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Effects of patch quality and network structure on patch occupancy dynamics of a yellow-bellied marmot metapopulation

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Summary

1. The presence/absence of a species at a particular site is the simplest form of data that can be collected during ecological field studies. We used 13 years (1990–2002) of survey data to parameterize a stochastic patch occupancy model for a metapopulation of the yellow-bellied marmot in Colorado, and investigated the significance of particular patches and the influence of site quality, network characteristics and regional stochasticity on the metapopulation persistence.

2. Persistence of the yellow-bellied marmot metapopulation was strongly dependent on the high quality colony sites, and persistence probability was highly sensitive to small changes in the quality of these sites.

3. A relatively small number of colony sites was ultimately responsible for the regional persistence. However, lower quality satellite sites also made a significant contribution to long-term metapopulation persistence, especially when regional stochasticity was high.

4. The northern network of the marmot metapopulation was more stable compared to the southern network, and the persistence of the southern network depended heavily on the northern network.

5. Although complex models of metapopulation dynamics may provide a more accurate description of metapopulation dynamics, such models are data-intensive. Our study, one of the very few applications of stochastic patch occupancy models to a mammalian species, suggests that stochastic patch occupancy models can provide important insights into metapopulation dynamics using data that are easy to collect.

Key-words: *Marmota flaviventris*, patch occupancy models, SPOMs, SPOMSIM, stochastic regional synchrony.

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Introduction

Many biological populations occupy spatially heterogeneous environments, and there is a growing realization that spatially mediated processes (e.g. dispersal, habitat connectivity) are vital for the regional persistence of populations. Ecologists are increasingly relying on metapopulation theory to understand the influence of spatial heterogeneity on dynamics and persistence of biological populations (e.g. Lankester *et al*. 1991; Lahaye, Gutierrez & Akçakaya 1994; Akcakaya & Atwood 1997; Hokit, Stith & Branch 2001).

The presence/absence of a species at a particular site is the simplest form of data that can be collected during ecological field studies (Hanski 1994b). A class of metapopulation models that capitalizes on such data is the stochastic patch occupancy models (SPOMs). The theory of SPOMs has been well developed, and these models have received much practical application (Moilanen &

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Hanski 1998; Hanski 1999; Moilanen 1999; Moilanen & Cabeza 2002). SPOMs assume that suitable habitat occurs in discrete patches surrounded by unsuitable matrix and that occupancy of each patch is determined by local colonization and extinction events. These turnover events are assumed to depend on factors such as patch area (a proxy for local population size), spatial arrangement of patches, dispersal ability of the species and spatially correlated environmental stochasticity (regional stochasticity). These assumptions are reasonable for many biological populations inhabiting highly fragmented landscapes, where only a small portion of the landscape often provides suitable habitat (Hanski & Ovaskainen 2003).

An important question that can be addressed using SPOMs is: what is the relative significance of particular patches or networks (patch groups) for patch occupancy dynamics? Intuitively, low quality patches that are poorly connected to other patches will have lesser influence on metapopulation dynamics than high quality patches that are well connected. However, low quality patches may, under certain conditions, significantly influence regional dynamics (Brown 1969; Gill *et al.* 2001). If there is no significant contribution of the low quality patches, metapopulation dynamics may depend only on the high quality patches, and the interactions between high and low quality patches may resemble source–sink (Pulliam 1988; Pulliam & Danielson 1991) or mainland–island dynamics (Schoener 1991). The importance of a particular patch (or network) can be investigated by comparing simulated patch occupancy dynamics with and without that patch (or network). Previous studies have observed that persistence of a particular patch network may depend on the presence of other networks (e.g. Moilanen, Smith & Hanski 1998).

SPOMs have been used mainly to model the metapopulation dynamics of large invertebrates or small vertebrates. The preference for small-bodied habitat specialists is dictated by the criteria of regional persistence as a classical metapopulation: high rate of population increase, short generation time and high habitat specificity (Murphy, Freas & Weiss 1990; Hanski 1999). However, some mammal populations that occupy discrete habitat patches also exhibit characteristics of metapopulations, and SPOMs can be applied to such populations as well (e.g. Moilanen *et al.* 1998).

A mammal species that meets the assumptions of the SPOMs is the yellow-bellied marmot, *Marmota flaviventris* (Audubon & Bachman 1841). Yellow-bellied marmots occupy discrete habitat patches that vary in quality (Svendsen 1974), and populations can go locally extinct and be recolonized by individuals from surrounding patches (Svendsen 1974; Armitage 2003). Although there is a gradient from low quality to high quality sites, marmot habitats can be grouped into two major quality types: (1) colony (high quality) and (2) satellite (low quality) sites. The persistence of the metapopulation is believed to be dependent mainly on the colony sites, but the relative influence of colony and satellite sites on the marmot metapopulation dynamics is unknown.

In this study, we used long-term (1990–2002) patch occupancy data and a SPOM to investigate the metapopulation dynamics of yellow-bellied marmots in the Upper East River Valley near the Rocky Mountain Biological Laboratory, Colorado (hereafter referred to as Colorado). Specifically, we investigated the relative influence of particular sites, site quality, network characteristics and regional stochasticity on the persistence of the yellow-bellied marmot metapopulation.

Materials and methods

THE YELLOW-BELLIED MARMOT METAPOPULATION IN COLORADO

The yellow-bellied marmot is a large, diurnal, burrow-dwelling rodent, distributed widely in the mountainous region of the western United States (Frase & Hoffmann 1980). Marmots typically occupy meadows with talus and large boulders, under which they dig their burrow systems (Svendsen 1974). The distribution of marmots in Colorado is patchy (Fig. 1), and is associated closely with the local mosaic of meadow and forest vegetation. The distinct habitat patches vary in size, ranging from 0·01 ha to 7·2 ha (K. B. Armitage, unpublished data). However, the density of marmots varied remarkably among sites, and local patch area does not necessarily represent the local population size (Armitage & Schwartz 2000). We use the term 'site quality' to describe the combined effect of multiple environmental factors (including patch area) on local population size. Satellite sites (lower quality patches) are occupied typically by a single adult female, her litter and sometimes an adult male. Colony sites (higher quality patches) are occupied by one or more matrilines, each consisting typically of one male, two or more closely related adult females, yearlings (1 year old) and young (Armitage 1991, 1998).

Typically, all yearling males and about half the yearling females disperse (Van Vuren 1990; Schwartz, Armitage & Van Vuren 1998). Recolonization occurs when an immigrant occupies an empty habitat patch. Matrilineal groups can exclude potential immigrants unless all individuals die and the habitat patch is empty, thus reducing the chance of a 'true' rescue effect (Armitage 1991, 2003). Local extinction occurs when a matriline dies out or deserts a site. However, local turnover events can be concealed by the immediate occupation of an empty site by immigrants, thus creating an 'apparent' rescue effect. The detailed biology of yellow-bellied marmots in Colorado is described by Armitage (1991, 2002).

Although the number of patches in the yellow-bellied marmot metapopulation in Colorado is smaller than that observed in some studies, our study system meets the four conditions of regional persistence as a metapopulation (Murphy *et al.* 1990; Hanski *et al.*

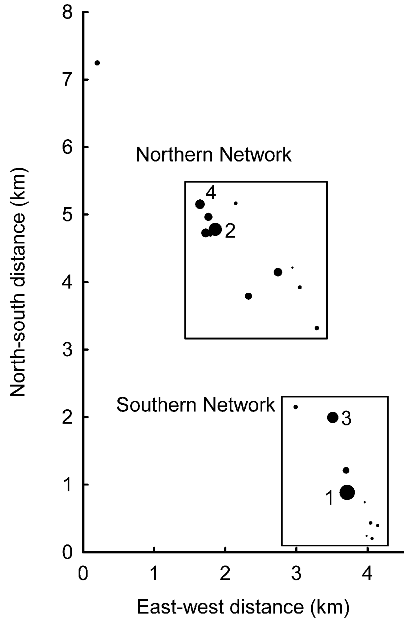

Fig. 1. The structure of the yellow-bellied marmot metapopulation in Colorado. Diameters of circles are proportional to the estimated quality of each site. Four highest quality sites are indicated with numbers. The figure also shows the division of the metapopulation into northern and southern networks.

1995). First, marmots live in spatially discrete habitat patches. Their burrow systems are located typically in open meadow patches with rocky outcrops (Svendsen 1974). Philopatric marmots rarely travel > 50 m away from burrows because of the predation risk. Secondly, all local populations face the risk of local extinction in the absence of a rescue effect. The average population size of the largest colony is approximately 20 animals, and local extinction is possible due to predation, disease, environmental and demographic stochasticity or catastrophes. Thirdly, the probability of survival during dispersal decreases with the distance moved (Van Vuren 1990). Therefore, low survival of the long-distance dispersers can result in a distance-dependent dispersal. Finally, the local population dynamics are sufficiently asynchronous (Armitage & Downhower 1974; Armitage 1977, 2003; Oli & Armitage 2004). Asynchrony in local population dynamics increases the probability that an extinct local population is reestablished, or a declining population is rescued by dispersers from other local populations (Hanski *et al.* 1995). Therefore, the yellow-bellied marmot system provides one of the few examples of naturally occurring mammalian metapopulations to which SPOMs can be applied (e.g. Bryant 1998; Moilanen *et al.* 1998; Stephens *et al.* 2002).

MODEL STRUCTURE

We used program SPOMSIM (Moilanen 2004) to parameterize and simulate a SPOM for the yellow-bellied marmot metapopulation. SPOMSIM is a computational modelling tool designed for the parameterization and analysis of SPOMs. In SPOMSIM, subfunctions can be chosen for describing the dispersal kernel, connectivity function, colonization probability, extinction probability and rescue effect (Moilanen 2004).

The shape of the dispersal kernel is important only when the metapopulation consists of several small networks that are far from each other, which was not the case in our system. Therefore, we used the simple negative exponential function for describing the dispersal kernel:

$$D(d_{ij},\alpha) = \exp(-\alpha d_{ij}), \qquad \text{eqn 1}$$

where d_{ij} is the distance between patches i and j, and α is the distribution parameter of the dispersal distances ($1/\alpha$ = average dispersal distance).

For the connectivity function, we used the subfunction that includes the effect of local patch area (patch quality in this study) on connectivity:

$$S_t(t) = A_i^c \sum_{j \neq i} O_j(t) D A_j^b, \qquad \text{eqn 2}$$

where $O_j(t)$ is the occupancy status of each patch at time t, D is the dispersal kernel (.1), and A_i is the quality of patch i. Parameter b scales emigration and parameter c scales immigration as a function of patch quality (Moilanen & Nieminen 2002).

Moilanen (2004) recommends that the choice of the colonization function be based on the biology of the studied species. Because marmot colonies typically contain only few individuals, we used the subfunction that includes the Allee effect in colonization (Hanski 1994b):

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

where $S_i(t)$ is the connectivity of patch i at time t (.2) and y is a model parameter.

For the extinction function we used two alternative subfunctions, one that was used in the incidence function model (IFM):

$$E_i = \frac{\mu}{A_i^x}, \qquad \text{eqn 4}$$

and the other in spatially realistic Levin's model (SRLM):

$$E_i = 1 - \exp\left(\frac{-\mu}{A_i^x}\right), \qquad \text{eqn 5}$$

where μ is the extinction probability of a patch of unit size, and parameter x scales the extinction risk as a function of patch area (for a discussion see Foley 1997).

The rescue effect can be included in the SPOM, and it essentially decreases the extinction probabilities of well-connected patches. We used the generalized version of the rescue effect function to determine the strength of the rescue effect:

$$E_i(t) = \min\{1, (1 - C_i(t))^R E_i\}, \qquad \text{eqn 6}$$

where parameter R determines the strength of the rescue effect.

Different models with alternative combinations of connectivity and extinction functions were parameterized and the most parsimonious model was identified using Akaike's information criterion corrected for small samples, AIC_c (Burnham & Anderson 2002; Grimm *et al*. 2004).

PARAMETER ESTIMATION

SPOMs can be parameterized with survey data from a single year; however, data from several years provide more robust estimates of parameters (Moilanen 1999). A long-term study in Colorado has provided occupancy data for most sites; however, some sites were not surveyed every year (Armitage 1991; Schwartz *et al*. 1998). We used data from 21 known sites surveyed between 1990 and 2002 to parameterize the SPOMs, as this period provided the most complete occupancy information (Fig. 2).

In SPOMs, patch area is often used to indicate local population size. This indicator is based on the assumption that as the patch area increases, local population size increases, hence the local extinction risk decreases. Patch area is preferred by many authors, because estimating area is generally easier than estimating local population size or other measures of patch quality. However, the density of marmots varied remarkably among sites. We used the average number of adult females per site (conditional upon occupied years) as a measure of patch quality, because it was a more accurate measure of local population size than was patch area.

Where possible, independent estimation of model parameters is preferable in order to reduce the number of parameters to be estimated from site occupancy data (Hanski 1999). Parameter α of the dispersal kernel was estimated using independent dispersal data, while the remaining model parameters (b, c, y, μ, x and R) were estimated from the site occupancy data using the Markov chain Monte Carlo method (Moilanen 1999). Analysis of local population dynamics during the last 40 years did not reveal any significant trend in population sizes (Schwartz *et al*. 1998; Schwartz & Armitage 2003; Oli & Armitage 2004). Therefore, it was reasonable to assume that the yellow-bellied marmot metapopulation was at a stochastic quasi-equilibrium.

MODEL SIMULATION

Metapopulation dynamics were simulated using the most parsimonious model, which was selected based on AIC_c as described above. Each scenario was simulated 1000 times for 100 years. Model predictions included changes in average proportion of occupied patches and proportion of simulated replicates that survived throughout 100 years, and average metapopulation lifetime (Hanski 1994b; Moilanen *et al*. 1998).

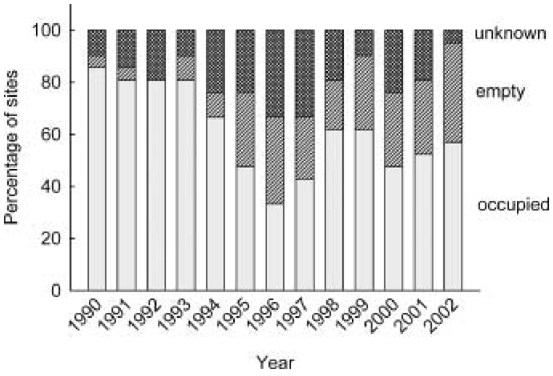

Fig. 2. Yearly proportions of occupied patches, empty patches and patches with unknown occupancy status, for the period between 1990 and 2002.

Influence of site quality and network structure

We classified each habitat patch either as a colony site or a satellite site based on the average number of adult females. Nine sites that had > 1 adult female on average were designated as colony sites, and 12 sites that had < 1 adult female on average as satellite sites.

Using the most parsimonious model, we simulated three alternative scenarios: (1) colony sites excluded; (2) satellite sites excluded; and (3) original configuration. Predictions of alternative models on metapopulation persistence were compared to assess the relative influence of colony and satellite sites on the overall metapopulation dynamics (e.g. Hanski 1994a).

The Colorado yellow-bellied marmot metapopulation can be divided into two networks, the northern and the southern, which are separated by areas of unsuitable habitat. The most parsimonious model was used to simulate three alternative scenarios: (1) northern network; (2) southern network; and (3) the entire network. The predictions of alternative models on metapopulation persistence were compared to assess the significance of compartmentalization among sites (e.g. Moilanen *et al*. 1998).

Significance of regional stochasticity

Spatial correlation in environmental stochasticity (regional stochasticity) can heavily influence metapopulation persistence (Hanski & Ovaskainen 2003). Regional stochasticity is included in SPOMSIM based on log-normal variation in patch area, which creates a yearly synchronous variation in both extinction and colonization rates (Moilanen 2004). The standard deviation (σ) of this variation quantifies the level of synchrony. The level of regional stochasticity could not be estimated directly; therefore, we used two levels of regional stochasticity ($\sigma = 0{\cdot}1$ and $0{\cdot}2$) and analysed the sensitivity of model predictions to regional stochasticity.

ADEQUACY OF THE SPOM

We used the robust design occupancy modelling approach (MacKenzie *et al*. 2002, 2003) to investigate the adequacy of the SPOM used for simulations of the yellow-bellied marmot system. The robust design occupancy model uses occupancy data and provides a framework for estimating the rate at which occupied sites go extinct (ε) and the rate at which unoccupied sites are recolonized (γ). We used program MARK version 4·0 (White & Burnham 1999) to implement the robust design occupancy model with parameters ψ (proportion of sites occupied), ε (probability of an occupied site becoming unoccupied), γ (probability of an unoccupied site becoming occupied) and ρ (detection probability on a visit to the site) (MacKenzie *et al*. 2002, 2003). Robust design occupancy models implemented in program MARK provides more flexibility in modelling recolonization and extinction probabilities, and allows comparison of several alternative model structures that are not included in SPOMSIM.

Program MARK can be used to estimate time-specific rates of extinction and colonization, and time-varying individual covariates can be used to incorporate site-specific information into the model. We estimated the site- and time-specific extinction and colonization rates for 21 sites for 13 years using the most parsimonious SPOM. We used these estimates as time-varying site covariates for estimating ε and γ parameters using MARK. Years for which the occupancy status was unknown were treated as missing values. Because we did not have > 1 sample occasion per year, we assumed that there were no false zeros (indicating that the site was not occupied) in our occupancy history, and set our detection probability parameter (ρ) to 1·0. Considering the conspicuousness of the presence of marmots at a given site and the high intensity of observation efforts, we believe that this is a reasonable assumption.

We used $\mathrm{AIC_c}$ for model comparison and for the identification of the most parsimonious model in the candidate model set. Candidate models differed in the way parameters ε and γ were modelled. We used four alternative model structures for modelling extinction rate, ε. First, we modelled ε as a constant rate [ε (.)]. Secondly, we modelled ε as a time-specific rate and let it vary among years [ε (*t*)]. Thirdly, we let ε vary among sites and used site quality as a constant site covariate [ε (*Q*)]. Finally, we used the extinction rate estimated from SPOM as a time-varying site covariate [ε (*E*)]. We also used four alternative model structures for modelling recolonization rate, γ. Similar to ε, we initially modelled γ as a constant [γ (.)] and a time-specific [γ (*t*)] rate. Then, we let γ vary among sites and through time, and used the colonization [γ (*C*)] and connectivity [γ (*S*)] parameters estimated from SPOM as time-varying site covariates. We expected the models in which the time-varying site covariates (estimated from SPOM) were used as predictors of extinction and recolonization rates to be more parsimonious than the time-specific or constant recolonization and extinction rate models.

Results

PARAMETER ESTIMATION

We used independent dispersal data from 90 radio-instrumented marmots (Van Vuren 1990) to estimate the dispersal kernel parameter, α. The average dispersal distance was 2·087 km, and α was estimated as the inverse of the average dispersal distance [α = 1/(2·087) = 0·479]. To evaluate the robustness of our estimate, we set α as a free parameter in SPOMSIM, and estimated it from patch occupancy data. This method gave an estimate of 0·337, which was slightly smaller than our independent estimate. These estimates indicated high dispersal ability, which was consistent with previous field observations (Van Vuren 1990). We performed simulations using both values of α, and found that the qualitative conclusions remained unchanged. Here, the independent estimate of α (0·479) was used for parameterizing the dispersal subfunction and simulation of alternative scenarios. The remaining model parameters were estimated using the 13 years' occupancy data (Fig. 2) and the Markov chain Monte Carlo estimation technique provided in SPOMSIM.

We used $\mathrm{AIC_c}$ weights to select the best model from a set of eight candidate models (Table 1). The most parsimonious model (model 5 in Table 1) included the following subfunctions:

- negative exponential function (.1) for describing the dispersal kernel (α fixed at 0·479);
- connectivity function that included the effect of local patch quality (.2);
- colonization function with the Allee effect in colonization (.3);
- extinction function from the original IFM; (.4) and
- rescue effect with parameter *R* (strength of the rescue effect) fixed at 1·0 (.6).

The differences in $\mathrm{AIC_c}$ values between the best model (model 5) and other alternative models were more than 2 except in two cases: model 1 (original IFM) and model 7 (Table 1). The model structure of the best model (model 5) differed from that of original IFM (model 1) in that model 5 included the effect of local patch quality on connectivity by including the model component A_i^c (in .2). Despite the small differences in $\mathrm{AIC_c}$ values, we used the model with the smallest $\mathrm{AIC_c}$ value (model 5) for simulating metapopulation dynamics. Parameter values of the most parsimonious model are given in Table 2.

Scaling of extinction risk with patch quality, parameter *x*, was in the higher end of the typical range ($0{\cdot}5 < x < 1{\cdot}5$; Moilanen 2004), indicating that local extinction probability decreased quickly with increasing population size. The intrinsic extinction probabilities for the smallest (0·3 adult females on average), average (1·3 adult females) and largest (3·8 adult females) patches were 0·78, 0·08 and 0·02, respectively. Incidentally, value of *x* estimated for the yellow-bellied marmots was very close to the one estimated for the

Table 1. Models and subfunction definitions used in SPOMSIM, and associated Akaike's information criterion corrected for small sample size ($\mathrm{AIC_c}$) values, number of parameters (# par) and model likelihoods. Connectivity function parameter c was fixed at '0' for the models without the effect of local patch, and it was set as a 'free' parameter for the models with the effect of local patch. 'IFM' is extinction probability function used in the original incidence function model, and 'SELM' is the one used in the spatially explicit Levin's model. Subfunction for the rescue effect was modelled with R (strength of the rescue effect) fixed at '1', and R set as a 'free' parameter during parameter estimation

Model	c	Extinction probability	R	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	# par	Model likelihood
1	0	IFM	1	161·4	0·8	5	0·670
2	0	IFM	Free	162·8	2·2	6	0·333
3	0	SELM	1	162·7	2·1	5	0·350
4	0	SELM	Free	164·7	4·1	6	0·129
5	Free	IFM	1	160·6	0·0	6	1·000
6	Free	IFM	Free	162·6	2·0	7	0·368
7	Free	SELM	1	161·4	0·8	6	0·670
8	Free	SELM	Free	163·5	2·9	7	0·235

Table 2. Markov chain Monte Carlo estimates of the parameters for the best stochastic patch occupancy model (model 5 in Table 1); 95% confidence intervals for the parameters that are estimated independently are given as 'fixed'. α is the dispersal function parameter, b and c are the connectivity function parameters, y is the colonization function parameter, u and x are the extinction function parameters and R is the rescue effect function parameter

Model parameters	Estimates	95% CI
a	0·479	Fixed
b	0·056	0·000–0·283
c	0·351	0·088–0·398
y	6·579	6·579–8·570
u	0·127	0·094–0·128
x	1·465	1·445–1·859
R	1	Fixed

American pika, *Ochotona princeps* in an earlier study (Moilanen *et al*. 1998).

Scaling of emigration with patch quality was weak ($b < 0{\cdot}2$), indicating that quality of a patch did not substantially influence the emigration rate. Scaling of immigration with patch quality was in the typical range ($c < 0{\cdot}5$), indicating that local patch quality had a significant influence on the immigration rates (Moilanen 2004).

MODEL SIMULATION

The patch occupancy dynamics of the yellow-bellied marmot metapopulation was simulated using the most parsimonious model (model 5 in Table 1) with the parameter estimates given in Table 2. For all simulations, the average proportion of occupied patches and the proportion of surviving simulation replicates were reported for two different levels of regional stochasticity ($\sigma = 0{\cdot}1$ and $s = 0{\cdot}2$).

As expected, simulations of the entire network showed equilibrium dynamics at the lower regional stochasticity, and higher regional stochasticity did not have a significant effect on long-term metapopulation persistence (Fig. 3a). To understand the influence of site quality on metapopulation persistence, we simulated sites of each quality type separately. The average proportion of occupied patches in nine colony sites showed a rapid decline followed by a long period of stability, in the absence of satellite sites (Fig. 3b). Despite their much lower quality, satellite sites seemed to contribute to the overall metapopulation persistence. When regional stochasticity was low, 12% of the simulated replicates went extinct within 100 years, whereas 20% went extinct when regional stochasticity was high. In the absence of the satellite sites, average persistence time of the metapopulation decreased from infinity to 2481 years.

Absence of colony sites significantly altered the overall metapopulation persistence. Even at the lower level of regional stochasticity, the proportion of occupied patches declined very rapidly to zero within 30 years when colony sites were excluded (Fig. 3c). None of the simulated replicates survived past 40 years in the absence of the colony sites (Fig. 3c). Average persistence time of the metapopulation that included only 12 satellite sites was only 10 years.

To evaluate the sensitivity of patch occupancy dynamics to changes in the quality of colony sites the quality of each colony site was gradually reduced, and patch occupancy dynamics were simulated using the new values. Our simulations showed that a 20% decline in quality of colony sites significantly affected regional persistence. The proportion of occupied patches declined to 60% at the end of 100 years at the lower regional stochasticity, whereas it declined to 46% at the higher regional stochasticity (Fig. 4a). At lower regional stochasticity, 96% of the simulated replicates persisted at the end of 100 years, whereas at higher regional stochasticity only 80% persisted (Fig. 4a). This 20% reduction in the quality of colony sites resulted in a decrease in average metapopulation lifetime from infinity to 3254 years.

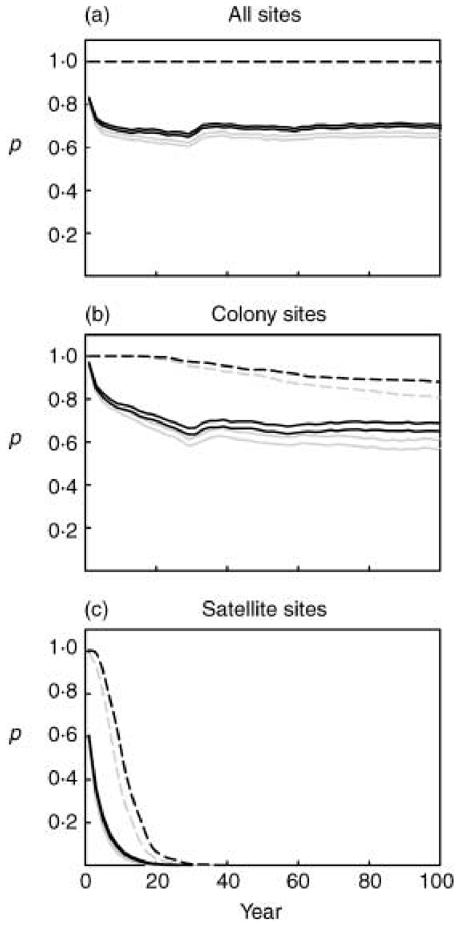

Fig. 3. Patch occupancy in 1000 replicate simulations of the yellow-bellied marmot metapopulation using the parameterized stochastic patch occupancy model. Confidence intervals (95%) for the proportion of occupied patches in all sites (a), colony sites only (b) and satellite sites only (c) are given as solid lines. Proportion of surviving replicates for all sites (a), in only colony sites (b), and in only satellite sites (c) are given as dashed lines. Simulation results with regional stochasticity set at $\sigma = 0{\cdot}1$ are shown as black lines, and for $s = 0{\cdot}2$ are shown as grey lines.

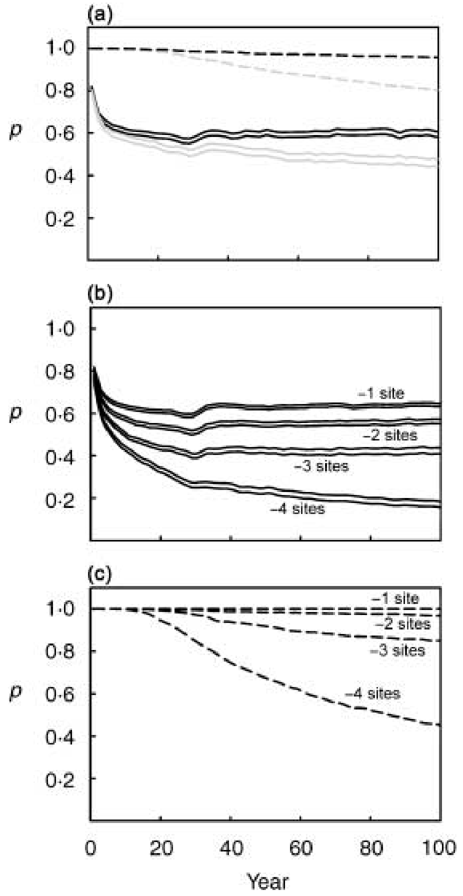

Fig. 4. Patch occupancy in 1000 replicate simulations (a) when the quality of colony sites was reduced by 20%, and (b, c) when one, two, three and four highest quality colony sites were excluded from the network. These sites are indicated in Fig. 1. Confidence intervals (95%) for the proportion of occupied patches are given as solid lines. Proportion of surviving replicates are given as dashed lines. Simulation results with regional stochasticity set at $\sigma = 0{\cdot}1$ are shown as black lines, and for $s = 0{\cdot}2$ are shown as grey lines.

These results indicated that persistence of the yellow-bellied marmot metapopulation in Colorado depended heavily on the quality of a few colony sites. To analyse the influence of these high quality sites on metapopulation persistence, we repeated the simulations by excluding one, two, three and four of the highest quality sites (Fig. 1). Simulations with the low level of regional stochasticity showed that the metapopulation persistence was relatively unaffected by the absence of the two best quality sites (Fig. 4b,c). However, in the absence of the best three sites site occupancy gradually declined to 42%, and 15% of the simulated replicates went extinct within 100 years (Fig. 4b,c). In the absence of the best four sites, the metapopulation was no longer persistent; the proportion of occupied patches declined rapidly, and only 45% of the simulated replicates persisted for 100 years (Fig. 4b,c).

We used connectivity-based clustering analysis available in SPOMSIM to test for the existence of hierarchical network structure of the metapopulation in terms of connectivity between networks (Moilanen 2004). This analysis revealed the existence of two networks: upper-valley (northern) and lower-valley (southern) networks (Fig. 1), which was also consistent with our biological understanding of the marmot system. Thus, we examined the differences in the dynamics of these two networks. The metapopulation in the northern network was more stable than the southern network. The proportion of occupied patches in the northern network did not decline during 100 years of simulations either under low or high regional stochasticity levels (Fig. 5a). On the other hand, the southern network was very unstable, and the proportion of occupied patches frequently declined to zero (Fig. 5b). Very few of the simulated replicates survived till the end of 100 years (Fig. 5b).

We repeated our simulations using values sampled from the 95% confidence interval of parameter estimates,

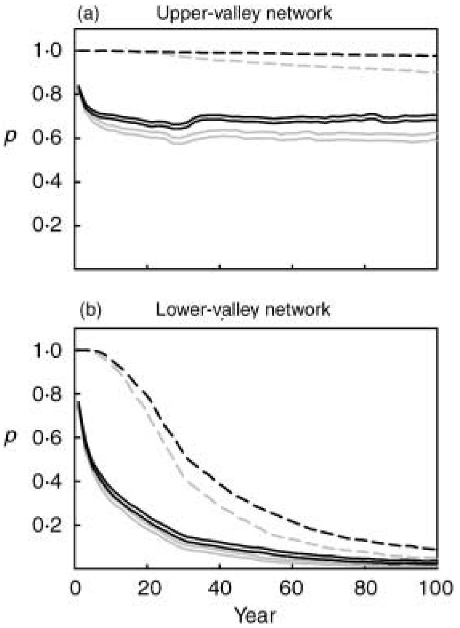

Fig. 5. Patch occupancy in 1000 replicate simulations for the northern and southern networks. Confidence intervals (95%) for the proportion of occupied patches in the northern (a) and the southern (b) network are given as solid lines. Proportion of surviving replicates in the northern (a) and the southern (b) network are given as dashed lines. Simulation results with regional stochasticity set at $\sigma = 0·1$ are shown as black lines, and for $s = 0·2$ are shown as grey lines.

Table 3. Definition of robust design occupancy models used for modelling colonization (γ) and extinction (ε) probabilities

Notation	Biological significance
ε (.)	Constant extinction rate
ε (t)	Time-specific extinction rate
ε (Q)	Extinction rate with *site quality* as a constant site covariate
ε (E)	Extinction rate with *extinction** as a time-varying site covariate
γ (.)	Constant colonization rate
γ (t)	Time-specific colonization rate
γ (C)	Colonization rate with *colonization** as a time-varying site covariate
γ (S)	Colonization rate with *connectivity** as a time-varying site covariate

*Estimated using the parameterized stochastic patch occupancy model.

and each replicate was run with the new set of parameter values. Our previous results remained unchanged, indicating that our results were fairly robust to small changes in the parameter values.

ADEQUACY OF THE SPOM

To investigate the adequacy of SPOM for the yellow-bellied marmot system, we compared a set of candidate models using the robust design occupancy modelling approach (Tables 3 and 4). In general, including time-specific, but not site-specific, variation in colonization and extinction rates resulted in poor model likelihoods (Table 4). Models with constant colonization and extinction rates had higher likelihoods compared to time-specific models that ignored site-specific differences. Model likelihoods were improved significantly when time- and site-specific extinction probabilities estimated using the SPOM were included as covariates. The models that included connectivity or colonization parameters as covariates did not differ significantly from constant colonization rate models (first three models in Table 4). None the less, two models with SPOM-predicted colonization rates were among the best models. These findings indicated the adequacy of the SPOM for modelling the dynamics of the yellow-bellied marmot metapopulation.

Table 4. Number of parameters (# par), Akaike's information criterion corrected for small sample size (AIC_c), deviances and model likelihoods for the robust design occupancy models fitted to the yellow-bellied marmot data. Parameters ε and γ are the extinction and colonization rates, respectively. Initial occupancy rate (Ψ) was estimated as a constant rate, and detection probability (ρ) was set to 1 in all models. For model definitions see Table 3

Extinction and colonization rates	# par	AIC_c	Deviance	ΔAIC_c	Model likelihood
ε (E) γ (S)	5	158·4	143·7	0	1·00
ε (E) γ (.)	4	158·9	148·1	0·5	0·75
ε (E) γ (C)	5	159·2	144·5	0·8	0·67
ε (Q) γ (S)	5	164·7	150·1	6·3	0·04
ε (Q) γ (.)	4	165·2	154·4	6·8	0·03
ε (Q) γ (C)	5	165·4	150·8	7	0·03
ε (.) γ (S)	4	176·2	165·3	17·8	0
ε (.) γ (C)	4	177·1	166·2	18·7	0
ε (.) γ (.)	3	178·1	170·5	19·7	0
ε (.) γ (t)	14	282·3	149·3	123·9	0
ε (t) γ (.)	14	284·6	151·6	126·2	0

Discussion

Our study suggests that (1) persistence of the yellow-bellied marmot metapopulation strongly depends on the colony sites; (2) overall metapopulation persistence was highly sensitive to small changes in number and quality of colony sites; (3) lower quality sites contributed to the long-term persistence of the yellow-bellied marmot metapopulation, especially when the regional stochasticity was high; and (4) the northern network was more stable compared to the southern network, and the persistence of the southern network depended strongly on the northern network.

Previous studies indicated that colony sites generally are more persistent than satellite sites mainly because of the fact that colony sites are occupied by matrilines that may persist for many generations (Armitage & Downhower 1974; Armitage & Schwartz 2000; Armitage 2003). Increased matriline sizes improve the persistence of the local population by affecting survival and net reproductive rate (Armitage & Schwartz 2000; Armitage 2003). Consistent with these observations, our results suggest that colony sites are the major drivers of the yellow-bellied marmot metapopulation dynamics, and that the quality of these sites was especially important; a small decline in site quality resulted in a significant decline in metapopulation persistence. Also, a small number of colony sites might be ultimately responsible for the metapopulation persistence. The dependence of metapopulation persistence on a small number of high quality sites has been suggested to be a general rule in long-lived species (Harrison 1991; Schoener 1991) and has been observed in American pika, *Ochotona princeps* (Moilanen *et al*. 1998), a species that shares similar life-history characteristics. These results emphasize the importance of local site quality, and of environmental factors that may influence local site quality, for metapopulation persistence.

Local population sizes of yellow-bellied marmots can fluctuate remarkably over time (Armitage & Downhower 1974; Schwartz *et al*. 1998; Oli & Armitage 2004). These fluctuations can occur at a local scale due to factors such as predation (Armitage 2004; Van Vuren 2001), or at the regional scale due to regional fluctuations in environmental conditions (Armitage 1994, 2003). Regional factors influencing local population dynamics are considered explicitly in the stochastic patch occupancy modelling approach; however, local population dynamics are assumed to be insignificant and generally overlooked (Hanski 1999). Given that the yellow-bellied marmot metapopulation persistence is highly sensitive to changes in the quality of a few colony sites, a complete understanding of marmot metapopulation dynamics probably requires consideration of factors and processes that influence the dynamics of local populations. Overall, however, SPOM provided a reasonable description of the dynamics of the marmot metapopulation.

Although the colony sites rarely went extinct during our study period, there remains a possibility that factors such as predation, disease, and demographic stochasticity can cause local extinctions of colony sites in the long term. Despite the high importance of colony sites for regional persistence, our results suggest that lower quality satellite sites may also contribute markedly to the long-term persistence of the yellow-bellied marmot metapopulation. The risk of metapopulation extinction increases in the absence of the satellite sites, especially when the fluctuations in site qualities are regionally synchronous. Although satellite sites are much lower in quality than colony sites, they create a buffer effect (Brown 1969; Gill *et al*. 2001) by increasing connectivity among colony sites and providing temporary sources of recolonization when surrounding colony sites locally go extinct. Observed importance of lower quality sites for the regional dynamics suggests that the yellow-bellied marmot system is not a perfect mainland–island system as suggested for other long-lived species (Harrison 1991; Schoener 1991), and it shows characteristics of a metapopulation in which the extinction–recolonization dynamics play an important role. Ignoring the relative role of satellite sites and considering only dynamics of colony sites can lead to underestimation of metapopulation extinction probability.

Patch occupancy dynamics in two networks indicated that the northern network was more stable and likely to persist longer than the southern network. Moreover, in the absence of the northern network the southern network was unlikely to persist. The observed difference between the persistence of the two networks was largely due to the difference in the number of higher quality sites; the northern network included six colony sites, whereas the southern network included only three colony sites. This observation is consistent with our results that the number and quality of colony sites were the most important factors affecting regional persistence of the yellow-bellied marmot metapopulation. These findings emphasize the importance of a few sites that act as a connection between the two networks for metapopulation persistence.

Moilanen & Nieminen (2002) found that including the effect of local patch area in SPOMs significantly improved the connectivity measure. In our study, the model that included the effect of local patch quality in the connectivity measure had a slightly better likelihood compared to alternative models including the original IFM, which ignored the effect of local patch quality on connectivity (Hanski 1994b). To investigate the differences between the predictions of the SPOM used in this study and IFM, we repeated the simulations with the parameterized IFM. Simulation results were qualitatively very similar to those of our original SPOM, but IFM predicted a higher contribution of satellite sites to metapopulation persistence. In the absence of satellite sites, IFM predicted substantially lower persistence of colony sites compared to those predicted by the SPOM used in this study. Including local patch quality in the estimation of the connectivity parameter increased the connectivity of higher quality sites, hence the overall persistence of the colony sites as well as of the entire metapopulation.

We assumed that the yellow-bellied marmot metapopulation was a discrete metapopulation with no connections to populations outside the study area. However, this assumption is unlikely to be correct. Based on 10 years of radiotelemetry study (Van Vuren 1990) and 41 years of intensive survey (Armitage 1991; Schwartz *et al*. 1998), we are confident that all major marmot sites inside or within close proximity of our study area are included in our analyses. However, immigration into and emigration out of the study metapopulation did occur (Van Vuren 1990). Ignoring the connectivity of the yellow-bellied marmot metapopulation to outside of the study area can result in an overestimation of colonization ability, hence in an overestimation of regional persistence (Moilanen

2002). It is also important to note that we assumed a detection probability of 1·0 during our analyses; however, it may be an unrealistic assumption for some of the remote satellite sites that have been surveyed less frequently. False zeros in these sites can result in slight overestimation of the intrinsic extinction rates, dispersal distances and colonization ability (Moilanen 2002). Therefore, our measures of persistence are not conservative, and should be interpreted with caution.

Finally, we utilized the robust design occupancy modelling approach to test the adequacy of the SPOM used for simulations of the yellow-bellied marmot system. We found that colonization and extinction events varied among sites; thus, an important assumption of the classical metapopulation model (Levins 1969) was not appropriate for the yellow-bellied marmot metapopulation. Considering site-specific connectivity measures and extinction probabilities estimated using the SPOM significantly improved the likelihood of the resulting model. Therefore, we believe that the SPOM adequately described the site occupancy dynamics of the yellow-bellied marmot metapopulation. Our study is one of the first studies to use the robust design occupancy modelling approach to test the adequacy of a SPOM. We suggest that this approach could also be utilized easily in other studies.

Behavioural interactions among individuals can influence population dynamics of social organisms (Grimm *et al*. 2003). The yellow-bellied marmot is a socially complex species (Blumstein & Armitage 1999; Armitage & Schwartz 2000), and an accurate description of the dynamics of marmot metapopulations may thus necessitate models that can incorporate behavioural interactions among individuals. However, models that allow explicit consideration of behavioural interactions (e.g. individual-based models) are structurally complex and data-intensive. Although models that consider behavioural interactions should be preferred when data are available to parameterize such models, it is important to know what we can learn about dynamics and persistence of a population by analysing models with simple data requirements. For many species, data to parameterize more complex models are usually lacking and simple models such as SPOMs or robust design patch occupancy models are the only option. Ovaskainen & Hanski's (2004) findings that SPOMs adequately mimic the behaviour of more complex models are encouraging to those who lack detailed demographic and behavioural data to parameterize individual-based models. Patch occupancy models are applied frequently to modelling metapopulation dynamics of many invertebrates (e.g. Hanski *et al*. 1996; Wahlberg, Moilanen & Hanski 1996; Appelt & Poethke 1997; Biedermann 2000; Kindvall 2000), but the applications of such models to avian or mammalian metapopulations are clearly under-represented (see Moilanen *et al*. 1998 for an exception). This study provides one of the very few applications of SPOMs as well as robust design occupancy models to study the dynamics and persistence of mammalian metapopulations.

In conclusion, this study demonstrated that the dynamics of yellow-bellied marmot metapopulation depended mainly on a few colony sites, and the regional persistence was highly sensitive to changes in the quality of these sites. None the less, satellite sites made an important contribution to the long-term persistence of the yellow-bellied marmot metapopulation. Given the high sensitivity of metapopulation persistence to local population size, future studies of the yellow-bellied marmot metapopulation should also consider local population dynamics. Our analyses based on simple site occupancy data provided an adequate description and several useful insights regarding the dynamics and persistence of the yellow-bellied marmot metapopulation.

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