_____

Metapopulations and the Sinai Baton Blue (*Pseudophilotes sinaicus* Nakamura): an introduction

Mike James
School of Biology, Nottingham University, Nottingham NG7 2RD

Patchy Populations

Most species on most spatial scales have a patchy distribution (Hanski & Gilpin 1997; Hanski 1999). Because species have evolved specific habitat requirements, only some habitats some of the time will provide the resources necessary for population persistence. The landscape is therefore complex, a mosaic of different habitat types changing in their quality over time.

On a large-scale, the patchy distribution of a species might occur because of the physical features of its landscape e.g. amphibians in small ponds (Sjögren Gulve 1994), or be a result of its history. Local breeding populations might be distributed in discrete habitat patches containing adequate resources; for example, the bog fritillary butterfly (*Proclossiana eunomia*) occurs only in the natural wet meadows in Belgium which contain its sole larval food plant, *Polygonum bistorta* (Baguette & Nève 1994). On a smaller-scale individuals may aggregate in response to the patchiness of resources within an area of suitable habitat; this is particularly the case for small species, or those with limited mobility. Patches may also be formed because of the spatial and temporal variation in the quality of the landscape elements (Wiens 1997).

In addition to naturally defined patches, human activities have directly altered the landscape, generally causing destruction of natural habitats, their increased fragmentation, and deterioration of habitat quality (Henle *et al.* 2004). Indirect human-induced factors, most notably global warming (Houghton *et al.* 2001), are also changing the quantity and quality of habitats available to many species (Parmesan *et al.* 1999; Thomas *et al.* 2001; Beever *et al.* 2003; Crozier 2003).

Thus for many species the world is becoming ever more patchy, and consequently an increasing number of species are gradually becoming more and more confined to networks of small habitat patches. This will have an effect on the size and connectivity of suitable habitat, and may also cause large changes in the physical environment (Saunders *et al.* 1991). The effects of habitat destruction and its impact on species survival in fragmented landscapes are likely to prove to be the greatest challenges to animal and plant conservation in the twenty-first century (Root *et al.* 2003; Travis 2003; Henle *et al.* 2004; Thomas *et al.* 2004).

Spatial considerations

Despite the real world being 'patchy', theoretical ecologists and population biologists had until recently considered populations to live in uniform environments (Wiens 2000). Traditional population models took no account of the heterogeneous environment in which the species lived, and assumed that populations were closed with only births and deaths contributing to population change (Hanski & Simberloff 1997). This was obviously an oversimplification because it overlooked the spatial aggregation of individuals and ignored the effect of immigration and emigration on the population. However, since the mid-1980's we have realised that the huge amount we know about within-population processes (births and deaths, competition and predation) needs to be augmented by between population processes (movement) (Hanski & Gilpin 1997). Indeed, in some (possibly many) situations the system is dominated by movement, e.g. the acorn woodpecker (*Melanerpes formicivorus*: Stacey & Taper 1992), the cougar (*Felis concolor*: Beier 1993), and Edith's checkerspot

butterfly (*Euphydryas editha*: Boughton 1999). Ecologists now recognise the importance of spatial considerations in understanding the processes that contribute to population regulation and long-term persistence. They recognise the usefulness of defining populations in the context of the discrete habitat patches they occupy, the dynamic nature of these biological units, and the influence of their interaction (Hanski & Gilpin 1997). Habitat fragmentation is likely to result in a non-random pattern of extinction among species because species are characterised by different levels of dispersal; the details are likely to depend on the taxa, habitats and regions considered (Thomas 2000). By increasing the isolation of remnant populations, fragmentation is likely to increase rates of local extinction whilst decreasing those of colonisation (Thomas *et al.* 1992). Indeed, spatial considerations now dominate ecology and population biology to the extent that some scientists regard it to be a new paradigm (Hanski & Simberloff 1997; Hanski 1999; Wiens 2000).

The metapopulation approach

The spatial structure of populations and its consequences for the behaviour of individuals and for population ecology, genetics, conservation and evolution, has provided the basis for much recent research (Thomas & Hanski 1997), which has developed the concept of the metapopulation (an assemblage of 'local' populations), originally proposed by Levins in 1969. This approach has provided significant insights into the importance of factors such as immigration and emigration, extinction, and randomness. It is unlike most of the past research on population dynamics and ecology because rather than focusing on single (usually large) populations, it studies the interactions of a group of local (often small) populations.

A metapopulation consists of extinction-prone local populations that survive in a stochastic balance between extinctions and colonisations. Metapopulation theory (Gilpin & Hanski 1991) assumes that the landscape consists of discrete habitat patches, each one potentially occupied by a distinct local population. These discrete breeding populations fluctuate asynchronously so extinctions do not occur at the level of the entire metapopulation. However, the local populations are connected to one another by migration so their dynamics are not entirely independent. Migration among discrete patches of suitable habitat has three main components: movement away from a patch (emigration), movement in the inhospitable matrix among patches (dispersal), and movement into a patch (immigration) (Ims & Yoccoz 1997). A colonist is an immigrant to an unoccupied patch that manages to reproduce successfully in that patch.

Thus, in addition to a healthy balance of births over deaths (within-patch processes), the role of movement among patches is now considered to be a vital component of the persistence of species occupying fragmented landscapes (Murdoch 1994; Hanski & Gilpin 1997). Any landscape structures that affect extinction and colonisation rates will affect population dynamics and persistence and, when combined with the characteristics of the local populations and characteristics of the inhabiting species, will determine the dynamics of the metapopulation.

The metapopulation approach has been applied to a wide variety of taxa, including arthropods (e.g. Caudill 2003; Bonte *et al.* 2003; Purse *et al.* 2003; Steffan-Dewenter 2003; Menéndez *et al.* 2002), fish (e.g. Armsworth 2003), amphibians (e.g. Sjögren Gulve 1994; Driscoll 1998; Rowe *et al.* 2000), mammals (e.g. Moilanen *et al.* 1998; Sweanor *et al.* 2000; Elmhagen & Angerbjörn 2001), and birds (e.g. Esler 2000; Hames *et al.* 2001; Inchausti & Weimerskirch 2002). However, as a model group of species, butterflies have played a dominant role in illuminating metapopulation dynamics, and studies involving them continue to stimulate and advance metapopulation biology (Thomas & Hanski 1997; Hanski 1999; Wahlberg *et al.* 2002a).

Butterfly metapopulations

Butterfly biologists have been particularly quick to utilise metapoplation theory because butterflies are probably the most well-studied and well-known of all invertebrates, and have been the subject of some of the most important research on the dynamics of natural populations (e.g. Ehrlich 1984). Butterfly populations are often structured in space in a manner that is generally consistent with the metapopulation concept (Thomas & Hanski 1997), and many species (Hanski & Kuussaari 1995; Thomas 1995) satisfy the four necessary conditions for metapopulation-level persistence proposed by Hanski *et al.* (1995); also rates of emigration and immigration are quick to be observable in reasonable time-scales. The metapopulation approach is also useful in conservation, and here again butterflies represent an important set of exemplars: they are high-profile species for conservation and have declined dramatically across much of their range (Hanski & Kuussaari 1995; Pullin 1995; Asher *et al.* 2001). Extinction processes important in butterflies are also important in many other taxa, and butterfly metapopulation studies have helped shift attention from the conservation of single populations towards a regional perspective. The need for this change in focus has been emphasised following the discovery that rare species often have extremely specific and subtle habitat requirements (Thomas 1991), meaning that many populations have been lost even from protected sites because of apparently minor habitat changes (Thomas 1995; Thomas & Hanski 1997; Hanski 1999).

The past decade has seen an explosion of metapopulation studies involving butterflies. A search of the title, keywords and abstract of articles on the ISI Web of Science§ between 1993 and the end of 2003 using the search term "butterfl* AND metapopulation" produced 197 articles (excluding work presented in this thesis). Of these, 74 did not have a butterfly species as the main study organism, did not involve aspects of a metapopulation study, or described general patterns / butterfly communities without detailing the butterfly species involved. The remaining 123 studies involved at least one species of butterfly as part of a metapopulation study; these studies are summarised in Table 1.1. The overriding pattern is the preponderance of studies involving species from northern temperate Europe (86%), dominated by work concerning species of fritillary in north-west continental Europe (e.g. Hanski *et al.* 2000; Wahlberg *et al.* 2002a,b; Schtickzelle *et al.* 2002), especially the Finnish population of the Glanville fritillary (*Melitaea cinxia*: Hanski *et al.* 1994,1995, 1996; Kuussaari *et al.* 1996; Drechsler *et al.* 2003), and in the UK the silver-studded blue (*Plebejus argus*: Thomas & Harrison 1992; Thomas *et al.* 1992; Lewis *et al.* 1997; Thomas *et al.* 2002). All of these studies concern the margins of the ranges of species with wide distributions.

Butterfly metapopulation studies have underlined the importance of spatial dynamics in explaining the occurrence and abundance of species, improved our knowledge of migration rates and distances, and increased our understanding of the effect of these on colonisation and extinction processes (Hanski 2003). Empirical studies have demonstrated that the number of dispersers reaching new habitats declines with distance from the source patch (Harrison 1989; Kuussaari *et al.* 1996; Wahlberg *et al.* 2002a), and that individuals emigrate disproportionately often from small areas with small populations and low habitat quality, factors which in nature are often interrelated (Hill *et al.* 1996; Sutcliffe *et al.* 1997; Petit *et al.* 2001). Migration into populations may postpone their extinction - the rescue effect (Brown & Kodric-Brown 1977; Hanski *et al.* 1995) - and patches of empty habitat may be (re)-colonised. Conversely, if emigration is too high from a small population this may increase the risk of extinction (Thomas & Hanski 1997).

Metapopulation studies have also greatly contributed to butterfly conservation (Hanski 1999). The design and successful application of spatially realistic models has highlighted key processes, such as distance-dependent colonisation and area-dependent extinction (Hanski 1994, 2003), and enabled us to predict the distribution of species in

fragmented landscapes (Hanski *et al.* 1996; Wahlberg *et al.* 1996). Recommendations for conservation and management have been made possible with the application of these models, for instance, predicting the likelihood of persistence under different scenarios of landscape change or under alternative management regimes (Wahlberg *et al.* 2002b), and more specifically identifying which patches in particular networks are critical for metapopulation survival (Ovaskainen & Hanski 2003), and which sorts of patch networks are required for long-term metapopulation persistence (Thomas & Hanski 1997). In some cases, conservation management based on metapopulation model predictions has now been initiated (Hanski 1999; Schtickzelle & Baguette 2004).

The Sinai Baton Blue butterfly

The Sinai Baton Blue butterfly, *Pseudophilotes sinaicus* Nakamura, is a narrow-endemic species occurring only in the high mountain region of the St. Katherine's Protectorate in South Sinai, Egypt. The species was discovered in 1974 (Nakamura 1975), and was seldom recorded again (let alone studied) until the start of my work in spring 2001. I chose to study this butterfly both as a model organism on which to apply the metapopulation approach, and more specifically for its intrinsic conservation value (James 2006a,b,c,d,e,f; James *et al.*, 2003; Hoyle & James, 2005).

The area around the town of St. Katherine is classified as being arid (<100 mm precipitation in an average year: Greenwood 1997), and is characterised by an extensive network of dry valleys (wadis) interspersed with high mountain peaks (up to 2,650 m) and ridges: a naturally fragmented landscape. These physical features form natural barriers to the dispersal of many species, consequently even areas that are relatively close to one another differ in subtle aspects of their ecology (Gilbert *et al.* 1996; Behnke *et al.* 2000, 2004; Zalat *et al.* 2001). The distribution of the Sinai Baton Blue is highly localised, mainly due to its dependence on its sole hostplant, Sinai Thyme (*Thymus decussatus* Benth.), which only grows in well-developed soils such as those found at the base of cliffs or in wadis (Nakamura 1975). Hence the thyme (and therefore the butterfly) has a patchy distribution in the mountainous landscape. The Baton Blue probably became isolated about 17,000 years ago at the end of the Würm glacial, but the restriction of its range is likely to be a more recent event (Nakamura 1975). Although human activities have undoubtedly altered its habitat, it is reasonable to assume that the species has existed in a patchy environment for all, or a large part of, its history. Nakamura (1975) also states that the butterfly is "sedentary", and is usually found "flying weakly" in the close vicinity of its hostplants which it "seldom leaves", suggesting that the species has limited powers of dispersal. Therefore this system provided an ideal opportunity for research to be undertaken in a metapopulation context.

With very few exceptions, other metapopulation studies have concentrated on species from the temperate zone (Table 1.1), and usually at or close to the northern limit of the range of species with wide distributions (e.g. Thomas & Jones 1993; Gutiérrez *et al.* 1999; Wahlberg *et al.* 2002a,b); fragmentation of suitable habitat in these regions has almost always been exacerbated by human activities. The narrow-endemic status of the Sinai Baton Blue means that its worldwide distribution is contained within a relatively small area, and so it was possible to study the species over its entire geographical range. This makes my research unique among metapopulation studies (see Table 1.1), and provides a valuable addition to previous work that has dealt with the distribution of species at a national (e.g. Hanski *et al.* 1994; 1995), regional (e.g.Thomas & Harrison 1992), or local scale (e.g. Lewis *et al.* 1997; Schtickzelle *et al.* 2001). My study system is also different to most other metapopulation studies because it deals with a species living entirely within a naturally fragmented ecosystem and in a very arid environment. Thus it advances our knowledge of the existence of

metapopulation processes and how they operate on endangered species from environments quite different to those in which metapopulation biology was developed and tested.

The St. Katherine's Protectorate is very little studied biologically and as such faces a severe lack of scientific information with which to develop an integrated management plan with scientifically based conservation objectives. Increasing pressure from settlement, rapidly expanding tourism (it is one of the world's most important cultural sites), and changing land-use practices by the native Bedouin compound this problem. The Sinai Baton Blue is of considerable conservation interest because:

1) it is one of only two endemic animals (both butterflies) in the St. Katherine's Protectorate, one of Egypt's most recently designated Protected Areas, and its newest UNESCO World Heritage Site. The butterfly's endemicity makes it a world conservation issue
2) it is one of the smallest butterflies in the world (Larsen 1990)
3) it is a flagship species for the area, highlighted as a priority for the Protectorate (St. Katherine Protectorate Management Unit, personal communication)
4) its only known larval hostplant, Sinai Thyme, is an IUCN Red List endangered plant (Walter & Gillet 1998), and is of great medicinal value (Batanouny 1999)

Table 1 Summary of studies involving at least one species of butterfly as part of a metapopulation study. Numbers reflect individual butterfly species used in the studies, not the number of studies

Family	Range of study species						Location of the study in relation to the whole range of the study species			
	Europe	N. America	S. America	Asia	Africa	Australasia	V. restricted	Limited	Most	Entire
Papilionidae	4	3	0	0	0	0	7	0	0	0
Pieridae	2	0	0	0	0	0	2	0	0	0
Lycaenidae	29	2	0	0	0	0	26	4	1	0
Nymphalidae	74	11	1	2	0	0	63	24	1	0
Hesperidae	6	0	0	0	0	0	6	0	0	0

The papers that follow are the result of three seasons of fieldwork undertaken during the spring and summer of 2001-2003. Together with James *et al* (2003) and Hoyle & James (2005), they form a series of linked papers describing the ecology and conservation of the Sinai Baton Blue butterfly in a metapopulation context.

In James *et al.* (2003) I described for the first time the known distribution of the Sinai Baton Blue, its local population sizes, and its hostplant. I attempted to understand its specific habitat needs, and this enabled me to characterise the network of patches of potential habitat in which the butterfly's distribution can be assessed throughout its known range and in which metapopulation processes might be operating. I also quantified the quality of habitat in each patch and used this to develop an index of habitat suitability applicable to every patch. Using this knowledge I determined why patches of apparently suitable habitat were unoccupied and tried to understand the distribution of its local population sizes. This enabled me to assess whether or not a metapopulation approach is informative when applied to the entire known range of this narrow-endemic species living in an arid environment.

Successful conservation policies and ecological theory require that the specific habitat requirements of a species are correctly identified and understood. During the fieldwork, it became apparent that not all the area of every thyme patch was being utilised, with butterflies sometimes only ever being seen in restricted parts of patches. Therefore in James (2006b), I

refined further the characteristics of the habitat occupied by Sinai Baton Blues, assessing their habitat requirements at the resolution of the individual plant. This study prompted the first-ever examination of myrmecophily in this species, and demonstrated that a very subtle and perhaps surprising factor was important to its survival and therefore influential in its distribution at a very local scale.

Quantifying abundance and determining the factors affecting it are critical to understanding and conserving small animal populations. In fragmented landscapes, information on local demographic processes (births and deaths), and the transfer of individuals among the network of habitat patches, are required when studying metapopulation dynamics (Hill *et al.* 1996; Hanski 1999; Thomas & Kunin 1999). Thus in James (2006c), I studied seasonal dynamics in one of the largest local populations of the Sinai Baton Blue. Using data representing virtually every individual present on every day during the adult flight season, I determined recruitment, the survival rate, the sex ratio, and the total adult population size, both within a season and between two seasons.

Migration of individuals among patches is a key process in metapopulation biology, so in James (2006d) I estimated the number of immigrants into and emigrants from a patch, and how and why these numbers change over time. This illustrates whether or not patches of habitat delimit the butterfly's local populations, and whether there is sufficient transfer of individuals among them to enable their long-term persistence: a fact of fundamental importance to a species surviving in a metapopulation. In James (2006e) I investigated movement of individuals within a patch of habitat, and quantify how sedentary the butterfly really is. I determined some of the environmental factors that affect its local movement, and examined whether these are altered by its age, sex or size. I asked whether factors determining how far individuals move within a patch, were related to factors influencing dispersal among patches.

Continued human-induced habitat destruction and predicted future increases in temperature (Houghton *et al.* 2001) mean that many patch networks are not static. Thus conservation biology needs to be able to predict metapopulation persistence in dynamic patch networks reliably, and so provide solutions for the conservation of rare and endangered species in both the short- and long-term. In Hoyle & James (2005) we modelled the metapopulation dynamics of the entire known network of habitat patches of the Sinai Baton Blue. We examined the effects of differential habitat destruction (from livestock grazing and over-collection by humans) on metapopulation persistence against a background of habitat change likely to be imposed by global warming. This was the first study to use a metapopulation model to investigate these effects, and also the first to examine their interaction using empirical data over the entire range of a species. The three habitat degradation scenarios modelled are realistic management problems faced by the St. Katherine's Protectorate Management Unit, and are applicable to many other species living in dynamic and fragmented landscapes.

Finally, in James (2006f) I present a detailed account of the natural history of the Sinai Baton Blue using data from all three field seasons. It starts with an introduction to the genus and reviews current knowledge of its species and their phylogeny. This emphasises the paucity of knowledge surrounding the butterfly and related species, and highlights the general differences in its ecology compared with other species used in metapopulation studies. This is followed by a description of all stages of the life cycle, including its larval stages (which have never before been described). I have also included considerable quantitative data relating to adult size that can be used to determine whether it really is the 'smallest butterfly in the world'. I then provide an account of behaviour with particular reference to subjects not covered in other papers, for example activity patterns, mating, and oviposition behaviour. It

includes a series of colour photographs that illustrate the habitus and aspects of its behaviour and ecology.

REFERENCES

Armsworth PR (2002) Recruitment and limitation, population regulation, and larval connectivity in reef fish metapopulations. *Ecology*, 84: 1092-1104 .

Asher J, Warren M, Fox R, Harding P, Jeffcoate G & Jeffcoate S (eds) (2001) The millennium atlas of butterflies in Britain and Ireland. Oxford University Press, Oxford.

Baguette M & Nève G (1994) Adult movements between populations in the specialist butterfly *Proclossiana eunomia* (Lepidoptera, nymphalidae). *Ecol. Entomol.*, 19: 1-5.

Batanouny KH (1999) Wild Medicinal Plants in Egypt. Palm Press, Cairo, Egypt.

Behnke JM, Barnard CJ, Mason N, Harris PD, Sherif NE, Zalat S & Gilbert FS (2000) Intestinal helminths of spiny mice (*Acomys cahirinus dimidiatus*) from St Katherine's Protectorate in the Sinai, Egypt. *J. Helminthol.*, 74: 31-44.

Behnke JM, Harris P, Bajer A, Barnard CJ, Sherif N, Cliff L, Hurst J, Lamb M, Rhodes A, James M, Clifford S & Gilbert FS (2004) Variation in the helminth community structure in spiny mice (*Acomys cahirinus dimidiatus*) from four montane wadis in the St.Katherine region of the Sinai Peninsula in Egypt. Parasitology (In Press).

Beever EA, Brussard PF & Berger J (2003) Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. *J. Mammal.*, 84: 37-54.

Beier P (1993) Determining minimum habitat areas and habitat corridors for cougars. *Conserv. Biol.*, 7: 94-108.

Bonte D, Lens L, Maelfait JP, Hoffman M & Kuijken E (2003) Patch quality and connectivity influence spatial dynamics in a dune wolfspider. *Oecologia*, 135: 227-233.

Boughton DA (1999) Empirical evidence for complex source-sink dynamics with alternative states in a butterfly metapopulation. *Ecology*, 80: 2727-2739.

Brown JH & Kodric Brown A (1977) Turnover rates in insular biogeography: effects of immigration on extinction. *Ecology*, 58: 445-449.

Caudill CC (2003) Empirical eveidence for non-selective recruitment and a source-sink dynamic in a mayfly metapopulation. *Ecology*, 84: 2119-2132 .

Crozier L (2003) Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris*. *Oecologia*, 135: 648-656.

Drechsler M, Frank K, Hanski I, O'Hara RB & Wissel C (2003) ranking metapopulation extinction risk: from patterns in data to conservation management decisions. *Ecol. Appl.*, 13: 990-998 .

13

Driscoll DA (1998) Genetic structure, metapopulation processes and evolution influence the conservation strategy for two endangered frog species. *Biol. Conserv.*, 83: 43-54.

Ehrlich PR (1984) The structure and dynamics of butterfly populations. The biology of butterflies (eds RI Vane Wright & PR Ackery), pp. 25-40. Academic Press, London.

Elmhagen B & Angerbjörn A (2001) The applicability of metapopulation theory to large mammals. *Oikos*, 94: 89-100.

Esler D (2000) Applying metapopulation theory to conservation of migratory birds. *Conserv. Biol.*, 14: 366-372.

Gilpin M & Hanski I (eds) (1991) Metapopulation dynamics: empirical and theoretical investigations. Academic Press, London.

Gilbert F, Willmer P, Semida F, Ghazoul J & Zalat S (1996). Spatial variation in a plant-pollinator system in the wadis of Sinai, Egypt. *Oecologia*, 108: 479-487.

Greenwood NH (1997) The Sinai: A physical geography. Univ. Texas Press, Austin, Texas.

Gutiérrez D, Thomas CD & León Cortés JL (1999) Dispersal, distribution, patch network and metapopulation dynamics of the dingy skipper butterfly (*Erynnis tages*). *Oecologia*, 121: 506-517.

Hames RS, Rosenberg KV, Lowe JD & Dhondt AA (2001) Site reoccupation in fragmented landscapes: testing predictions of metapopulation theory. *J. Anim. Ecol.*, 70: 182-190.

Hanski I (1994) A practical model for metapopulation dynamics. *J. Anim. Ecol*. 63: 151-162.

Hanski I (1999) Metapopulation Ecology. Oxford University Press, Oxford

Hanski I (2003) Biology of extinctions in butterfly metapopulations. Butterflies: Ecology and Evolution taking Flight (eds CL Boggs, WB Watt & P R Ehrlich), pp. 577-602. University of Chicago Press, Chicago.

Hanski I & Kuussaari M (1995) Butterfly metapopulation dynamics. Population dynamics: New approaches and synthesis (eds N Cappuccino & PW Price), pp. 149-171. Academic Press, London.

Hanski I & Gilpin M (eds) (1997) Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press, London.

Hanski I & Simberloff D (1997) The metapopulation approach, its history, conceptual domain, and application to conservation. Metapopulation Biology: Ecology, Genetics and Evolution (eds I Hanski & ME Gilpin), pp. 5-26. Academic Press, London.

Hanski I, Kuussaari M & Niemenen M (1994) Metapopulation structure and migration in the butterfly *Melitae cinxia*. *Ecology*, 75: 747-762.

Hanski I, Pakkala T, Kuussaari M & Lei G (1995) Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos*, 72: 21-28.

Hanski I, Moilanen A, Pakkala T & Kuussaari M (1996) The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Conserv. Biol.*, 10: 578-590.

Hanski I, Alho J & Moilanen A (2000) Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology*, 81: 239-251.

Harrison S (1989) Long-distance dispersal in the bay checkerspot butterfly. *Ecology*, 70: 1236-1243.

Henle K, Lindenmayer DB, Margules CR, Saunders DA & Wissel C (2004) Species survival in fragmented landscapes: where are we now? *Biodivers. Conserv.*, 13: 1-8.

Hill JK, Thomas CD & Lewis OT (1996) Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *J. Anim. Ecol.*, 65: 725-735 .

Houghton JT, Ding Y, Dai X, Griggs DJ, Johnson CA, Maskell K, Noguer M & van der Linden PJ (eds) (2001) Climate Change 2001: The Scientific Basis. Contribution of Working Group 1 to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge .

Hoyle M & James M (2005) Global warming, human population pressure and viability of the world's smallest butterfly. *Conservation Biology* 19(4): 1113-1124.

Ims RA & Yoccoz NG (1997) Studying transfer processes in metapopulations: emigration, migration and colonization. Metapopulation Biology: Ecology, Genetics and Evolution (eds I Hanski & ME Gilpin), pp. 247-265. Academic Press, London.

Inchausti P & Weimerskirch H (2002) Dispersal and metapopulation dynamics of an oceanic seabird, the wandering albatross, and its consequences for its response to long-line fisheries. *J. Anim. Ecol.*, 71: 765-770.

James, M. (2006b) Interactions among species in a tri-trophic system: the influence of ants on the distribution of the Sinai Baton Blue butterfly. *Egyptian Journal of Biology* 8: 17-26

James, M. (2006c) Demographic processes in a local population: seasonal dynamics of the Sinai Baton Blue butterfly. *Egyptian Journal of Biology* 8: 27-38

James, M. (2006d) Immigration and emigration in the Sinai Baton Blue butterfly: estimates from a single patch. *Egyptian Journal of Biology* 8: 39-50

James, M. (2006e) Intra-patch movement in the Sinai Baton Blue butterfly: influence of micro-habitat and individual characteristics. *Egyptian Journal of Biology* 8: 51-66

James, M. (2006f) The natural history of the Sinai Baton Blue: the smallest butterfly in the world. *Egyptian Journal of Biology* 8: 67-85

James M, Gilbert F & Zalat S (2003) Thyme and isolation for the Sinai Baton Blue butterfly (*Pseudophilotes sinaicus*). *Oecologia*, 134: 445-453.

Kuussaari M, Niemenen M & Hanski I (1996) An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia. J. Anim. Ecol.*, 65: 791-801.

Larsen TB (1990) The Butterflies of Egypt. Apollo Books, Svendborg, Denmark.

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Amer.*, 15: 237-240 .

Lewis OT, Thomas CD, Hill JK, Brookes MI, CraneTPR, Graneau YA, Mallet JLB & Rose OC (1997) Three ways of assessing metapopulation structure in the butterfly *Plebejus argus. Ecol. Entomol*., 22: 283-293.

Menéndez R, Gutiérrez D & Thomas CD (2002) Migration and Allee effects in the six-spot burnet moth *Zygaena filipendulae. Ecol. Entomol.*, 27: 317-325.

Moilanen A, Smith AT & Hanski I (1998) Long-term dynamics in a metapopulation of the American Pika. *Am. Nat*., 152: 530-542.

Murdoch WW (1994) Population regulation in theory and practice Ecology, 75: 271-287.

Nakamura I (1975) Descriptions of two new species of butterflies (Lepidoptera, Lycaenidae) from the South Sinai. *J. Entomol*. 44(B): 283-295.

Ovaskainen O & Hanski I (2003) How much does an individual habitat fragment contribute to metapopulation dynamics and persistence? *Theor. Popul. Biol.*, 64: 481-495.

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennett WJ, Thomas JA & Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399: 579-583.

Petit S, Moilanen A, Hanski I & Baguette M (2001) Metapopulation dynamics of the bog fritillary butterfly: movements between patches. *Oikos*, 92: 491-500.

Pullin AS (ed.) (1995) Ecology and Conservation of Butterflies. Chapman and Hall, London.

Purse BV, Hopkins GW, Day KJ & Thompson DJ (2003) Dispersal characteristics in a rare damselfly. *J. Anim. Ecol.*, 40: 717-728.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C & Pounds A (2003) Fingerprints of global warming on wild animals and plants. *Nature*, 421: 57-60.

Rowe G, Beebee TJC & Burke T (2000) A microsatellite analysis of natterjack toad, *Bufo calamita*, metapopulations. *Oikos*, 88: 641-651.

Saunders DA, Hobbs RJ & Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol*., 5: 18-32.

Schtickzelle N & Baguette M (2004) Metapopulation viability analysis of the bog fritillary butterfly using RAMAS/GIS. *Oikos*, 104: 277-290.

Schtickzelle N, Le Boulengé E & Baguette M (2002) Metapopulation dynamics of the bog fritillary butterfly: demographic processes in a patchy population. *Oikos*, 96: 349-360.

Sjögren Gulve P (1994) Distribution and extinction patterns within a northern metapopulation case of the pool frog, *Rana lessonae. Ecology*, 75: 1357-1367.

Stacey PB & Taper ML (1992) Environmental variation and the persistence of small populations. *Ecol. Appl.*, 2: 18-29.

Steffan Dewenter I (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conserv. Biol.*, 17: 1036-1044.

Sweanor LL, Logan KA & Hornocker MG (2000) Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conserv. Biol.*, 14: 798-808.

Sutcliffe OL, Thomas CD & Peggie D (1997) Area-dependent migration by ringlet butterflies generates a mixture of patchy population and metapopulation attributes. Oecologia, 109: 229-234.

Thomas CD (1995) Ecology and conservation of butterfly metapopulations in the fragmented British landscape. Ecology and Conservation of Butterflies (ed. AS Pullin), pp. 46-63, Chapman and Hall, London.

Thomas CD (2000) Dispersal and extinction in fragmented landscapes. *Proc. R. Soc. Lond*. 267(B): 139-145.

Thomas CD & Harrison S (1992) Spatial dynamics of a patchily distributed butterfly species. *J. Anim. Ecol.*, 61: 437-446.

Thomas CD & Jones TM (1993) Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges: lessons for conservation in a fragmented landscape. *J. Anim. Ecol.*, 62: 472-481.

Thomas CD & Hanski I (1997) Butterfly metapopulations. Metapopulation Biology: Ecology, Genetics and Evolution (eds I Hanski & ME Gilpin), pp. 359-386. Academic Press, London.

Thomas CD & Kunin WE (1999) The spatial structure of populations. *J. Anim. Ecol.*, 68: 647-657.

Thomas CD, Thomas JA & Warren MS (1992) Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia*, 92: 563-567.

Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M & Conradt L (2001) Ecological and evolutionary processes at expanding range margins. *Nature*, 411: 577-581.

Thomas CD, Wilson RJ & Lewis OT (2002) Short-term studies underestimate 30-generation changes in a butterfly metapopulation. *Proc. R. Soc. Lond*. 268(B): 1791-1796.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega Huerta MA, Peterson AT, Phillips OL & Williams SE (2004) Extinction risk from climate change. *Nature*, 427: 145-148.

Thomas JA (1991) Rare species conservation: case studies of European butterflies. The scientific management of temperate communities for conservation (eds I Spellenberg, B Goldsmith & MG Morris), pp. 149-197. Blackwell, Oxford.

Travis JMJ (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc. R. Soc. Lond*. 270(B): 467-473.

Wahlberg N, Moilanen A & Hanski I (1996) Predicting the occurrence of endangered species in fragmented landscapes. *Science*, 273: 1536-1538.

Wahlberg N, Klemetti T, Selonen V & Hanski I (2002a) Metapopulation structure and movements in five species of checkerspot butterflies. *Oecologia*, 130: 33-43.

Wahlberg N, Klemetti T & Hanksi I (2002b) Dynamic populations in a dynamic landscape: the metapopulation of the marsh fritillary butterfly. *Ecography*, 25: 224-232.

Walter KS & Gillett HJ (eds) (1998) 1997 IUCN Red List of threatened plants. Complied by the World Conservation Monitoring Centre. IUCN – The World Conservation Union, Gland, Switzerland & Cambridge, UK.

Wiens JA (1997) Metapopulation dynamics and landscape ecology. Metapopulation Biology: Ecology, Genetics and Evolution (eds I Hanski & ME Gilpin), pp. 43-62. Academic Press, London.

Wiens JA (2000) Ecological heterogeneity: an ontogeny of concepts and approaches. The ecological consequences of environmental heterogeneity (eds MJ Hutchings, EA John & AJA Stewart). Blackwell Science, Oxford.

Zalat S, Semida F, Gilbert F, El Banna S, Sayed E, El-Alqamy H, Behnke J (2001) Spatial variation in the biodiversity of Bedouin gardens in the St Katherine Protecorate, South Sinai, Egypt. *Egypt. J. Biol.*, 3: 147-155.