vol. 173, no. 4 the american naturalist april 2009 Ⓔ

Influence of Local Demography on Asymptotic and Transient Dynamics of a Yellow-Bellied Marmot Metapopulation

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Submitted June 20, 2008; Accepted October 14, 2008; Electronically published February 27, 2009

Online enhancements: appendix figures.

abstract: Despite recent advances in biodemography and metapopulation ecology, we still have limited understanding of how local demographic parameters influence short- and long-term metapopulation dynamics. We used long-term data from 17 local populations, along with the recently developed methods of matrix metapopulation modeling and transient sensitivity analysis, to investigate the influence of local demography on long-term (asymptotic) versus short-term (transient) dynamics of a yellow-bellied marmot metapopulation in Colorado. Both long- and short-term dynamics depended primarily on a few colony sites and were highly sensitive to changes in demography at these sites, particularly in survival of reproductive adult females. Interestingly, the relative importance of sites differed between long- and short-term dynamics; the spatial structure and local population sizes, while insignificant for asymptotic dynamics, were influential on transient dynamics. However, considering the spatial structure was uninformative about the relative influence of local demography on metapopulation dynamics. The vital rates that were the most influential on local dynamics were also the most influential on both long- and short-term metapopulation dynamics. Our results show that an explicit consideration of local demography is essential for a complete understanding of the dynamics and persistence of spatially structured populations.

Keywords: conservation of fragmented populations, *Marmota flaviventris*, matrix metapopulation model, patch value, transient sensitivity analysis, vec-permutation matrix.

Introduction

Loss and fragmentation of habitat are the most important factors contributing to biodiversity loss worldwide (Lawton and May 1995; Laurance and Bierregaard 1997; Young and Clarke 2000; Fahrig 2001). The remaining habitats continue to be fragmented to accommodate the needs of expanding human populations, and many species of conservation concern occur in fragmented populations (Thrall et al. 2000; Brito and Fernandez 2002). Understanding the dynamics and persistence of populations that are spatially structured (either naturally or by human-caused fragmentation of habitat) and assessing their conservation needs necessitate an explicit consideration of spatial heterogeneity (McCullough 1996; Akçakaya 2000; Akçakaya and Sjögren-Gulve 2000; Hanski and Ovaskainen 2000; Hanski and Gaggiotti 2004). Consequently, ecologists and conservation biologists have relied on metapopulation theory and models to understand the effect of spatial structure on population dynamics (reviewed by Hanski and Simberloff [1997] and Hanski [1999]). The theory has advanced substantially in recent decades, and several models with varying degrees of complexity (e.g., from patch occupancy to spatially explicit individual-based models) have been developed (reviewed by Akçakaya and Sjögren-Gulve [2000] and Hanski and Gaggiotti [2004]). However, empirical tests of the theory and its application to wildlife conservation have been mostly limited to modeling approaches that do not explicitly consider local demographic processes (Hanski 1999; Sjögren-Gulve and Hanski 2000; Lopez and Pfister 2001; Moilanen 2004). As a result, we still have a limited understanding of the interplay between local demography and metapopulation dynamics.

Prospective perturbation (i.e., sensitivity and elasticity) analyses have proved to be a useful and robust tool to discern the relative influence of demographic parameters on single-population dynamics (Benton and Grant 1999; Caswell 2001). However, similar tools for perturbation analysis of spatially structured populations have been lacking until recently (Hunter and Caswell 2005; but see Pascarella and Horvitz 1998). Our understanding of the in-

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Am. Nat. 2009. Vol. 173, pp. 517–530. © 2009 by The University of Chicago. 0003-0147/2009/17304-50553$15.00. All rights reserved.
DOI: 10.1086/597225

terplay between local demography and metapopulation dynamics has been limited to a few simulation-based studies tailored to specific conservation questions and species (e.g., Lankester et al. 1991; Lahaye et al. 1994; Akçakaya and Atwood 1997). Consequently, little is known about how demographic elasticities change when the spatial structure of a population is considered or what demographic factors determine the relative contribution of local populations to metapopulation dynamics.

The relative contribution of local populations (patches) to metapopulation dynamics and the factors that determine the importance of patches (i.e., patch values) are interesting questions from both theoretical and applied perspectives (Brito and Fernandez 2002; Ovaskainen and Hanski 2003; Figueira and Crowder 2006; Pellet et al. 2006). Most studies evaluating the relative importance of patches are based on models that do not explicitly consider local population dynamics (Ovaskainen and Hanski 2003; Pellet et al. 2006). However, where data are available, explicit consideration of local dynamics can elucidate the demographic determinants of what constitutes an important patch. Furthermore, dispersal of individuals is often age or stage specific for most species and is influenced by local demographic processes (e.g., Lahaye et al. 1994; Bowler and Benton 2005; Matthysen 2005). Hence, consideration of local demographic processes can also provide important insights into the regional processes driving metapopulation dynamics.

It has long been recognized that transient population dynamics can differ in important ways from asymptotic dynamics (Coale 1972; Koons et al. 2006; Caswell 2007). Just as perturbation analysis of the asymptotic growth rate reveals the effects of vital rates on long-term population growth, the perturbation analysis of transient dynamics can reveal the relative importance of vital demographic parameters in determining short-term population dynamics. Although asymptotic perturbation analyses are widely used in demographic studies (Caswell 2001), perturbation analysis of transient dynamics is a relatively new concept in population ecology (Fox and Gurevitch 2000; Yearsley 2004; Caswell 2007; Haridas and Tuljapurkar 2007).

Our goal was to quantify the relative contribution of local demographic and dispersal rates to both long-term (asymptotic) and short-term (transient) population dynamics of a spatially structured population of the yellow-bellied marmot (*Marmota flaviventris*). Specifically, we addressed the following questions: (1) What are the demographic causes of spatial variation in population dynamics? (2) How do demographic rates influence population dynamics, and does the pattern of influence change when population's spatial structure is considered? (3) How much does each local population contribute to metapopulation dynamics, and what are the demographic factors influencing their relative contributions? Finally, (4) do answers to these questions differ for short-term (transient) versus long-term (asymptotic) dynamics?

The yellow-bellied marmot is an ideal model species for understanding the dynamics and persistence of spatially structured populations. Marmots in the East River Valley (Colorado) live in spatially distinct habitat patches in a matrix of aspen-spruce forest (Svendsen 1974). Philopatric marmots typically stay within 50 m of their burrows to minimize predation risk. Thus, local populations are distinctly defined and are interconnected through dispersal (Schwartz and Armitage 1980; Van Vuren 1990; Ozgul 2006). Our long-term (1962–2005) study provided adequate data to parameterize a spatially and demographically structured population model. The recently developed vec-permutation matrix approach (Hunter and Caswell 2005) and the MATLAB symbolic toolbox enabled us to construct a complex metapopulation matrix model, a task that would otherwise be tedious and error prone.

Methods

Study System and Field Methods

The yellow-bellied marmot is a large, diurnal, burrow-dwelling rodent occupying montane regions of western North America (Frase and Hoffmann 1980; Armitage 2003). The biology of yellow-bellied marmots in Colorado is described in detail by Armitage (1991, 2003). This study was conducted in the upper East River Valley near the Rocky Mountain Biological Laboratory, Gothic, Colorado (38°57′N, 106°59′W). The marmots in our study area occupied discrete habitat patches that varied in size and quality (Armitage 1991, 1998). We identified 17 distinct habitat patches (hereafter "sites") within the study area and grouped these sites into eight categories (four colonies and four satellite groups) on the basis of site quality and location (for details, see Ozgul et al. 2006*b*, 2007). The four major colonies were (1) Picnic, (2) River (two adjacent sites), (3) Marmot Meadow, and (4) Gothic. Smaller satellite sites were grouped with respect to their location: (5) North (two sites), (6) West (two sites), (7) East (four sites), and (8) South (four sites) satellites. Colony sites are larger habitat patches occupied by one or more matrilines, each typically consisting of one male, two or more closely related adult females, yearlings, and young. Satellite sites are smaller habitat patches that are typically occupied by a single adult female, her litter, and sometimes an adult male (Armitage 1991, 1998).

From 1962 to 2005, yellow-bellied marmots were live-trapped at the 17 sites and individually marked with numbered ear tags (details in Armitage 1991). Animal identification number, sex, mass, and reproductive condition were recorded for each animal. Ages for females that were captured as juveniles were known, whereas ages for other females were estimated based on body mass (≤ 2 kg = yearling, >2 kg = adult; Armitage et al. 1976).

Local Population Dynamics

Previous studies have shown that survival and reproductive rates of marmots differ among life-history stages and among sites (Armitage and Downhower 1974; Schwartz et al. 1998; Oli and Armitage 2004; Ozgul et al. 2006*b*, 2007). We used a postbreeding census, stage-structured matrix model to investigate the dynamics of the female segment of the population at each site. We considered four stages: juveniles (subscript j; 0–1 yr), yearlings (subscript y; 1–2 yr), prereproductive adults (subscript p; ≥2 yr and yet to reproduce), and reproductive adults (subscript r; ≥2 yr and having reproduced at least once). This stage structure is depicted as a life-cycle graph (fig. 1), which can be expressed in the form of a population projection matrix:

$$\begin{bmatrix} 0 & S_y\psi_y m_2 & S_p\psi_p m_{\geq 3} & S_r\psi_r m_{\geq 3} \\ S_j & 0 & 0 & 0 \\ 0 & S_y(1-\psi_y) & S_p(1-\psi_p) & 0 \\ 0 & S_y\psi_y & S_p\psi_p & S_r \end{bmatrix},$$

where S_x is the probability of an individual in stage x surviving until the following year, ψ_x is the probability of an individual in stage x reproducing the following year, conditional on survival, and m_x is the number of daughters per reproducing female (hereafter, litter size) at age x. We assumed a postbreeding census such that births occur just before the census (Caswell 2001); consequently, all females except juveniles have a nonzero probability of breeding before the next census (fig. 1).

Estimation of Demographic Parameters. We used the long-term (1962–2005) trapping data and the multistate capture-mark-recapture (CMR) model (Hestbeck et al. 1991; Brownie et al. 1993; Williams et al. 2001; Fujiwara and Caswell 2002; Morris and Doak 2002) implemented in the program MARK (White and Burnham 1999) to estimate and model stage-specific annual apparent survival (S), recapture (ρ), and breeding probabilities (ψ) at each site group. The parameter ψ is the probability of breeding during the following year; thus, both yearling and prereproductive adult stages have $\psi > 0$. Yellow-bellied marmots disperse during the yearling stage (1–2 yr). Thus, the apparent survival rates for the yearlings (S_y) were confounded by permanent emigration. To derive the site-specific true survival rates for the yearlings, we divided the site-specific apparent survival rates by the estimated dispersal probability, P_d (for more detail, see "Dispersal"). If the derived true survival rate for yearlings was higher than that for the reproductive adults (S_r) at a given site, we used the value of S_r as the true survival rate for the yearlings. Litter size was estimated as the number of weaned female young that emerged from the natal burrows

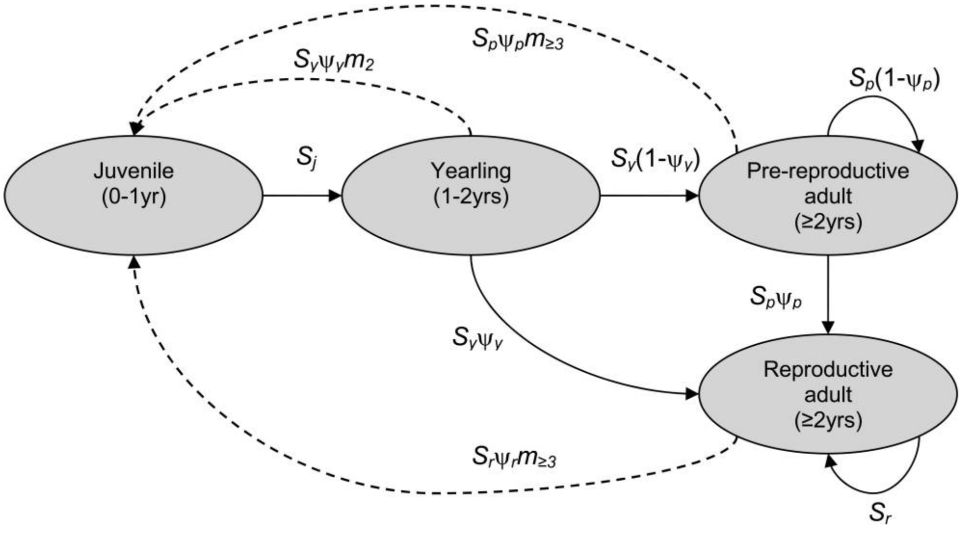

Figure 1: Life cycle of the yellow-bellied marmot, with four life-history stages: juvenile (*j*), yearling (*y*), prereproductive adult (*p*), and reproductive adult (*r*). S_x is the probability of an individual in stage x surviving until the next census, ψ_x is the probability of an individual in stage x reproducing in the following year, conditional on survival, and m_x is the number of daughters per reproducing female at age x. We have assumed a postbreeding census; consequently, both yearlings and prereproductive adults have a nonzero probability of reproducing in the following year.

(Schwartz et al. 1998; Oli and Armitage 2004). Litter sizes varied among site groups and differed between 2-year-olds (m_2) and older females ($m_{\geq 3}$; Schwartz et al. 1998; Ozgul et al. 2007). Thus, we obtained separate estimates of m_2 and $m_{\geq 3}$ for each site group.

Perturbation Analyses. For each site, the local population growth rate (λ) was estimated as the dominant eigenvalue of the population projection matrix. First, we investigated the relative influence of demographic rates on local population dynamics. We implemented prospective perturbation methods using elasticity analysis and investigated the sensitivity of λ to proportional changes in local demographic rates (de Kroon et al. 2000; Caswell 2001). Next, we identified the demographic causes of the observed spatial variation in local population dynamics. We implemented retrospective methods using the random-design life-table response experiment analysis (Caswell 2001) and investigated the actual contributions of the variance of and the covariation among demographic parameters to observed variation in λ among site groups.

Metapopulation Dynamics

We used Hunter and Caswell's (2005) vec-permutation-matrix approach and the MATLAB Symbolic Toolbox (R2006a, MathWorks, Natick, MA) to construct a matrix metapopulation model using demographic and dispersal data from 17 sites. We assumed that demography and dispersal occurred sequentially within the projection interval; demographic changes took place within each site, and then dispersal redistributed individuals among sites. The corresponding metapopulation projection equation is

$$\underbrace{\begin{bmatrix}\eta_1\\ \vdots \\ \eta_{17}\end{bmatrix}_{t+1}}_{\mathbf{n}_{t+1}} = \underbrace{\mathbf{P}^T\mathbf{MPB}}_{\mathbf{A}}\underbrace{\begin{bmatrix}\eta_1\\ \vdots \\ \eta_{17}\end{bmatrix}_{t}}_{\mathbf{n}_{t}},$$

where $\mathbf{n}_t$ is the metapopulation vector at time t, written in terms of stage distributions within each site, and η_i is the population vector for the ith site. The matrix product $\mathbf{A} = \mathbf{P}^T\mathbf{MPB}$ is the metapopulation projection matrix (Hunter and Caswell 2005). The matrix $\mathbf{B}$ is the block-diagonal matrix for demography,

$$\mathbf{B} = \begin{bmatrix}\mathbf{K}_1 & 0 & \dots & 0\\ 0 & \mathbf{K}_2 & \dots & 0\\ & & \ddots & \\ 0 & 0 & \dots & \mathbf{K}_{17}\end{bmatrix},$$

where the ith diagonal block $\mathbf{K}_i$ is a 4 × 4 population projection matrix for site i. The matrix $\mathbf{M}$ is the block-diagonal matrix for dispersal,

$$\mathbf{M} = \begin{bmatrix}\mathbf{L}_\mathrm{j} & 0 & 0 & 0\\ 0 & \mathbf{L}_\mathrm{y} & 0 & 0\\ 0 & 0 & \mathbf{L}_\mathrm{p} & 0\\ 0 & 0 & 0 & \mathbf{L}_\mathrm{r}\end{bmatrix},$$

where the ith diagonal block $\mathbf{L}_i$ is a 17 × 17 matrix of dispersal probabilities for stage i. The matrix $\mathbf{P}$ is a 68 × 68 vec-permutation matrix, defined as

$$\mathbf{P} = \sum_{i=1}^{4}\sum_{j=1}^{17}\mathbf{E}_{ij}\otimes\mathbf{E}_{ij}^T,$$

where $\mathbf{E}_{ij}$ is a 4 × 17 matrix with 1 in the (i, j) position and 0s elsewhere and $\otimes$ denotes the Kronecker matrix product (Hunter and Caswell 2005).

Dispersal. In yellow-bellied marmots, dispersal is age specific, with dispersal occurring predominantly at the yearling stage (1–2 yr; Armitage 1984; Van Vuren 1990). Using the findings of Van Vuren and Armitage (1994), we assumed that the probability of dispersal (P_d) was 0.45 for the yearling females. We further assumed that the Colorado metapopulation was a closed system, and we forced the individuals to disperse within the metapopulation according to distances between sites. We repeated our analyses at nine different dispersal levels (from 0.25 to 0.65 in increments of 0.05) to understand the influence of dispersal level on elasticity patterns. We assumed that dispersal was distance dependent (e.g., Akçakaya and Atwood 1997; Hanski 1999) and used the dispersal distances of 38 radio-tagged yearling marmots to model dispersal (Van Vuren 1990). Proportion of dispersers dispersing to each distance class (in kilometers) was used as the dependent variable (D) and the midpoint of each distance class was the independent variable (d) in a negative exponential model:

$$D = a\cdot e^{-(d/b)},$$

where b is the average dispersal distance (estimated as 1.44 km for female marmots; Van Vuren 1990) and a was estimated with a nonlinear regression model ($a = 0.084$). We used the estimated D to distribute dispersing individuals (i.e., 45% of the yearlings) among sites. Van Vuren and Armitage (1994) reported that dispersing marmots suffer an additional 13% mortality; thus, we imposed an additional 13% mortality on dispersing yearling females ($S_\mathrm{d} = 0.87$). The resulting dispersal matrix for yearlings, $\mathbf{L}_y$, has the probability of staying at the natal site (0.55) along the diagonal and 0.45 × 0.87 (i.e., $P_\mathrm{d} \times S_\mathrm{d}$) =

0.39 as the column sums for the subdiagonal elements. Dispersal matrices for marmots belonging to other stages ($\mathbf{L}_j$, $\mathbf{L}_p$, and $\mathbf{L}_j$) have 1s along the diagonal and 0s elsewhere.

Asymptotic Analysis (λ_{MP}*).* The asymptotic metapopulation growth rate (λ_{MP}) was estimated as the dominant eigenvalue of the metapopulation projection matrix **A**. The elasticities of λ_{MP} to changes in the local demographic rates (8 site groups × 9 vital rates = 72 parameters) and dispersal rates (P_{d} and S_{d}) were calculated by using the chain rule, as described by Caswell (2001) for single-population models.

Transient Perturbation Analysis (N_{t}*).* We performed a perturbation analysis of transient metapopulation dynamics using a matrix calculus approach recently developed by Caswell (2007). The sensitivity of the metapopulation vector at time t ($\mathbf{n}_t$) to changes in the local demographic and dispersal rates (vector $\boldsymbol{\theta}$) was calculated as

$$\frac{d\mathbf{n}_t}{d\boldsymbol{\theta}^T} = \mathbf{A}_{\mathrm{MP}}\frac{d\mathbf{n}_{t-1}}{d\boldsymbol{\theta}^T} + \left(\mathbf{n}_{t-1}^T \otimes \mathbf{I}\right)\frac{d\mathrm{vec}(\mathbf{A}_{\mathrm{MP}})}{d\boldsymbol{\theta}^T},$$

where $\otimes$ denotes the Kronecker product, **I** is a 68 × 68 identity matrix, and vec($\mathbf{A}_{\mathrm{MP}}$) stacks the columns of $\mathbf{A}_{\mathrm{MP}}$ into a column vector. The initial metapopulation vector $\mathbf{n}_0$ (number of individuals at each stage at each site) is the average number of females in each stage observed from 2000 to 2005. The sensitivity of total metapopulation size (N_t) to changes in $\boldsymbol{\theta}$ was calculated as

$$\frac{dN_t}{d\boldsymbol{\theta}^T} = \mathbf{e}^T\frac{d\mathbf{n}_t}{d\boldsymbol{\theta}^T},$$

where **e** is a vector of 1s (i.e., the weight vector for each stage per site). The elasticity of total metapopulation size (N_t) to changes in $\boldsymbol{\theta}$ was calculated as

$$\frac{\mathrm{diag}(\boldsymbol{\theta})}{N_t}\frac{dN_t}{d\boldsymbol{\theta}^T},$$

where diag($\boldsymbol{\theta}$) is a matrix with $\boldsymbol{\theta}$ on the diagonal and 0s elsewhere.

We investigated the relative influence of the overall demography at each site on long-term (λ_{MP}) and short-term (N_t) population dynamics, using elasticity of metapopulation growth rate to demographic variables at each site. The elasticity of λ_{MP} (or N_t for transient metapopulation dynamics) to changes in the overall demography at a given site was calculated by summing the elasticity of λ_{MP} (or N_t) to the nine demographic rates (S_{j}, S_{y}, S_{p}, S_{r}, m_2, $m_{\geq 3}$, ψ_{y}, ψ_{p}, and ψ_{r}) at that site; these values quantify the relative influence on λ_{MP} (or N_t) of each site. Next, we examined the relative influence of local demographic and dispersal rates on long- and short-term population dynamics. The elasticity of λ_{MP} (or N_t) to a specific local demographic rate was calculated by summing the elasticities of λ_{MP} (or N_t) to that specific demographic rate at all sites; these values were then used to quantify the relative influence on λ_{MP} (or N_t) of each demographic variable.

Results

Local Population Dynamics

Annual local population growth rate λ (mean ± SE) showed significant variation among sites. In general, λ was higher in colony sites (Marmot Meadow: 1.12 ± 0.09, Picnic: 1.10 ± 0.12, River: 1.08 ± 0.09, Gothic: 1.02 ± 0.07) than in satellite sites (North: 0.88 ± 0.06, East: 0.81 ± 0.10, South: 0.87 ± 0.11, West: 0.80 ± 0.09). The λ calculated using a single projection matrix for the overall population (i.e., all sites pooled) indicated a slowly increasing population trajectory (1.02 ± 0.07).

Despite the observed spatial variation in λ, vital-rate elasticities did not vary substantially among sites (see fig. A1 in the online edition of the *American Naturalist*). In general, the elasticity of λ was the highest to S_{r} and the second-highest to S_{j} and S_{y} (except in West satellites, where elasticity of λ to S_{p} was the second-highest). We used a random-design analysis of the life-table response experiment to decompose spatial variation in local population growth rate, $V(\lambda)$, into contributions from variance of and covariance among vital rates at each site. The largest spatial variation (quantified by the coefficient of variation) was observed in ψ_{y} and ψ_{p} (see fig. A2 in the online edition of the *American Naturalist*); however, these variables contributed little to $V(\lambda)$. In contrast, S_{r} varied among sites less than most vital rates did but made the largest contribution to $V(\lambda)$. Other demographic variables that made meaningful contribution to $V(\lambda)$ included S_{p} and $m_{\geq 3}$.

Metapopulation Dynamics

At the estimated dispersal level ($P_{\mathrm{d}} = 0.45$), annual λ_{MP} was ~1.00, indicating a stable metapopulation (fig. 2). This estimate was lower than the λ estimated using a single-population matrix for the entire region (1.02). As expected from a deterministic model, λ_{MP} was lower at higher dispersal levels (0.96 at $P_{\mathrm{d}} = 0.65$) and higher at lower dispersal levels (1.05 at $P_{\mathrm{d}} = 0.25$). The λ_{MP} approached the largest local λ's (1.12) as P_{d} approached 0.

At the estimated dispersal level ($P_{\mathrm{d}} = 0.45$), λ_{MP} was the most sensitive to demographic changes in the Marmot Meadow colony, the site with the highest local λ (fig. 3*A*). Two other colony sites, Picnic and River, also had relatively

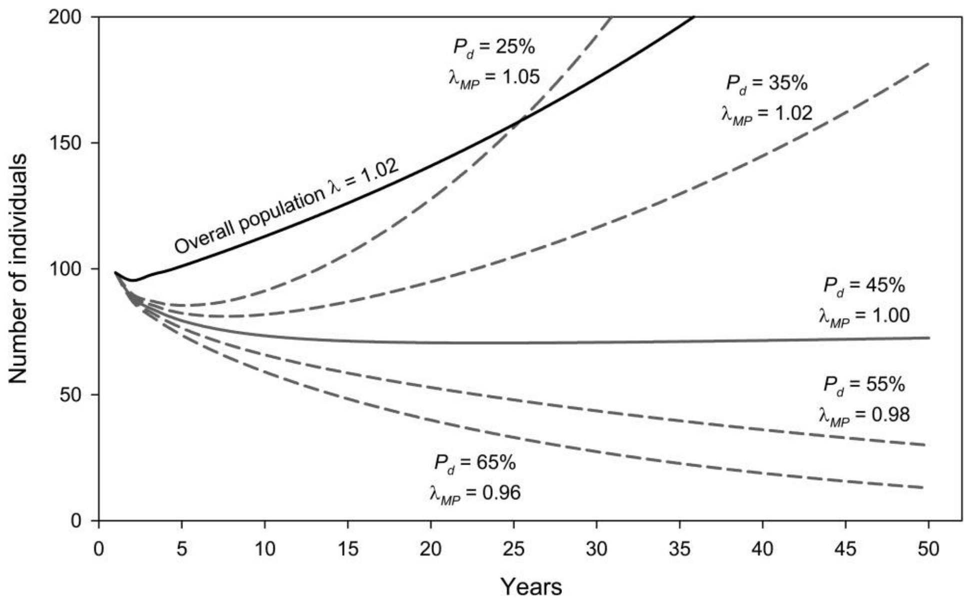

Figure 2: Projected overall population size (*solid black line*) and metapopulation sizes (*gray lines*) at different dispersal levels P_d.

high influence on λ_{MP}. The sum of the elasticities of λ_{MP} to demographic changes in these three colony sites (0.92) was substantially greater than that in the rest of the sites (0.08), suggesting that the overall dynamics of the marmot metapopulation is driven primarily by the demography of these three sites. At lower dispersal levels, the site with the highest local λ had a proportionately greater influence on λ_{MP}, whereas at higher dispersal levels, the River colony had the greatest influence on λ_{MP} (fig. 3*A*). The relative influence of lower-quality sites on λ_{MP} slightly increased at higher dispersal levels. At $P_d = 0.65$, the sum of the relative influence of the three colony sites on λ_{MP} decreased to 0.76, and that of other sites increased to 0.24.

We examined the elasticity of metapopulation size at year 23 (N_{23}) to the overall demography at each site to examine whether transient elasticity patterns differed from asymptotic elasticity patterns (fig. 3*B*). We chose $t = 23$ as the transient time period because the projected population size at the estimated dispersal level ($P_d = 0.45$) reached its minimum at $t = 23$ (fig. 2); hence, 23 years provided an adequate time frame to investigate transient dynamics. Like the asymptotic elasticities, N_{23} was proportionately most sensitive to changes in the demography of the three major colony sites; however, the relative influence of each site was different from that in the asymptotic analysis. At $P_d = 0.45$, N_{23} was the most sensitive to demographic changes in the River colony, followed by Picnic and Marmot Meadow. The rest of the sites generally had a higher influence on N_{23} (0.20) than on λ_{MP} (0.08). Unlike results of the asymptotic analysis, transient elasticities of N_{23} for each site did not vary substantially among dispersal levels. At lower dispersal levels, the three major colony sites had similar influences on N_{23}, whereas at higher dispersal levels, the River colony had the greatest influence on N_{23} (fig. 3*B*).

We also examined how the pattern of transient elasticities changed over time, using the metapopulation projection matrix constructed at the estimated dispersal level ($P_d = 0.45$; fig. 4*A*). The elasticity of N_t to overall demography in the three major colony sites increased gradually during the first ~30 yr. The order of importance for these three sites differed between the short- and long-term projections. For the first ~80 yr, N_t was the most sensitive to proportional changes in the demography at the River colony, followed by those at the Picnic and Marmot Meadow colonies. In the long run, transient (N_t) elasticities approached the asymptotic (λ_{MP}) elasticities; Marmot Meadow (i.e., the site with the highest local λ) became the most influential site, followed by the Picnic and River colonies.

Next, we investigated the relative influence of local demographic and dispersal rates on long-term (λ_{MP}) and short-term (N_t) population dynamics. We calculated the elasticities of λ_{MP} and N_{23} to two dispersal rates (P_d and S_d) and nine local demographic rates (S_j, S_y, S_p, S_r, m_2, $m_{\geq 3}$ ψ_y, ψ_p, and ψ_r), where the elasticities for each local demographic rate were summed across sites. The overall elasticity pattern was qualitatively similar between the asymptotic (fig. 5*A*) and transient (fig. 5*B*) analyses. After an initial transient period of ~20 yr, the elasticity patterns

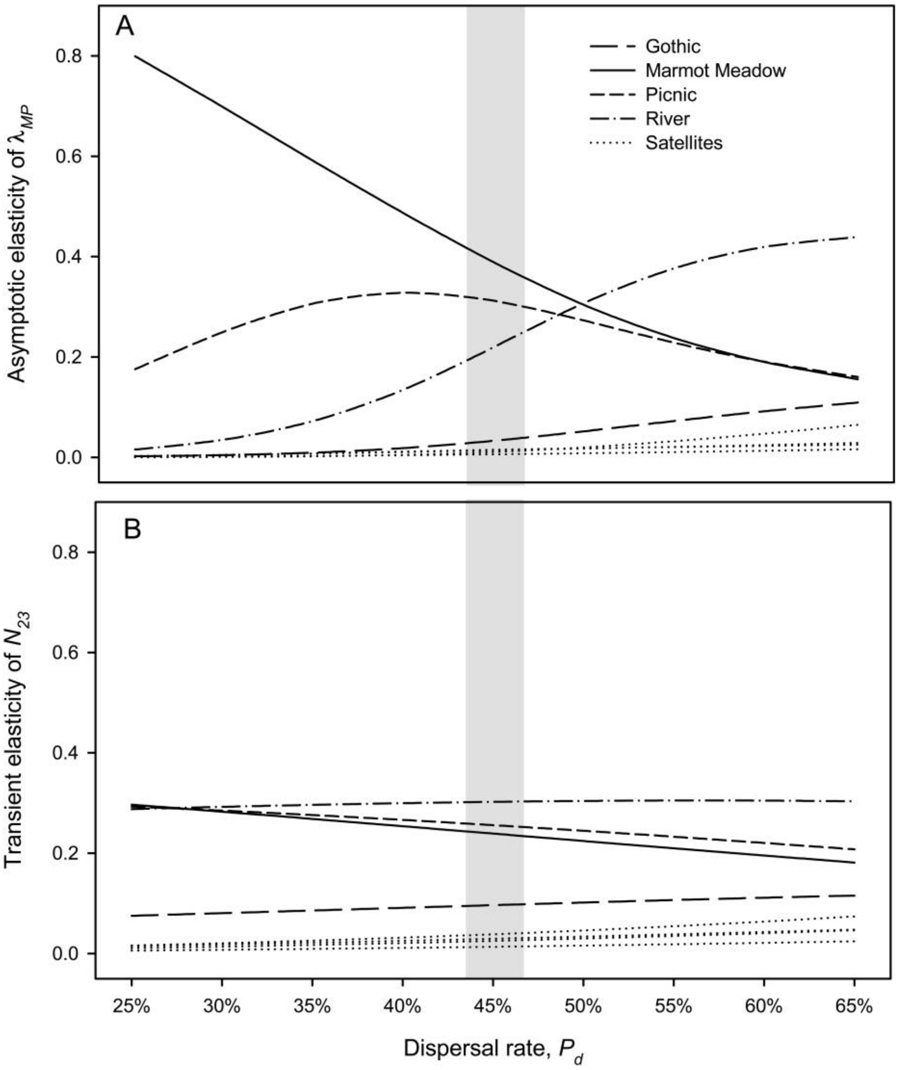

Figure 3: Relative influence of the overall demography at each site on metapopulation growth rate (λ_{MP}; *A*) and metapopulation size at $t = 23$ (N_{23}; *B*) at different dispersal levels ($25\% \leq P_d \leq 65\%$). Relative influences were calculated by summing the lower-level elasticities of λ_{MP} or N_t to the nine demographic rates at a given site. Summed elasticities for each site were rescaled to add to 1. Shaded areas indicate the estimated dispersal level, $P_d = 0.45$.

did not change (fig. 4*B*). Furthermore, elasticities of long- and short-term metapopulation dynamics to the local demographic rates were very similar to the elasticity pattern observed for the local population models. Both λ_{MP} and N_{23} were the most sensitive to proportional changes in S_r, followed by S_j, S_y, and $m_{\geq 3}$. As expected from a deterministic model, λ_{MP} was negatively influenced by P_d. However, the potential influence of P_d and S_d on λ_{MP} (or N_{23}) was relatively small. At higher dispersal levels, the elasticity of λ_{MP} (or N_{23}) to S_r and S_p increased and that to S_j, S_y, and P_d decreased (fig. 5); however, these changes in the elasticity values were minute and did not affect the overall elasticity pattern.

Discussion

Because of their simple data requirements, well-developed theory, and mathematical tractability, stochastic patch occupancy models (SPOMs) have received much attention in both theoretical explorations and practical applications (e.g., Moilanen et al. 1998; Sjögren-Gulve and Hanski 2000; Vos et al. 2000; Hanski 2001; Ovaskainen 2002; Hanski and Ovaskainen 2003; Etienne et al. 2004; Frank 2005). A potential shortcoming of SPOMs is that they do not explicitly consider within-patch population processes, which can be important for population dynamics at both local and regional scales (Harrison and Taylor 1997; Ba-

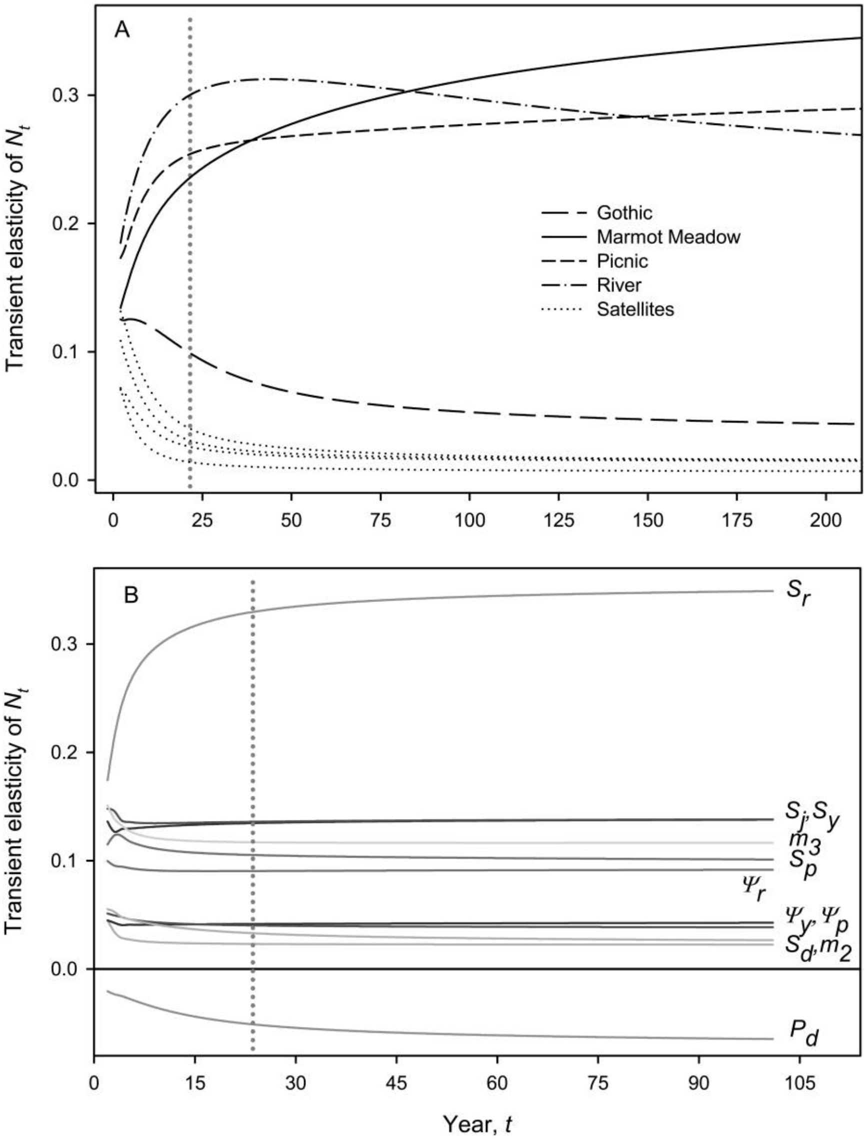

Figure 4: Temporal change in the relative influences of the overall demography in each site group (*A*) and the local demographic and dispersal rates on the metapopulation size at $t = 23$ (N_{23}; *B*). The dotted vertical lines indicate the year at which the metapopulation size reached its minimum (fig. 2). Elasticities of N_{23} are evaluated at the estimated dispersal level, $P_d = 0.45$.

guette and Schtickzelle 2003; Baguette 2004; Baguette and Mennechez 2004; Driscoll 2007). A modeling approach for spatially structured populations that addresses this potential shortcoming is to use spatially and demographically structured matrix metapopulation models (Akçakaya 2000; Hunter and Caswell 2005). When data are adequate, this modeling framework explicitly considers within-patch demography, does not require large number of patches or population turnover, and also has the advantage of a fully developed theory of matrix population models. Using long-term, multisite demographic data obtained from individually marked marmots and recent developments in matrix metapopulation models (Hunter and Caswell 2005) and transient sensitivity analysis (Caswell 2007), we examined various aspects of asymptotic and transient population dynamics at local as well as regional scales.

Local and Metapopulation Growth Rates

Vital demographic rates of yellow-bellied marmots varied among sites (Ozgul et al. 2006*b*, 2007), and this naturally led to spatial variation in population dynamics. The most

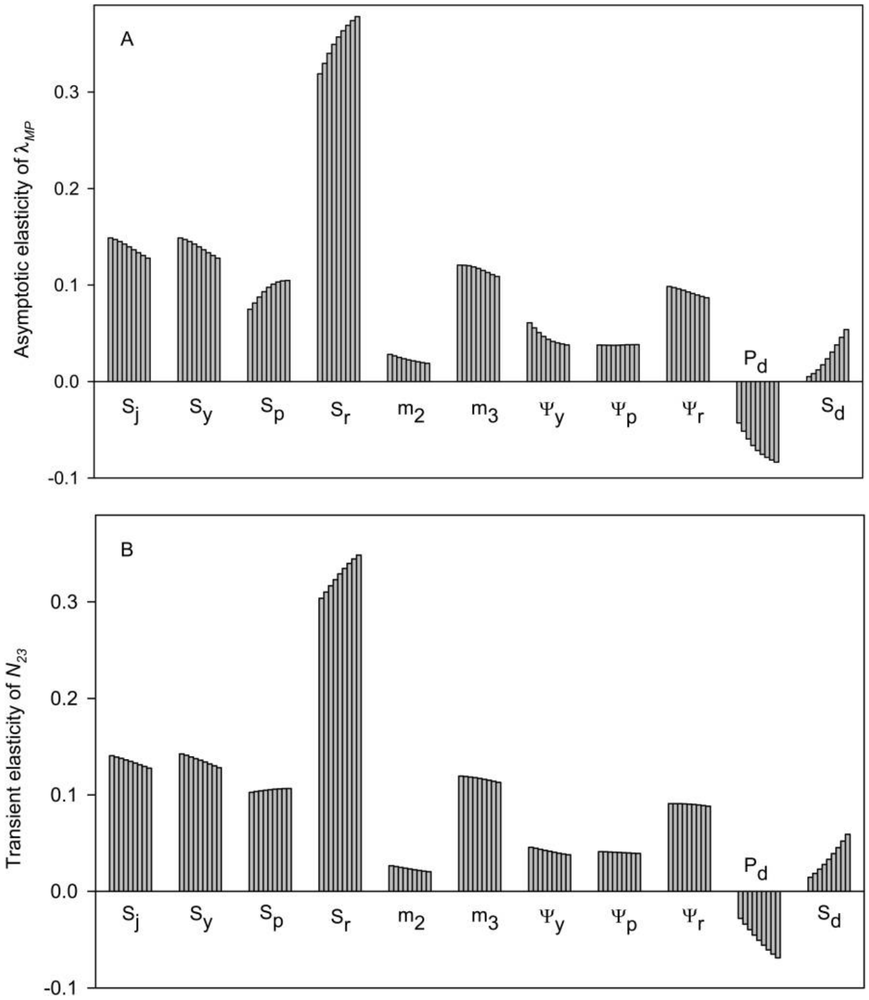

Figure 5: Relative influence of local demographic and dispersal rates on metapopulation growth rate (λ_{MP}; *A*) and metapopulation size at $t = 23$ (N_{23}; *B*) at different dispersal levels ($25\% \leq P_d \leq 65\%$). The elasticity values for the local demographic rates are summed across all the sites. The narrow bars represent the elasticity estimates at nine different dispersal levels: 0.25–0.65 by increments of 0.05, from left to right. See figure 1 for definitions of the vital rates.

influential vital rate, survival of the reproductive adults, showed the least amount of variation, but even a small variation in this rate resulted in significant differences among local population growth rates (λ). Local λ's were ≥1 at colony sites and <1 at satellite sites, suggesting that long-term persistence of satellite sites depended on dispersal from colony sites. Despite a substantial spatial variation in demographic rates and local λ's, the pattern of elasticities did not vary among sites; local λ's had, in general, higher elasticity to survival rates than to reproductive rates, as is true for most long-lived species (Morris and Doak 2002; Oli and Dobson 2003; Stahl and Oli 2006).

Including the spatial structure of the population substantially altered both the asymptotic population growth rate and the transient population dynamics. The asymptotic metapopulation growth rate (λ_{MP}) was lower than that estimated for the overall population ignoring the spatial structure, indicating the importance of spatial structure and dispersal to population dynamics.

Spatial Structure and Elasticity Pattern

Elasticity analysis is a flexible yet tractable tool to understand the association between demographic processes and population dynamics (Caswell 2001). It has become an integral part of demographic studies (de Kroon et al. 1986;

Caswell 2001), and important generalizations regarding the relative importance of vital demographic rates to population growth rates have emerged (Pfister 1998; Heppell et al. 2000; Oli and Dobson 2003; Stahl and Oli 2006). However, it remains unknown whether and to what extent elasticity patterns are altered when the spatial structure of the population is considered. Interestingly, we found that including the spatial structure of the population did not yield substantially different information regarding the relative influence of local demographic rates on population dynamics. Elasticities of λ_{MP} and N_t to local demographic rates were qualitatively similar to those of λ for the overall population (i.e., without spatial structure). Survival of reproductive adults, followed by that of juveniles and yearlings, was the most influential vital rate. This pattern did not differ between short-term (transient) and long-term (asymptotic) population dynamics. Demographic rates that were the most influential on the overall population (i.e., no spatial structure) dynamics were also the vital rates most influential for both long- and short-term metapopulation dynamics.

Demography or Dispersal?

Much of the theory of SPOMs is based on the premise that within-patch demography and population dynamics are relatively unimportant and can be ignored. This notion, however, has been questioned, and some authors have argued that local population dynamics are too important to be ignored (Baguette and Schtickzelle 2003; Baguette 2004; Baguette and Mennechez 2004; Driscoll 2007). We empirically tested the relative importance of local demography and dispersal by comparing elasticity of λ_{MP} or N_t to demography and dispersal parameters (Caswell 2001; Hunter and Caswell 2005). We found that dispersal rate negatively influenced both asymptotic and transient dynamics of the yellow-bellied marmot population. However, the magnitude of the influence of dispersal rate and dispersal mortality on regional population dynamics was generally lower than that of the local demographic rates; changes in dispersal rates did not substantially alter these elasticity patterns. We suggest that the indifference of vital-rate elasticities to spatial structure and the relatively small influence of dispersal rate and dispersal mortality are due to the fact that dispersal in yellow-bellied marmots takes place at the least costly age (as indicated by relatively low elasticities). Although this is not a surprising result, it has important implications for the evolution of dispersal in long-lived species. Furthermore, the relatively minor influence of dispersal rates on metapopulation dynamics highlights the need for explicit consideration of within-patch demography in studying the dynamics of demographically and spatially structured populations (Baguette and Schtickzelle 2003; Baguette 2004; Baguette and Mennechez 2004).

Patch Values and Metapopulation Dynamics

An understanding of the relative importance of a habitat patch to the dynamics and persistence of metapopulations ("patch value") is of tremendous importance for conservation of fragmented or otherwise spatially structured populations (Brito and Fernandez 2002; Ovaskainen and Hanski 2003; Figueira and Crowder 2006). Within the SPOM framework, the relative importance of patches is frequently quantified by using measures such as the contribution of a patch to metapopulation capacity, metapopulation size, or to metapopulation persistence (Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2003). Similar measures of patch values are not currently available for demographically structured metapopulation models. We suggest that the sum of the elasticities of metapopulation growth rate to vital demographic rates for each patch rigorously quantifies the relative contribution of a patch to the overall metapopulation dynamics. This measure of patch value has several desirable properties. First, elasticities are directly interpretable as contributions to λ_{MP}; the elasticity sum for each patch represents the contribution of that patch to the metapopulation growth rate (Caswell 2001; Hunter and Caswell 2005). Second, this approach appropriately considers both within- and between-patch processes that can potentially influence metapopulation dynamics. Also, when elasticities are estimated for the elements of the demographic matrix, they sum to 1.0 (de Kroon et al. 1986; Caswell 2001; Hunter and Caswell 2005); thus, the sum of elasticity for each patch precisely quantifies the relative contribution, or importance, of each patch. Finally, recent developments in the theory of matrix population models allow sensitivity analysis of transient metapopulation dynamics (Caswell 2007); thus, the relative importance of patches can be calculated for both long-term (asymptotic) and short-term (transient) dynamics.

We assessed the patch value of each marmot site by examining elasticities of λ_{MP} and N_t to changes in the overall demography at each site (i.e., lower-level elasticities for local demographic rates summed for each site). The three major colony sites (River, Picnic, and Marmot Meadow) were substantially more influential on both λ_{MP} and N_t than the remaining sites. The dependence of regional persistence on a small number of high-quality sites has been suggested as a general rule in long-lived species (Harrison 1991; Schoener 1991; Beier 1993) and has also been observed in empirical studies (e.g., Moilanen et al. 1998). Consistent with these observations, three of the 17 sites were the major drivers of marmot metapopulation dynamics.

Interestingly, the relative patch values differed between long- and short-term population dynamics. At the estimated dispersal level, λ_{MP} was most sensitive to changes in the demography of the site with the highest local λ. Only at very high dispersal levels did the spatial structure have some influence on the relative importance of sites, and a site with a lower local λ became the most influential site. On the other hand, transient perturbation analysis showed that, during the transient period of ~30 yr, N_t was also influenced by the initial population sizes. During this period, N_t was relatively more sensitive to overall demography in two major colony sites that had lower local λ's, but higher initial population sizes, than it was in the site with the highest λ. Also, lower-quality sites had substantially more influence on N_t than on λ_{MP}. The observed difference in the patch values for the short- and long-term population dynamics is important to note. Spatial structure and sizes of local populations, while insignificant for asymptotic dynamics, were very influential during the transient period. These results emphasize the need for explicit consideration of transient population dynamics for conservation of spatially and demographically structured populations.

Clearly, smaller (or lower-quality) sites had lower patch values and thus little influence on both short- and long-term metapopulation dynamics in yellow-bellied marmots. At higher dispersal levels, the influence of lower-quality sites on λ_{MP} slightly increased, but this reduced λ_{MP}. These results may seem to indicate a mainland-island or source-sink situation (Pulliam 1988; Harrison 1989), in which the viability of the best-quality sites is of predominant importance for the regional dynamics, whereas that of other sites is of minor importance. However, even lower-quality sites can significantly contribute to regional persistence, especially when local population dynamics are asynchronous (Ozgul et al. 2006*a*). Furthermore, the number of marmots inhabiting even the largest habitat patches was small, and no single local population of yellow-bellied marmot is invulnerable to extinction. For example, the mean number of female marmots in two of the best sites (North Picnic and Marmot Meadows) was 16.3 and 14.8, respectively. Given the small sizes of local populations inhabiting an unpredictable and highly variable environment, the probability that even the largest of these populations would become extinct because of demographic and environmental stochasticities, disturbances, diseases, and extreme weather conditions is high. Thus, lower-quality sites most likely contribute substantially more to the persistence of the metapopulation than is indicated by our deterministic model when larger patches become extinct or sources of uncertainties and disturbances are considered. Revealing these interplays, however, would require individual- or population-based simulation models (DeAngelis and Gross 1992; Grimm and Uchmanski 2002; Baguette 2004; Baguette and Mennechez 2004; DeAngelis and Mooij 2005; Grimm et al. 2006) and is beyond the scope of this article.

The yellow-bellied marmot is a socially complex species, and events such as dispersal, breeding, and survival are intricately connected with social behavior (Armitage 1977; Blumstein and Armitage 1999). Stephens et al. (2002) compared models with varying degrees of complexity, using data from a similar species (alpine marmot *Marmota marmota*), and showed that models that include spatial structure but ignore the social behavior can result in unlikely dispersal events (e.g., individuals dispersing even when reproductive opportunity exists in the natal site). Also, Grimm et al. (2003) showed that social behavior can moderate the effect of environmental fluctuations on population dynamics. The matrix metapopulation model used in our study, although flexible and powerful, did not provide a framework for evaluating the population dynamic consequences of sociality.

Conclusion

Elasticity analyses have proved to be useful tools in conservation planning (Caswell 2000) because they provide conceptual clarity that can direct future research and management actions (e.g., Crowder et al. 1994; Gerber and Heppell 2004). Our study exemplifies the application of these tools to the analysis of demographically and spatially structured populations. Our findings that vital-rate elasticities did not change substantially when the spatial structure was considered but that the relative importance of patches differed, depending on timescales (transient vs. asymptotic), have important conservation implications. Given the limited time and resources for conservation, it is important to know that a basic understanding of the most influential vital rates for population growth can still be gained when the spatial structure of a population is ignored.

Both long- and short-term dynamics of the yellow-bellied marmot metapopulation depended primarily on a few colony sites and were highly sensitive to changes in the overall demography at these sites (particularly survival of reproductive adult females). However, the relative influence of sites was different for long- and short-term dynamics. The spatial structure and the sizes of local populations, while insignificant for long-term dynamics, were very influential during the transient period, suggesting that care must be exercised in using results of asymptotic analyses for conservation of spatially structured populations and reserve design. Given that most populations under pressure are unlikely to be at a stable age or stage distribution or to exhibit nonasymptotic behavior, we propose that patch values based on transient elasticities provide a better understanding of the importance of different patches in conservation planning. Finally, our results show that local demographic factors are important drivers of metapopulation dynamics, and we suggest that an explicit consideration of local demography is essential for a thorough understanding of the dynamics and persistence of demographically and spatially structured populations.

Acknowledgments

We thank all the "marmoteers" who participated in the fieldwork; this work would not have been possible without their dedicated help. Two anonymous reviewers reviewed our manuscript and provided many insightful comments. Our research was partially supported by the Lee R. G. Snyder Memorial Fund (A.O.), a Sigma Xi Grant-in-Aid of Research (A.O.), the Florida Agricultural Experiment Station, and National Science Foundation grants DEB-0224953 (M.K.O.), G-16354, GB-1980, GB-6123, GB-32494, BMS-7421193, DEB-7807327, BSR-8121231, BSR-8614690, BSR-9006772 (K.B.A.), and DBI-0242960 (to Rocky Mountain Biological Laboratory).

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