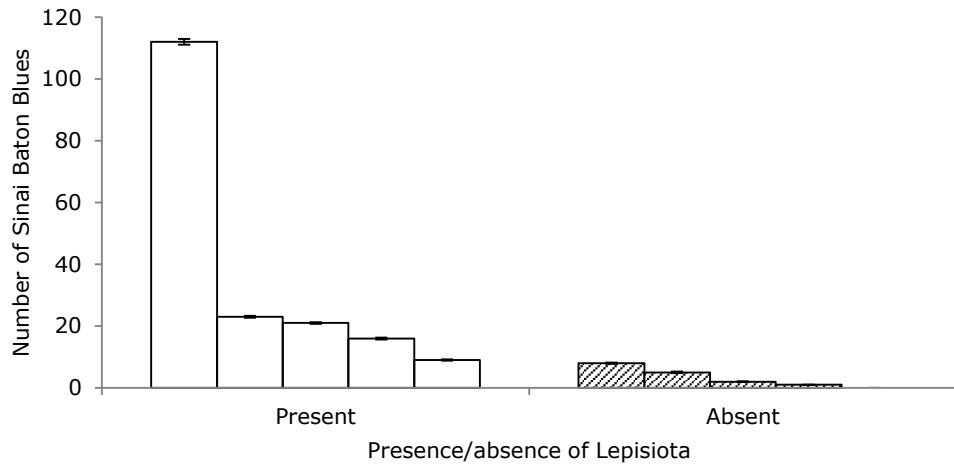
Figure 4.10. The population sizes of Sinai Baton Blues in the separate patches in 2011 either in the presence (white) or absence (striped) of the attendant *Lepisiota* species.
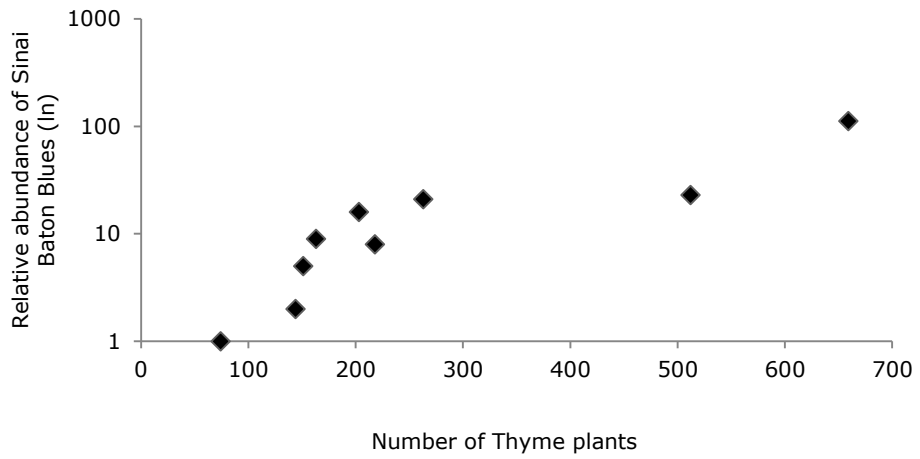
Figure 4.11. The logged abundance of Sinai Baton Blues and the number of thyme plants in 2011.
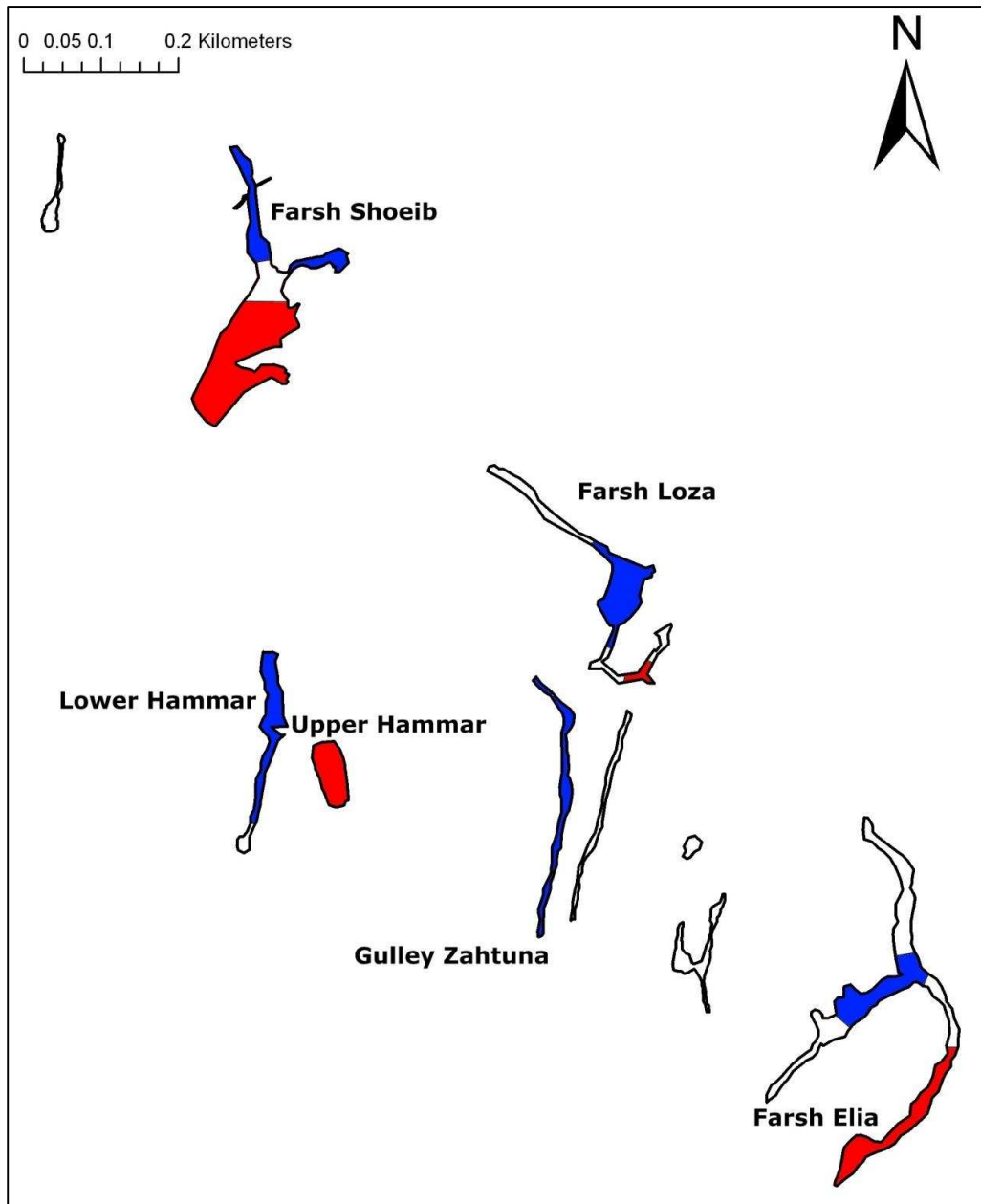
Figure 4.12. The distribution of *Crematogaster antaris* and *Lepisiota* spp. on the Mt. Sinai massif. The blue illustrates the range of the attendant *Lepisiota* spp., whilst the red shows the predatory *Crematogaster antaris*. The data for Farsh Shoeib are from Shepherd (2010).

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Chapter 5.

Plant quality governs the larval distribution of the Critically Endangered Sinai Baton Blue butterfly (*Pseudophilotes sinaicus*)

The larva tended by two *Lepisiota* ants

Plant quality governs the larval distribution of the Critically Endangered Sinai Baton Blue butterfly (*Pseudophilotes sinaicus*)

Abstract

The larval distribution of herbivorous insects play an important role in their development and hence future fitness. Here we study larval distribution of the critically endangered Sinai Baton Blue butterfly, *Pseudophilotes sinaicus*, who feed exclusively on the buds and flowers of the also endangered Sinai Thyme, *Thymus decussatus*. The study was carried out in 2009 where we looked at the larval distribution over 131 plants, recording the size, quality and phenological stage of the plants along with the presence of beneficiaries. Using linear mixed models we found that the larval distribution was non-random; larvae were found on plants with a high number of flowers, a relatively advanced flowering phenology and the presence of tending ants. This highlights the importance of the vitality and quality of the thyme, as the resource level influences the larvae's spatial distribution. A migratory polyphagous moth, *Heliothis peltigera*, larvae were also found feeding on the thyme, but large size appeared to be the only selection criterion.

Introduction

Resource availability in arid environments is primarily governed by water (Pueyo et al., 2008) and spatial variation in rainfall and the subsequent soil moisture plays a large role in determining plant quality and abundance and hence resource levels (Reynolds et al., 2004). Abiotic and biotic conditions can vary across a localised spatial scale and as a consequence this will impact the realised species niche of associated herbivores (Anthes et al., 2008). Population density of many butterfly species is primarily determined by the quality and condition of the host plant (Thomas et al., 2011). Insect herbivores utilise different host plant characteristics depending upon their developmental stage and the availability of resources in turn influence survivorship (Hellmann, 2002). A critical driver for population size and persistence is the availability of suitable sites for larval development, as mortality at this stage can govern population dynamics, with either explosive growth when there are an abundance of resources or

potential extinction if mortality rates are too high (Ehrlich & Hanski, 2004; Thomas et al., 2011). Adequate feeding at the larval stage is essential for future fitness. Starvation, even just over a short period, affects larval growth and development; small larvae develop into small adults with lower fecundity and reduced survival (Boggs & Freeman, 2005; Bauerfeind & Fischer, 2009).

Many butterfly species are constrained to a single genus or species of host plant (Dennis et al., 2004) and variation in host plant quality can leave some plants incompatible for larval development (Singer & Lee, 2000). This will result in spatial variation in respect to occupied larval host plants (Roy & Thomas, 2003) with varying conditions enhancing larval development (Davies et al., 2006). Micro-climate characteristics play an important role in successful offspring development, with variation in temperature and photoperiod preventing desiccation in arid environments (Weiss et al. 1988; Anthes et al. 2008). Larvae frequently have a narrower habitat range than the adult stage (Warren, 1987) and often it is essential to identify suitable habitat in order to successfully conserve rare and endangered butterflies, such as the Heath Fritillary (*Melitaea athalia*: Nymphalidae) (Warren, 1987; Thomas et al., 2011).

Due to the vital role of larval habitats, I am looking into larval distribution of the Critically Endangered Sinai Baton Blue butterfly, *Pseudophilotes sinaicus*, to see which host plant characteristics govern its spatial spread. This study was carried out patch level to see which conditions are necessary for larval development.

Materials & Methods

The study system

The Sinai Baton Blue butterfly (*Pseudophilotes sinaicus* Nakamura 1975) has a narrowly endemic distribution localised to the St Katherine Protectorate in South Sinai. It was the subject of a 3-yr study by James (2006a-f). It is Critically Endangered, with the total 2001 population estimated at less than 3000 adults, and an Extent of Occurrence of less than 7 km^2 (Thompson & Gilbert, 2012). Because of its status as one of

only three animal species endemic to Egypt, and one of two endemic to the St Katherine Protectorate (the other is the Sinai Hairstreak *Satyrium jebelia* Nakamura 1975), it is not possible to obtain permission for manipulative experiments and I have had to rely only on observational data.

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

The study site was Farsh Shoeib (Fig. 5.1), a flat open area within the arid rocky mountains where a patch of thyme plants had one of the largest populations of Sinai Baton Blues in 2001 (James et al., 2003). Farsh Shoeib is near the summit of Gebel Safsafa on the Mt. Sinai massif, close to the town of St Katherine in South Sinai, at an altitude of approximately 1950 m above sea level. It has an area of 14,000 m^2, containing 669 thyme plants in 2010. The majority of the patch has been fenced off as a conservation effort to prevent public access, grazing and any damage to the plants, with

only a few plants of the patch found outside the enclosure. The fieldwork was carried out from March until late June 2010. The main flight period typically lasts from the start of May to mid-June.

Fieldwork

Detailed larval counts were made on thyme plants in Farsh Shoeib. The majority of butterfly sightings in the patch were within the main gulley (Fig. 5.1) outside the foraging range of colonies of the predatory *Crematogaster antaris*, which only forage in wide open spaces. It is a section of the site containing 148 thyme plants, 131 of which were searched thoroughly once a week. For each plant, the number of Sinai Baton Blue larvae, flowering phenology and the number of flowers present were recorded weekly. Flowering phenology was recorded according to a 0-7 scale (Table 5.1). Five randomly selected inflorescences from the most advanced flowering area of the plant were scored and averaged to get the phenological status for each plant at that time. The height (m), two perpendicular widths (m) and condition (percentage green) of each plant were recorded in the field once before the beginning of the adult flight season, and later the resource area (m^2, assuming an ellipsoidal shape for the plant) calculated from these measurements.

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

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

Two weeks before the first Sinai Baton Blue larva was seen, at the start of the thyme's flowering season, another green caterpillar was found feeding

upon the buds and flowers of the thyme. Until now there have been no previous records of any other larvae feeding upon Sinai Thyme. This species was later identified as *Heliothis peltigera* (Denis & Schiffermüller, 1775)(Noctuidae), confirmed by Dr. Luigi Sannino (Consiglio per la Ricerca e Sperimentazione i Agricoltura, Italy). *Heliothis peltigera* is a polyphagous migratory pest with a widespread distribution across South and Central Europe, the Middle East, Africa, India and Israel (Manjunath, 1976). 2010 was a huge migration year for this and many other Lepidoptera. It was possible to categorize these larvae into three size classes, and hence approximate survival rates could be calculated by comparing the number of larvae in different size classes through time.

Analysis of data

ArcGIS 9.3 was used to map plants and observations. All analysis used the statistical package R 2.14.1 (R Development Core Team, 2012) to assess the predictability of larval distribution from characteristics of the thyme plants. Models were simplified in accordance to Zuur et al. (2009). I ran linear mixed models (*lmer* from the *lme4* package) using the individual plant identity as the random factor and two response variables: the presence/absence of larvae, and larval counts for plants in the gulley. The error structures for the presence/absence of both the Sinai Baton Blue and *Heliothis peltigera* larvae were binomially distributed, whilst a Poisson model was used for the larval counts of both species. I simplified the full model based on the AIC criterion using stepwise backwards deletion of model terms and significance was assessed with a χ^2 test.

Results

In the main gulley a total of 64 Sinai Baton Blue larvae were found, but on just 33 plants, i.e. only 24% of those available. On plants with larvae, there were an average of 1.6 larvae found per visit, with no more than six on a plant at one time. The distribution of larvae was scattered across the gulley, with few larvae found in the southern and northern sections and the majority located in the central plant cluster (Fig. 5.4), on plants with high numbers of flowers and with *Lepisiota*. *Lepisiota* species were not found in the southern section of the gulley which may have influenced the lack of

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

Plants with larvae had on average more flowers (χ^2= 6.64, df=1, p<0.001) (Fig. 5.2a), a higher phenological score (χ^2=24.0, df=1, p<0.001; Fig. 5.2b) and were more likely to have *Lepisiota* ants (χ^2=13.8, df=1, p<0.001), compared with plants with no larvae detected. The phenological state of the plants was the most influential predictor of presence/absence of larvae (i.e. it had the greatest change in deviance upon deletion from the model); plants with larvae were more advanced in seasonal development than those that did not have larvae. The presence of a tending ant species and the number of flowers on the thyme plant were both strongly significant predictors of larval distribution. No larvae were ever found on a thyme plant without either of the *Lepisiota* species. There was no evidence that height, width, condition or resource area affected whether a plant had *Pseudophilotes* larvae.

Phenology was again the most significant predictor of the number of larvae, with more larvae on plants with an advanced phenological score (χ^2= 30.7, df=1, p<0.001). The number of flowers (χ^2= 21.1, df=1, p<0.001)(Fig. 5.3), and *Lepisiota* presence (χ^2= 17.5, df=1, p<0.001) were again significant predictors. The height, width, condition and resource area, again had no significant effect on how many larvae were on the plant.

Heliothis peltigera were abundant throughout the entire patch, with 432 individuals found in the main gulley, in comparison to the 63 Sinai Baton Blue larvae. The majority of *H. peltigera* were found before the first Sinai Baton Blue larva was discovered (Fig. 5.5). They were abundant before all the plants had all of their flowers open, and were seen feeding upon the buds before the flowers were fully in bloom. They peaked in numbers during the main flowering season, when the majority of the flower heads were open (Fig. 5.5). These larvae may have been able to move between plants because they were significantly larger in size than those of the Sinai Baton Blue, and considerably more mobile whilst moving around the plant. The apparent survival rate of *Heliothis* from small- to medium-sized larvae was 24.3%, whilst that from medium- to large-sized larvae was more than

double at 66.2%, suggesting that larger larvae have a higher survival rate. The overall survival rate from small to large larvae was 16%. The survival rate of medium- to large-sized larvae may be underestimated because some categorized as 'medium' may have pupated during the week, thus appearing to have died. The extent to which these values may reflect movement among plants is unknown.

Heliothis peltigera and Sinai Baton Blue larvae were rarely found together on a plant at the same time (17% of the recordings of the Sinai Baton Blue larvae concurrently recorded *H. peltigera*) but no interactions were seen between the two species. *Heliothis* larvae were never seen to be tended by any ant species, but elsewhere on the site they were also found on plants within the foraging range of *Crematogaster antaris*, possibly indicating that this ant does not prey on it.

For presence/absence of *Heliothis peltigera*, the width of the plant was the only significant predictor of the distribution of the larvae; wider plants were more likely to contain larvae (χ^2 =46.8, df=1, p<0.001)(Fig. 5.6). There was no evidence that the characteristics found to influence Sinai Baton Blue distribution (the presence of either *Lepisiota* species, phenology and number of flowers) affected the distribution of *H. peltigera* larvae. For counts of the *Heliothis peltigera* as the response variable, plant width was again the only significant factor for the number of larvae (χ^2= 45.6, df=1, p<0.001).

Discussion

This study highlights the importance of the vitality of the host plant for the Sinai Baton Blue larvae, as the number of flowers and hence resource level influences the larvae's spatial distribution. There were more larvae on plants with a high number of flowers, an advanced phenological stage and with tending ant species, *Lepisiota obtusa* and *Lepisiota hirsuta*. The larvae's distribution is suited to maximise fitness, as there would be an expected lower larval mortality rate where there more resources (Boggs & Freeman, 2005) and the presence of beneficiaries (Berenbaum & Feeny, 2008). The first two instars feed exclusively upon the buds, with the later stages feeding upon the flowers (James, 2006b); thus it makes sense that

the number of flowers influences the larval distribution (James, 2006f; Berenbaum & Feeny, 2008). Arid environments are predominately resource limited, and are often governed by bottom up forces through herbivorous competition (Schwinning et al., 2004; Letnic & Dickman, 2010). Where insect larvae have reduced resources, the resulting adults are generally smaller in size and tend to have a lower survival rate and reduced fecundity (Gibbs et al., 2004; Boggs & Freeman, 2005).

The average number of larvae found on a plant was just below two, very similar to that found previously by James (2006f) in 2001. Intraspecific competition reduces food resources, leading to longer development and reduced survivorship, or it could lead to density-dependent mortality from threats such as predators or parasitoids (Gibbs et al., 2004; Sato et al., 2004; Strausz et al., 2012) and hence this spatial distribution may increase offspring survival. There appears to be microsite selection within Farsh Shoeib, with the majority of the larvae found in the central cluster of plants: this could be due to climatic factors such as variation in photoperiod or temperature (Strausz et al., 2012).

There was an interesting difference in host plant effects between the generalist (*H. peltigera*) and specialist (*P. sinaicus*). The distribution of *H. peltigera* larvae was only significantly affected by plant size (width) and was not restricted to plants of a higher vitality or the presence of beneficiaries. The moth larvae were seen feeding upon leaves and not just the buds of the thyme which may explain the difference in the relationship between the migratory moth larvae and host plant, with larger plants representing more resources. We know nothing about any possible interactions between *H. peltigera* and ants, but these are unlikely. Appeasement is common in interactions between lycaenid larvae and ants, but not with other Lepidoptera (Pierce et al., 2002). It is possible that the abundant and earlier occurrence of *H. peltigera* larvae on thyme may perhaps have increased mortality in the Sinai Baton Blue larvae. Increases in larval density do seem to reduce survival (James, 2006f). Since in 2010 the larvae of both species were feeding on the same resource, a number of outcomes is possible, the most likely being reductions in growth and survival rate (Sato et al., 2004).

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

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

Facultative ant species may be used as cues because they can signal the presence of enemy-free space. This would be the situation here since the attendant ant *Lepisiota* spp. has a mutually exclusive distribution in relation to the predatory *Crematogaster* (James, 2006b). Therefore the presence of *Lepisiota* would signal to a gravid female the absence of *Crematogaster*, and therefore enemy-free space. For ants to be good cues they need to have a consistent foraging range and consistently to occupy the same individual plants. *Lepisiota* spp appeared to consistently forage

on the same plants, with the surveys noting similar foraging patterns across multiple weeks (indeed, across many years too: Shepherd, 2010).

Overall, this study has highlighted the importance of the density of flowers and hence the quality of host plant in determining the Sinai Baton Blue's larval distribution in this arid environment. The thyme is already a limited resource, currently in relatively poor condition (Chapter 2), so further conservation work needs to be carried out on improving the quantity and quality of the host plants, and thus the number of inflorescences to ensure there are sufficient resources for the butterfly to complete its life cycle.

Table 5.1. The way flowering phenology was scored (from James, 2006e).

Phenological score	Appearance of plant
0	100% pre bud
1	sepals visible, buds not yet visible
2	sepals apparent, buds starting to develop
3	large buds <2 flowers open
4	50-90% buds, 10-50% flowers open
5	1-50% buds, 50-100% flowers open
6	1-50% flowers over/seed heads
7	>50% flowers over/seed heads

Figure 5.1. Map of Farsh Shoeib upon the Mount Sinai massif.
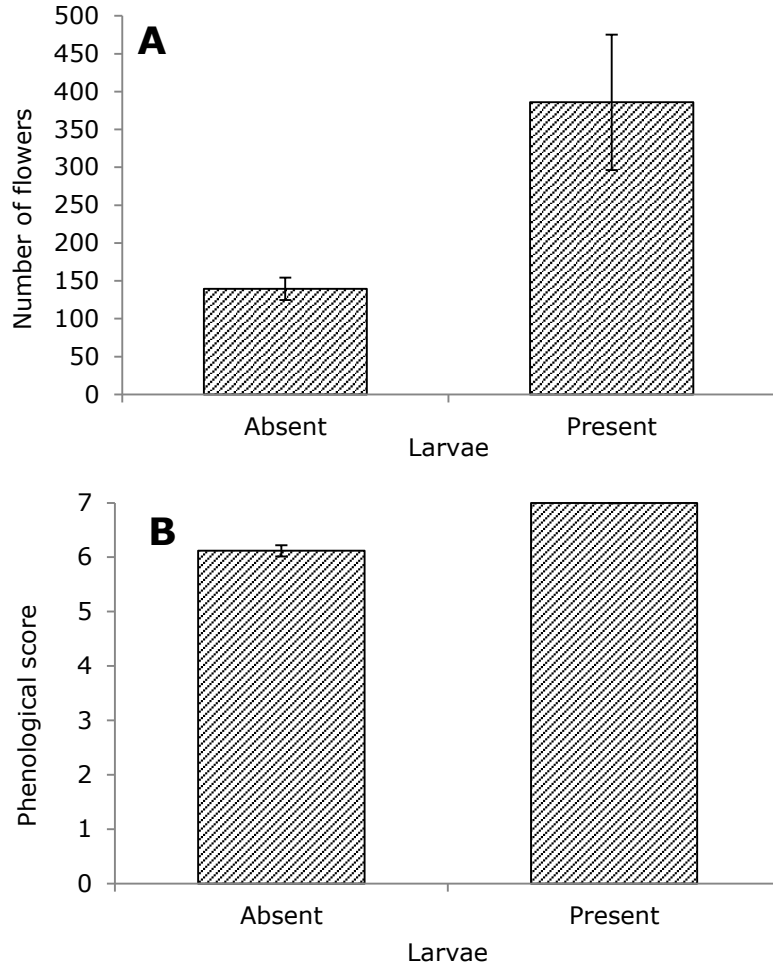
Figure 5.2. Differences between a) the number of flowers and b) the phenological scores of thyme plants (n = 131) where Sinai Baton Blue larvae were present or absent. Mean values ± SE.
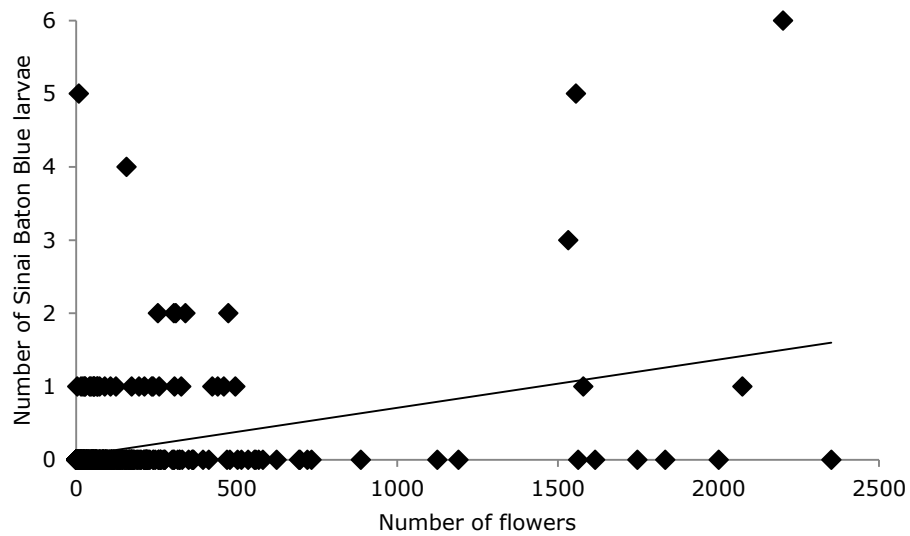
Figure 5.3. The relationship between the number of Sinai Baton Blue larvae and the number of flowers for the plants (n = 131) in the main gulley.
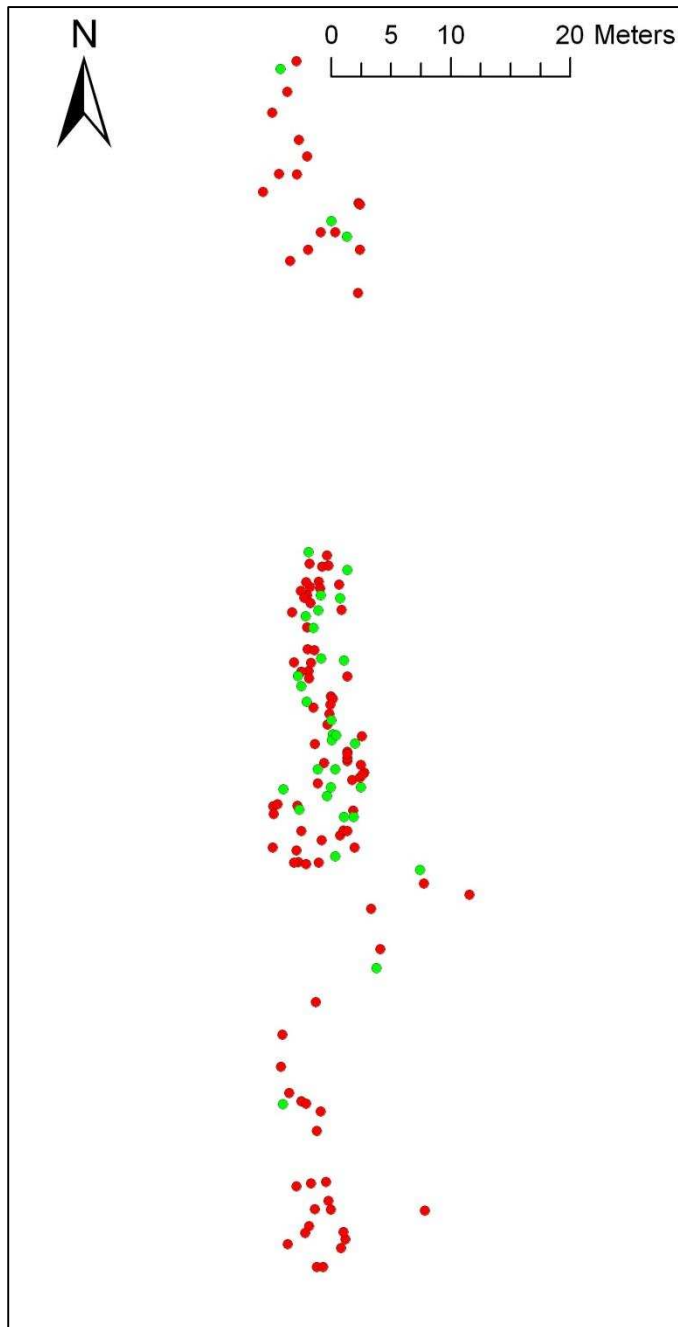
Figure 5.4. The distribution of the Sinai Baton Blue larvae in the main gulley. Red circles indicate thyme plants without larvae; green circles indicate plants where larvae were found.
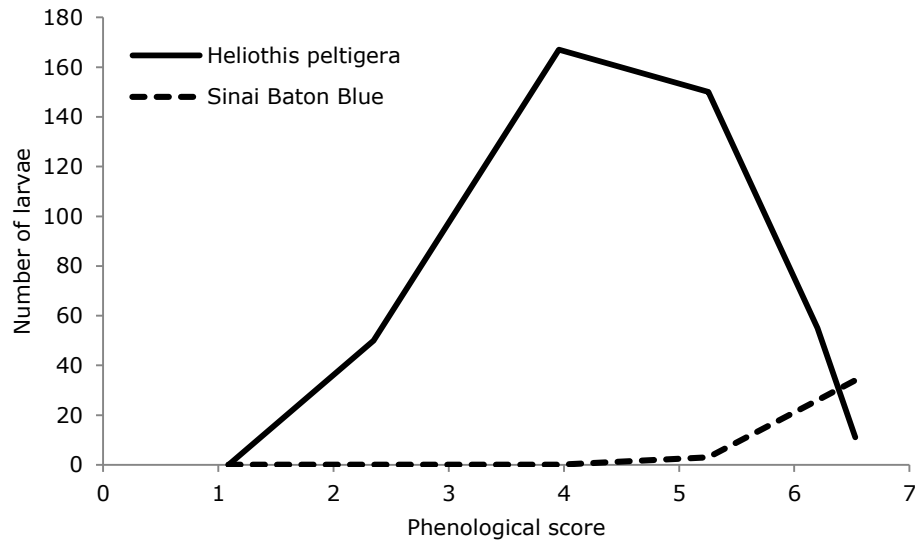
Figure 5.5. The number of Sinai Baton Blue (dashed line) and *Heliothis peltigera* larvae (solid line) and the phenology of plants.

Heliothis peltigera larvae

Figure 5.6. Comparison of the width of the plants with and without *Heliothis peltigera* larvae. Mean values ± SE.

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Craig, T. & Itami, J. 2008. Evolution of preference and performance relationships. *In:* Tilmon, K. (ed.) *Specialization, speciation, a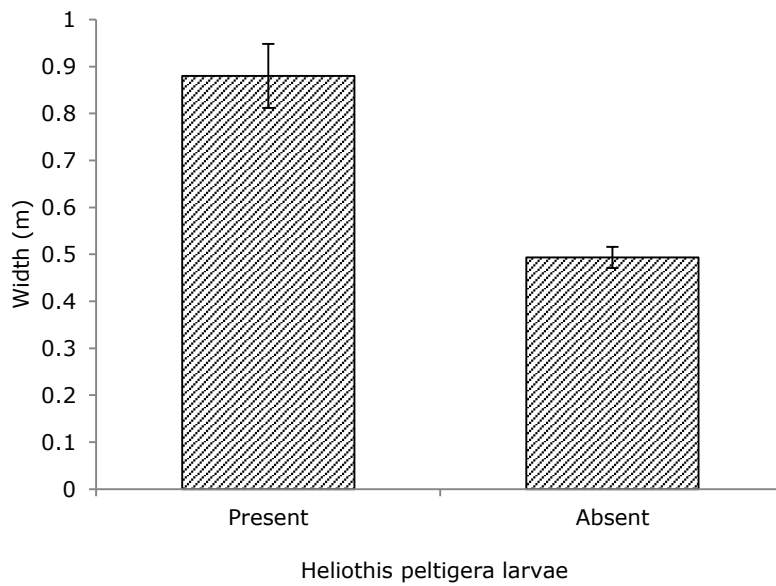nd radiation: the evolutionary biology of herbivorous insects.* Berkeley and Los Angeles, California: University of California Press, Ltd.

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Chapter 6.

The effects of grazing on the endangered *Thymus decussatus* in a hyper-arid environment

Goats in Farsh Loza

The effects of grazing on the endangered *Thymus decussatus* in a hyper-arid environment

Abstract

Herbivores play a key role in determining plant community composition. Historically grazing has been deemed detrimental for plants, but recent theoretical and empirical studies suggest that grazing may in fact be beneficial. Grazing is more likely to improve primary productivity in areas with a grazing history, where the plants are adapted to tolerate grazing, and also in arid environments because water stress and grazing select for comparable plant traits. Sinai Thyme (*Thymus decussatus*) in the arid St Katherine Protectorate of South Sinai has high apparent mortality rates and poor condition, both of which have detrimental consequences for its associated herbivores, particularly the Critically Endangered Sinai Baton Blue (*Pseudophilotes sinaicus*) whose larval stage feeds exclusively upon this plant. One recent conservation action banned grazing but there has been no obvious improvement in the thyme with continued high mortality, and local Bedu claim that grazing is in fact advantageous for plant health. I carried out a factorial experiment that manipulated simulated grazing, fertilizing and watering of thyme. This showed no evidence of any negative response to grazing or that watering or fertilizing had any effect either, presumably their impact is smaller than the current inter-annual variability caused by climatic fluctuations.

Introduction

Grazing has traditionally been considered detrimental for many plant species, reducing photosynthetic area, removing the apical meristem and causing a loss of nutrients stored in the stem (Noy-Meir, 1993; Cingolani et al., 2005; Rutherford & Powrie, 2010). However, the effects of grazing vary with species and ecological conditions, and current theories and studies have shown that grazing can in fact improve productivity (Luo et al., 2012). The removal of old leaves can improve overall quality and prevent senescence (Fulkerson & Donaghy, 2001), whilst moderate grazing has been found to increase species richness, plant cover and biomass when compared to ungrazed or intensely grazed areas (Taddesse et al., 2003).

The excretions of herbivores can enhance soil fertility and plant productivity through adding minerals, and can improve soil hydrological properties such as water infiltration: the result is an increase in plant biomass (Willott et al., 2000; Taddesse et al., 2003). The impact of grazing also depends upon grazing history. In areas that are consistently grazed, plants would be expected to have phenotypic plasticity so as to be able to respond positively to grazing with compensatory growth. This should enhance primary productivity and fitness by initiating new growth and reducing senescence (Noy-Meir, 1993; Strauss & Agrawal, 1999; Klein et al., 2007; Knapp et al., 2012).

Herbivores play a key role in determining species composition in communities, and changes to traditional management practices can trigger rapid reductions in species richness and alterations to species composition (Spiegelberger et al., 2006; Carmona et al., 2012; Loydi et al., 2012). Where there has been a history of grazing, the community is dominated by plants tolerant to grazing, with resistant traits such as small leaves (Navarro et al., 2006; Komac et al., 2011) or unpalatability (Loydi et al., 2012). If grazing ceases then such resistant plants lose their competitive advantage and can be outcompeted by grazing-intolerant species. This process has been noted in the Alps, where long-term pastoral grazing has shaped the environment and community. Grazing has recently declined in the area with considerable effect on species composition (Laiolo et al., 2004).

Milchunas et al. (1988) studied the impact of water availability on grazing. Plants in an arid environment experience high levels of below-ground competition for limited resources such as water, whilst grazing also negatively impacts roots. Therefore water stress and grazing are thought to select for similar traits (Milchunas & Lauenroth, 1993; Carmona et al., 2012). As a consequence, plants in arid environments are expected to show either a neutral or positive grazing response (Milchunas et al., 1988; Milchunas & Lauenroth, 1993; Adler et al., 2004). Morphological adaptations include small size, unpalatability and the ability to change chemical composition so as to decrease forage quality or biomass lost to herbivory (Adler et al., 2004). The genus *Thymus* contains species regarded as indicators for degraded landscapes in arid environments with long-standing grazing pressures, because they have favourable

characteristics that resist the impact of disturbance. They have small seeds and exposed flowers adapted to temperature stress, whilst small leaves and seeds help limit the effects of drought and grazing (Navarro et al., 2006). In a general review of grazing studies, 17% found a positive correlation between grazing pressure and above-ground productivity; these were studies of unproductive environments with long evolutionary histories of grazing, consistent with Milchunas' theory. Where grazing caused a decline in above-ground productivity, in some studies there can be a positive effect on root mass, indicating that grazing can alter the balance of investment between root and shoot. In general, however, there was no relationship between grazing pressure and root mass (Milchunas & Lauenroth, 1993).

There are studies inconsistent with Milchunas' model, where grazing pressure in resource-poor areas with a long grazing history apparently degrades the environment. An example is in the Mongolian desert, where current grazing levels apparently reduce plant resources and hence flowering, but here climate is a key component of the degradation (Wesche et al., 2010). This study emphasizes that water is the major limiting factor in the majority of arid environments, and water stress can mask the effects of grazing and disturbance (Pueyo et al., 2008; Kikvidze et al., 2011). The Simpson Desert of Australia has a light grazing history prior to the past 20 years of heavy grazing by domestic stock; despite this lack of grazing history, a positive relationship was found between grazing pressure and the species richness and diversity of perennial plants, coupled with a lack of any shift to degraded states (Fensham et al., 2010). Plants with a long grazing history in resource-poor areas are more resilient and can quickly recover when grazing ceases (Cingolani et al., 2005). However, irreversible damage can occur if there are drastic changes in local management, or if grazing levels exceed those encountered in evolutionary history: these can result in a rapid decline in biodiversity (Cingolani et al., 2005).

Water is the main limiting factor behind primary productivity in arid environments, with resource pulses associated with sporadic rainfall (Boyer et al., 1982; Schwinning et al., 2004). Water stress can reduce available resources by lowering the abundance and activity of micro-organisms, with knock-on effects on the levels of available nitrogen (Aguilera et al., 1999). It has a negative impact on nutrient uptake from the soil, and impairs

acropetal translocation (Hu & Schmidhalter, 2005). Consequentially in arid environments nutrient movement is often greater after precipitation events, and nitrogen is the second most limiting factor, behind water (Gebauer & Ehleringer, 2000). The response to simulated herbivory is often rapid; significant differences were observed on Sweet Thorn (*Acacia karroo*; Fabaceae*)* within three months of clipping and additional fertiliser in South Africa (Scogings & Mopipi, 2008), whilst perennial grasses in arid zone of Tunisia showed a response within 6 weeks (Chaieb et al., 1996).

Here I study experimentally the effects of artificial grazing and nutrient additions, and try to assess the success of recent conservation actions on a rare plant growing in the arid mountains of South Sinai. Because the plant is the exclusive host of the Critically Endangered Sinai Baton Blue butterfly (see James, 2006a-f; Thompson & Gilbert 2012), the flagship conservation target of the Protectorate, its response to grazing and conservation techniques is a vital concern of the park management.

Materials & Methods

The study system

The endangered plant is Sinai Thyme (*Thymus decussatus* Bentham, 1834: Lamiaceae)(James, 2006a), whose flowers constitute the only food of the larvae of the Sinai Baton Blue butterfly (*Pseudophilotes sinaicus* Nakamura, 1975: Lycaenidae), the World's smallest butterfly, categorized as Critically Endangered (Thompson & Gilbert, 2012). The butterfly is one of two species endemic to the St Katherine Protectorate (South Sinai) in Egypt, the most arid country in the world (Hoyle & James, 2005; FAO, 2012; Thompson & Gilbert, 2012). The butterfly has been marooned by post-Pleistocene climate change on mountaintop islands that create a fragmented landscape of host-plant patches; it is considered a flagship conservation target for the Protectorate (James et al., 2003).

Since 2003 conservation efforts have been focussed upon one key patch of thyme, Farsh Shoeib, a patch found to contain one of the largest butterfly populations with approximately 500 individuals in 2002 (James 2006). Water is predominantly the limiting factor in arid environments (Pueyo et

al., 2008): from 2002 to 2010 there was a prolonged drought with many years with little or no water, which decreased the quantity and quality condition of the thyme (Chapter 2). To rectify this problem, the Protectorate management built dams in Farsh Shoeib to prevent surface run off and to increase water infiltration after flash floods (El-Deen, 2010). If these dams are successful then they could be replicated across the park wherever thyme patches occur. The fence was built after the 2002 survey, which did not locate each plant precisely enough to enable their identification with the plants of 2010. Thus it is impossible to get an individual-based measurement for survival inside and outside of the fence between 2002 and 2010 because the precise location of the deaths is unknown.

The collection of thyme has recently been banned with fines enforced; however there may still be illegal harvesting of the host plant due to its high medicinal value in Cairo. Local support and awareness is essential as this could prevent further anthropogenic habitat damage and discourage the collection of thyme (El-Deen, 2010). Over-grazing by goats of the local Bedouin was identified as a threat by Egyptian botanists in the 1980s (see Gilbert, 2010) and subsequently repeated by Hoyle & James (2005). As a consequence of this apparent grazing threat, a fence was erected around Farsh Shoeib in 2003 to restrict human or animal access. Fences are commonly used to protect wild species from threats, in this case the illegal collection of thyme and grazing damage from livestock (Hayward & Kerley, 2009). However, there is little evidence regarding the success of fencing because the results of exclosure experiments in the St Katherine Protectorate have never been published. In Farsh Shoeib, no base-line data were collected before the fence was erected, and hence the success of this action can only be evaluated via a comparison of a single fenced area with surrounding unfenced areas (Hayward & Kerley, 2009).

In the past half-century, Bedouin lifestyles have changed drastically as many have become increasingly settled, abandoning their traditional semi-nomadic lifestyle to live close to towns. The resulting pressure on surrounding grazing has meant that livestock are increasingly fed with imported food and as a consequence herd sizes have declined (Gilbert, 2010). Bedouins are increasingly employed in regular waged work, such as tourism, meaning that herding is now a secondary vocation, only kept as

an insurance policy for poor years (Perevolotsky et al., 1989). Although settlement has the potential to result in a higher local grazing pressure, in fact there is hardly any current grazing around St Katherine because the Bedouin have strongly reduced livestock numbers in response to recent lack of rain. Instead of supplying them with food and profit, their herds actually cost them money because they have to buy imported alfalfa as feed (Rashad et al., 2003; Gilbert, 2010).

The Bedouin maintain that grazing helps rather than restricts many forage plants, so it could certainly be the case that prevention of grazing is exactly the wrong management technique (Murphee et al., 2008). Natural grazers in the protectorate include the Nubian ibex (*Capra nubiana*: Bovidae). In the past this probably would have provided significant historical grazing pressure; the Himalayan ibex (*Capra sibirica*: Bovidae) definitely feeds upon other thyme species (Awasthi et al., 2003). In the 20th century ibex numbers declined drastically because of the ready availability of guns after the First World War (Alkon et al., 2008). Current grazing pressures are likely to be from local goat herds around the town of St Katherine, inversely proportional to the distance from settlements and altitude (Rashad et al., 2003). Because the patches of thyme are at high altitudes well away from settlements in the wadi bottoms, grazing pressure is likely to be low. Grazing pressure is also very variable across the butterfly's distribution; Wadi Gebel and Gebel Safsafa have higher apparent grazing intensities than Wadi Ahmar (Guenther et al., 2005). Despite these apparently higher grazing pressures, Wadi Gebel and Gebel Safsafa have one of the highest levels of plant vigour and health (Guenther et al., 2005).

Grazing might indeed be a threat to the thyme and hence to the butterfly, but such a view needs to be seen also as part of an environmental narrative that drives policy in spite of rather than because of scientific evidence (Gilbert, 2013). Research carried out by the Protectorate rangers (Rashad et al., 2003) showed that grazing intensity is higher in open places than on the rough terrain selected by the butterfly. Furthermore, only 10% of grazing occurs at altitudes above 2000 m, while the butterfly only occupies patches above 1900 m (James et al., 2003; Rashad et al., 2003). Observations on the feeding behaviour of goats and sheep for over 250 hours detected no feeding upon thyme (Rashad et al., 2003). Local Bedouin say that thyme is unpalatable and their goats avoid it, or take just

one bite before moving on, a behaviour also observed in donkeys and camels (Nasr Mansour, 2011, pers. comm.). Taken together, all these lines of evidence suggest that grazing may not be such a large threat to thyme, especially since wild plants are currently such a small secondary component of the diets of livestock. Irrespective of whether goats forage on thyme or not, preventing animal access into Farsh Shoeib could gradually reduce soil fertility and change pH, and hence in the long term negatively impact the condition and quality of the thyme (Taddesse et al., 2003). Soil characteristics such as pH have been found to affect species composition more acutely than grazing (Fensham et al., 2010).

The majority of the fieldwork was carried out in Farsh Shoeib (Fig. 6.1), found near the summit of Gebel Safsafa on the Mt. Sinai massif, close to the town of St Katherine. It sits at an altitude of approximately 1950 m with an area of 14,000 m^2 that contained 652 thyme plants in 2012. The other site for experimental manipulation was the nearby area of Lower Hammar (Fig. 6.1), which contained 163 plants in 2011, but has not been the focus of any conservation efforts. They are less than 0.5 km apart. Fieldwork was carried out in three, four-month periods starting in March 2010 and 2011 and April 2012.

Experimental manipulations

Sinai Thyme is an endangered plant, and the host plant of a Critically Endangered butterfly: this limited the sample sizes allowed for the experiment under the permission given to us by the Egyptian Environmental Affairs Agency, as conveyed to us by the Protectorate management. I therefore randomly selected ten plants per treatment within both the fenced area of Farsh Shoeib and within Lower Hammar; an additional five plants per treatment were randomly selected from the area of Farsh Shoeib outside the fence – this was smaller because of the low number of plants there. Plants were excluded if they were less than 10% green to reduce the likelihood of natural mortality. Each plant was individually labelled in 2011 when the treatments were carried out, and subsequently measured in 2011 and 2012. Thyme quality was measured using four characteristics; height, two perpendicular widths and condition (percentage green). The 'resource area' for each plant was then calculated

from the surface area (assuming each plant was a hemi-ellipsoid) multiplied by the condition (as a proportion).

There were three treatment factors, each with a control and a treated group: simulated grazing, the addition of dry goat faeces and the addition of water. These were factorially combined to create eight treatment groups, each with the sample sizes outlined above. Artificial grazing was simulated by clipping the top 2 cm from 12.5% of the plant before the flowering season, the maximum allowed under our permit. 'Light grazing' is usually simulated by clipping 30% of a plant, but there are many cases where 15% clipping has generated over-compensatory growth (Oba et al., 2000; Klein et al., 2007). Goat faeces have constituted a natural fertiliser for many centuries in South Sinai. I collected fresh pellets from the immediate surroundings on Safsafa: ten pellets were placed under each selected plant. The effect of increased soil moisture was investigated by watering appropriate plants with 150 ml once each week for 12 weeks before and during the flowering season. The treatments began in early March, six weeks before the beginning of the flowering season.

The resources for Sinai Baton Blue larvae are the flowers and flower buds; the response variable was therefore flower density on each plant. To measure this, a 10 x 10 cm quadrat was placed on the most advanced area of flowering on the plant to count the density of flowers. This was done each week for six weeks, commencing the week sepals were noted in the patch. In addition, the phenological state of the thyme was recorded weekly for 13 consecutive weeks, using the phenological scale created by James (2006e). Once a week, from the start of April, five inflorescences were randomly selected from the most advanced area of flowering on the plant and scored phenologically on a scale of 0-7 (Table 6.1): the average of the five scores represents the phenological state of the plant at that time. This was then repeated from mid-April until the end of June in 2012.

Analysis of data

To assess the long-term effects of grazing on thyme quality, data for 2010 and 2011 from the plants inside the fenced enclosure of Farsh Shoeib were compared to those outside, using the statistical package R 2.14.1 (R Development Core Team, 2012) and models were simplified in accordance

to Zuur et al. (2009). Any changes were investigated by testing plant size (assuming the hemi-ellipsoidal shape) and condition as response variables. Since I measured the same individuals, I ran a linear mixed model (*lmer* from the *lme*4 package) using year and location (inside & outside) as factors and individual plant as the random measure. Factors were assessed by the change in deviance upon deletion from the model, tested with a χ^2 value. The experiment reduced the number of unmanipulated plants outside the fence to fewer than twenty individuals making it impossible to compare those inside and outside the fence in 2012. To see if there was a significant difference in the proportion of flowering plants inside and outside of the fence, I ran a one-way GLM with whether the plant flowered or not as the response variable and the year (2010 and 2011) and location as factors. The model was run with the R routine *glm*, with a binomial error structure and significance was assessed with a χ^2 value. To compare the location of the mortalities since 2010, I ran a one-way GLM with mortality as the response variable and location (inside or outside the fence) as the factor. The model was run with the R routine *glm*, with a binomial error distribution and significance was assessed with a χ^2 value.

To assess the relatively short-term (two years) effects of the experimental treatments, I used seven response variables: the condition, peak density of flowers, the total number of flowers across six weeks, whether a plant flowered, and the flowering phenology using three summary indices (the average score across the first 13 weeks of surveys; the week where the first flower was seen; and the week of peak flowering). Weeks were counted from the 1st April. When comparing flowering phenology, I removed non-flowering plants from the analysis: fewer plants flowered in 2012, a pattern observed across the whole massif (Chapter 4). I ran a linear mixed model (*lmer* from the *lme*4 package) using the year (2011 & 2012) and the three kinds of treatment as fixed factors, with individual plant as the random effect. The error structure for the response variable 'whether a plant flowered' was binomial, and 'condition' was Poisson; all remaining response variables were normally distributed. All factors were assessed by the change in deviance following deletion from the model, tested with a χ^2 value.

Results

There was significant spatial variation in mortality across Farsh Shoeib between 2002 and 2010 (Chapter 2). The Southern area (outside the fence) had the highest mortality rate (66%), however, the adjacent area (Farsh II) had a similarly high mortality rate (63%), and two-thirds of these individuals would definitely have been located inside the enclosure: thus these deaths cannot solely be attributed to fencing.

Between 2010 and 2012 there was a significantly higher proportion of mortalities outside the fence (χ^2= 5.37, df=1, p<0.05); five of the 17 deaths were outside the enclosure and 12 were inside. When comparing the size of the plants inside and outside of the fence, there were marginally non-significant differences in size (χ^2= 3.49, df=1, p=0.06) and condition (χ^2=3.01, df=1, p=0.08). The plants were smaller outside the fence with a lower condition across both years. However the large individual variability coupled with the small number of plants found outside the fence may have masked any significance (Fig. 6.2). Both variables showed temporal fluctuations between years (size: χ^2=4.1, df=1, p<0.05; condition: χ^2=13.81, df=1, p<0.001) but there was no interaction between year and inside/outside (size: χ^2=0.001, df=1, p=0.97; condition: χ^2= 0.03, df=1, p=0.87). The proportion of flowering plants did not significantly differ between locations (χ^2=0.379, df=1, p=0.538) or between years (χ^2=1.18, df=1, p=0.277), nor was there an interaction between the two factors (χ^2=0.364, df=1, p=0.546), although the flowering rate was higher outside the patch in both years (Fig. 6.3).

Experimental treatments

The treatments were simulated grazing, the addition of dry goat faeces and the addition of water and they were factorially combined to create eight categories. Those with additional water had a significantly lower proportion of flowering plants (χ^2=6.55, df=1, p<0.01), but of the watered treatments, those which received all three treatments (clipping, dung and water) had the highest proportion of flowering plants (χ^2=5.19, df=1, p<0.001)(Fig. 6.4). The proportion of flowering plants had significant temporal variation (χ^2=115.8, df=1, p<0.001), with every plant flowering in 2011. The peak density of flowers and total density of flowers across 6

weeks did not significantly vary with treatment and showed no interaction with year, only showing yearly variation (peak density: χ^2=63.3, df=1, p<0.001; total: χ^2=67.4, df=1, p<0.001)(Fig. 6.5 & 6.7, Appendix 6.1). However the peak number of flowers was slightly lower in the clipped plants than those unclipped (χ^2=3.124, df=1, p=0.077)(Fig. 6.6). The total number of flowers also appears to have an interaction between dung and clipping, with the combination of the two treatments slightly reducing the flowering output. However the difference was insignificant (χ^2=2.824, df=1, p=0.093)(Fig. 6.8). The condition was significantly affected by an interaction between the year, dung and clipping (χ^2=4.38, df=1, p<0.05), but again the other treatments did not have any effect (Fig. 6.9).

When comparing the phenology there were significant yearly differences in the week of first flower (χ^2=25.7, df=1, p<0.001), week of peak flowering (χ^2=52.6, df=1, p<0.001) and average score across the thirteen weeks (χ^2=15.3, df=1, p<0.001). The average phenological score also had a significant interaction between year, water and clipping (χ^2=5.16, df=1, p<0.01), with the average phenology being earlier in 2012 in every group except for the dung only treatment (Fig. 6.10). The week of the first flower had a significant interaction with year and dung (χ^2=4.26, df=1, p=0.039), whilst there are signs of an interaction between year, water and clipping (χ^2=3.34, df=1, p=0.068)(Fig. 6.11). The remaining treatments did not affect flowering phenology (Appendix 6.1).

Thus in summary, the plants show a very diverse response to the experimental treatments with no clear trend amongst treatments and responses; for example the water only and water with clipping treatments had low proportion of flowering plants in 2012 yet they had a high average condition in 2012 (Fig. 6.4 & 6.9).

Discussion

The plants were generally smaller and in a poorer condition where grazing was permitted, however the differences were marginally insignificant and overall treatments had inconsistent effects on the plants' vitality. The response to the treatments did not mitigate against the inter-annual variability in quality, suggesting that grazing and disturbances within

natural boundaries might not have a negative impact on the thyme (Lewis, 2001).

It is hard to compare the effectiveness of the fence on plant quality and density because there is only a single fenced area, and there are no base-line data before fencing: thus we can only compare grazed and ungrazed areas. Only a few plants were found outside the enclosure, giving a poor sample size for direct comparisons within Farsh Shoeib, whilst spatial variation across the massif make comparisons with other populations impossible (Chapter 4). The plants in Farsh Shoeib where natural grazing is permitted are not significantly different, but they are smaller and in a poorer condition; however, this could be attributed to the collection of thyme (which I observed on multiple occasions despite the current ban, whereas I never observed grazing). Thyme is very slow growing, with very small differences in plant resource area between seasons (Chapter 2), so any disparities in size and quality may take longer to become apparent (although it has been almost 10 years!). In 2003 two artificial dams were created inside the enclosure to hold more water in the soil after heavy rainfall, and these dams may also have enhanced plant vigour within the enclosure. The mortality rate was higher outside the enclosure between 2002 and 2010 but this was highly variable across the whole patch, with the section just inside the fence having a similarly high mortality (Chapter 2). However, mortality has remained higher outside the patch since 2010.

The experimental plants did not perform worse than the controls, and plants had a variable response to treatments. The groups with the largest decline in the proportion of flowering plants had higher condition in 2012. Overall the thyme plants have large variability in quality; other work showed that Farsh Shoeib has large intra-patch variation in size and condition (Chapter 2). 2012 had a significantly lower flowering rate compared to 2011, a pattern observed across the whole massif (Chapter 4). Flowering entails a high water cost, so presumably this was a response to the dry 2011/2012 winter, with flowering commonly reduced under limited resources (Harrison, 2001). The drought and high variability in plant quality may have masked the effects of the experiment, with the drought being more influential on productivity (Pueyo et al., 2008). Water is predominately the limiting factor in arid environments, with additional nitrogen having a smaller impact on above-ground primary productivity in

drier systems (Yahdjian et al., 2011). Consequentially the dry winter may have masked the effects, if they exist, of nitrogen limitation and additional fertiliser on the thyme. Overall flowering phenology was not affected by the treatments. Cues for phenological timings are currently unknown for this system, but thyme may be insensitive to changes in water, fertilisation or grazing; air temperature may be the main cue that controls flowering, as in many other plant species (Crepinsek et al., 2006; Matesanz et al., 2009).

Current grazing pressures, if any, are likely to be from local goat herds around the town of St Katherine (Rashad et al., 2003). Any grazing threat coupled with dry conditions would select for grazing-tolerant plants (Milchunas et al., 1988; Navarro et al., 2006; Carmona et al., 2012). However, Sinai's unpredictable weather causes large fluctuations in water availability (Chapter 2), creating highly variable herbivory between years. There may have been no consistent selection pressure for grazing-tolerant plants, despite a long evolutionary history. Elsewhere this can result in two sets of plants; grazing-tolerant but less competitive plants, which would succeed under high grazing pressures, whilst less grazing-tolerant plants would dominate during other years (Cingolani et al., 2005; Rutherford & Powrie, 2010).

The state and transition model of rangeland management suggests that a system can be pushed between stable states when thresholds are crossed by natural or management changes in stocking levels (Westoby et al., 1989). This may be occurring here; preventing grazing might result in a shift between states, disturbing species composition, promoting grazing-intolerant or palatable plants (Knapp et al., 2012). If the Bedouin are correct in believing that thyme is unpalatable, this would have negative implications for thyme. Its small leaves and seeds are grazing-tolerant traits (Navarro et al., 2006). Elsewhere in subalpine habitats in Spain, *Thymus praecox* is known to be favoured by grazing (Komac et al., 2011). These adaptations mean if grazing ceases, thyme may lose its adaptive advantage and be outcompeted by grazing-intolerant species. Perhaps this was responsible for the high mortality rates of thyme within Farsh Shoeib.

Further studies need to be carried out on the effects of grazing, especially by native herbivores such as ibex relative to domestic livestock. Rashad et al. (2003) cast doubt on the reality of the grazing threat to high-mountain

plants, and this study did not find any evidence of negative consequences of natural or artificial grazing. It may in fact be masked by the climatic fluctuations and the large variability in the quality of the time. The high mortality rates in Farsh Shoeib over the past decade suggest that current conservation strategies may be ineffective. There needs to be more long-term monitoring to get clearer insight into how conservation actions can help to improve the abundance and quality of Sinai thyme.

Table 6.1. Scoring of flowering phenology scale (from James, 2006e).

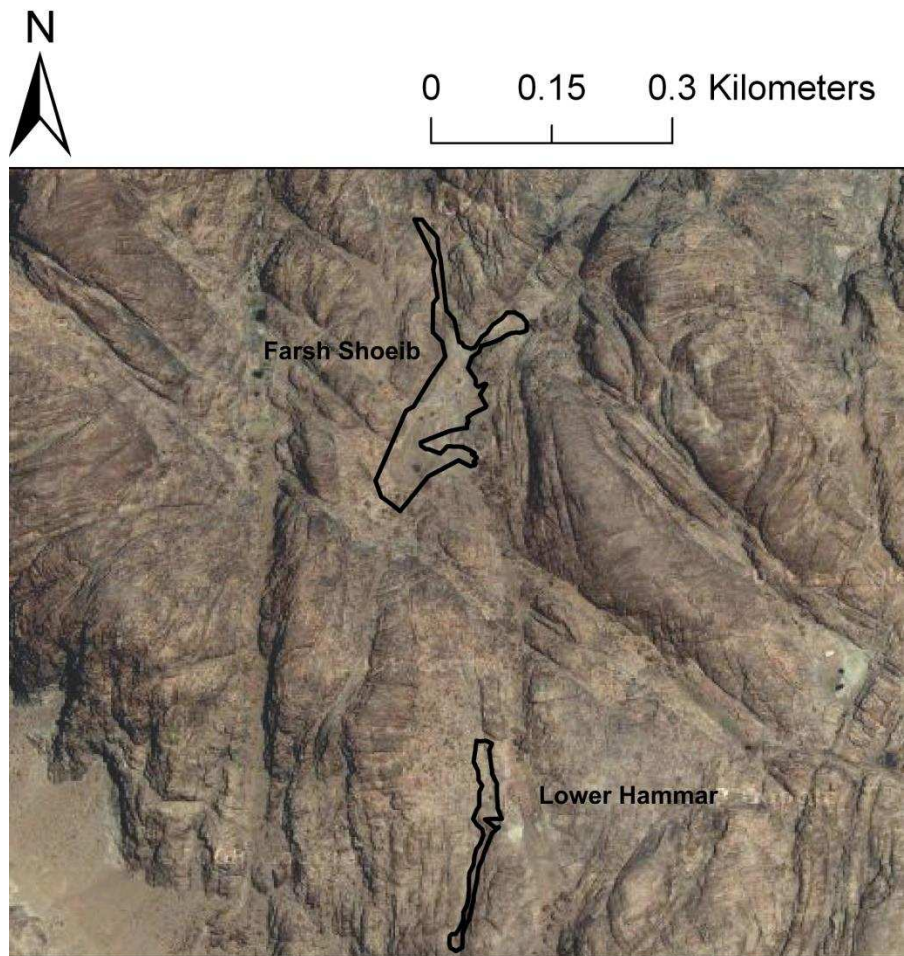| Phenological score	Appearance of plant
0	100% pre-bud
1	sepals visible, buds not yet visible
2	sepals apparent, buds starting to develop
3	large buds but fewer than 2 flowers open
4	50-90% buds, 10-50% flowers open
5	1-50% buds, 50-100% flowers open
6	1-50% flowers over/seed heads
7	more than 50% flowers over/seed heads

Figure 6.1. The locations of the experimental sites; Farsh Shoeib and Lower Hammar.
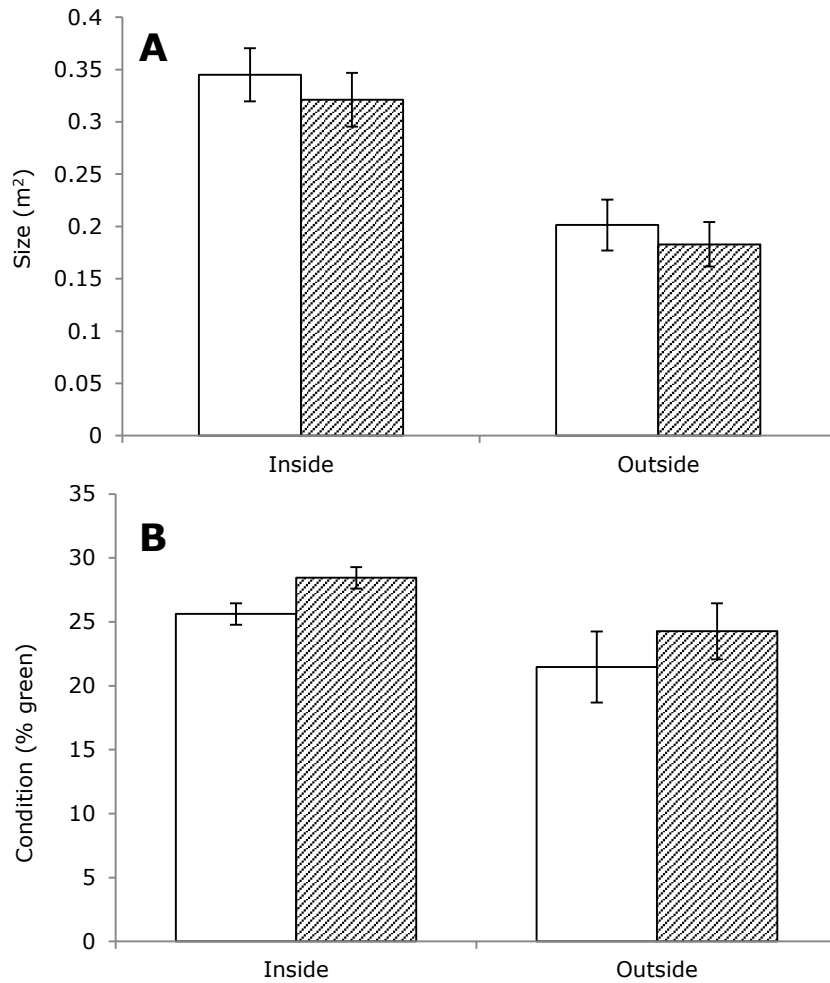
Figure 6.2 Differences in a) size and b) condition of the plants inside and outside of the fence in 2010 (white bars) & 2011 (striped). Mean values (± SE).
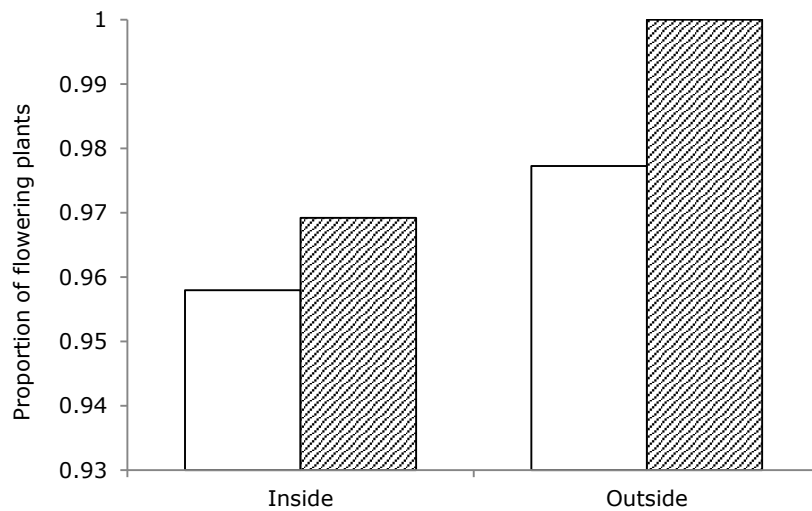
Figure 6.3 Differences in the proportion of flowering plants inside and outside of the fence in 2010 (white bars) & 2011 (striped).
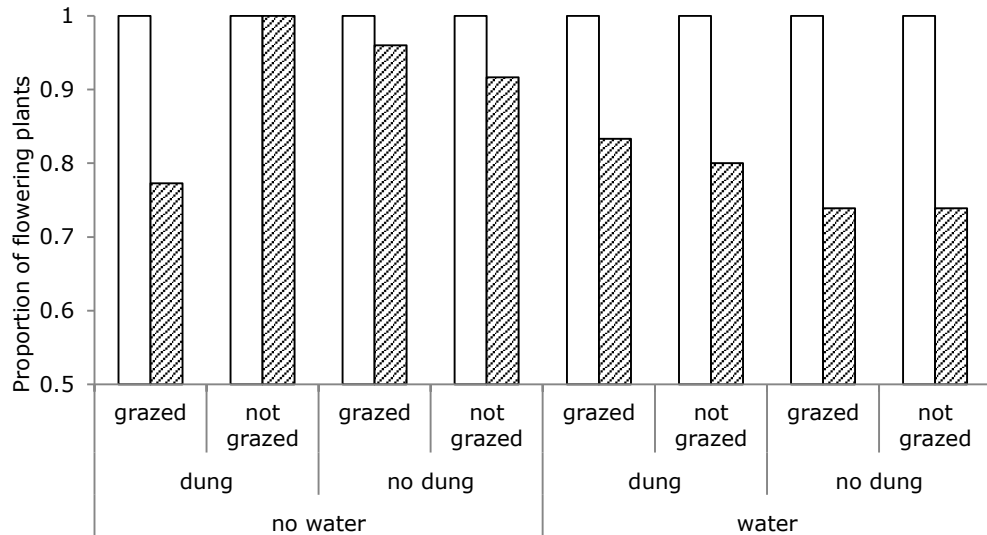
Figure 6.4 The proportion of flowering plants in 2011 (white bars) & 2012 (striped) per treatment category.
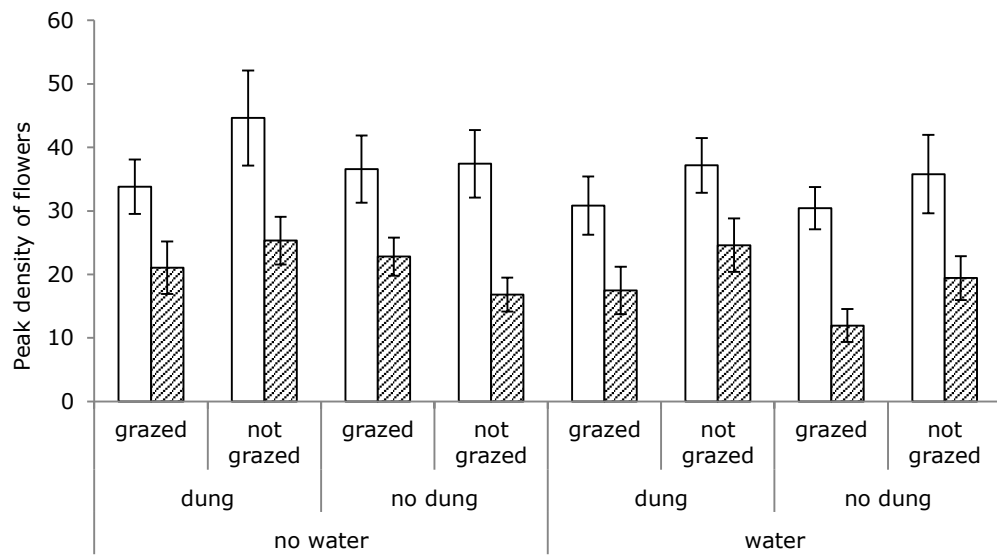
Figure 6.5 The peak density of flowers of the plants in 2011 (white bars) & 2012 (striped) per treatment category. Mean values (± SE).
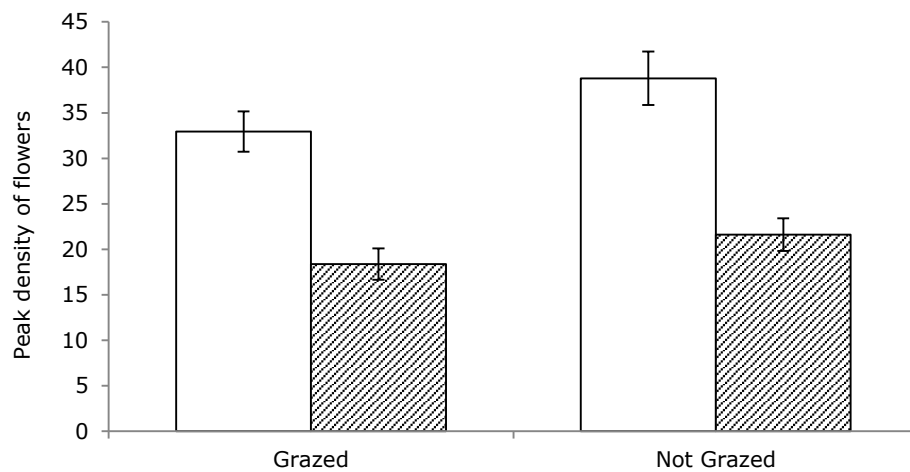
Figure 6.6 The peak density of flowers of the grazed and ungrazed treatments in 2011 (white bars) & 2012 (striped). Mean values (± SE).
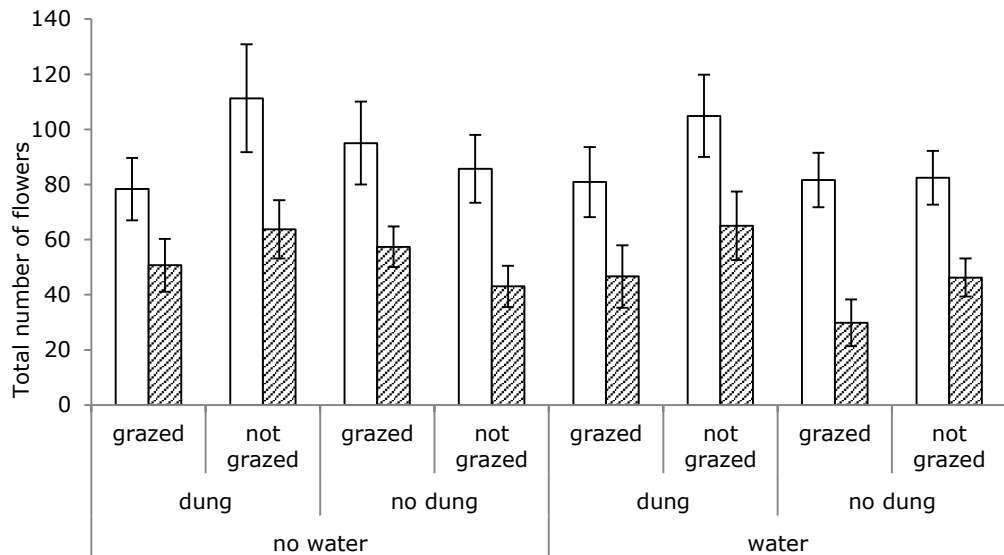
Figure 6.7 Total number of flowers of the plants in 2011 (white bars) & 2012 (striped) per treatment category.. Mean values (± SE).
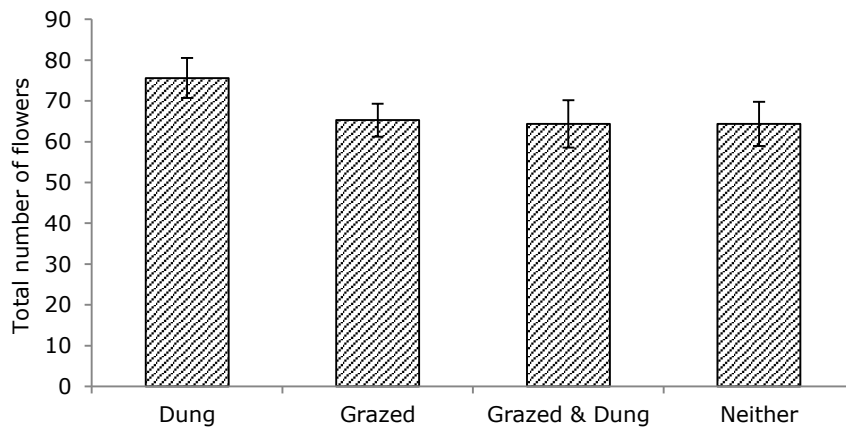
Figure 6.8 The total number of flowers of the dung and grazed treatments across both years. Mean values (± SE).
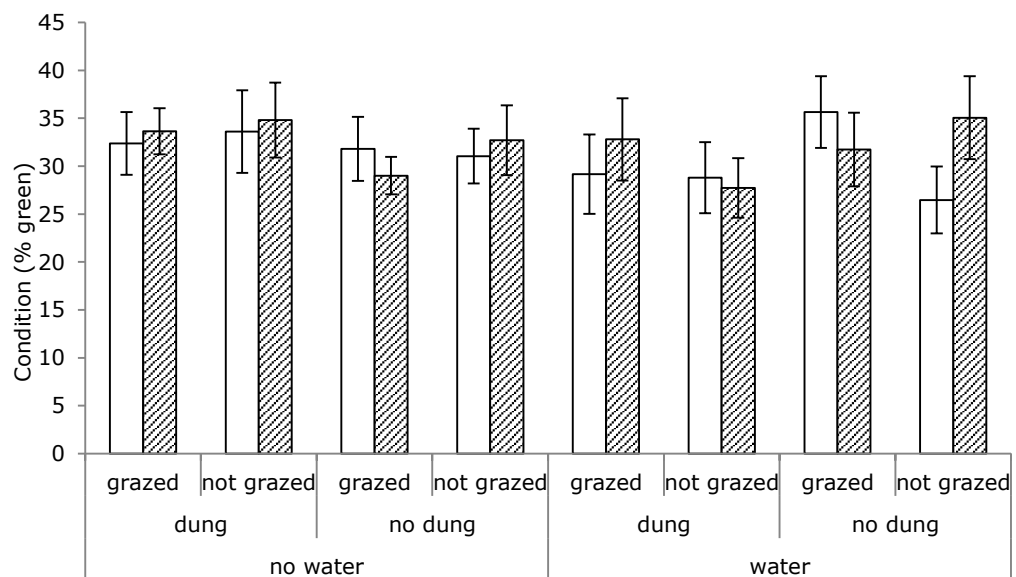
Figure 6.9 The condition (% green) of the plants in 2011 (white bars) & 2012 (striped) per treatment category. Mean values (± SE).

Figure 6.10 The average phenology scored across 13 weeks in 2011 (white bars) & 2012 (striped) per treatment category. Mean values (± SE).
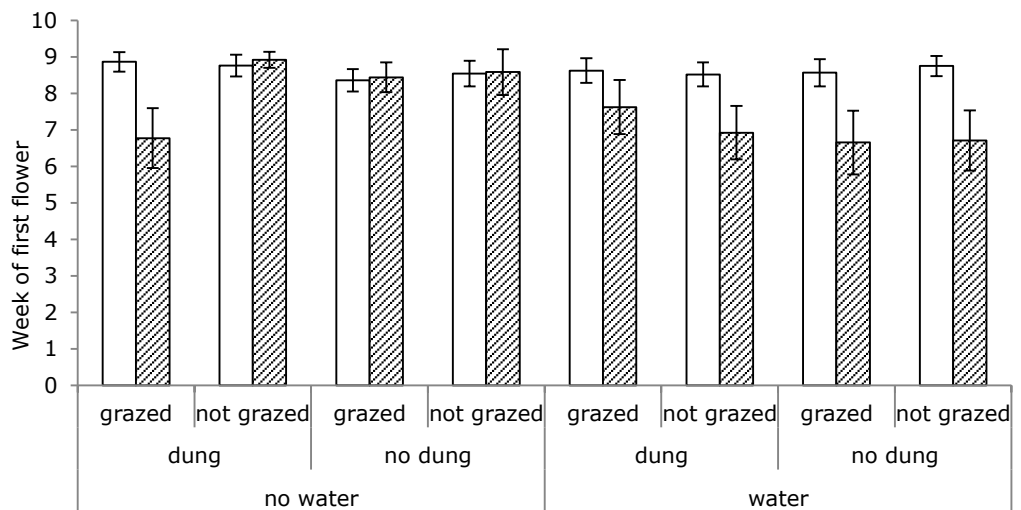
Figure 6.11 The week of the first flower in 2011 (white bars) & 2012 (striped) per treatment category. Mean values (± SE).
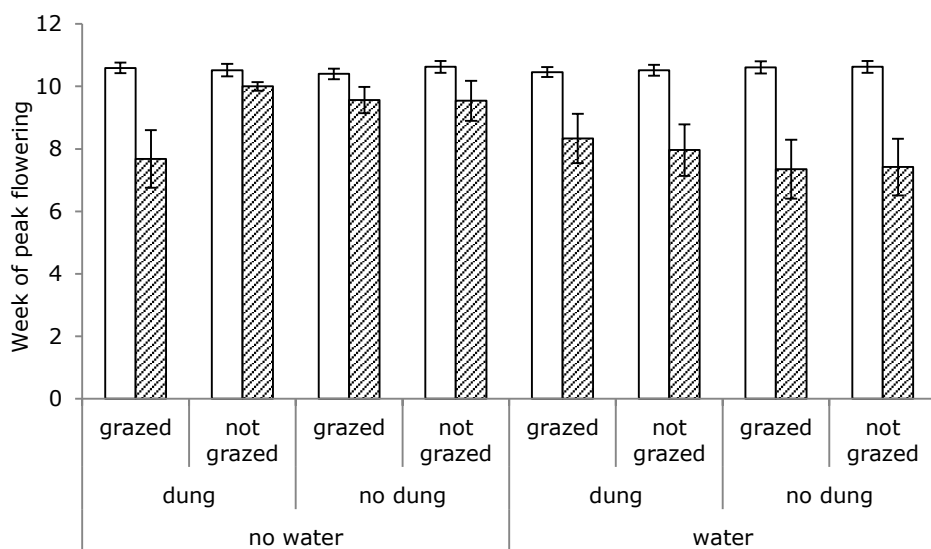
Figure 6.12 The week of peak flowering in 2011 (white bars) & 2012 (striped) per treatment category. Mean values (± SE).

References

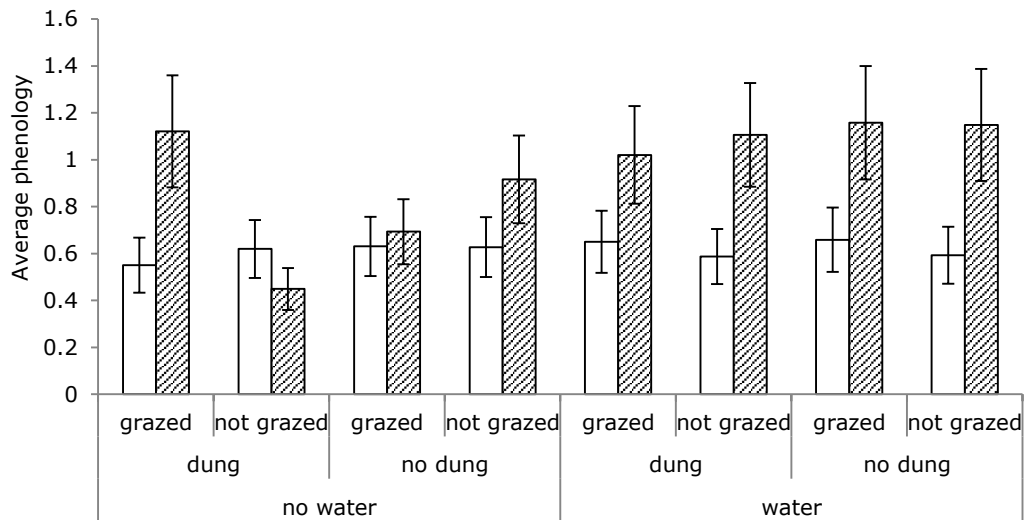Adler, P. B., Milchunas, D. G., Lauenroth, W. K., Sala, O. E. & Burke, I. C. 2004. Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology,* 41, 653-663.

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Appendix 6.1 The ANOVA table for the mixed effects model investigating the response of thyme to varying treatments. The levels of significance are * ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001.

Response variable		Chi	df	p	
Condition	Year	0.638	1	0.424	
	Water*Dung*Graze	0.041	1	0.839	
	Water*Dung	1.369	1	0.242	
	Water*Graze	0.982	1	0.322	
	Dung*Graze	0.032	1	0.858	
	Water	0.505	1	0.477	
	Dung	0.121	1	0.932	
	Graze	0.115	1	0.734	
	Year*Water*Dung*Graze	1.473	1	0.225	
	Year*Water*Dung	0.300	1	0.584	
	Year*Water*Graze	0.092	1	0.762	
	Year*Dung*Graze	4.38	1	0.036	*
	Year*Water	0.325	1	0.569	
	Year*Dung	0.037	1	0.848	
	Year*Graze	1.311	1	0.252	
Peak flowers	Year	63.251	1	<0.001	***
	Water*Dung*Graze	0.921	1	0.337	
	Water*Dung	0.029	1	0.864	
	Water*Graze	0.671	1	0.413	
	Dung*Graze	1.046	1	0.306	
	Water	2.362	1	0.124	
	Dung	1.277	1	0.259	
	Graze	3.124	1	0.077	
	Year*Water*Dung*Graze	0.013	1	0.910	
	Year*Water*Dung	0.236	1	0.627	
	Year*Water*Graze	1.242	1	0.265	
	Year*Dung*Graze	0.009	1	0.927	
	Year*Water	0.179	1	0.672	
	Year*Dung	0.569	1	0.451	
	Year*Graze	0.518	1	0.472	
Total flowers	Year	67.389	1	<0.001	***
	Water*Dung*Graze	0.613	1	0.434	
	Water*Dung	0.354	1	0.552	
	Water*Graze	0.473	1	0.492	
	Dung*Graze	2.824	1	0.093	
	Water	0.766	1	0.382	
	Dung	1.997	1	0.158	
	Graze	2.060	1	0.151	
	Year*Water*Dung*Graze	0.039	1	0.854	
	Year*Water*Dung	0.236	1	0.627	
	Year*Water*Graze	0.985	1	0.321	
	Year*Dung*Graze	0.211	1	0.901	
	Year*Water	0.179	1	0.672	
	Year*Dung	0.569	1	0.451	
	Year*Graze	0.518	1	0.472	
Proportion of flowering plants	Year	115.840	1	<0.001	***
	Water*Dung*Graze	5.186	1	0.023	*
	Water*Dung	1.221	1	0.269	
	Water*Graze	1.967	1	0.161	
	Dung*Graze	0.718	1	0.396	
	Water	6.55	1	0.010	*
	Dung	0.032	1	0.858	
	Graze	0.485	1	0.486	
	Year*Water*Dung*Graze	0.001	1	0.974	
	Year*Water*Dung	0.003	1	0.971	
	Year*Water*Graze	0	1	0.995	
	Year*Dung*Graze	0.001	1	0.993	
	Year*Water	0.005	1	0.935	
	Year*Dung	0.208	1	0.742	
	Year*Graze	0.400	1	0.527	

Response variable		Chi	df	p	
Average phenology	Year	15.28	1	<0.001	***
	Water*Dung*Graze	0.542	1	0.462	
	Water*Dung	0.437	1	0.509	
	Water*Graze	0.460	1	0.497	
	Dung*Graze	1.028	1	0.311	
	Water	0.026	1	0.871	
	Dung	0.007	1	0.934	
	Graze	0	1	1	
	Year*Water*Dung*Graze	1.824	1	0.177	
	Year*Water*Dung	1.271	1	0.260	
	Year*Water*Graze	5.162	1	0.023	*
	Year*Dung*Graze	0.586	1	0.444	
	Year*Water	0.0192	1	0.890	
	Year*Dung	2.281	1	0.131	
	Year*Graze	0.325	1	0.569	
Week of first flower	Year	25.694	1	<0.001	***
	Water*Dung*Graze	0.069	1	0.792	
	Water*Dung	0.401	1	0.526	
	Water*Graze	0.432	1	0.511	
	Dung*Graze	1.053	1	0.305	
	Water	0.044	1	0.834	
	Dung	0.001	1	0.973	
	Graze	0.010	1	0.919	
	Year*Water*Dung*Graze	0.452	1	0.501	
	Year*Water*Dung	1.495	1	0.222	
	Year*Water*Graze	3.343	1	0.068	
	Year*Dung*Graze	0.346	1	0.555	
	Year*Water	0.462	1	0.497	
	Year*Dung	4.265	1	0.039	*
	Year*Graze	0.089	1	0.765	
Week of peak flowering	Year	52.629	1	<0.001	***
	Water*Dung*Graze	1.02	1	0.312	
	Water*Dung	0.002	1	0.966	
	Water*Graze	0.412	1	0.521	
	Dung*Graze	0.612	1	0.434	
	Water	0.032	1	0.858	
	Dung	0.334	1	0.563	
	Graze	0.310	1	0.578	
	Year*Water*Dung*Graze	0.265	1	0.607	
	Year*Water*Dung	2.19	1	0.139	
	Year*Water*Graze	1.093	1	0.296	
	Year*Dung*Graze	0.225	1	0.635	
	Year*Water	0.615	1	0.433	
	Year*Dung	0.176	1	0.675	
	Year*Graze	0.002	1	0.989	

Chapter 7.

Predicting the future of the World's Smallest butterfly, *Pseudophilotes sinaicus*

Predicting the future of the World's Smallest butterfly, *Pseudophilotes sinaicus*

Abstract

The Sinai Baton Blue butterfly, *Pseudophilotes sinaicus*, is Critically Endangered, with a tiny endemic distribution in the St Katherine Protectorate, South Sinai. Its range is restricted to within the distribution of its sole host plant, the near-endemic endangered Sinai Thyme, *Thymus decussatus*. The butterfly metapopulation was modelled using the population viability software Vortex, incorporating catastrophes to simulate the impact of droughts, and variability in some life history traits whose parameters are uncertain. The metapopulation was very sensitive to fluctuations in the mortality rate, reproductive rate and carrying capacity, whilst varying the dispersal rate did not affect the outcome. The results underline the need for action to conserve this fragile species, focused on improving the patches of the host plant to enhance butterfly survival rates, carrying capacity and reproductive output.

Introduction

Population viability analysis tries to assess the likely course of (meta-) population dynamics under current conditions or under various scenarios of altered environmental conditions. Its most obvious use is to project the future risk of extinction. Sensitivity analysis can provide further insights by identifying the parameters which most influence the dynamics (Reed et al., 2002; Jaric et al., 2010). This makes such models useful in evaluating potential management options for endangered species, and thus in selecting strategies likely to improve species persistence (Drechsler et al., 2003). Predictions depend on the initial (meta-)population size coupled with the frequency and magnitude of demographic and environmental stochasticity and catastrophic events (Verboom et al., 2010).

Reviews of published population viability analyses of 21 long-term ecological studies demonstrated the accuracy of the simulations: the projected population sizes were not significantly different from the real outcomes (Brook et al., 2000; Schoedelbauerova et al., 2010). The

concordant results of simulations using five different software packages showed that all implementations of population viability models provide dependable results, and hence the methodology is usable as a practical tool in the conservation of threatened species (Brook et al., 2000). There are some who question this: for example, Verboom et al (2010) argue against the future accuracy of population viability because of the unpredictability of climate change. Climate change is expected to increase the frequency and duration of adverse conditions thus amplifying fluctuations in demographic rates and increasing the extinction risk. It is certainly true that the data used to test the results of simulations usually underestimates current or future fluctuations (Pimm & Redfearn, 1988), and of course many biological aspects are omitted, such as genetic constraints or phenological mismatches between interacting species (Verboom et al., 2010).

I study here the possible fate of the Sinai Baton Blue butterfly (*Pseudophilotes sinaicus* Nakumara 1975), a Critically Endangered species endemic to the St Katherine Protectorate in South Sinai (Egypt): it is a flagship species for the conservation of the area (Hoyle & James, 2005; Thompson & Gilbert, 2012). Its larval stage is entirely dependent on an endangered plant, Sinai Thyme (*Thymus decussatus* Bentham, 1834), itself highly restricted in its distribution (James, 2006a). The Sinai Baton Blue lives in a fragmented landscape of thyme patches, occupying only 39 of them in 2001 in an apparent metapopulation structure: its total Extent of Occurrence is less than 7 km^2 (James et al., 2003). The Sinai Baton Blue lives in an arid environment, confined to the slightly wetter and cooler tops of the highest mountains in Egypt with a volatile climate. Its future is threatened by anthropogenic deterioration in its habitat and climate. As a conservation effort, for both plant and butterfly, the majority of the patch was fenced off in 2003 to prevent public access, grazing and any damage to the plants: only a few plants are found outside the enclosure. Two large dams were built within the main farsh in 2003 to hold more water in the soil after flash floods.

Hoyle & James (2005) used an Incidence Function Model implemented in the stochastic patch occupancy model SPOMSIM (Moilanen, 2004) to predict the Sinai Baton Blue's long-term population dynamics, modelling presence/ absence on the set of habitat patches in the face of stochastic events and processes coupled with gradual habitat deterioration. Three

possible causes of habitat loss were simulated: over-grazing by goats (negatively related to the distance to settlements, and negatively to altitude), climate change (via gradual reductions in patch area as plants are forced to higher altitudes) and the random loss of entire thyme patches from over-collection for medicinal use (Murphee et al., 2008). Probably the impact of over-grazing has been exaggerated because stocking rates are actually very sensitive to levels of available vegetation, rather than the other way round (Perevolotsky & Seligman, 1998; Murphee et al., 2008; H Gilbert, 2010). The results of the SPOMSIM model showed that if current conditions were maintained, the butterfly would persist as a metapopulation for the next 200 years. Under increased intensity of global warming, there was a threshold level of grazing intensity beyond which the probability of metapopulation extinction rapidly increased to a level of inevitable extinction. Modelling the loss of random patches via over-collection showed the importance of two key central patches in sustaining the entire metapopulation: the loss of either would result in an 80% probability of metapopulation extinction within the next 200 years.

Materials & Methods

I use here a very different kind of model of population viability, Vortex (Lacy et al., 2003). It models at the level of the individual and separately analyses populations, and hence can include the impact of various types of environmental variation on demographic parameters. It explicitly models catastrophic events, such as the droughts which could potentially threaten the Sinai Baton Blue. Vortex was designed to assist in understanding how deterministic forces along with stochastic demographic, environmental and genetic events could influence the fate of any particular species (Miller & Lacy, 2003).

In this model I ignore the long-term effects of habitat loss considered by Hoyle & James (2005), and concentrate on the risk of extinction under current conditions of habitat distribution. While the effects of climate change are believed to be very real, those of over-grazing and over-collection are less certain. Over the last 50 years the local Bedouin have become less nomadic and increasingly sedentary, especially close to the town of St Katherine. This resulted in a rise in grazing intensity in the

surrounding gebels and wadis, and a dramatic reduction in flock size was the response (Perevolotsky et al., 1989; Rashad et al., 2003; Gilbert, 2010). Grazing intensity has the potential to cause damage and loss to the host plant, increasing fragmentation amongst patches and thus decreasing connectivity, a key component of metapopulations (Hanski, 1999). However, sustained droughts in the area coupled with increased competition for grazing have led to the almost complete loss of flocks of sheep and goats (Gilbert, 2010). Anthropogenic climate change is currently a realistic threat via the likely increase in the frequency and severity of drought (Giannakopoulos et al., 2009), and consequentially affects the quality and distribution of the host plant and the Sinai Baton Blue (Harrison, 2001; Boggs & Freeman, 2005). Thus my rationale is to try to understand the effects of the host plant on butterfly populations, and in particular the way in which it copes with stochastic and sparse rainfall. Annual fluctuations in the number of inflorescences on the host plant directly impact the larval stage of the Sinai Baton Blue (Hoyle & James, 2005).

I ran population viability analyses for the Sinai Baton Blue using the modelling software Vortex 9.99b. Values for the parameters were taken from the series of papers by James (2006a-f; James et al 2003; Hoyle & James 2005) based on data collected from 2001 to 2003. I performed sensitivity analyses by running multiple scenarios varying the adult mortality rate, reproductive rate, dispersal rate and carrying capacity to assess which factors have the biggest impact on long-term survival. I included catastrophes to simulate re-occurring droughts, a realistic consequence of climate change. The initial population sizes of each patch was taken as that at the start of data collection in 2001. Some of the options of Vortex (harvest, supplementation and genetic management) were not relevant and were not included.

Table 7.1 summarises the parameters used, and I comment briefly here on the necessary assumptions made. James (2006f) observed that an average of 26 eggs were laid per female in Farsh Shoeib in 2002, and found 42 in a dissected female: I set the maximum number of progeny at 46. The standard deviation of the number of eggs laid was set at 7. This was selected as it was the standard deviation of the number of eggs seen in a close relative of the Sinai Baton Blue, *Pseudophilotes barbagiae* (Leigheb &

Cameron-Curry, 1998). The environmental variation in the percentage of individuals that breed was set at a low number (4) because eclosing females mated almost immediately and nearly all are thought to lay at least a few eggs (James, 2006f).

The Sinai Baton Blue is a polygynous species, with males mating with multiple females. I assumed that all females mated, but it is likely that good-quality males will gain more than their fair share of matings. In 2002 James (2006f) observed 32% of females and 23% of males mating in Farsh Shoeib. James did not observe all matings, but his observations indicate a clear difference in mating success between males and females. Presuming 96% of females mated, I estimated that James only managed to observe one third of all matings: if he missed the same fraction of male matings, there would be 69% (23 x 3) of males in the breeding pool.

It is impossible to calculate the carrying capacity accurately, so to estimate the carrying capacities of each patch I plotted Ln (patch area) against the estimated patch populations for 2001 from data collected by James (Fig. 7.1). I assumed that in 2001 some of the patches were at or near carrying capacity; extrapolating backwards from the population cycle (Gilbert et al., 2010) the species would potentially have had a peak year in 2001. By regression I calculated the relationship between patch area and population size, excluding the four patches with larger populations of 200 or more individuals, and then shifted the regression line up slightly so that it was just skimming the uppermost points, which were assumed to be at carrying capacity (see Fig. 7.1). From this line the carrying capacity was calculated for each patch. The four excluded patches were presumed to be at their carrying capacity in 2001. This resulted in the total carrying capacity for the entire metapopulation at slightly more than 3500 individuals, with the metapopulation able to hold 1200 more individuals than the 2001 estimate. The carrying capacity was later systematically varied during sensitivity analysis. The standard deviation of the carrying capacity of each patch due to environmental variation was estimated at 20%, which was the observed variation in the available resource area within Farsh Shoeib between 2010 and 2011 (Chapter 2): it was subsequently varied during sensitivity analysis.

I ran multiple runs of the model to explore the sensitivity of the results to the values of particular parameters. Thus I ran several scenarios with different mortality rates (5% to 99.1%) in order to assess sensitivity to pre-adult mortality rates, set initially at 93% with a standard deviation of 4.3 (the estimate for 2002) and also run ± the standard deviation (88.7 & 97.3) and also at 99.1% (the observed rate for 2003)(James, 2006c,f). All simulations were run at the 93% mortality and also at the lower 88.7% mortality (for which the species was predicted to persist over the next century).

Sensitivity to carrying capacity was explored by increasing or decreasing all values used in the standard simulation in 5% steps. The environmental variation around the carrying capacity was set for the simulations at 20%, and was varied from 5 to 130% for sensitivity analysis; 5% decline was observed in available thyme 2011 - 2012, a 40% reduction was seen between 2002-2010, the numbers of flowers differed by 60% between 2011- 2012 and 130% between 2010-2011 (Chapter 2).

I varied reproductive rates by systematically altering the mean number of offspring per female from 20 to 44; *Pseudophilotes barbagiae* laid between 20-30 eggs in captivity and 42 eggs were found in a dissected Sinai Baton Blue female (Leigheb & Cameron-Curry, 1998, James, 2006f).

The survival of dispersers was determined at 89.5% (the difference between immigration and emigration), with the dispersal rate set at 14% (James, 2006d); the dispersal rate was varied systematically to determine the sensitivity of the outcome to their values. For these sensitivity analyses all other parameters were kept constant at their values of Table 7.1 but were run with a 93% mortality rate (2002 mean) and also at a lower mortality rate of 88.7% (2002 mean – SD) where the population persisted across the next century.

Catastrophic droughts were added to incorporate the realistic threat that these pose to this species. I estimated the severity of a typical drought using the data collected in the drought year of 2003, where reproductive output dropped to a third of that in the previous year (James, unpublished data). In 2003 the adult population was 14% of the 2002 total number of individuals (James, 2006c). So taking these responses as typical in a

drought, I chose 'severity values' within Vortex of 0.33 (on reproduction) and 0.14 (on survival). The other parameters were constant (Table 7.1) except that the optimistic mortality rate of 88.7% was used. A climatic catastrophe such as a drought would affect all patches equally, so this catastrophe was set at a global level. The frequency of the 'drought' catastrophe was incrementally increased from 2% (where two droughts would occur in the next century) up to 20% (where 20 droughts occurred) to simulate the effects that increasing climate change might have on this species.

Results

The future of the butterfly was very sensitive to varying mortality rates (Fig. 7.2). The mortality rate of 93% estimated in 2002 implies an inevitable extinction, with fewer than five individuals remaining after 30 years. In 2003, a year of winter drought, a higher mortality rate of 99.1% was estimated; if sustained, this implies rapid extinction within 3 years. At 89% mortality (the mean minus the typical environmental variation), the Sinai Baton Blue will survive the next 100 years with a final metapopulation size of approximately 700 individuals. When the mortality rate is 83% or below the metapopulation persists indefinitely, with a positive trajectory towards the carrying capacity.

Variations in the carrying capacity, environmental fluctuations in carrying capacity and reproductive output all had a greater impact on the projected metapopulation size when run at the lower mortality rate of 88.7% (2002 average minus the SD). When simulations were run at the higher mortality rate of 93% (the 2002 average), where the baseline conditions resulted in an inevitable extinction within 30 years) it is harder to assess the effects of varying the parameters due to their smaller influence on the downward trajectory.

Varying the carrying capacity in increments of 10% (Fig. 7.3a) only affected the early dynamics without altering the generally downwards trajectory with time. The metapopulation never reached carrying capacity, suggesting that other factors limit butterfly numbers. Variations in the carrying capacity at the higher mortality rate (Fig. 7.3b) had a smaller

impact on the predicted future of the metapopulation, with a small range of responses, and the species still approaching an inevitable extinction within 20 years.

Variation in the carrying capacity caused by environmental fluctuation were varied from 5% to 130%, with severe detrimental effects on the outcome (Fig. 7.4a). Its effects were non-linear, with a large fall in metapopulation size when the environmental variation increased from 30% to 40%, and above 50% the metapopulation was very close to extinction after 100 years. Again, when the environmental fluctuations were varied at the higher mortality (Fig. 7.4b) there was a smaller range of outputs, with fluctuations of just 5% still unable to save the species.

The metapopulation dynamics were sensitive to the mean number of offspring per female, with small changes in reproductive output making a large difference in the outcome (Fig. 7.5). When run at the 89% mortality, as the reproductive output increased there was a reduced decline in numbers, but the metapopulation never reached the carrying capacity and there was always a downward projection, even when simulations were run with a reproductive output of 44, considerably higher than the average of 26 eggs. The reproductive rate had a larger influence on the metapopulation size when run at the higher mortality rate (Fig. 7.5b), but nevertheless the future still appeared ominous, with fewer than 100 individuals after 30 years.

In contrast, metapopulation numbers were not affected by dispersal rate (Fig. 7.6). Using dispersal rates ranging from 5% to 30% the outcomes were very similar to that of the observed dispersal rate (14%), with no effect on the overall rate of metapopulation decline: greater carrying capacities had no impact on this result.

If faced with catastrophes (such as droughts) at a frequency of only two per century, the species looks to be critically endangered with only 300 individuals remaining after 100 years (Fig. 7.7). When the frequency of catastrophic events increases to five per century, fewer than 100 individuals remain. Catastrophes occurring more frequently than 10 per century result in extinction within 100 years.

Discussion

The results from the Vortex simulations indicate that the metapopulation is most sensitive to changes in the mortality rate, which determines whether the metapopulation reaches its carrying capacity or declines to extinction. They suggest that the estimates of James (2006f) were probably too high: that a mortality of 99.1% for 2003, if continued every year, would have caused extremely rapid extinction, according to the Vortex model. At mortality rates of 83% or lower, mortality became no longer a limiting factor, with metapopulation size being restricted by carrying capacity. High mortality in butterfly populations can occur during any of the four life stages: embryonic miscarriage with the failure of eggs to hatch, predation of the eggs, caterpillars or the adult butterflies, or death during the pupal state with a butterfly failing to eclose the following spring (Tammaru et al., 2002; James, 2006f). James (2006f) found some evidence of the effect of intraspecific competition in increasing larval mortality, presumably acting via the availability of their food, the flowers. The metapopulation was also sensitive to fluctuations in the reproductive output of females, and in fact the estimate of 26 eggs per female is the most uncertain parameter put into the simulation. It is possible that the reproductive and mortality rates are both proportional to available resources, as in other butterflies (Boggs & Freeman, 2005; Bauerfeind & Fischer, 2009).

A further parameter, the carrying capacity of patches, also depends upon the condition and abundance of the host plant (James et al., 2003). The carrying capacity was an uncertain estimate, but the fact that the metapopulation failed to reach the carrying capacity in the majority of simulations means that this would not have affected the overall conclusions from the model. The biggest threat to the Sinai Thyme is now climatic: an increasing occurrence of adverse years would have a severe impact on its populations. Since 2002 the amount of available resource has dramatically declined in the stronghold of Farsh Shoeib, with nearly 30 m^2 of thyme lost between 2002 and 2010, roughly equating to a 40% decline in carrying capacity. If this occurred in multiple patches, this would leave the metapopulation with just 300 individuals after the next century. In addition there are substantial instabilities in available resources, and thus carrying capacities between years, with yearly fluctuations from 5% to 130% observed since 2002 (Chapter 2). In the model the metapopulation was

very responsive to this factor, with fluctuations above 20% having strong negative consequences. The butterfly's metapopulation only reached the carrying capacity when the mortality rates were below 83%, considerably lower than the estimated 2002 rate of 93%. When varying other parameters with an 89% mortality rate, the metapopulation never reached the carrying capacity, indicating that mortality is the most restrictive parameter. The assumption of density dependence was therefore not relaxed because this was basically irrelevant - populations never reached carrying capacity due to the restrictive mortality rates.

The Sinai Baton Blue exists in a spatially structured metapopulation, thought to be close to a classical metapopulation (James et al 2003; Hoyle & James 2005). In a classic metapopulation, inter-patch dispersal is essential to maintain the metapopulation and rare dispersal events prevent extinctions and assist re-colonisations (Hanski, 1999). This model shows no apparent sensitivity to dispersal rates, suggesting that connectivity and isolation may not be a critical factor behind metapopulation survival: mortality and fecundity may be more important in a few large/mainland populations. This supports recent findings by Hodgson et al. (2011) who suggest that habitat area and quality are more important than the effects of isolation in population persistence, and should thus be the focus of conservation. Increases in habitat quality and area increase the resources available to the butterflies, enhancing fecundity and survival. This has been observed in many butterfly species, such as the Carson Valley silverspot butterfly, *Speyeria nokomis carsonensis* (Nymphalidae)(Sanford et al., 2011). There are other causes of spatial population structure where dispersal is not a critical component, such as populations where habitat quality is the key factor, which may be the case here (Driscoll et al., 2010).

The occurrence of 'catastrophes' such as droughts, however, clearly is important. Climate change and a rise in temperature is predicted to increase the likelihood of droughts (Giannakopoulos et al., 2009). Drought stress directly impacts the thyme's condition and hence the availability of larval resources. This is expected to increase larval intraspecific competition and the mortality rate (James 2006f), decreasing the metapopulation size (Boggs & Freeman, 2005).

These simulations show very different predictions to those of Hoyle & James (2005). For 2001 conditions, their model predicts a stable metapopulation for the next 200 years. Our model forecasts a variety of outcomes ranging from rapid extinction to stability, dependent mainly on the availability and condition of the host plant. Both models agree that global warming will increase the probability of extinction. Yearly monitoring since 2002 has shown that this species appears to undergo population cycles with crashes every three years (Gilbert et al., 2010). The majority of the data used for these simulations was collected before and during a crash year (2003), so perhaps suggesting a more pessimistic outcome than is likely: in general population viability models provide rather pessimistic outcomes (Brook et al., 2000). Replicated measures, especially of the mortality rate and reproductive output, during different points in the population cycle would enable more accurate predictions and fewer assumptions.

These results reiterate the urgent need for conservation of this butterfly (James 2006f). Although needing to be interpreted with caution because of several imprecise parameters, nevertheless this model suggests that the butterfly is in trouble, and identifies particular life-history traits that need further study. Conservation needs to be focused on the endangered Sinai Thyme, preferably with targets to increase its condition and abundance. This would probably improve all of the aspects of the butterfly life-history crucial to its long-term survival: i.e. mortality of the different stages, fecundity and patch carrying capacity. Connectivity amongst patches is probably not critical here. In many butterfly species the quality of habitat is an important factor as well as connectivity between patches (Thomas et al., 2001), and quality is possibly much more important (Hodgson et al., 2009).

Methods of improving the host-plant are as yet unclear. Although suffering from drought, rain in 2010 did not prevent the death of many thyme plants in Farsh Shoeib (Chapter 2), and water by itself may not increase flowering and condition (Chapter 2 & 6). In 2009 two dams were built in Farsh Shoeib to hold water in the hope of increasing soil moisture and hence thyme quality and abundance (El-Deen, 2010), but there is little sign of any effect as yet (Chapter 2). Improving the quality of the thyme would

have a positive impact on other species in the community, affecting the ecosystem on a wider scale (Launer & Murphy, 1994).

Table 7.1. The parameters for simulations of the metapopulation dynamics of the Sinai Baton Blue, obtained from the data in James et al. (2003), Hoyle & James (2005), James (2006a-f).

Parameter	Value
Iterations	500
Number of years	100
Extinction definition	Only 1 sex remains
Number of populations	39
Environmental variation concordance of reproduction and survival	0.7
Number of catastrophes*	0
Dispersal ages	1 (with both sexes dispersing)
% survival of dispersers**	89.5%
Reproductive system	Polygynous
Age of first offspring for males/females	1
Max age of reproduction	1
Max broods per year	1
Max number of progeny per brood	46
Sex ratio at birth	50:50
% adult female breeding	96
Environmental variance in % breeding	4
Mean offspring per female per brood (SD)**	26 (7)**
Mortality from age 0-1 (SD)***	93 (4.3)**
Annual mortality after age 1	100
% males in breeding pool	69.1

* later changed to model the potential effects of catastrophes.

** indicates the parameters whose means were later varied for sensitivity analysis.

*** All simulations were run with a 93% mortality rate (as seen in 2002) and at a 88.7% mortality rate (the 2002 mean- SD).
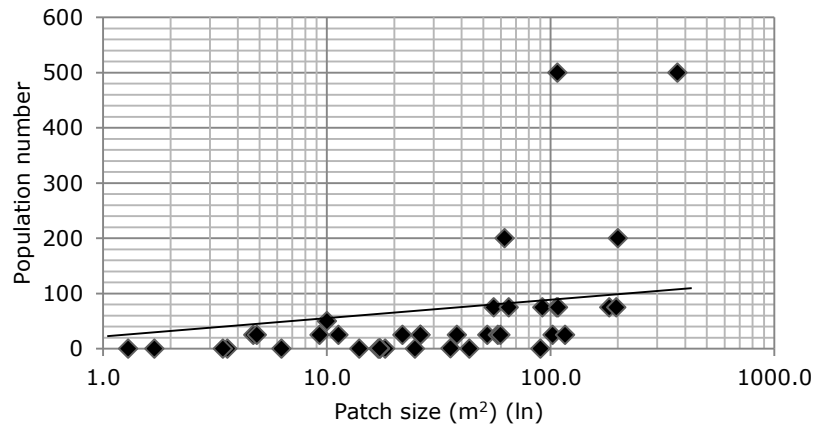
Figure 7.1. Calculation of the theoretical carrying capacity of populations of the Sinai Baton Blue butterfly dependent on patch size. The data come from a thorough census in 2001 (James et al. 2003). The regression line was calculated omitting the four patches with populations of 200 or more, considered to be outliers for this purpose, and then was shifted upwards so as to skim the top of the data (as shown). This was used to estimate the carrying capacities of all but the omitted four patches (assumed to be at their carrying capacity in 2001). The equation of the line was: pop number = 13 [ln(patch size)] + 20.
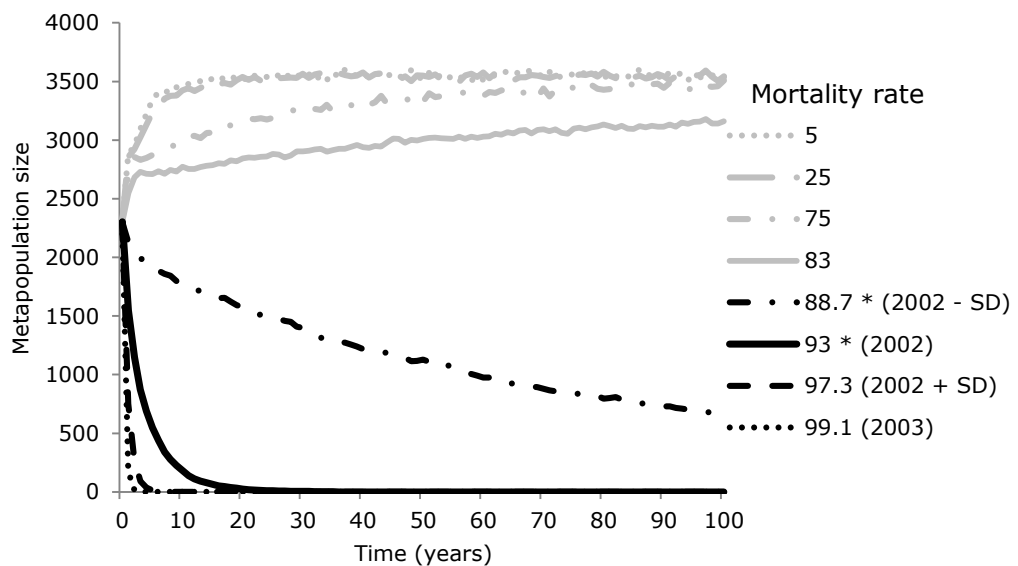

Figure 7.2. Metapopulation size of the Sinai Baton Blue butterfly simulated using Vortex over the next 100 years, varying the mortality rate for each run. The black lines are values observed in the field; the mortality rate was 93% (± S.D. of 4.3) in 2002 and 99.1% in 2003, whereas the grey lines are theoretical values. *Mortality rates of 93% & 88.7% were used in other simulations.
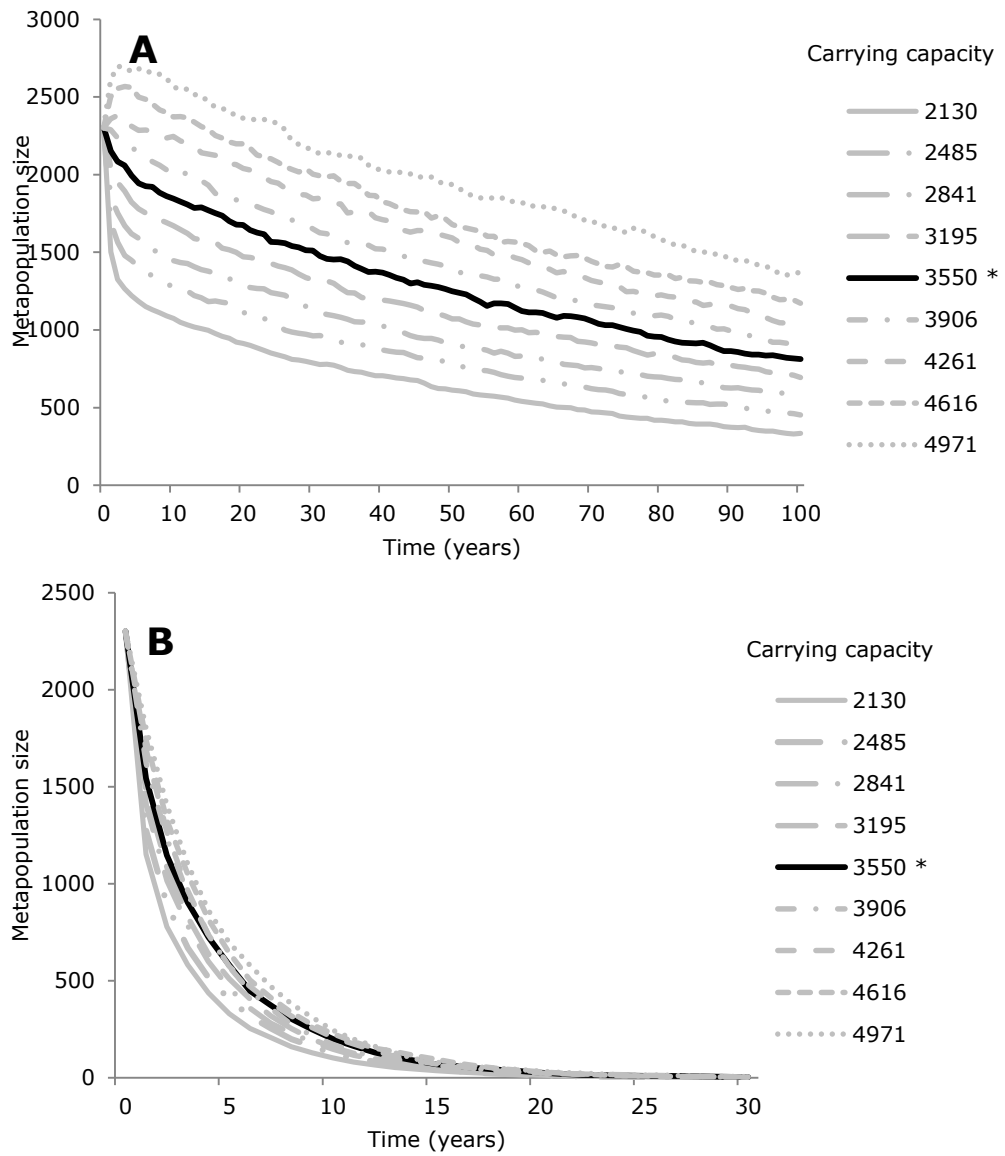
Figure 7.3. Metapopulation size of the Sinai Baton Blue butterfly simulated using Vortex varying the carrying capacities of the patches for each run, using a mortality rate of a) 88.7% and b) 93%. The figures show the total metapopulation carrying capacity. *A carrying capacity of 3550 was used in the other simulations whilst the other values are theoretical.
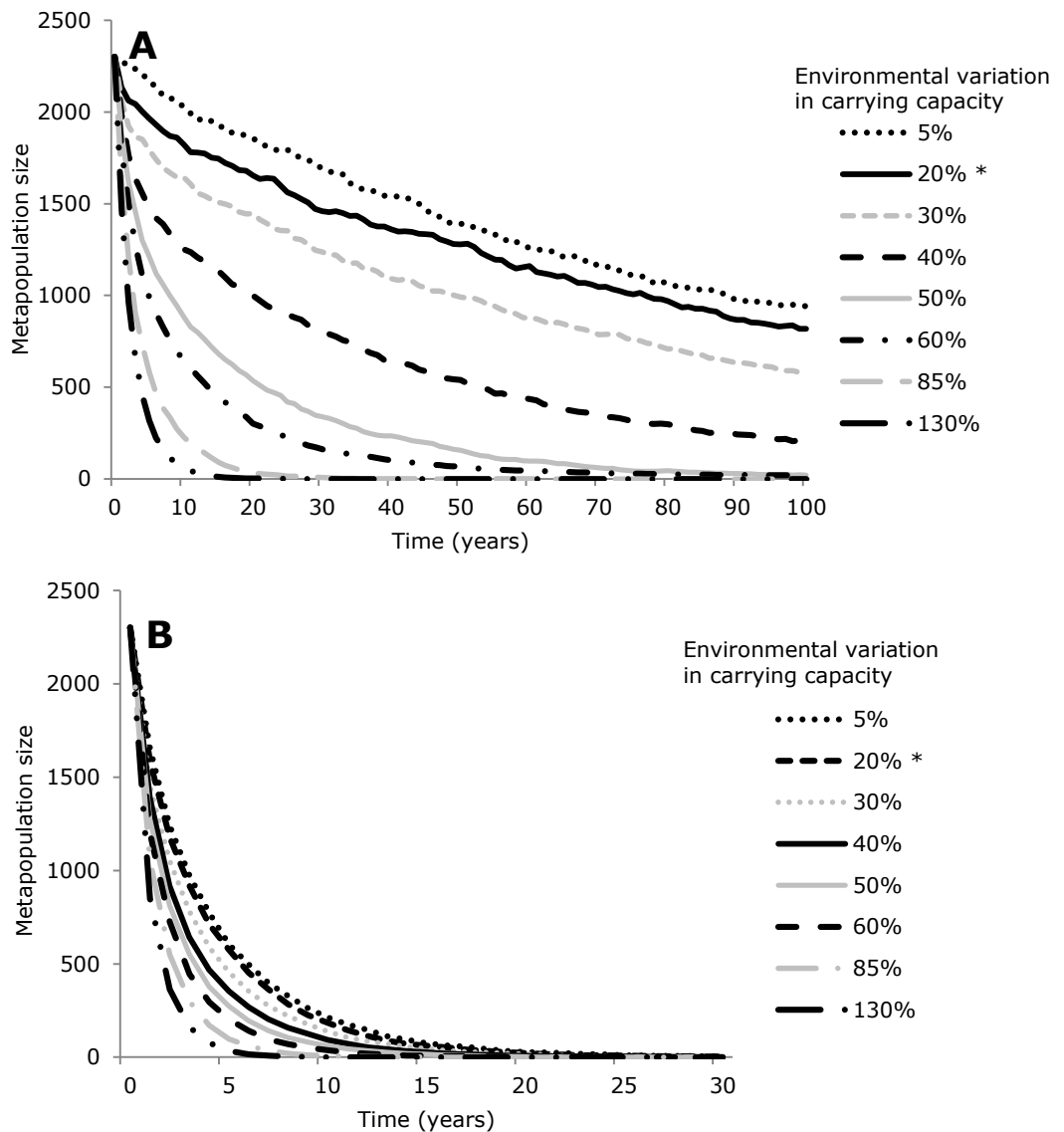
Figure 7.4. Metapopulation size of the Sinai Baton Blue butterfly simulated using Vortex, varying the level of environmental fluctuations in the carrying capacity with each run, using the mortality rate of a) 88.7% and b) 93%. The black lines show simulations run using values from field data; the available thyme varied by 5% between 2011-2012, 20% between 10-11 and by 40% between 02-10 whilst the number of flowers differed by 60% in 11-12 and by 130% 10-11. The grey lines are theoretical values. *20% fluctuation in carrying capacity was used in other simulations.
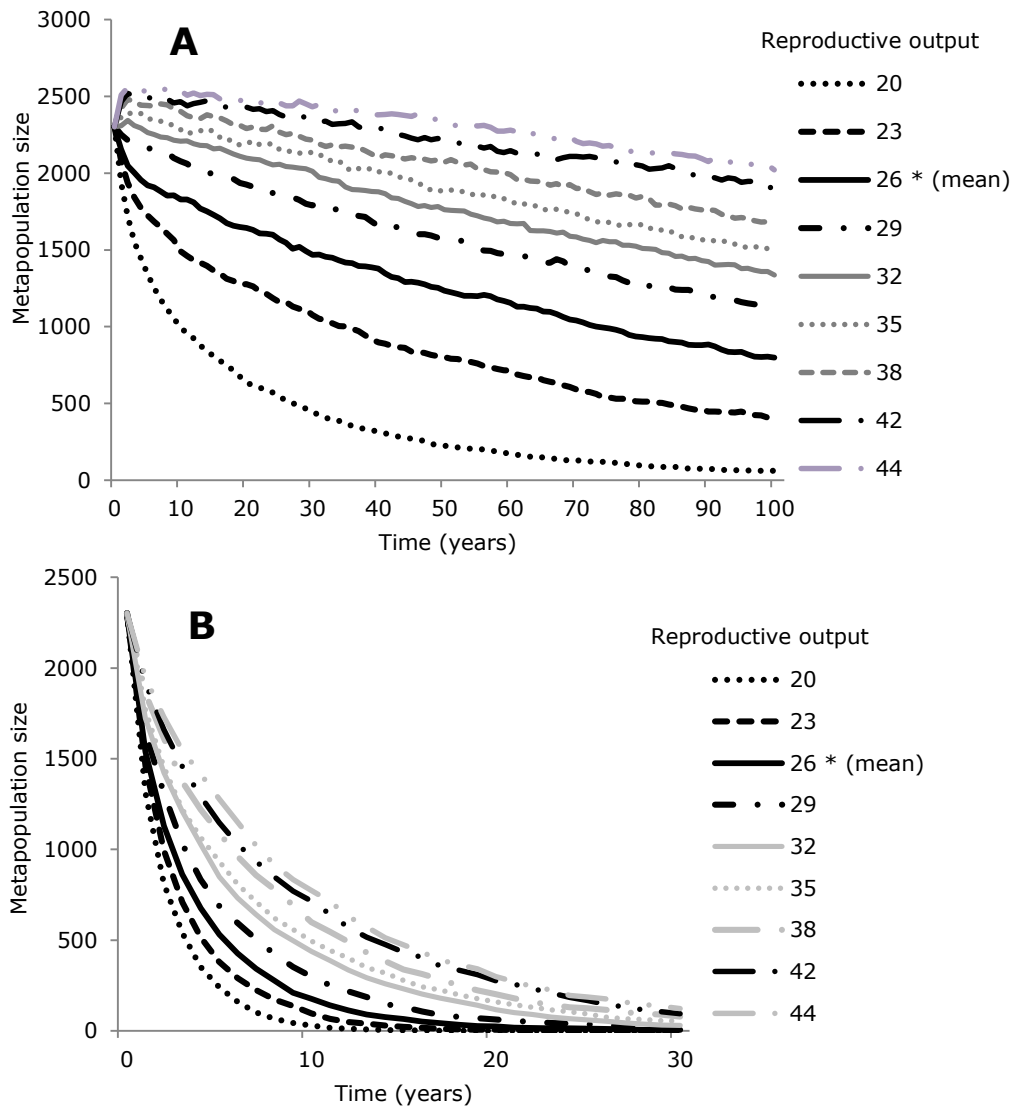
Figure 7.5. Metapopulation size of the Sinai Baton Blue butterfly simulated using Vortex, varying the mean number of offspring per female per brood with each run. a) used the mortality rate of 88.7%, b) used 93% mortality. The mean number of eggs for the Sinai Baton Blue was 26. The black lines show when the reproduction rate was varied within the range of the closely related *Pseudophilotes barbagiae*, whilst 42 eggs were observed in a dissected Baton Blue female. The grey lines are theoretical values. *A reproductive output of 26 was used in other simulations.
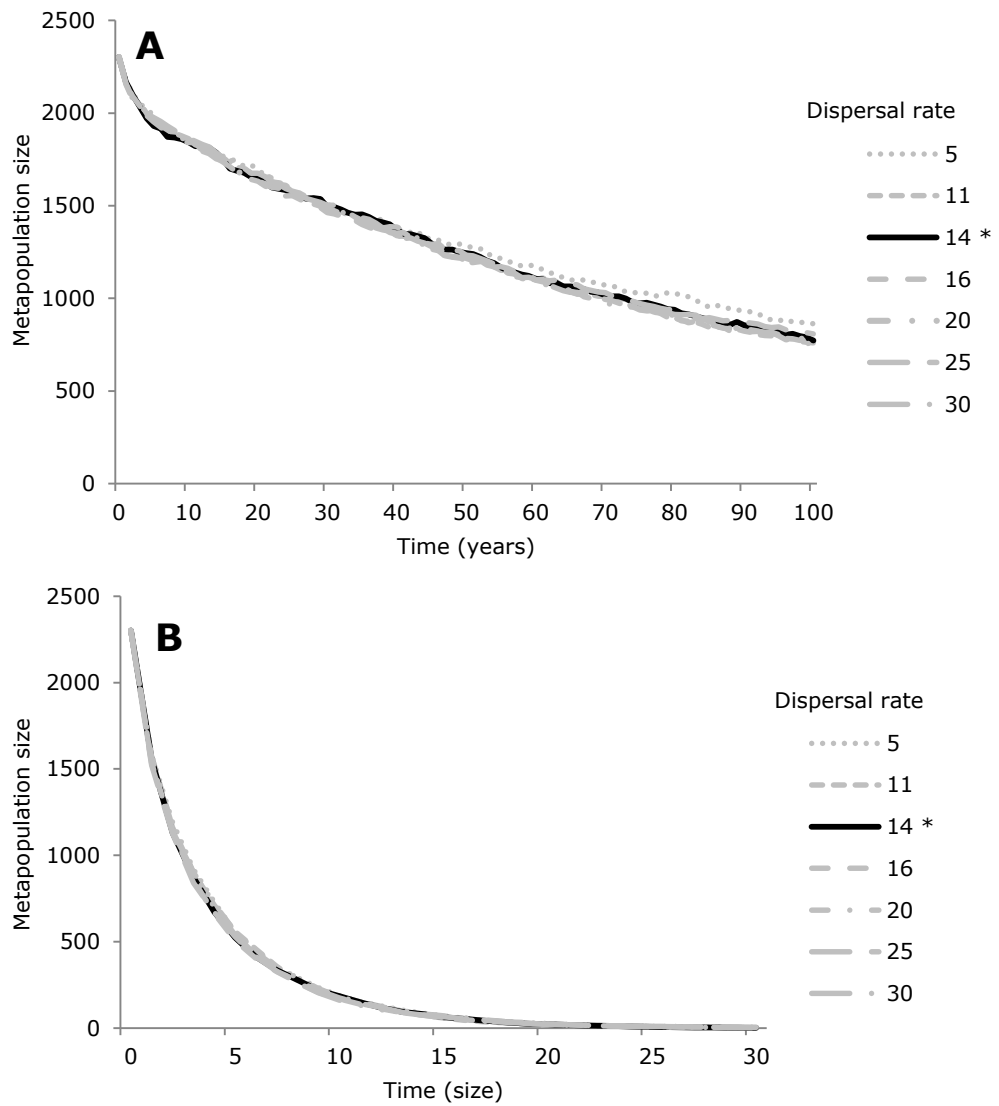
Figure 7.6. Metapopulation size of the Sinai Baton Blue butterfly simulated using Vortex varying the dispersal rates with each run. a) used the mortality rate of 88.7% whilst b) used a 93% mortality. * A dispersal rate of 14% was used in other simulations whilst the other rates are theoretical values.
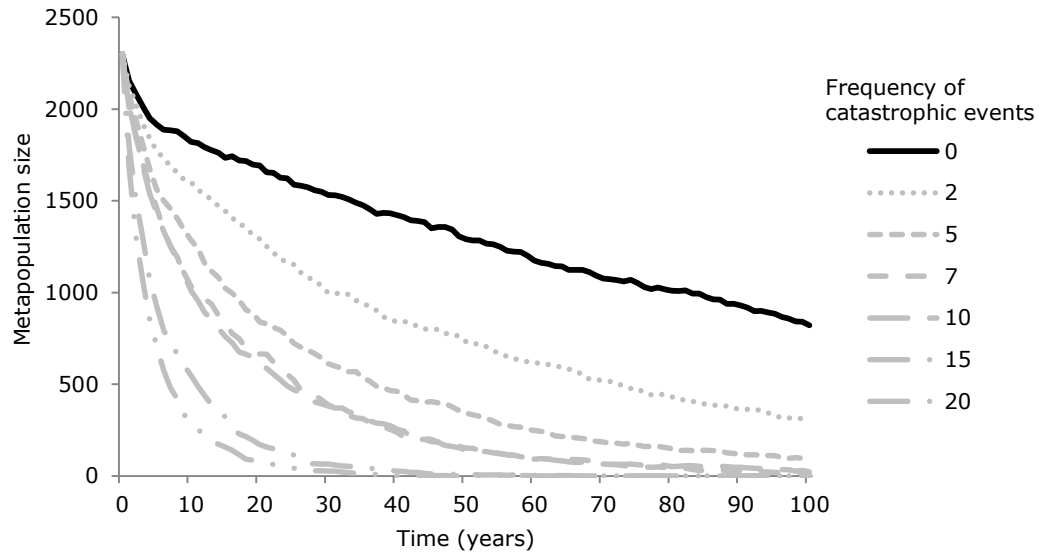
Figure 7.7. Metapopulation size of the Sinai Baton Blue butterfly simulated using Vortex over the next 100 years, varying the frequencies of catastrophic events with each run. The mortality rate was set at 88.7%. The black line shows a metapopulation without any catastrophic events.

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Chapter 8.

Future directions; passing on the Baton

Future directions; passing on the Baton

Biodiversity levels are currently decreasing at a faster rate than any historically recorded level (Thompson & Starzomski, 2007). The majority of predicted extinctions are accredited to anthropogenic climate change which acts synergistically with other threats, such as changes in land use, in speeding up extinction (Stork, 2010), with arid environments believed to be the most sensitive to anthropogenic climate change (Schwinning et al., 2004). Butterflies are increasingly vulnerable as they respond quickly to changes in land management and increased fragmentation, elevating their extinction risk (Heer et al., 2013). Each system will react differently to the future uncertainties of climate change, making it hard to predict future responses (Fronhofer et al., 2012): for example, specialist butterflies will be more restricted by fragmentation than generalists (Ye et al., 2013). As a consequence conservation strategies need to be tailored to the particular circumstances; generic management strategies will not be as successful. Poverty and poor biological guidance in developing countries can result in higher levels of habitat loss and higher extinction rates, with an estimated annual shortfall of $1.3 billion for the management of protected areas in developing countries (Bruner et al., 2004). This highlights the importance of quantitative appraisals to determine optimum conservation strategies (Fronhofer et al., 2012; Heer et al., 2013).

This study has advanced our understanding of the current threats to both the Sinai Baton Blue and the Sinai Thyme, and has gained sufficient data to register the butterfly as Critically Endangered on the IUCN Red List (Thompson & Gilbert, 2012). It has given us insight into population fluctuations over the past decade, during which there has been considerable environmental variation, particularly in rainfall. Water is the key limiting factor in many in arid environments (Pueyo et al., 2008), and consequentially there have been large inter-annual fluctuations in the quality of thyme (Fig. 8.1) from the butterfly's standpoint. Dams were built in Farsh Shoeib as a conservation effort in 2003 and have been successful in holding water in the patch after rainfall in 2010 and 2011, leaving parts of the patch submerged for over a week (Fig. 8.2). The dams stopped the fast surface run-off after irregular heavy rainfall, holding more water in the soil, increasing its availability for the thyme.

Conservation for the Sinai Baton Blue started in 2002 and has been solely focused within Farsh Shoeib. Monitoring the host plant in Farsh Shoeib has shown nearly 50% mortality since 2002, with the loss of smaller individuals. Presumably this happened by size-dependent mortality because smaller individuals had insufficient resources to survive consecutive dry years (Chapter 2; Hamerlynck & McAuliffe, 2008). This is alarming because it occurred in the only site where conservation measures have been enacted, suggesting that current conservation methods may be ineffective. We need to keep monitoring the thyme within Farsh Shoeib and also across other patches on the massif to see whether this exceptionally high mortality rate is replicated in other patches, and whether it is continuing in Farsh Shoeib.

Changing climate threatens interacting species, with some species responding differently to environmental cues, causing problems for insect herbivores where ecological success is correlated with the degree of synchrony (Powell & Logan, 2005; Phillimore et al., 2012). This is the case for the Sinai Baton Blue, with an already narrow window when the thyme is flowering and the larvae are present (James, 2006f). The flowering phenology of thyme appears to have large inter-annual fluctuations: there was a two-week shift noted between years, although the 2012 flowering season appears to be more condensed. The flight season of the butterfly seems to have remained relatively static amongst years; years when phenologies do not match will reduce available resources. It is, however, perhaps a good sign that flowering seems to be tracking the changing climate, as this will increase its ability to cope in comparison to species which do not exhibit phenotypic plasticity (Willis et al., 2008; Johansson et al., 2013). The butterfly seems to have had severe population cycles over the past decade, with the causes still unclear. It could be due to fluctuating levels of resources from the large temporal variations in thyme quality and density of inflorescences accompanied by varying degrees of asynchrony. It is good that the butterfly has so far successfully recovered from multiple crash years, perhaps a result of dispersal from neighbouring patches rescuing Farsh Shoeib from extinction. This highlights the importance of neighbouring patches and that conservation should be focused on a wider scale, not exclusively in Farsh Shoeib.

This study has highlighted the importance of the thyme: butterfly abundance is governed by the number of plants and their flowering, whilst patch connectivity appears to be insignificant (Chapter 4). This appears to be consistent with other studies, since bottom-up forces are often suggested to regulate community composition in arid environments; resource pulses alleviate competition, resulting in a corresponding boom in associated herbivores and pollinators (Schwinning et al., 2004; Letnic & Dickman, 2010). Increased resources will reduce larval competition, and this should have a larger fitness-enhancing impact on the population dynamics of short-lived herbivores with highly specific interactions, such as the Sinai Baton Blue (Ostfeld & Keesing, 2000; Boggs & Freeman, 2005; Kay et al., 2010). Larval habitat quality plays an important role in population dynamics in other butterfly species: increases in quality reduce the probability of extinction in many ways, including by attracting more migrating individuals (Thomas et al., 2011). The number of flowers significantly influences the Sinai Baton Blue's larval distribution, indicating that resources play a key role in offspring survivorship (Chapter 5). Ovipositing females also appear to avoid larval over-crowding, presumably with positive fitness consequences (Boggs & Freeman, 2005). This can direct future conservation with focus on improving the quality of the host plants, to increase the number of inflorescences and also the quantity of host plants to reduce over-crowding.

Population viability analysis has also highlighted the importance of management techniques aimed at increasing survivorship, especially of larvae since the highest mortality occurs during the larval stage (James, 2006b). Sensitivity analysis illustrated the positive effects of enhancing the carrying capacity; dispersal and hence connectivity did not affect the dynamics (Chapter 7). This suggests that conservation should be focused on improving the quality and abundance of plants within patches. Better habitats would be able to support larger populations which would generate more dispersing individuals, which in turn would enhance connectivity and flow amongst patches (Hodgson et al., 2009). It is often more efficient to focus conservation efforts on the patch level; it is cheaper and more successful to enhance what is already present, rather than to recreate additional corridor habitats (Hodgson et al., 2009, 2011). It can also be hard to estimate and then create an optimum level of structural connectivity (Hodgson et al., 2009, 2011); too little connectivity could

result in extinction, and too much could lead to high levels of patch synchrony (Koelle & Vandermeer, 2005). These uncertainties make it hard to focus conservation on connectivity, whereas the association between habitat area and population size is very general (Hodgson et al., 2009).

The results of artificial clipping and fertilisation do not show any negative effects on the thyme, suggesting that grazing may not be a threat to the species (Chapter 6). Sinai has large climatic fluctuations, with many years of little or no rainfall whilst some years have heavy rainfall and flash flooding. This suggests that there would have historically been large variations in available thyme flowers, and therefore the butterfly has clearly coped with these in the past. The Chiquibul forest of Belize has a high frequency of natural disasters and the butterfly species present appear to have adapted to such disturbances: experimental logging did not appear to affect butterfly assemblages (Lewis, 2001). Thus in the Sinai case, grazing within the boundaries of natural variation may not have any negative impacts on associated herbivores.

After the heavy rainfall in 2010 and 2011 the general vegetation in the area made an astonishing recovery from the extended drought, and consequentially there were more Bedouin women walking with their goatherds in the mountains to take advantage. In 2011 I noticed more Bedouin flocks upon the massif, but I saw no grazing damage to the thyme whilst there were obvious and considerable impacts on other plant species. This suggests that the Bedu may be correct in that goats find thyme unpalatable. The thyme also has favourable traits for coping with grazing and water stress, with their small flowers, seeds and leaves (Navarro et al., 2006), and other thyme species do benefit from grazing (Komac et al., 2011). Banning grazing may cause a shift in dynamics, changing the plant species composition, and the thyme may then lose its adaptive advantage and be outcompeted by grazing-intolerant plants (Knapp et al., 2012). It would be interesting to study the plant community composition upon the massif, to see whether there has been a shift in Farsh Shoeib to fewer grazing-tolerant species. Such a shift may have contributed to the high thyme mortality observed in Farsh Shoeib over the past decade.

To further our understanding of the species, we must continue monitoring both the thyme and the butterfly. Only through long-term monitoring will

we be better able to understand their interaction and how best to conserve them. We should therefore:-

> ➢ Continue regular surveying in Farsh Shoeib to follow the relative abundance of the butterfly.
> ➢ Record the flowering stages (sepals, bud or flowers) in Farsh Shoeib when surveying butterfly numbers; even a small sample size would enable us to match thyme flowering phenology to climate, and to study temporal synchrony between host plant and butterfly.
> ➢ Record density of inflorescences on 50 plants within Farsh Shoeib once a year to study the extent of resource fluctuations. Following resource levels, synchrony and butterfly numbers would materially help in identifying potential causes of fluctuations in butterfly numbers.
> ➢ Continue intermittent monitoring of the host plant (every few years) within Farsh Shoeib and other patches upon the massif to determine patterns of plant mortality rate upon the massif.

Conservation efforts should focus on improving the quality and condition of host plants within patches. We need to understand the causes of the high mortality and loss of condition in thyme plants. The quantity of thyme appears to be the key limiting factor for the Sinai Baton Blue: we need to focus on improving its abundance and health. This will have positive implications for both the Sinai Baton Blue and other co-existing species within the same system.

The local Bedouin have been living in the area for hundreds of years, accumulating a wealth of local knowledge which can help conserve the biodiversity of the Protectorate. Such knowledge was useful here in finding new patches of thyme and hence potential butterfly populations. I believe that Bedouin indigenous knowledge will prove vital in the battle to conserve Egypt's heritage. Western ideas and policies are often assumed to be correct, whilst the importance of local land management in creating and maintaining biodiversity is often downplayed or ignored (Chatty, 2006). One such Western myth is the perception of nature as untouched unpeopled land. In Syria, Westernised policies and untested assumptions have in the past held the Bedouin responsible for destroying the land, despite the lack of baseline data to prove any degradation had even occurred. As a result, in the 1960's the Bedouin were evicted from their

homes in order to 'rehabilitate' the land, but after four years of poor results they were allowed back to take over once again the safeguarding of the land. Unable to learn from their previous mistakes, within the next decade the government decided that stocking rates were too high, so once again the Bedouin were dispossessed without consultation (Chatty, 2006). With hindsight, it was only the decade with local cooperation in land management that led to successful conservation efforts; contradictory to predictions, no tragedy of the commons occurred (Chatty, 2006). There may be lessons to be learned that could be implemented in Sinai; perhaps the best conservation might result from encouraging, consulting and cooperating with the local Bedouin residents in maintaining and conserving the land, the bedrock essential for successful conservation.

Figure 8.1. Inter-annual fluctuations in the quality of thyme within Farsh Loza in a) May 2010

b) May 2012

Figure 8.2. A dam in Farsh Shoeib holding water inside the patch after heavy rainfall in May 2010 left sections submerged for more than a week.

Figure 8.3. A local Bedouin woman with her goat herd sheltering from the midday sun within Farsh Loza.

Figure 8.4. A herd of goats grazing in Upper Hammar.

Figure 8.5. Anthropogenic damage to a thyme plant in Farsh Loza, with the majority of the plant uprooted.

Figure 8.6 A discrete and isolated patch of thyme (Farsh Elia Circle).

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