Short-term studies underestimate 30-generation changes in a butterfly metapopulation

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Most studies of rare and endangered species are based on work carried out within one generation, or over one to a few generations of the study organism. We report the results of a study that spans 30 generations (years) of the entire natural range of a butterfly race that is endemic to 35 km² of north Wales, UK. Short-term studies (surveys in single years and dynamics over 4 years) of this system led to the prediction that the regional distribution would be quite stable, and that colonization and extinction dynamics would be relatively unimportant. However, a longer-term study revealed unexpectedly high levels of population turnover (local extinction and colonization), affecting 18 out of the 20 patches that were occupied at any time during the period. Modelling the system (using the 'incidence function model' (IFM) for metapopulations) also showed higher levels of colonization and extinction with increasing duration of the study. The longer-term dynamics observed in this system can be compared, at a metapopulation level, with the increased levels of variation observed with increasing time that have been observed in single populations. Long-term changes may arise from local changes in the environment that make individual patches more or less suitable for the butterfly, or from unusual colonization or extinction events that take metapopulations into alternative states. One implication is that metapopulation and population viability analyses based on studies that cover only a few animal or plant generations may underestimate extinction threats.

Keywords: colonization; conservation biology; extinction; incidence function model; population dynamics; population viability analysis

1. INTRODUCTION

Metapopulation theory describes the effects of local population extinction and subsequent recolonization of empty habitat patches on regional persistence (Hanski 1998, 1999). This theory is relevant to species that inhabit naturally patchy habitats, and to many additional species that now occupy fragmented landscapes where natural habitat remnants are surrounded by crops and other anthropogenic environments.

Most empirical assessments of metapopulation model predictions have examined static distributions (i.e. snapshot surveys conducted in a single year or a generation), short-term population turnover and invasions of empty habitat networks (e.g. Hanski 1994; Hanski & Thomas 1994; Lindenmayer & Possingham 1995, 1996; Wahlberg *et al.* 1996; Moilanen *et al.* 1998; Lindenmayer *et al.* 1999; Sjögren-Gulve & Ebenhard 2000; Thomas *et al.* 2001). The ability to match empirical and model-generated patterns has led to the widespread use of a metapopulation approach by conservation biologists wishing to reconstruct and forecast the responses of rare species to habitat fragmentation (e.g. Burgman *et al.* 1993; Lahaye *et al.* 1994; Wahlberg *et al.* 1996; Brook *et al.* 2000; Brito & Fernandez 2000; Sjögren-Gulve & Ebenhard 2000).

However, there are several difficulties in testing model-generated predictions using empirical data. Two particular concerns are that model output has inevitably been tested against short-term data, given the short duration of most empirical studies and long generation times of many ani-

mals and plants, and that long-term changes may not be generated by the same blend of factors that affect short-term dynamics. We studied and modelled the dynamics and distributions of a 'metapopulation-like species' over a relatively long period, to understand how short-term and longer-term dynamics differ (if they do) and to evaluate the ability of a metapopulation model to forecast longer-term dynamics on the basis of short-term data.

2. MATERIAL AND METHODS

The silver-studded blue butterfly *Plebejus argus* has been studied between 1970 and 1999, in the 35 km² Creuddyn Peninsula, in north Wales, UK (Dennis 1972, 1977; Thomas 1985a,b; Thomas & Harrison 1992; Dennis & Bardell 1996; figure 1). This represents the entire natural distribution of *P. a. caernensis*, an endemic race thought to have evolved and persisted within the peninsula since the last ice age (it has recently been introduced elsewhere, but we only consider its native distribution (de Worms 1949; Dennis, 1972, 1977; Thomas *et al.* 1999)). The race *caernensis* shows local adaptations to the host plants and mutualist ants (*Lasius alienus*) that are common on south-facing limestone grasslands in the area (Thomas 1985a; Jordano & Thomas 1992; Jordano *et al.* 1992; Thomas *et al.* 1999), allowing us to define habitat patches. The race has a low rate of dispersal, with an estimated 1.4% exchange of adults between habitat patches that are 13 to 200 m apart (Lewis *et al.* 1997). Extinction risk is highest for small local populations in small habitat patches (area and population size are correlated), colonization probability decreases with distance from source populations (Thomas & Harrison 1992), and genetic bottlenecks have been detected following colonization (Brookes *et al.* 1997). Therefore, *P. a. caernensis* meets all the criteria that are generally regarded as necessary for designation as a metapopulation (and

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Figure 1. Map of Creuddyn Peninsula, showing the coastline and distributions of habitat patches at four times (solid circles, occupied; open circles, unoccupied), X shows 1997 populations extinct by 1999. The size of the symbols is proportional to patch area.

has been modelled as such (Hanski & Thomas 1994)), meeting the assumptions as well as any other terrestrial organism for which data have been published.

The only major deviation from 'normal' metapopulation assumptions is that habitat patch quality may vary through time, as a consequence of changes in vegetation height of a few centimetres, which are generated by the interaction between grazing intensity (mainly sheep) and rainfall. In vegetation less than 3 cm tall, *P. a. caernensis* is present at a low density, or absent. In taller vegetation, *L. alienus* is more abundant, provided that there are some areas of broken ground, and *P. a. caernensis* typically occurs at higher density, when present (Thomas 1985b; Jordano & Thomas 1992; Jordano *et al.* 1992). Slight changes in vegetation frequently (but not always) precede colonization (i.e. when habitat quality is improving—usually vegetation becoming longer) and extinction (usually vegetation becoming shorter) (Thomas 1996). Thus, although the spatial distribution of habitat patches remains constant, their relative suitability may vary. In a modelling context, this does not necessarily cause a problem provided that the stochastic probability of extinction captures the environmental stochasticity due to changes in both habitat condition and weather.

Surveys of all limestone grassland on the peninsula were carried out in 1970 and 1971 (hereafter 1971; Dennis 1972, 1977), 1983 (Thomas 1985b), 1990 (Thomas & Harrison 1992) and 1997, with additional surveys in 1996, 1998 and 1999, providing a total span of 30 years. There is one butterfly generation per year. This paper concentrates on patterns of presence and absence, but abundance data were collected using transect counts in 1983 and 1997 (see Thomas (1985b) for methods

used). Most of the analyses relate to 27 generations of adult butterflies, from 1971 to 1997. Patches were defined as separated by 25 m or more of unsuitable open habitat, or 10 m or more of dense scrub (the southwest facing side of Great Orme's Head on the peninsula is designated as one patch, whereas some previous papers treated this area as several very closely linked patches). In 1983 and 1990, three very small patches of grassland near the main population on Great Orme's Head (figure 1) were not surveyed: all subsequent analyses of the empirical data, and comparisons of empirical and model results, refer to the remaining 33 patches. The three unsurveyed patches are known to have shown population turnover, so they are included in the 18 out of 20 occupied patches that showed turnover, and in figures 1 and 2, but excluded from figure 3.

We used a metapopulation model that can be applied to landscapes containing distinct habitat patches—the incidence function model (IFM) (Hanski 1994). The results from this model have been found to be comparable with those of other metapopulation models (METAPOP, RAMAS) so the results are likely to be broadly representative (Kindvall 2000). The IFM has already been parameterized and tested successfully in several butterfly metapopulations (e.g. Wahlberg *et al.* 1996; Thomas & Hanski 1997; Hanski 1999; Thomas *et al.* 2001).

Extinction probability in the IFM increases with decreasing habitat area, and colonization probability increases with patch connectivity (an exponential function of distance to all existing populations in the system), leading to dynamics and distributions that are consistent with those observed empirically (Hanski 1998, 1999). By assuming that extinction is due to area and colonization is due to connectivity, the processes of

Figure 2. Patch occupancy and turnover in relation to habitat area and distance to the nearest larger patch of populated habitat (to the second largest for the largest patch). (a) 1997 snapshot (diamonds, occupied; circles, unoccupied), and (b) all four surveys (diamonds, occupied in 1971, 1983, 1990 and 1997; squares, occupied in 1971, 1983 and 1990; circles, unoccupied in each census year).

Figure 3. Simulated (dashed lines) and observed (solid line and solid squares) turnover: the number of separate patches showing a change in population occupancy, between pairs of years. Simulations were based on parameters that were derived separately from each of the four census years (diamonds, 1971; triangles, 1983; open circles, 1990; open squares, 1997), and from all four surveys together (solid circles, 27 years). Means (+1 s.d.) are shown for simulation results.

extinction and colonization can be deduced even from a single snapshot survey of the distribution (Hanski 1994). The snapshot approach only works if there is an assumption that the organism's dynamics, and the landscape itself, were at a 'stochastic steady state' when the parameters were estimated (Moilanen 2000). The limestone grassland inhabited by *P. a. caernensis* is persistent: it is found on shallow soils, and is effectively permanent, provided that grazing is continued (the case for hundreds, probably thousands, of years). Historical reconstruction of land-use changes on the Creuddyn Peninsula between 1901 and 1997

revealed only very minor changes to *P. a. caernensis*' limestone habitat: 9% of all limestone grassland was lost during this period (242 reduced to 221 ha) (Cowley *et al.* 1999). Given the low rate of habitat loss per year in this system, censuses seven or more years apart, and the intrinsic rate of increase of a butterfly (Hanski & Thomas 1994), we would not expect the metapopulation dynamics of *P. a. caernensis* to lag far behind the dynamics of this landscape.

IFM parameters e , y and x (Hanski 1994) were estimated from patterns of occupancy of *P. a. caernensis* at four snapshots (1971, 1983, 1990 and 1997), over a network of 33 patches. In the IFM, annual extinction probability of patch i is area dependent, $E_i = (e/A_i^x)(1 - C_i)$, where A_i is patch area (ha). The risk of extinction is unity where minimum patch area $A_0 = e^{1/x}$, and the annual risk of extinction of a patch of area 1 ha is e . Annual colonization probability is connectivity dependent, $C_i = S_i^2/(S_i^2 + y^2)$. Connectivity of patch i is $S_i = \sum \exp(-\alpha d_{ij})A_j^B$ where d_{ij} is the distance (km) between patch i and each other occupied patch (j). On the basis of field data, parameters α (the slope of the negative exponential dispersal kernel) and A_0 were estimated as -3 and 0.008 ha, respectively. Following previous studies, the parameter scaling migration relative to patch area (B) was fixed at 0.5 (A. Moilanen, personal communication).

Parameters were estimated separately using each single snapshot survey year, all four occupancy states (27-year parameter estimates) and all possible combinations of two and three census dates. On the basis of previously published parameter estimates for butterfly species (Hanski 1994; Wahlberg *et al.* 1996), parameters entered into the estimation were $x = 1$, $e = 0.01$ and $y = 5$. Initial estimates of parameters were obtained using nonlinear regression (NLR and then NLRB) methods, each with 250 replicates in estimation, 300 function evaluations in initiation and 1000 function evaluations in estimation (Moilanen 1999). The final estimates were obtained using a Monte Carlo Markov chain (MCMC) model with 1000 function evaluations in initiation and 4000 function evaluations in estimation (Moilanen 1999). The estimates based on more than one census use turnover information but assume that single snapshots are representative of a stochastic steady state (Moilanen 1999, 2000). In the absence of good data, regional stochasticity was taken to be zero for single snapshot surveys (i.e. patches vary independently; see § 3). Estimations for the multiple-year datasets using MCMC always yielded a regional stochasticity estimate of 0.0005 , that was used for the simulations (Moilanen 1999). Further simulations carried out with a much higher level of regional stochasticity (0.3) did not alter the overall conclusions (see § 4).

The four single-year and all of the multi-year sets of IFM parameters were then iterated, starting with each of the four observed distributions. We concentrated on the single-year and four-census parameter simulations. Results based on two or three census periods largely fell within the range of the results generated using single-year and four-census parameter combinations. One hundred replicates of 200-year simulations were run using each of the sets of parameter estimates, starting with each of the four observed regional distributions. Short-term output was used to compare observed and modelled population turnover. The 200th year of each simulation was used to establish long-term occupancy patterns. Observed and model-generated turnover (figure 3) were measured as the number of patches that showed a change in population status between two census dates (ignoring intervening surveys, if there were any).

Table 1. Relationship between potential population size (measured, or based on patch area $\times$ average density) and patch history in the *P. a. caermensis* metapopulation.

potential adult population size	number of patches occupied for 30 years	number of patches occupied, but for less than 30 years	number of patches not occupied
<100	0	4	3
100–999	1	6	6
1000–9999	0	7	7
10 000–99 999	0	1	0
>100 000	1	0	0

Table 2. Incidence function model parameters based on single snapshot surveys, or on two, three or four surveys. (CI, confidence interval.)

years used in estimation		95% CI			95% CI			<i>y</i>	<i>e</i>
		<i>x</i>	lower	higher	<i>e</i>	lower	higher		
1971		1.665	0.804	2.249	0.520	0.087	0.771	40.11	0.00032
	1983	1.079	0.109	1.884	0.106	0.002	0.310	4.40	0.0055
		1.190	0.668	1.551	0.056	0.026	0.153	4.17	0.0032
		1.130	0.517	1.712	0.042	0.008	0.134	3.13	0.0043
1971	1983	0.744	0.245	1.076	0.225	0.052	0.468	2.89	0.0276
1971		0.697	0.150	1.068	0.226	0.054	0.456	2.55	0.0346
1971		0.749	0.237	1.088	0.119	0.054	0.162	2.11	0.0269
	1983	1.027	0.548	1.557	0.085	0.016	0.188	3.49	0.0070
	1983	0.847	0.189	1.280	0.038	0.006	0.267	1.51	0.0167
		0.410	0.000	1.441	0.057	0.011	0.187	0.64	0.1380
1971	1983	0.666	0.134	1.311	0.259	0.025	0.442	2.54	0.0401
	1983	0.825	0.160	1.764	0.063	0.005	0.153	1.84	0.0186
1971	1983	0.714	0.230	0.914	0.134	0.032	0.370	2.05	0.0318
1971		0.716	0.000	1.086	0.216	0.042	0.397	2.62	0.0328
1971	1983	0.619	0.331	1.102	0.167	0.025	0.365	1.82	0.0503

3. RESULTS

(a) Empirical patterns

Population turnover was recorded in just two patches between 1996 and 1999. The two most isolated populations in the landscape became extinct (marked X in figure 1d). These patches of habitat were not populated in 1990, but may have been colonized in 1995 (Dennis & Bardell 1996). Six observations of adults (probably including repeat observations of the same individuals) were made in eight visits to each of these sites in 1996. At Gloddaeth (northwest of the two sites), six, two, two and zero adults were observed from 1996 to 1999, respectively. At Llangwstenin (southeast of the sites), six, two, zero and zero were seen from 1996 to 1999, respectively.

The longer the period of observation, the more patches showed population turnover, affecting 18 of 20 patches ever occupied during the 30-year period; a further 16 patches remained unoccupied throughout the survey period (table 1; figures 1 and 2). The overall pattern has been one of growth in metapopulation size between 1971 and 1997, although there have also been extinctions. The number of occupied patches grew on Great Orme's Head between 1971 and 1983, remained fairly stable there between 1983 and 1990, and then grew again between 1990 and 1997 (figure 1).

Population size changes between 1983 and 1997 were

not synchronized across 10 sites where the species persisted, with no overall change in abundance (five increased, five decreased; paired *t*-test, *p* = 0.19).

(b) Simulation results

The simulation results, parameterized from any one of the four snapshot distributions, underestimated turnover after seven years (measured as the number of separate patches showing a change in occupancy state) and seriously underestimated longer-term turnover, after 26 years (figure 3). The especially poor performance of the 1971 parameters may be because they are based on only three occupied patches. However, the 1971 distribution was observed and it is worth contemplating how improbable it would have been to predict changes between 1971 and 1997, based on the 1971 data alone.

The metapopulation parameter estimates based on multiple surveys tended to fall outside those for the four single snapshot years (table 2). The colonization parameter (*y*) decreased (more colonization) weakly with the increasing span of years between the first and last survey included ($r^2 = 0.18$, $n = 15$ estimates), and the extinction parameter (*e*) increased strongly (more extinction expected) with the increasing span of years ($r^2 = 0.79$, $n = 15$ estimates: probability values are not ascribed because different sets of parameter estimates are not independent). This translates into increased estimates of population turnover with

Table 3. Number of standard deviations between observed occupancy and simulated occupancy after 200 years, predicted by various parameter combinations and starting distributions. (Numbers in bold indicate significant mismatches between predicted and observed distributions.)

	single snapshots				all four surveys			
starting distribution	1971	1983	1990	1997	1971	1983	1990	1997
parameters	1971	1983	1990	1997	27-year	27-year	27-year	27-year
comparison year								
1971	0.20	4.13	11.9	17.2	5.54	13.8	14.6	21.0
1983	22.1	0.08	2.87	9.12	2.58	5.15	5.54	10.5
1990	25.7	0.76	1.43	7.83	2.11	3.77	4.09	8.83
1997	45.6	4.52	6.63	0.63	0.53	3.92	3.96	0.57

increased length of study (e.g. figure 3). The four-census parameter estimates provided the best fit, but tended to overestimate turnover over short periods and underestimate turnover over longer periods, suggesting that the model was not behaving in the same way as the real metapopulation.

Estimates of parameter x , which describes the shape of the relationship between patch area and the extinction risk, also reveal an important difference between deduced short-term and longer-term dynamics. Snapshots produced moderately high values of x , indicating a *relatively* mainland-island type of dynamics (small patches having a very high risk of extinction, with larger patches surviving better). By contrast, multiple surveys generally produced lower estimates of x , indicating a *relatively* Levins type of dynamics (in which extinction risk is more comparable for patches of different area). Furthermore, observed turnover events were more evenly distributed across patches than in the simulation results, during which a subset of patches showed repeated extinction and recolonization. This is illustrated by the relatively high number of turnover events per patch that did undergo extinction or colonization in the simulation output, compared with those observed (sampling the model output with the same temporal pattern as in the real surveys; figure 4).

Patch occupancy (the fraction of patches occupied) is frequently used to compare model output with empirical observation. Table 3 shows the number of standard deviations between observed occupancy in each census year and mean predicted occupancy (in simulated generation 200; see § 2) based on the various starting distributions and parameter combinations. The snapshot sets of parameter estimates faithfully reconstructed patch occupancy observed empirically in the same year (values less than 2, top-left to bottom-right diagonal in table 3a). To use the model as a predictive tool, however, the relevant question is whether single-year parameters and starting distributions predict the occupancy patterns actually observed in any of the other three surveys—they did not. In 11 out of 12 cases, observed occupancies were outside the 95% confidence limits of predictions (bold values in table 3a). The longer the interval between the year used to estimate the parameters and the observed 'test' year, the worse the fit (table 3a). Parameters based on all four surveys were explored in the same way, starting in turn with each of the four empirically observed distributions. Observed occupancy was outside the 95% confidence limits in 14 out of the 16 tests (table 3b).

Figure 4. Observed and simulated turnover events per patch that did show turnover, starting with the 1971 distribution, with model output sampled after 12, 19 and 26 years (squares, forecast; circle, observed). Means of the different parameter combinations and 95% confidence limits (± 1.96 s.d.) are shown.

4. DISCUSSION

This unusually long-term study of an endemic butterfly race revealed an increasing number of patches involved in population turnover as the work progressed, and hence showed the increasing relevance of a metapopulation approach. A four-year study would have given the impression that metapopulation dynamics were trivial: one could argue that virtually all important habitat patches would be (permanently) occupied, with minor levels of population turnover at the metapopulation periphery. This has been a general criticism that has been made of the applicability of metapopulation theory to species with patchy distributions (Schoener & Spiller 1987; Harrison 1991, 1994).

Over a longer period, however, the high level of turnover (affecting 90% of populated patches and 50% of all patches) shows that a metapopulation or landscape approach is required, and population turnover was not limited to small and peripheral patches. A comparable impression was obtained from the simulation modelling. The longer the period of data used to parameterize the model, the greater the turnover predicted.

The exceptionally long colonization distances (2.5 and 5 km; cf. Lewis *et al.* 1997) observed at the metapopulation

periphery between 1990 and 1996 almost certainly represent the arrival of single, mated females. Although they colonized relatively large habitat patches, the populations only grew to a small size (probably less than 10 adults in any one year) prior to their extinction, possibly due to demographic stochasticity or inbreeding. Extinction of small populations at the periphery of the metapopulation occurred in the late 1940s or 1950s (*P. a. caernensis* occurred in one or more patches in the southernmost part of our study area in the 1940s (Ellis 1950)), after 1971, and again between 1997 and 1999. These extinctions initially seem rather trivial, but may not be so on a longer time-scale. Many of the empty habitat patches away from Great Orme's Head could contain populations of hundreds to thousands if *P. a. caernensis* were to establish in these sites. It is quite possible that *P. a. caernensis* could in future have a much wider distribution on the Creuddyn Peninsula.

To evaluate the potential for such an alternative state for the metapopulation, we simulated *P. a. caernensis* dynamics in the peripheral patch network to the southwest of Great Orme's Head. The simulation was started first with populations in the two patches observed to be occupied in 1997, assuming that these populations had grown to their local estimated carrying capacities, and using the four-census parameter combination. The median time to extinction was 30 years, with seven out of 100 simulations surviving for more than 100 years. Starting with all patches in this region that were populated, the median time to extinction was 59 years (53 years with regional stochasticity of 0.3). On the basis of the experience of the past 30 years and these simulations (the real range of possibilities is probably wider than simulated), it seems equally plausible that the number of occupied patches could: (i) remain at approximately 1997 levels; (ii) increase further (colonizing empty habitat away from Great Orme's Head); or (iii) decline back to the 1971 distribution size over the next 30 years.

In our study system, increasing time leads to increasing variation, perhaps as a result of temporal population lags and gradual changes in local habitat quality, which may affect even the largest habitat patches. Unusual colonization and extinction events may also generate long-term changes, potentially giving rise to alternative metapopulation states (see Moilanen *et al.* 1998). The overall pattern is analogous to the concept by Pimm & Redfearn (1988) of a reddened spectrum in population dynamics (Halley & Kunin 1999), here expressed at the metapopulation level. Over short periods, small populations or patches may be seen to go extinct and be recolonized, but large populations do not become extinct. Over the same time periods, large populations may nonetheless become smaller, making them susceptible to extinction at a later time. Short-term colonizations predominantly affect nearby patches that are unoccupied either because they are very small or because they contain low-quality habitat. Observed colonizations and extinctions in *P. a. caernensis* over three decades, however, affected patches that can contain thousands and tens of thousands of individuals, far larger than would be expected to succumb to inter-annual (white noise) variation in environmental stochasticity (table 1; cf. Hanski & Thomas 1994).

We were able to increase the modelled range of out-

comes by incorporating regional stochasticity into the model, to mimic the possibility that all populations might be affected in the same way by the same weather events (leading to correlated extinction events). However, increased regional stochasticity did not otherwise increase the match between observed and predicted patterns, and we are loath to include high levels of regional stochasticity as a *post hoc* means of increasing the range of modelled dynamics, when we have no evidence that local abundances change synchronously (see also Thomas 1991). Nonetheless, regional stochasticity may represent an important source of long-term changes in the size of many metapopulations.

Great caution is required if one wishes to deduce long-term dynamics by extrapolating from short-term dynamics and patterns. Two long-term metapopulation studies have now been completed (our 30-year study of *P. a. caernensis* and a 21-year study of the American pika, *Ochotona princeps* (Moilanen *et al.* 1998)), both of which revealed long-term dynamics that were not predicted on the basis of the initial, short-term studies. Short-term studies may miss long-term trends, and may miss the potential existence of alternative states, making it extremely difficult to assess (usually underestimating) minimum viable metapopulation sizes. However, conservation actions are often required long before such data can be gathered. It may still be possible to assess the *relative* benefits of alternative conservation strategies by comparing predicted metapopulation trajectories and metapopulation capacities of, say, alternative patterns of habitat management across entire landscapes (Thomas 1996; Hanski & Ovaskainen 2000), without making any numerical statement about the long-term probability of persistence.

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