Global Warming, Human Population Pressure, and Viability of the World's Smallest Butterfly

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Abstract: *The effects of climate change and habitat destruction and their interaction are likely to be the greatest challenge to animal and plant conservation in the twenty-first century. We used the world's smallest butterfly, the Sinai baton blue (*Pseudophilotes sinaicus*), as an exemplar of how global warming and human population pressures may act together to cause species extinctions. We mapped the entire global range of this butterfly and obtained extensive data on the intensity of livestock grazing. As with an increasing number of species, it is confined to a network of small habitat patches and is threatened both by indirect human-induced factors (global warming) and by the direct activities of humans (in this case, livestock grazing and collection of medicinal plants). In the absence of global warming, grazing, and plant collection, our model suggested that the butterfly will persist for at least 200 years. Above a threshold intensity of global warming, the chance of extinction accelerated rapidly, implying that there may be an annual average temperature, specific to each endangered species, above which extinction becomes very much more likely. By contrast, there was no such threshold of grazing pressure—the chance of extinction increased steadily with increasing grazing. The impact of grazing, however, decreased with higher levels of year-to-year variation in habitat quality. The effect of global warming did not depend on the future level of grazing, suggesting that the impacts of global warming and grazing are additive. If the areas of habitat patches individually fall below certain prescribed levels, the butterfly is likely to go extinct. Two patches were very important for persistence: if either were lost the species would probably go extinct. Our results have implications for the conservation management of all species whose habitats are at risk because of the direct activities of humans and in the longer term because of climate change.*

Key Words: grazing, habitat fragmentation, incidence-function model, Lycaenidae, metapopulation, *Pseudophilotes*, Sinai

Calentamiento Global, Presión de la Población Humana y Viabilidad de la Mariposa más Pequeña del Mundo

Resumen: *Probablemente, los efectos del cambio climático y de la destrucción del hábitat y su interacción son el mayor reto para la conservación de animales y plantas en el siglo veintiuno. Utilizamos a la mariposa más pequeña del mundo,* Pseudophilotes sinaicus*, como ejemplo de cómo pueden actuar conjuntamente el calentamiento global y las presiones de la población humana para causar la extinción de especies. Elaboramos un mapa de la distribución global de esta mariposa y obtuvimos datos copiosos sobre la intensidad del apacentamiento de ganado. Como sucede con muchas especies, está confinada a una red de pequeños parches de hábitat y esta amenazada tanto por factores inducidos indirectamente por humanos (calentamiento global) como por actividades humanas directas (en este caso, apacentamiento de ganado y recolección de plantas medicinales). En ausencia de calentamiento global, apacentamiento y recolecta de plantas, nuestro modelo sugirió que la mariposa persistirá por lo menos 200 años. Por encima de una intensidad umbral de calentamiento global, la probabilidad de extinción se aceleró rápidamente, lo que implica que puede haber una temperatura media anual, específica para cada especie amenazada, sobre la cual la extinción es más probable. En contraste, no hubo tal umbral de presión de apacentamiento— la probabilidad de extinción aumenta*

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constantemente con el incremento de apacentamiento. Sin embargo, el impacto de apacentamiento decreció con niveles mayores de variación anual en la calidad del hábitat. El efecto del calentamiento global no dependió del nivel de apacentamiento en el futuro, lo que sugiere que los impactos del calentamiento global y del apacentamiento son aditivos. Si las áreas de parches de hábitat caen individualmente bajo ciertos niveles prescritos, es probable que la mariposa se extinga. Dos parches fueron muy importantes para la persistencia: si ambos desaparecieran la especie probablemente se extinguiría. Nuestros resultados tienen implicaciones para la conservación de todas las especies cuyo hábitat esta en riesgo debido a las actividades directas de humanos y, en el largo plazo, debido al cambio climático.

Palabras Clave: apacentamiento, fragmentación del hábitat, Lycaenidae, metapoblación, modelo función-incidencia, *Pseudophilotes*, Sinai

Introduction

Human activities have directly altered the landscape, substantially destroying and fragmenting natural habitats. Indirect human-induced factors, most notably global warming (Easterling et al. 1997; Watson et al. 1998), are also changing the quantity and quality of habitats available to many species. The majority of range shifts in the northern hemisphere have been in a northward direction in response to environmental change (Parmesan et al. 1999), and climate change may have forced one mammal, the American pika (*Ochotona princeps*), to move to higher elevations in search of suitable habitat (Beever et al. 2003). Consequently, an increasing number of species are becoming confined to networks of small habitat patches.

Currently, the most popular approach to studying populations in fragmented landscapes is based either on population viability analysis (e.g., Ball et al. 2003; Grimm et al. 2003; Schultz & Hammond 2003; Bergman & Kindvall 2004) or on the metapopulation concept (Gilpin & Hanski 1991; Hanski 1994; Hanski & Gilpin 1997). A metapopulation approach has been applied to a variety of taxa (e.g., Esler 2000; Elmhagen & Angerbjörn 2001) and to many conservation strategies (e.g., Lindenmayer & Possingham 1996; Gonzalez et al. 1998; Schtickzelle & Baguette 2004).

Many species inhabit early successional habitats, so their network of suitable habitat patches changes with time (Stelter et al. 1997; Hanski 1999; Johnson 2000; Wahlberg et al. 2002). But relatively few metapopulation studies (e.g., Amarasekare & Possingham 2001; Akçakaya et al. 2004) have focused on species occupying patch networks that are dynamic as a result of disturbance. This is surprising given that continued (direct) habitat destruction and predicted future increases in temperature (Houghton et al. 2001) mean that many patch networks are not static. Thus, we need to be able to reliably predict metapopulation persistence in dynamic patch networks and so provide solutions for the conservation of rare and endangered species over the short and long term.

Spatially realistic models allow quantitative predictions to be made for particular metapopulations and are useful tools for managers trying to conserve species inhabiting fragmented landscapes. The incidence-function model (IFM; Hanski 1994) is a stochastic patch occupancy model, which describes how the processes of local extinction and recolonization of empty habitat patches are related to patch areas and isolation. Researchers using this model have tested its predictive ability (Wahlberg et al. 1996) and its power when faced with hypothetical management problems (Drechsler et al. 2003), evaluated its assumptions (Eber & Brandl 1996; Conradt et al. 2000), or compared it with other models that attempt to reconcile ecological theory and conservation practice (Wiegand et al. 2003). These researchers have concluded that the model is a useful tool in conservation ecology, but it has been applied directly only to conservation for northern temperate species with wide distributions (e.g., the butterflies *Melitaea diamina* [Wahlberg et al. 1996], *M. cinxia* [Moilanen & Hanski 1998], and *Euphydryas aurinia* [Wahlberg et al. 2002] and the mammal *Ochotona princeps* [Moilanen et al. 1998]).

We used the IFM on the entire known range of an endangered, narrow-endemic species living at high elevation in an arid environment and in a metapopulation structure (James et al. 2003; James 2004). Such a species allows one to examine the effects on metapopulation persistence of differential habitat destruction in a network of habitat patches against a background of habitat change likely to be imposed by global warming. Anthropogenic climate change is likely to be a major cause of extinctions in the near future (Thomas et al. 2004), and the effects of climate change and habitat destruction and their interaction are likely to be the greatest challenge to animal and plant conservation in the twenty-first century (Root et al. 2003; Travis 2003). Our study is the first we know of to use a metapopulation model to investigate these effects and the first to examine their interactions based on empirical data collected over the entire range of a species.

We simulated the metapopulation dynamics of the Sinai baton blue butterfly (*Pseudophilotes sinaicus*) throughout its known range. The butterfly has a highly localized distribution mainly because of its dependence on Sinai thyme (*Thymus decussatus* Benth.: Labiatae), which

occurs as discrete patches in the mountains (James et al. 2003). The patch network is likely to be dynamic as a consequence of disturbance: patches are differentially affected by grazing (Alqamy et al. 2003), threatened by global warming (Watson et al. 1998; Houghton et al. 2001; Ragab & Prudhomme 2002), and at risk of being extirpated because of overcollection for medicinal purposes (Batanouny 1999; GEF 2000). These variables will affect the spatial pattern and size of the butterfly's habitat and are problems managers face with many species elsewhere that live in dynamic and fragmented landscapes. This butterfly is of considerable conservation interest because (1) it is one of only two endemic animals in the St. Katherine's Protectorate (one of Egypt's most recently designated protected areas and its newest World Heritage Site); (2) it is probably the world's smallest butterfly (minimum forewing length 6.25 mm); (3) it is a flagship species for the area highlighted as a priority for the protectorate (St. Katherine's Protectorate Management Unit [SKPMU], M.J., personal communication); and (4) its only known larval host plant, Sinai thyme, is on the World Conservation Union (IUCN) Red List of Endangered Plants (Walter & Gillett 1998) and is of great medicinal value (Batanouny 1999; GEF 2000). Specifically, we investigated the expected persistence time of the baton blue metapopulation under the following scenarios: direct human-induced habitat destruction caused by grazing, indirect human-induced habitat destruction caused by global warming, and random loss of individual patches caused by medicinal plant collectors.

Methods

Study System

St. Katherine's Protectorate is in south Sinai (Egypt) and is dominated by mountain peaks (to 2650 m) and dry valleys. The Sinai baton blue has been recorded only from a small area of the protectorate and probably occurs only above 1500 m, where Sinai thyme grows (Fig. 1). It has one generation per year, with adults present from mid April to early July.

The species fulfills all conditions necessary to exist as a metapopulation (Hanski et al. 1995). It lives in discrete habitat patches, and local populations are small (the largest contains approximately 500 individuals; James et al. 2003) and so face a significant risk of extinction. Most individuals remain in their natal patch of thyme, but the degree of interpatch movement (emigration from patch
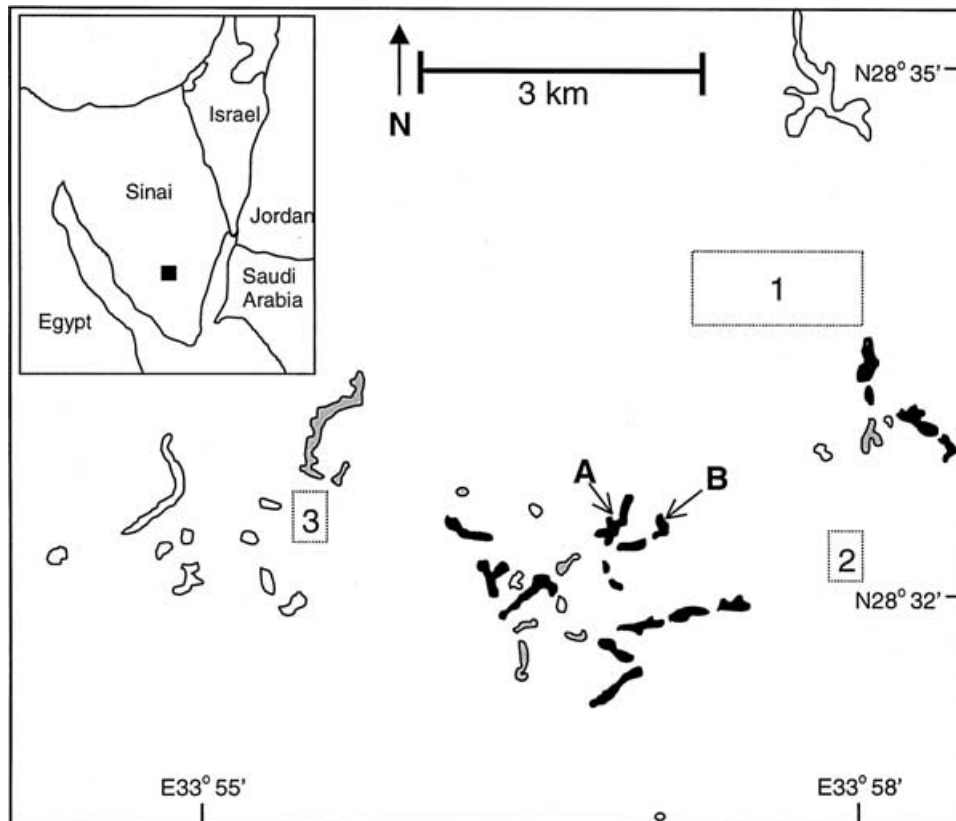

Figure 1. Location of Sinai thyme in St. Katherine's Protectorate. Black shapes represent patches in which a Sinai baton blue colony was present; open shapes represent patches of thyme in which a colony was absent in 2001; grey shapes represent patches in which a colony was present in 2001 but not in 2003. The geographical size (exaggerated for clarity) and shape of the habitat patches are shown. Patch sizes do not represent the amount of Sinai thyme because the density of thyme varies among patches. Patches A and B are important to metapopulation persistence. Numbered boxes are the main settlements in the area (size of the box indicates relative size of each settlement): 1, town of St. Katherine; 2, Wadi Arbaein; 3, Wadi Zuwetein.

estimated at 14%; James 2004) is sufficient for the species to persist as a metapopulation, and migration appears to be distance dependent (the probability of patch occupancy falls significantly with increasing patch isolation) (James et al. 2003).

Sinai thyme grows in areas of well-developed soil above 1500 m. It has a patchy distribution but can be locally abundant. Patches are well delimited from the surrounding environment and are usually bordered by steep, bare cliffs. They are often separated from one another by ridges or mountains. Butterflies rarely move more than 40 m in or between days (James 2004); hence, we defined a thyme patch as an area of thyme separated from any other area of thyme by more than 100 m. Locations of patches were established using a global positioning system (GPS 12 MAP; Garmin, Kansas, U.S.A.) accurate to +10 m and were recorded at the center of each patch. The butterfly has an intimate relationship with Sinai thyme, so rather than measuring the physical area of these patches, we recorded the amount of thyme present in each patch (average surface area of 58 m^2 of thyme per patch) (James et al. 2003).

In May and June 2001 (coinciding with the main flight period), we surveyed the entire network of suitable habitat patches. Each patch was visited at least twice, with one or more visits occurring within a week of the day of peak adult emergence (approximately end of May). Adults are conspicuous, fly weakly around thyme plants, and are easy to detect. If two or more butterflies were seen in a patch at any time, then a breeding colony was defined as present. Hence, we are confident that patches observed to be empty were not in fact occupied. To ascertain the size of the breeding colony in each patch, we performed either transect counts or mark-recapture experiments (James et al. 2003).

We repeated the survey in 2003, a time that coincided with the worst drought in the last 50 years (personal communication with Bedouin experts). Numbers of baton blues were dramatically lower in 2003 than in 2001 (85% fewer; M.J., unpublished results), and thyme plants were much reduced in area.

The Model

We used the IFM (Hanski 1994; Hanski et al. 1995; Moilanen et al. 1998), implemented in the stochastic patch occupancy model simulator (SPOMSIM, Moilanen 2004), to model the butterfly's long-term population dynamics. Data requirements of the model match the data obtainable, and the model is robust and has been successfully used to model the population dynamics of many species, most of them butterflies (Hanski et al. 1995; Wahlberg et al. 1996; Moilanen et al. 1998).

The IFM models the presence or absence of a species in each habitat patch of a metapopulation, ignoring local population dynamics. The probability of occupancy of patch i at time t, $p_i(t)$ depends on the colonization $C_i(t)$ and extinction E_i probabilities in that patch:

$$p_i(t) = \frac{C_i(t)}{C_i(t) + E_i - C_i(t)E_i}, \qquad (1)$$

where E_i is assumed to be a function of population size in patch i. This function in turn is assumed to be related to patch area A_i by a power function. Hence,

$$E_i = \frac{u}{A_i^x}, \qquad (2)$$

where u and x are parameters. The colonization probability $C_i(t)$ of an empty patch is described by the sigmoid function of the connectivity of patch i, $S_i(t)$:

$$C_i(t) = \frac{S_i(t)^2}{S_i(t)^2 + y^2}, \qquad (3)$$

where y is a parameter and

$$S_i(t) = \sum_{i \neq j} p_j(t) \exp(-\alpha d_{ij})A_j^b, \qquad (4)$$

where a is a parameter determining the effect of distance on colonization, d_{ij} is the distance between the centers of patches i and j, and b is a parameter that transforms patch area to expected population size (Hanski et al. 2000).

Essential data include patch area, patch position, and one or more butterfly presence/absence snapshots (Hanski 1994; Ter Braak et al. 1998). Important assumptions of the model are that the probability of local extinction depends on population size via patch size (Eq. 2); migration is distance dependent (Eq. 4); and the spatial structure of the landscape is allowed for (Eq. 4). The baton blue metapopulation satisfies the important requirements of the IFM (Hanski 1994): the network of local populations conforms to the characteristics of a metapopulation; the metapopulation is at quasi-equilibrium (i.e., the "typical" dynamic state of the metapopulation before eventual extinction, where colonization and extinction probabilities for all patches do not vary over time) (Hanski 1994; Moilanen 1999; Moilanen 2000); there are at least 30 habitat patches (we had 41); the fraction of occupied patches at equilibrium is between 0.2 and 0.8 (0.6 in 2001); and there is considerable variation in patch size and isolation (true in this case).

With sufficient information, patch area can be corrected for spatially varying habitat quality (Hanski & Ovaskainen 2000). In a previous study (James et al. 2003), we demonstrated the importance of certain environmental variables (amount of shelter, size of individual thyme plants, diversity of other plant species) when describing habitat for the butterfly and used these variables to calculate an index of patch quality. If variation in habitat quality is linearly related to population density (possibly after a suitable transformation), the simplest way to incorporate patch-specific habitat quality is to multiply the patch area

by a scaled quality measure (Hanski 1994). Habitat quality could have an important influence on metapopulation dynamics for certain species or in particular landscapes (Moilanen & Hanski 1998). Thus, we defined the adjusted patch area (A_{adj}) as

$$A_{adj} = AQ^k, \qquad (5)$$

where A is the unadjusted patch area, Q is the patch quality index (James et al. 2003), and k is a constant. The parameter b (Eq. 4) is best estimated from patch population sizes (Moilanen et al. 1998). Here, we used the statistics package "R" (Ihaka & Gentleman 1996) to estimate both b and k from a linear regression of log(population size) versus log(A) and log(Q), from Eq. 5.

The Sinai baton blue inhabits an arid landscape and is not closely related to butterfly species previously investigated with the IFM. Thus parameters a, x, u, and y were estimated from our data. The SPOMSIM allows for two parameter-estimation methods: nonlinear regression and Monte Carlo methods (Moilanen 1999). Although presence and absence data were recorded for both 2001 and 2003 (an exceptionally dry year), only the 2001 data were used for the presence-absence model input because in 2003 low baton blue numbers meant that the probability of obtaining "false zeros" was unacceptably high. The SPOMSIM cannot implement the Monte Carlo method with only a single patch-occupancy snapshot with estimated turnover rates (A. Moilanen, personal communication); hence, we used the nonlinear regression method. With only one snapshot, it is necessary to supply an estimate of the number of turnover events (patch extinctions and colonizations) per year (A. Moilanen, personal communication). Between 2001 and 2003 there were 8 turnover events, all extinctions (Fig. 1). Because 2003 was so dry, 8 turnovers is likely to represent a maximum number of extinctions in 2 years. The sensitivity of other parameter estimates to the turnover rate was modeled based on a range of 1–12 turnover events per year, each with four runs of 4800 function evaluations.

An estimate must be provided of the probability that a given patch is observed to be empty but is in fact occupied (false zero). We set this probability to zero because the butterflies are highly visible and each patch in the network was surveyed intensively at least twice. Each survey of the same patch yielded the same result (i.e., 00 or 11).

Regional stochasticity, σ, is the year-to-year temporal variation in patch area or quality affecting all patches simultaneously (Hanski 1991). It is affected by the weather and is especially likely to be significant in arid environments. The greater the correlation in population sizes, the lower the expected persistence time of the metapopulation (Moilanen 1999). The SPOMSIM cannot estimate regional stochasticity, so it is incorporated by multiplying patch areas in each year with a standard $\log_{10}$ normally distributed variable with variance σ^2 (Moilanen et al. 1998). The general formula for the cumulative distribution function of the standard lognormal distribution is $F(x) = \Phi(\frac{\log(x)}{\sigma})$, where Φ is the cumulative distribution function of the standard normal distribution. To assess the impact of the 2003 drought on thyme plants, we counted the number of inflorescences on every thyme plant in one large patch and compared this number with the number of inflorescences counted on the same plants the previous year. In the drought year the number of inflorescences was reduced on average by 40%. Hence, setting $x^* = 1 - 0.4 = 0.6$ and $F(x^*) = 1/50$, our best estimate of regional stochasticity was $\sigma \cong 0.1$. Because σ was estimated with only limited data, we used a range of σ values (0, 0.1, 0.2, 0.4) for some simulations to test for sensitivity.

Habitat Degradation Processes

One hundred simulations were iterated on the patch network (with the parameter values in Table 1), assuming no future change in habitat patch areas. We modeled three

Table 1. Parameter values for the incidence-function model used to analyze the population dynamics of the Sinai baton blue compared with values from other butterfly studies.[a]

	Butterfly			
Parameter[b]	Pseudophilotes sinaicus *(this study)*	Melitaea cinxia *(Hanski et al. 1996)*	Melitaea diamina *(Wahlberg et al. 1996)*	Euphydryas aurinia *(Wahlberg et al. 2002)*
b	0.58	0.5	0.5	—[d]
x	1.50	0.952	0.884	1.30
α^c	0.85	1	1.0	0.42
y^c	3.72	4.04	3.62	4 and 48.13
u^c	0.01	0.01	0.014	0.08
σ	0.1	0–0.5	—[d]	—[d]

[a] *Values were estimated from the 2001 patch occupancy assuming the metapopulation was in quasi-stationary equilibrium. Distances used to generate parameter values were measured in kilometers.*
[b] *See Eqs. 1–4 for parameter definitions.*
[c] *Highly species and landscape specific (A. Moilanen, personal communication).*
[d] *Not published.*

factors that would alter the spatial structure of the network of habitat patches available to the butterfly: grazing, global climate change, and random loss of patches.

GRAZING

Bedouin have inhabited the area continuously for the last 1500 years (Hobbs 1995). Today, most families keep a small herd of goats and sheep. The high price of fodder means the herd is usually completely sustained by grazing. In the last 70 years, the Bedouin tribe living in St. Katherine's Protectorate (the *Jabaliya*) has undergone dramatic changes. Their population has more than tripled (from 400 to 1200 between 1930 and 1980; between 1980 and 1989 the number of families increased by 50% [Hobbs 1995]), and their lifestyle has switched from pastoral seminomadism to one that is largely sedentary. Their settlements are based in St. Katherine's town and a few smaller outlying settlements (Fig. 1) (Perevelotsky et al. 1989; GEF 2000). This has meant a shift in patterns and intensity of land use. Based on data from GPS-tagged livestock (Alqamy et al. 2003), the SKPMU quantified present-day grazing pressure: the closer a habitat patch is to the settlements and the lower (nonlinearly) the elevation, the higher the grazing pressure.

We converted this information into relative grazing pressure for each habitat patch (γ_i for patch i). Then the future effect of grazing on all patches was expressed by a single parameter, grazing intensity (GR), which is directly proportional to the local human population. A value of zero implied no change in future patch areas compared with 2001. At GR = 0.04, all but two patches were destroyed, and at GR = 1 all patches were destroyed. The area of patch i, already adjusted for patch quality, was then adjusted for grazing intensity: $(A_{\mathrm{adj}})_i(1 - \gamma_i\mathrm{GR})$. We used a GR in the range of 0 to 0.008 because this provided a complete range of extinction probabilities.

GLOBAL CLIMATE CHANGE

The average temperature in the Middle East has increased by approximately 0.7° C over the last 100 years, and climate models project temperatures in the region will increase another 1–2° C by 2050, although changes in precipitation are unlikely to be significant (Watson et al. 1998; Houghton et al. 2001; Ragab & Prudhomme 2002). An increase in temperature can affect species in several ways. For example, the density of a species may change at given locations as it becomes able to occupy new areas within its metabolic temperature tolerances. In the past few decades many butterfly species have shifted their range poleward (Hill et al. 1999; Parmesan et al. 1999), and species of butterflies and plants have expanded their range up an elevational gradient (Grabherr et al. 1994; Klanderud & Birks 2003; Konvica et al. 2003). Global warming may also cause changes in the timing of events

(phenology) that rely on temperature-related cues (e.g., migration, flowering, or egg laying). Root et al. (2003) demonstrated a consistent temperature-related shift in a wide variety of species of plants and animals: in the temperate zone the spring phenology of events (e.g., breeding, flowering) is now an average of 5 days earlier than a decade ago. These phenological responses are greatest at higher latitudes (which have warmed more than lower latitudes in the past century), and they suggest that species will react more strongly in other areas where temperature changes are large (e.g., at high elevations).

Because it is difficult to predict the response of Sinai baton blue and Sinai thyme to such warming, we modeled the effect of global warming simply by reducing the area of every thyme patch by a certain proportion: the global warming intensity (GW). This is the most likely scenario in Sinai, where thyme is already restricted near mountain tops. Each value of global warming intensity corresponds to a future average annual temperature. This parameter varied from zero (no effect of global warming) to unity (complete destruction of all patches), and six equidistant levels from 0 to 1.0 were used. The area of patch i with GR and GW factored in was calculated as $(A_{\mathrm{adj}})_i(1 - \gamma_i\mathrm{GR})(1 - \mathrm{GW})$. Thus, any combination of GR and GW corresponded to an area of thyme per habitat patch. The patch areas were assumed to change instantly, not gradually (see Discussion). The key differences between these two parameters were that (1) global warming, but not grazing, reduced patch area by the same proportion; and (2) as grazing intensity increased, patches were steadily eradicated. Conversely, patches were removed only when global warming reached the maximum value.

Twenty simulations were performed for each combination of regional stochasticity (0, 0.1, 0.2, 0.4), grazing intensity (0, 0.002, 0.004, 0.006, 0.008), and global warming intensity (0, 0.2, 0.4, 0.6, 0.8, 1). The resulting metapopulation extinctions and survivals were modeled by logistic regression, with predictors being these three variables and all second- and third-order terms and interactions. In the model it is not possible to introduce the degradation of the habitat patches resulting from grazing and global warming in a gradual fashion over time (A. Moilanen, personal communication). So we had to subject the metapopulation to a shock, with an instantaneous decrease in patch area.

RANDOM LOSS OF PATCHES

The disappearance of medicinal plant species has become a problem in Egypt due largely to overzealous harvesting by medicinal plant wholesalers and academic institutions (GEF 2000). Rough surveys have estimated that more than 100 species of plants have disappeared from the St. Katherine Protectorate in the last 10 years as a result of unmanaged human activity (GEF 2000). Because

Sinai thyme is used as a medicinal plant by the Bedouin and can also fetch high prices when sold in Cairo, it is highly threatened by overcollection (GEF 2000). A realistic scenario is the complete eradication of one or more patches of Sinai thyme because of the medicinal value of this plant. Modeling the effect of the loss of a single patch to the persistence of the butterfly metapopulation provides a measure of the importance of each patch to the metapopulation network.

We modeled the impact of the loss of individual patches on metapopulation persistence and proportion of habitat patches occupied after 200 years as a function of grazing and global warming intensities separately, assuming the best estimate of regional stochasticity $\sigma = 0.1$. Only the 12 patches remaining at a grazing intensity of 0.008 were considered. Twenty simulations for each patch singly removed were repeated for GW = 0, GR = 0 to 0.008, and GR = 0, GW = 0 to 1. Then logistic regressions were performed on the number of metapopulation extinctions and survivals and on the average number of patches occupied, with habitat patch as a factor and the linear and quadratic grazing or global warming intensities as covariates. The logistic algorithm for the probability of metapopulation extinction as a function of global warming intensity did not converge, so we used a model that was transformed to arc-sine square root.

Results

The estimated parameter values for the IFM (Table 1) were similar to those used in other butterfly studies, which gave us more confidence in our estimates, especially because we used only one presence-absence snapshot. Parameter *b*, which connects patch area to expected patch population size, was on the boundary of the normal range of 0.1–0.5 for butterflies (Moilanen & Nieminen 2002). The exponent *k*, which connects the unadjusted and adjusted patch areas, was 3.63. The number of turnover events was not critical for parameter estimation (as in Wahlberg et al. 2002) because parameter estimates obtained from 1-12 turnover events did not differ significantly (within the 95% confidence limits) from those reported in Table 1.

Given our best estimate of regional stochasticity ($\sigma = 0.1$), no global warming, and no increase in grazing, the metapopulation persisted for at least 200 years (probability of metapopulation extinction <0.01) (Fig. 2, point $*$). The probability of metapopulation extinction within 200 years increased with regional stochasticity squared (i.e., with the variance of the log-normal distribution of year-to-year patch area), increased linearly with grazing intensity and with global warming intensity squared, and decreased with the interaction between regional stochasticity and grazing intensity (Fig. 2, Table 2). There was no interaction between regional stochasticity and global warming
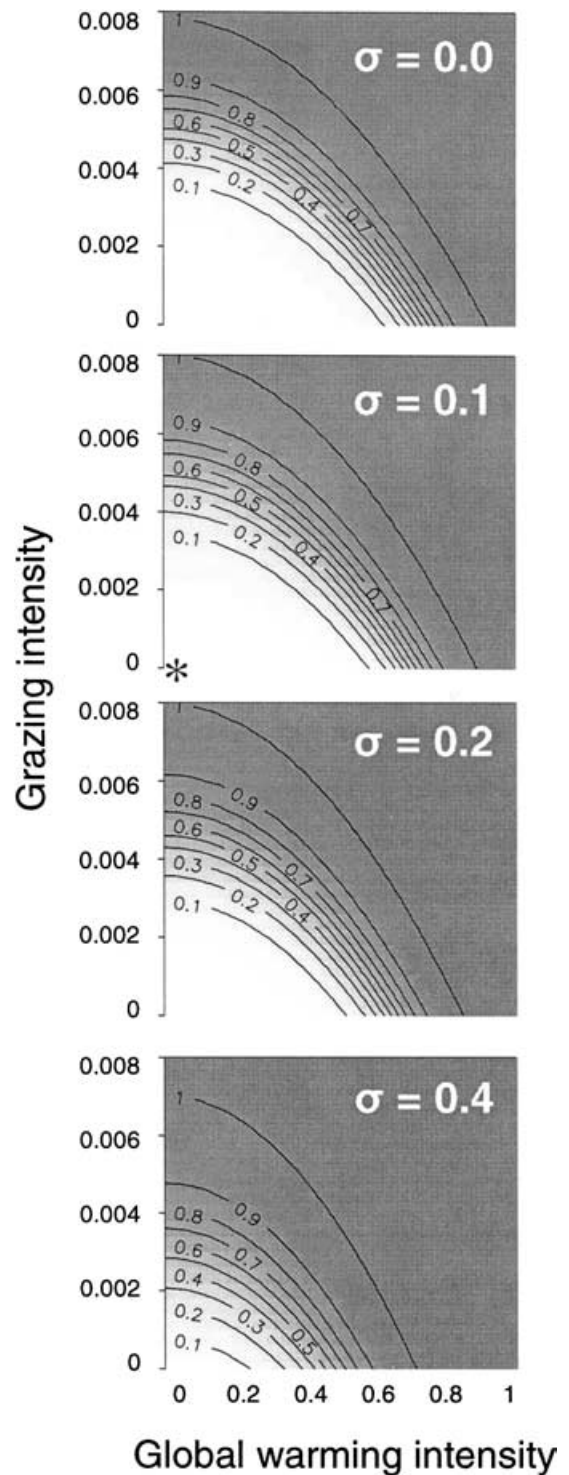

Figure 2. Effect of global warming and grazing intensities and regional stochasticity (σ) on the probability of extinction (numbers on contours: 0.1 to 1 from bottom to top) of the Sinai baton blue butterfly metapopulation within 200 years. See Table 2 for significance of parameter values. At the origin ($*$) (i.e., best estimate of σ, no future change in global warming and grazing intensities), the metapopulation will persist with high probability.

Table 2. Significance of intensities of global warming (GW), grazing (GR), regional stochasticity (σ), and second-order interactions on the extinction probability of the Sinai baton blue butterfly within 200 years, based on logistic regression (Fig. 2).[a]

Statistical term	χ^2_1[b]	Significance	Influence on extinction probability	Interpretation
σ	na	na	+	na
GW	1.30	ns	ns	effect of GW not linear
GR	na	na	+	na
σ : GW	0.49	ns	ns	effect of GW not dependent on σ
σ : GR	9.02	$p < 0.005$	-	effect of grazing decreases with increasing σ
GW : GR	0.13	ns	ns	effect of GW not dependent on grazing
σ^2	6.18	$p < 0.05$	+	effect of σ quadratic
$(GW)^2$	935	$p < 0.005$	+	effect of GW quadratic
$(GR)^2$	<0.00	ns	ns	effect of grazing not quadratic

[a]*No third-order term (not shown) was significant. Terms were deleted from the maximal to the minimum adequate model. Abbreviations: na, values are not shown because the σ: GR term was significant; ns, not significant; p > 0.05.*
[b]*The reduction in deviance after single-factor deletion is distributed as χ^2_1.*

intensity (because the two effects were perfectly correlated) or between grazing and global warming intensities. Given our best estimate $\sigma = 0.1$ and no effect of global warming, the metapopulation was safe for only small increases in grazing intensity, and the extinction probability rose in a linear fashion for larger increases (above 0.004). With no increase in grazing, the metapopulation extinction probability was substantially affected by a global warming index above 0.6. Above a threshold (whose precise value was defined by the grazing intensity and regional stochasticity) the chance of extinction accelerated (Fig. 2, Table 2).

Individual removal of two patches (A and B) at grazing intensities of above 0.004 greatly increased the chance of metapopulation extinction (Fig. 3). Individual removal of the other patches increased the metapopulation extinction risk by only a small amount. Metapopulation extinction probability and proportion of patches occupied were nonlinearly related to global warming intensity (Table 3). Occupancy was nonlinearly related to grazing intensity, but the chance of metapopulation extinction was linearly related. The importance of habitat patches to metapopulation persistence and occupancy varied significantly with grazing but not with global warming intensity (Fig. 3, Table 3). The interactions between habitat patch and the quadratic intensity terms were not significant, and the interaction between patch and grazing was not significant for the metapopulation extinction probability but highly significant for the proportion of patches occupied.

Discussion

There is some evidence that thyme patches vary in quality and position over time (James et al. 2003). If so, the pattern of patch occupancy for 2001 reflects not only patch connectivity and area, as assumed by the IFM, but also the past history of patch positions and sizes. Unfortunately there are no data regarding the past distribution of

the Sinai baton blue, which means it is impossible to be sure that the metapopulation is at stochastic equilibrium (another important assumption of the IFM). In recently deteriorated landscapes, species may be doomed to extinction but have not yet had time to go extinct (Diamond 1972). But the butterfly has inhabited the area since at least 1974, and Nakamura (1975) believes it was first collected in St. Katherine's (and misidentified) in 1942. He suggests that the species probably became isolated about 17,000 years ago (at the end of the Würm glacial) but that the restriction of its range is a much more recent event.

Three types of error commonly occur in metapopulation data sets, and all can cause significant biases in parameter estimates (Moilanen 2002): patch area may be misestimated, patches observed to be empty may in fact be occupied, and suitable habitat patches may be undetected. We accurately measured patch area by recording the size of individual thyme plants in each patch, and each patch was searched intensively for butterflies at least twice during the peak flight period, minimizing the likelihood that our data were affected by these inaccuracies. Missing patches are likely to be small and on the perimeter of the patch network (Moilanen 2002); hence, they are unlikely to affect our modeling predictions substantially. The stochastic patch occupancy model simulator did not allow us to introduce a gradual change in patch areas, so we were forced to change patch areas instantaneously. Such a shock to the metapopulation would probably merely bring forward the new quasi-stable equilibrium state in time. It is unlikely, then, that this method affected our conclusions.

The best estimate of regional stochasticity was calculated using data from the reduction in area of a single habitat patch between 2002 (a normal year) and 2003 (the dry year). All other patches were assumed to be affected to the same extent because all local populations of the butterfly fell by similar percentages between 2001 (another normal year) and 2003 (personal observation). The degree of environmental correlation among patches,
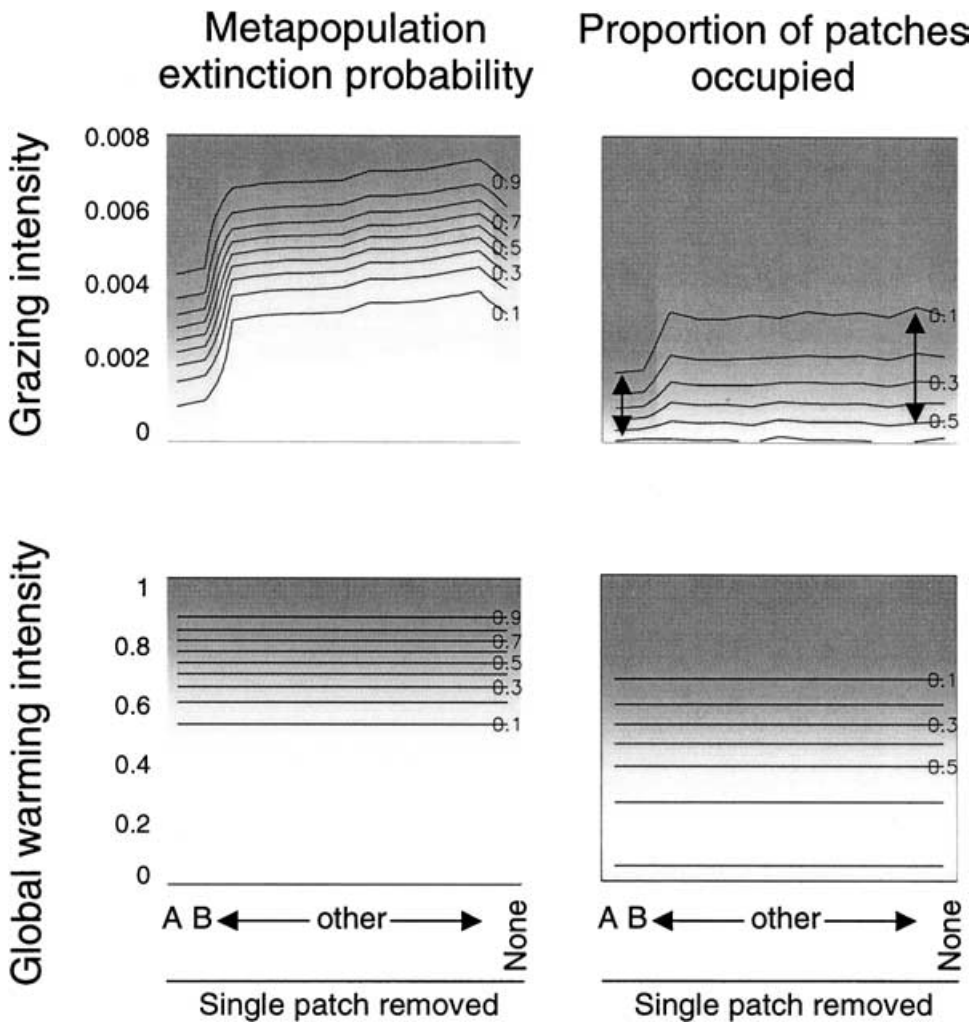
Figure 3. Effect of removal of single patches of Sinai thyme as a function of grazing and global warming intensity (σ = 0.1) on the probability of extinction of the Sinai baton blue butterfly metapopulation within 200 years (numbers on contours: 0.1 to 1 from bottom to top) and on patch occupancy (numbers on lines: 0.9 to 0.1 from bottom to top). The x-axis represents the patches in rank order of decreasing influence on metapopulation persistence, culminating in a value for no patches deleted. The effect of grazing on the proportion of patches occupied varied according to which single patch was removed and is displayed graphically by the difference in lengths of the double-arrow lines.

however, may in fact be low because of their varying elevational range (1825 to 2600 m) and the extremely localized weather (e.g., rainfall) characteristic of mountain landscapes. The simulations show that the degree of regional stochasticity strongly influences metapopulation extinction, so because of the uncertainty in its value, it is wise to be cautious in suggesting exact probabilities of metapopulation extinction.

Implications for Conservation

If global warming and grazing intensities do not increase in the future, the model predicts that the metapopulation will persist for at least 200 years. The metapopulation extinction probability, however, was nonlinearly related to regional stochasticity. Hence, if regional stochasticity has been underestimated the chance of extinction

Table 3. Effect of removal of a single patch of Sinai thyme on the probability of extinction of the Sinai baton blue butterfly metapopulation and proportion of all 41 patches occupied at 200 years (assuming σ = 0.1) by (1) setting global warming intensity = 0 and varying the grazing intensity and (2) setting grazing intensity = 0 and varying the global warming intensity, based on either logistic regression or transformation to arc-sine square root (see Fig. 3).*

Habitat patch factor	Linear	Quadratic	Linear interaction with patch	Quadratic interaction with patch
Metapopulation extinction probability				
1 $\chi^2_{12} = 358, p < 0.005$	$\chi^2_1 = 998, p < 0.005$	$\chi^2_1 = 2.45$ ns	$\chi^2_{12} = 18.4$ ns	$\chi^2_{12} = 12.1$ ns
2 $F_{1,26} = 0.17$ ns	$F_{1,62} = 258, p < 0.005$	$F_{1,62} = 76.5, p < 0.005$	$F_{12,26} = 0.04$ ns	$F_{12,26} = 0.10$ ns
Proportion of patches occupied				
1 $\chi^2_{12} = 41.8, p < 0.005$	$\chi^2_1 = 1810, p < 0.005$	$\chi^2_1 = 8.57, p < 0.005$	$\chi^2_{12} = 71.2, p < 0.005$	$\chi^2_{12} = 0.89$ ns
2 $\chi^2_{12} = 1.22$ ns	$\chi^2_1 = 237, p < 0.005$	$\chi^2_1 = 173, p < 0.005$	$\chi^2_{12} = 0.21$ ns	$\chi^2_{12} = 0.43$ ns

Terms were deleted from the maximal to the minimum adequate model. No third-order term was significant. Abbreviation: ns, not significant.

rises rapidly. For any level of regional stochasticity, the metapopulation extinction probability was relatively unaffected by global warming when its intensity was below about 0.2. Above 0.2, however, global warming became increasingly influential. This is an important result because it indicates that the persistence of a metapopulation may be nonlinearly related to the intensity of global warming. In particular, as the level of global warming increased its impact on metapopulation extinction accelerated rapidly, implying that there may be an annual average temperature, specific to each endangered species, above which extinction becomes much more likely.

In contrast, there was no such threshold of grazing pressure. In the short term, grazing intensity is likely to increase more quickly than global warming intensity. Given the best estimate of regional stochasticity, no effect of global warming, and no loss of entire patches because of overharvesting, the metapopulation was safe for grazing intensities of <0.004. Between grazing intensities of 0.004 to 0.006, however, the metapopulation extinction probability rose rapidly from 0.1 to 0.9 in a linear fashion. It is impossible to predict the future intensity of grazing. Any combination of grazing and global warming intensities corresponds to a predicted area of thyme per habitat patch. Therefore, if the areas of thyme fall to a certain level (corresponding to a grazing intensity of 0.004), then the metapopulation (and so the butterfly) is likely to go extinct within 200 years. The probability of extinction can be estimated by inspection of Fig. 2, which provides management with a useful tool for conservation. Managers can estimate the chance of extinction simply by measuring the areas of thyme patches. If this probability is unacceptably high, they can recommend a reduction in grazing pressure.

Two patches were important to metapopulation persistence because they had high quality indices, were located at high elevation (hence relatively unaffected by grazing), and contained a large amount of thyme. Best estimates indicated that if either of these two patches were to be lost (in the absence of global warming and at a grazing intensity of 0.004), there would be an 80% chance of metapopulation extinction within 200 years, compared with only about 20% when any other single patch is removed. Furthermore, there was virtually no increase in extinction probability on removal of any other single patch. Neither the chance of metapopulation extinction nor the occupancy varied significantly according to which single patch was removed for varying global warming and assuming no effect of grazing because global warming was assumed to have the same impact on all patches.

The effect of grazing and global warming on the chance of metapopulation extinction did not depend on which single patch was removed. The same was true for the effect of varying global warming on the occupancy. But the proportion of occupied patches was much more sensitive to grazing intensity on removal of either of the two

important patches than for the other patches. As grazing intensity increased, the metapopulation persisted with high probability (approximately 90%) even when the proportion of occupied patches was very low (approximately 10%). The two important patches sustained the metapopulation even at high grazing intensities because they were proportionally less affected by grazing (they are at high elevation and relatively far from settlements). They were less able to sustain the metapopulation with increasing global warming, however, because they were affected by global warming to the same degree as the other patches.

Hanski (1994) cautions that the IFM's predictions are more likely to be qualitatively rather than quantitatively accurate because the model requires little data. Hence, the model can be used to rank scenarios of future landscape change to identify the best of a range of management strategies (Wahlberg et al. 1996; Moilanen 2000; McCarthy et al. 2003).

We have used the world's smallest butterfly as an exemplar of how global warming and human population pressures may act together to cause species extinctions. Thus, we studied a real system in urgent need of conservation to provide a clear and practical example of the importance of studying climate change and other stresses, in particular habitat destruction, by themselves and concomitantly.

Acknowledgments

Literature Cited

Akçakaya, H. R., V. C. Radeloff, D. J. Mladenoff, and H. S. He. 2004. Integrating landscape and metapopulation modelling approaches: viability of the Sharp-tailed Grouse in a dynamic landscape. Conservation Biology **18:**526–537.

Alqamy, H., T. Wacher, S. Rashad, M. Hemeed, and Y. Abd Elbasset. 2003. Grazing patterns in the high altitude mountain area around St. Katherine Town, South Sinai, Egypt: a GIS integrated approach. Nature Conservation Sector, Egyptian Environmental Affairs Agency, Cairo. Available from http:www.geocities.com/stkatherinesprotectorate/Alqamy_etal_GrazingStudy.pdf (accessed July 2004).

Amarasekare, P., and H. Possingham. 2001. Patch dynamics and metapopulation theory: the case of successional species. Journal of Theoretical Biology **209:**333–344.

Ball, S. J., D. B. Lindenmayer, and H. P. Possingham. 2003. The predictive accuracy of population viability analysis: a test using data from two small mammal species in a fragmented landscape. Biodiversity and Conservation **12:**2393–2413.

Batanouny, K. H. 1999. Wild medicinal plants in Egypt. Palm Press, Cairo.

Beever, E. A., P. F. Brussard, and J. Berger. 2003. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. Journal of Mammalogy **84:**37–54.

Bergman, K. O., and O. Kindvall. 2004. Population viability analysis of the butterfly *Lopinga achine* in a changing landscape in Sweden. Ecography **27:**49–58.

Conradt, L., E. J. Bodsworth, T. J. Roper, and C. D. Thomas. 2000. Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. Proceedings of the Royal Society of London Series B **267:**1505–1510.

Diamond, J. M. 1972. Biogeographic kinetics estimation of relaxation times for avifaunas of southwest Pacific islands. Proceedings of the National Academy of Science—Biology **69:**3199–3203.

Drechsler, M., K. Frank, I. Hanski, R. B. O'Hara, and C. Wissel. 2003. Ranking metapopulation extinction risk: from patterns in data to conservation management decisions. Ecological Applications **13:**990–998.

Easterling, D. R., et al. 1997. Maximum and minimum temperature trends for the globe. Science **277:**364–367.

Eber, S., and R. Brandl. 1996. Metapopulation dynamics of the tephritid fly *Urophora cardui*: an evaluation of the incidence-function model assumptions with field data. Journal of Animal Ecology **65:**621–630.

Elmhagen, B., and A. Angerbjörn. 2001. The applicability of metapopulation theory to large mammals. Oikos **94:**89–100.

Esler, D. 2000. Applying metapopulation theory to conservation of migratory birds. Conservation Biology **14:**366–372.

GEF (Global Environmental Facility). 2000. Conservation and sustainable use of medicinal plants in arid and semi-arid ecosystems. GEF, Washington, D.C. Available from http:www.gefonline.org/projectDetails.cfm?projID=776 (accessed July 2004).

Gilpin, M. E., and I. Hanski. 1991. Metapopulation dynamics: empirical and theoretical investigations. Academic Press, London.

Gonzalez, A., J. H. Lawton, F. S. Gilbert, J. M Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundances, and distribution in a micro-ecosystem. Science **281:**2045–2047.

Grabherr, G., M. Gottfried, and H. Pauli. 1994. Climate effects on mountain plants. Nature **369:**448.

Grimm, V., N. Dorndorf, F. Frey-Roos, C. Wissel, T. Wyszomirski, and W. Arnold. 2003. Modelling the role of social behaviour in the persistence of the alpine marmot *Marinota marmota*. Oikos **102:**124–136.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Pages 17–38 in M.E. Gilpin and I. Hanski, editors. Metapopulation dynamics. Academic Press, London.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology **63:**151–162.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, United Kingdom.

Hanski, I., and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, London.

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. Nature **404:**755–758.

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

Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation Biology **10:**578–590.

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

Hobbs, J. 1995. Mount Sinai. University of Texas Press, Austin.

Houghton, J. T., Y. Ding, X. Dai, D. J. Griggs, C. A. Johnson, K. Maskell, M. Noguer, and P. J. van der Linden. 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, United Kingdom.

Hill, J. K., C. D. Thomas, and B. Huntley. 1999. Climate and habitat availability determine 20th century changes in butterfly's range margin. Proceedings of the Royal Society of London Series B **266:**1197–1206.

Ihaka, R., and R. Gentleman. 1996. R: A language for data analysis and graphics. Journal of Computational and Graphical Statistics **5:**299–314.

James, M. 2004. Ecology and conservation of the Sinai Baton Blue butterfly, *Pseudophilotes sinaicus*. Ph.D thesis. University of Nottingham, Nottingham, United Kingdom.

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

Johnson, M. P. 2000. The influence of patch demographics on metapopulations, with particular reference to successional landscapes. Oikos **88:**67–74.

Klanderud, K., and H. J. B. Birks. 2003. Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. Holocene **13:**1–16.

Konvicka, M., M. Maradova, J. Benes, Z. Fric, and P. Kepka. 2003. Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. Global Ecology and Biogeography **12:**403–410.

Lindenmayer, D. B., and H. P. Possingham. 1996. Ranking conservation and timber management options for Leadbeater's possum in Southeastern Australia using population viability analysis. Conservation Biology **10:**235–251.

McCarthy, M.A., S. J. Andelman, and H. P. Possingham. 2003. Reliability of relative predictions in population viability analysis. Conservation Biology **17:**982–989.

Moilanen, A. 1999. Patch occupancy models of metapopulation dynamics: efficient parameter estimation using implicit statistical inference. Ecology **80:**1031–1043.

Moilanen, A. 2000. The equilibrium assumption in estimating the parameters of metapopulation models. Journal of Animal Ecology **69:**143–153.

Moilanen, A. 2002. Implications of empirical data quality to metapopulation model parameter estimation and application. Oikos **96:**516–530.

Moilanen, A. 2004. Stochastic patch occupancy model (SPOMSIM 1.0). Metapopulation Research Group, Helsinki, Finland. Available from http://www.helsinki.fi/science/metapop (accessed September 2004).

Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology **79:**2503–2515.

Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. Ecology **83:**1131–1143.

Moilanen, A., A. T. Smith, and I. Hanski. 1998. Long-term dynamics in a metapopulation of the American pika. The American Naturalist **152:**530–542.

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

Parmesan, C., et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature **399:**579–583.

Perevolotsky, A., A. Perevolotsky, and I. Noy-Meir. 1989. Environmental adaptation and economic change in a pastoral mountain society: the case of the Jabaliyah Bedouin of the Mt. Sinai region. Mountain Research and Development **9:**153–164.

Ragab, R., and C. Prudhomme. 2002. Climate change and water resources management in arid and semi-arid regions: prospective

challenges for the 21st century. Biosystems Engineering **81:**3–34.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature **421:**57–60.

Schtickzelle, N. and M. Baguette. 2002. Metapopulation viability analysis of the bog fritillary butterfly using RAMAS/GIS. Oikos **104:**277–290.

Schultz, C. B., and P. C. Hammond. 2003. Using population viability analysis to develop recovery criteria for endangered insects: case study of the Fender's blue butterfly. Conservation Biology **17:**1372–1385.

Stelter, C., M. Reich, V. Grimm, and C. Wissel. 1997. Modelling persistence in dynamic landscapes: lessons from a metapopulation of the grasshopper *Bryodema tuberculata*. Journal of Animal Ecology **66:**508–518.

Ter Braak, C. J. F., I. Hanski, and J. Verboom. 1998. The incidence function approach to the modelling of metapopulation dynamics. Pages 167–188 in J. Bascompte and R. V. Solé, editors. Modelling spatiotemporal dynamics in ecology. Springer-Verlag, Berlin.

Thomas, C. D., et al. 2004. Extinction risk from climate change. Nature **427:**145–148.

Travis, J. M. J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proceedings of the Royal Society of London Series B **270:**467–473.

Wahlberg, N., T. Klemetti, and I. Hanski. 2002. Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. Ecography **25:**224–232.

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

Walter, K. S., and H.J. Gillett. 1998. 1997 IUCN Red List of threatened plants. Compiled by the World Conservation Monitoring Centre. The World Conservation Union, Gland, Switzerland, and Cambridge, United Kingdom.

Watson, R. T., M. C. Zinyowera, and R. H. Moss. 1998. The regional impacts of climate change: an assessment of vulnerability. Intergovernmental Panel on Climate Change and Cambridge University Press, Cambridge, United Kingdom.

Wiegand, T., F. Jeltsch, I. Hanski, and V. Grimm. 2003. Using pattern-oriented modelling for revealing hidden information: a key for reconciling ecological theory and application. Oikos **100:**209–222.