

YELLOW-BELLIED MARMOT POPULATION DYNAMICS: DEMOGRAPHIC MECHANISMS OF GROWTH AND DECLINE

MADAN K. OLI^{1,3} AND KENNETH B. ARMITAGE²

¹Department of Wildlife Ecology and Conservation, 110 Newins-Ziegler Hall, University of Florida, Gainesville, Florida 32611-0430 USA

²Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045-2106 USA

Abstract. Multiple environmental factors may act synergistically to influence demographic characteristics, and ultimately the dynamics, of biological populations. Using prospective and retrospective analyses of demographic data from a 40-year study of individually marked animals, we investigated the demographic mechanisms of the temporal and spatial dynamics of a yellow-bellied marmot (*Marmota flaviventris*) population. Prospective elasticity analyses indicated juvenile survival (P_j) would have the largest relative influence on the projected population growth rate (λ). Relative magnitudes of elasticities did not differ between years characterized by positive ($\lambda > 1.0$) and negative ($\lambda < 1.0$) population growth. However, retrospective analyses of a life table response experiment (LTRE) revealed that changes in fertility (F), followed by age of first reproduction (α) made the largest contributions to observed annual changes in λ . Changes in F and α made the largest contributions to annual declines in λ , whereas changes in P_j also were important to cause increases in λ . Population dynamic differences among marmot colonies were due primarily to spatial variations in α and P_j . Our results indicate that changes in reproductive parameters (α and F) primarily drive the temporal dynamics of our study population, and that demographic mechanisms of population increases might differ from those of population declines. Studies of the regulation of yellow-bellied marmot populations should focus on the factors or processes influencing reproductive parameters.

Key words: demographic mechanisms of population dynamics; elasticity analysis; LTRE analysis; *Marmota flaviventris*; partial life-cycle model; population dynamics and regulation; yellow-bellied marmot demography.

INTRODUCTION

An important goal of population ecology is to explain why populations fluctuate as they do (Royama 1992). This seemingly simple problem has been a major challenge to modern ecology, and we only have a limited understanding of the causes or consequences of population fluctuations. Clearly, population sizes change in response to environmental perturbations, but environmental factors influence the dynamics of a population through their influences on demographic variables because population dynamics are governed by changes in population growth rates, which in turn are functions of demographic variables (Cole 1954, Oli and Dobson 1999, Dobson and Oli 2001). Thus, a complete understanding of the dynamics and regulation of biological populations requires an understanding of demographic changes that underlie changes in growth rate or size of a population (hereafter “demographic mechanisms of population dynamics”).

Varley and Gradwell (1960) recognized the need for “identifying the [demographic] cause of population change,” and developed a method (key factor analysis)

for this purpose. The key factor analysis attempts to explain changes in population size in terms of total mortality (K), which is the sum of age- or stage-specific mortality rates (k_i) on log scale. The k_i that covaries most closely with K is then identified as the “key factor,” and is assumed to be primarily responsible for observed population changes. The key factor may be identified visually by plotting K and k_i , or based on regression analyses (Smith 1973, Podoler and Rogers 1975). Although popular among ecologists until recently, the key factor analysis has been shown to be conceptually and statistically flawed and is no longer considered to be a reasonable approach to identifying demographic causes of population fluctuations (Royama 1996, Sibly and Smith 1998).

Of currently available demographic techniques, prospective and retrospective perturbation analyses (Horvitz et al. 1997, Tuljapurkar and Caswell 1997, Sibly and Smith 1998, Caswell 2000, 2001, Heppell et al. 2000) are particularly appropriate for discerning the demographic mechanisms of population dynamics. Prospective methods, such as sensitivity and elasticity analyses, explore the functional dependence of projected population growth rate (λ) on demographic variables, and quantify likely changes in λ in response to small absolute (sensitivity) or proportional (elasticity) changes in demographic variables. Sensitivities and

Manuscript received 28 July 2003; revised 3 January 2004; accepted 23 February 2004. Corresponding Editor: B. J. Danielson.

³ E-mail: olim@wec.ufl.edu

elasticities quantify *potential* influences on λ of absolute or proportional changes in demographic variables, but they do not consider observed changes in demographic variables (Caswell 2000, 2001, Oli et al. 2001). Retrospective analyses, on the other hand, look backward and ask how variation in demographic variables expressed themselves in observed changes in λ (Caswell 2000). In particular, the analysis of life table response experiments (LTRE; Caswell 1989, 1996, 2001), a technique for retrospective perturbation analysis (also referred to as “ λ contribution analysis”; Sibly and Smith 1998), allows decomposition of observed changes in λ into contributions from individual demographic variables. The LTRE analysis simultaneously considers the changes in demographic variables and sensitivity of λ to changes in those variables, and thus adequately quantifies the *actual* contributions of demographic variables to observed changes in λ . Moreover, LTRE analyses also adequately address conceptual and statistical problems inherent in the traditional key factor analyses (Sibly and Smith 1998, Dobson and Oli 2001, Oli et al. 2001), and have been used to investigate population-level responses to naturally occurring or experimentally induced perturbations to the environment (Brault and Caswell 1993, Levin et al. 1996, Horvitz et al. 1997, Cooch et al. 2001, Dobson and Oli 2001, Oli et al. 2001).

Experimental studies of population dynamics within the framework of density perturbation experiments (Murdoch 1970, Harrison and Cappuccino 1995) permit quantification of demographic mechanisms and rigorous tests of specific hypotheses (Dobson and Oli 2001, Oli et al. 2001). However, such field experiments usually are of short durations, and logistics do not permit simultaneous manipulation of multiple environmental factors. In the natural world, biological populations are subjected to synergistic effects of multiple environmental factors that may vary unpredictably over time and space. While density perturbation experiments allow rigorous tests of specific hypotheses, an understanding of the dynamics of biological populations that experience the effects of temporal changes in multiple environmental factors can only be gained from long-term demographic studies. This is because unpredictable temporal variation in several environmental factors is a rule, rather than an exception, and experimental manipulations of all factors that can potentially influence the dynamics of a population generally are not feasible.

Using prospective and retrospective analyses of long-term demographic data, we investigated the demographic mechanisms of the dynamics of a yellow-bellied marmot (*Marmota flaviventris*) population in East River Valley, Colorado. First, we used elasticity analysis to identify potentially influential demographic variables. Second, we applied LTRE analysis with time as a treatment, and decomposed observed annual changes in λ into contributions from individual de-

mographic variables. LTRE analyses allowed us to identify key demographic variables that made the largest contributions to observed annual changes in λ , and thus to discern the demographic mechanisms of the dynamics of our study population. Third, we compared the pattern of actual influences of demographic variables on λ between years with positive and negative changes in λ to test if the same demographic mechanisms underlay increases and decreases in λ . Local variation in environmental factors can potentially cause spatial differences in population dynamics (Tilman and Kareiva 1997). Thus, we also investigated population dynamic differences among marmot colonies using prospective and retrospective demographic methods.

Detailed demographic data based on individually identified animals were collected for 40 years. Given the long duration of the study, our study population was subjected to a wide range of environmental conditions that were translated into temporal fluctuations in demographic variables as well as in size and growth rate. Thus, our data were ideal for discerning the spatiotemporal patterns in demographic mechanisms of the long-term dynamics of our study population under natural conditions.

MATERIALS AND METHODS

Study species, study area, and field methods

Yellow-bellied marmots are widely distributed in the mountainous region of the western United States (Frase and Hoffmann 1980). They occupy open, montane habitats dominated by perennial forbs and grasses (Svendsen 1974). Individual marmots live in social groups that consist of closely related females (mothers, daughters, sisters) that may persist for several generations and are known as matriline (Armitage 1998). The matriline occupying a habitat patch form a colony. All yearling males and about half of the yearling females disperse.

The study was conducted in the East River Valley, near Rocky Mountain Biological Laboratory, Gunnison County, Colorado, USA. The study area is described in detail in Svendsen (1974) and Armitage (1986).

Each year, from 1962 to 2001, all marmots within our study area were live-trapped. Sex, age, mass, and reproductive status were noted, and each animal received a pair of uniquely numbered ear tags at first capture. Age of first reproduction of a female was determined as the age at which the first litter of a female emerged from the natal burrow. Litter size was estimated from the number of pups that emerged from a natal burrow (Schwartz et al. 1998). Fate and reproductive history of each female was monitored until she disappeared from the study area. We assumed that a female that disappeared from a colony and was not captured within the study area had died. This assumption may have introduced a bias in our estimates of juvenile survival rate; however, this bias is likely to be

small because (1) all sites occupied by marmots were intensively trapped each year, and attempts were made to capture all animals present. Successful trapping was verified by visual observation. Thus, absence of an animal from the study area was most likely due to death. (2) Immigration is very rare in established colonies unless residents die such that some or all of the habitat patch becomes available for occupancy (Armitage 1991). (3) Dispersing females suffer a high mortality, and probability of dispersing females' finding a suitable habitat patch and realizing reproduction is very low (Van Vuren and Armitage 1994). However, we recognize that some yearling females might have survived dispersal and formed a new matriline outside of our study sites; our estimates of juvenile survival rates may thus be biased downward.

Although our study began in 1962, we did not have adequate data for demographic analyses prior to 1964 because marked females of known age did not begin reproduction until that year. For each year of the study during 1964–2001, we estimated annual juvenile survival rate P_j as the proportion of nulliparous females that survived the year. Likewise, annual adult survival rate P_a was estimated as the proportion of adult females (i.e., females that had attained reproductive maturity) that survived the year and emerged from hibernation the following year. This approach to estimating juvenile and adult survival rates was adequate because our intensive trapping protocol ensured that capture probability was close to one. Average fecundity m was estimated as the average number of daughters per adult female per year; annual fertility rate F was then estimated as: $F = m \times P_a$. Age of first reproduction (α) was the average age of females that reproduced for the first time in a given year. Age of last reproduction (ω) could not be estimated for several years of the study, and was thus assumed to be 11 years; this corresponds to the oldest recorded age at which ≥ 2 female yellow-bellied marmots reproduced in our study area. Given the insensitivity of λ to changes in ω in other ground-dwelling sciurids (Dobson and Oli 2001, Oli et al. 2001, Oli and Dobson 2003), this assumption is unlikely to influence our results.

Demographic analyses

We used a postbreeding census partial life-cycle model for demographic analyses (Oli and Zinner 2001a). This model was appropriate for our study for several reasons. First, this model can be parameterized with five demographic variables (α , ω , P_j , P_a , and F), and we had sufficient data to estimate these parameters for each year of the study. Second, ages of first and last reproduction explicitly appear as model parameters in the partial life-cycle model, and potential and actual contributions of these variables to changes in λ can be directly estimated. This is significant, because α has been suggested to be an important variable with substantial fitness and population dynamic consequences

(Cole 1954, Stearns 1992, Oli and Dobson 1999, Oli et al. 2002, Oli and Armitage 2003, Oli and Dobson 2003). Finally, dynamical properties of age-structured models are generally retained in the partial life-cycle model (Oli and Zinner 2001a, b, Oli 2003). In a partial life-cycle model, age-specific fertilities F_i are approximated by an average fertility parameter F , age-specific survival P_i prior to reproduction by a juvenile survival parameter P_j , and age-specific survival from α until ω by an adult survival parameter P_a . The characteristic equation for the postbreeding census partial life-cycle model is as follows (Oli and Zinner 2001a):

$$1 = FP_j^{\alpha-1}\lambda^{-\alpha} - FP_j^{\alpha-1}P_a\lambda^{-\alpha-1} + FP_j^{\alpha}\lambda^{-\alpha-1} - FP_j^{\alpha}P_a^{\omega-\alpha}\lambda^{-\omega-1} + P_a\lambda^{-1}. \quad (1)$$

For each year of study, the projected population growth rate (λ) was estimated as the largest real root of Eq. 1. We estimated covariance among demographic variables using data from the entire study period, and we estimated approximate variance of λ as follows (Lande 1988, Caswell 2001):

$$\text{var}(\lambda) \approx \sum_{p,q} \text{cov}(p,q) \frac{\partial \lambda}{\partial p} \frac{\partial \lambda}{\partial q}$$

where $\text{cov}(p,q)$ is the covariance between demographic variables p and q , $\partial \lambda / \partial p$ is the sensitivity of λ to changes in variable p , and $\partial \lambda / \partial q$ is the sensitivity of λ to changes in variable q .

The sensitivity of λ to changes in a model parameter p was estimated as the partial derivative of λ with respect to p (i.e., $\partial \lambda / \partial p$, where p is α , ω , P_j , P_a , or F) and was obtained by implicit differentiation of Eq. 1 (Caswell 2001, Oli and Zinner 2001a). Elasticity (proportional sensitivity) of λ to changes in p was estimated as $([\partial \lambda / \partial p][p/\lambda])$ (de Kroon et al. 1986, Caswell 2000, de Kroon et al. 2000, Caswell 2001, Oli and Zinner 2001a). For brevity, elasticity of λ to changes in a demographic variable p will be denoted by $e(p)$. As scaled, dimensionless quantities, elasticities adequately quantify potential influence on λ of changes in demographic variables, and also are directly comparable among demographic variables (de Kroon et al. 2000). Thus, we used elasticities as measures of potential influence of demographic variables on λ .

We used LTRE analyses to quantify the demographic mechanisms of observed temporal changes in λ of our study population. Observed annual change in a demographic variable p (Δp) between year t and the following year $t + 1$ was estimated as: $\Delta p = p^{(t+1)} - p^{(t)}$. Likewise, observed annual change in λ ($\Delta \lambda$) between year t and $t + 1$ was estimated as: $\Delta \lambda = \lambda^{(t+1)} - \lambda^{(t)}$. We then decomposed $\Delta \lambda$ into contributions from observed changes in a model parameter p (Caswell 1989, 2001, Dobson and Oli 2001):

$$\Delta \lambda \approx \sum_p \Delta p \frac{\partial \lambda}{\partial p} \Big|_{(p^{\text{year } t} + p^{\text{year } t+1})/2}. \quad (2)$$

Sensitivities were evaluated at the mean values of the

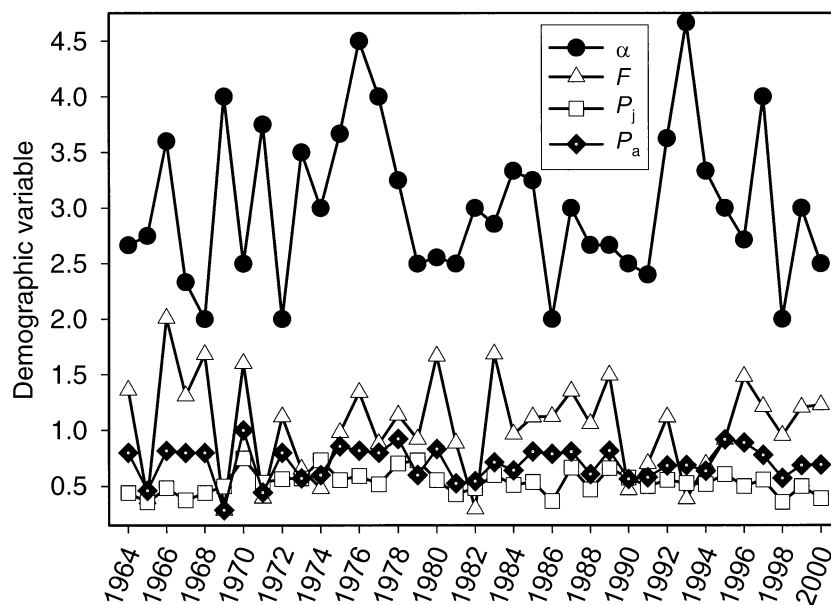


FIG. 1. Estimates of age of first reproduction (α), juvenile survival rate (P_j), adult survival rate (P_a), and fertility rate (F) for a population of yellow-bellied marmots in the East River Valley, Colorado, USA, 1964–2000.

parameters for the two years being compared. A close correspondence between $\Delta\lambda$ and sum of LTRE contributions would indicate adequacy of the LTRE model.

We used two-sample t tests to compare elasticity of λ to changes in demographic variables between years with positive ($\lambda > 1$) and negative ($\lambda < 1$) population growth, and to compare LTRE contributions of demographic variables during years with positive ($\Delta\lambda > 0$) and negative ($\Delta\lambda < 0$) change in λ .

Environmental factors can vary locally, which can cause spatial demographic and population-dynamic differences. Thus, we also asked if demographic mechanisms of spatial variation in population dynamics differed among three major marmot colonies (River, elevation 2867 m; Marmot Meadow, elevation 2930 m; and Picnic, elevation 2992 m). Because we did not have adequate data to estimate model parameters for each colony for each year of the study, we grouped our data into six temporal “periods”: period 1 (≤ 1970), period 2 (1971–1976), period 3 (1977–1982), period 4 (1983–1988), period 5 (1989–1994), and period 6 (1995–2000). We estimated parameters for the partial life-cycle model for each colony–period combination, and estimated λ and $e(p)$ as described previously. The patterns of elasticities were compared to test if they differed among colonies. Finally, we applied LTRE analysis to compare each pair of colonies for each period to discern the demographic mechanisms of spatial variation in the dynamics of our study population. LTRE analyses proceeded as described earlier, except that each colony was compared with the two other colonies for each temporal period.

Data from all colonies and satellite sites were pooled for the analyses involving temporal population dynam-

ics, whereas data from three colonies (River, Marmot Meadow, and Picnic colony) were used for the analyses of spatial population dynamics.

RESULTS

The size of our study population exhibited substantial temporal fluctuations, ranging from 34 individuals in 1970 to 137 individuals in 1988 (mean ± 1 SE = 80.68 ± 4.67). The average age of first reproduction (α) ranged from 2.0 to 4.67 yr, with an overall mean (± 1 SE) of 3.01 ± 0.11 yr. Likewise, P_j ranged from 0.36 to 0.75 and averaged 0.53 ± 0.02 , and P_a ranged from 0.29 to 1.00 and averaged 0.71 ± 0.03 . F ranged from 0.28 to 2.01, and averaged 1.04 ± 0.07 (Fig. 1). Temporal variation in demographic variables naturally caused temporal variation in λ , which ranged from 0.56 ± 0.20 in 1969 to 1.47 ± 0.24 in 1970, with an overall mean of 0.96 ± 0.20 . Demographic variables and λ generally fluctuated around their respective mean values, and there was no discernible temporal trend. λ was >1 (i.e., increasing population) in 12 years and <1 (declining population) in 25 years of study. The average age of first reproduction was three years or less in all years characterized by $\lambda > 1$, whereas delayed age of first reproduction generally characterized years of low λ .

For comparative purposes, we also parameterized the age-structured Leslie matrix model using data for the entire study period. The projected population growth rate (λ) estimated from the age-structured model was 0.97 ± 0.03 , and agreed closely with that reported by Schwartz et al. (1998).

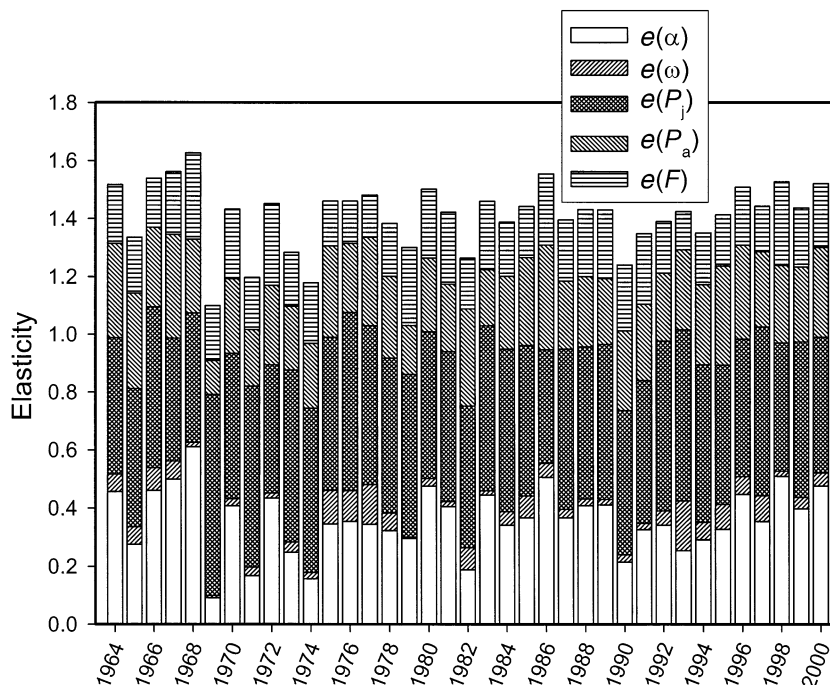


FIG. 2. Elasticity (proportional sensitivity) of the projected population growth rate (λ) to changes in demographic variables, $e(p)$, for a population of yellow-bellied marmots in the East River Valley, Colorado. Elasticities are given for each year during 1964–2000. Demographic variables are: α , age of first reproduction; ω , age of last reproduction; P_j , juvenile survival; P_a , adult survival; and F , fertility.

Temporal dynamics

Prospective analyses.—Mean (± 1 SE) $e(\alpha)$; absolute values), $e(\omega)$, $e(P_j)$, $e(P_a)$, and $e(F)$ was 0.36 (± 0.02), 0.05 (± 0.01), 0.53 (± 0.01), 0.27 (± 0.01), and 0.21 (± 0.01), respectively. Overall, elasticity of λ to changes in α and P_j ranked first (i.e., the largest absolute value of elasticity) in 5 and 32 years of the study, respectively; elasticity of λ to changes in other demographic variables never ranked first and rarely second (Fig. 2). Elasticity of λ to changes in α ($t = 2.44$, $df = 35$, $P = 0.020$) and F ($t = 3.14$, $df = 35$, $P = 0.005$) was significantly higher during years characterized by positive population growth ($\lambda > 1$) than in years characterized by negative population growth ($\lambda < 1$); elasticity of λ to changes in other demographic variables did not differ between years with positive and negative population growth. Overall, however, the relative magnitudes of mean elasticities in years characterized by positive population growth were identical to those characterized by negative population growth: $e(P_j) > e(\alpha) > e(P_a) > e(F) > e(\omega)$.

Retrospective analyses.—Using estimates of demographic variables for 37 years of study, we conducted 36 LTRE comparisons, and decomposed observed annual changes in λ ($\Delta\lambda$) into contributions from individual demographic variables. Observed annual change in λ was negative (i.e., $\Delta\lambda < 0$) in 17 years, whereas it was positive ($\Delta\lambda > 0$) in 19 years. There was a substantial variation in the contribution of demographic

variables to $\Delta\lambda$. In some years, some demographic variables contributed to $\Delta\lambda$ in opposite directions (Fig. 3). For example, during 1966–1967 and 1985–1986, α made a positive contribution to $\Delta\lambda$ whereas most other demographic variables made negative contributions; consequently, λ remained essentially unchanged. The sum of LTRE contributions was practically indistinguishable from $\Delta\lambda$ ($r = 0.999$, $P < 0.0001$), indicating the adequacy of the LTRE model.

Because LTRE contributions of some demographic variables were in the opposite direction (i.e., some variables made positive contributions while others made negative contributions; Fig. 3) for some years of the study, we compared absolute values of LTRE contributions. Overall, α and F made the largest contribution to $\Delta\lambda$ most frequently, in 27.8% and 38.9% ($n = 36$) of the comparisons, respectively; contributions of P_a to $\Delta\lambda$ were rather insubstantial (Fig. 3). During periods when λ declined ($\Delta\lambda < 0$), α and F made the largest contributions to $\Delta\lambda$ most frequently, in 29.4% and 47.1%, respectively ($n = 17$) of the comparisons. In contrast, F and P_j made the largest contributions to increases in λ ($\Delta\lambda > 0$) most frequently, in 31.6% of the comparisons each, followed closely by α (26.3%, $n = 19$).

Spatial dynamics

Prospective analyses.—The projected population growth rate exhibited temporal fluctuations in all col-

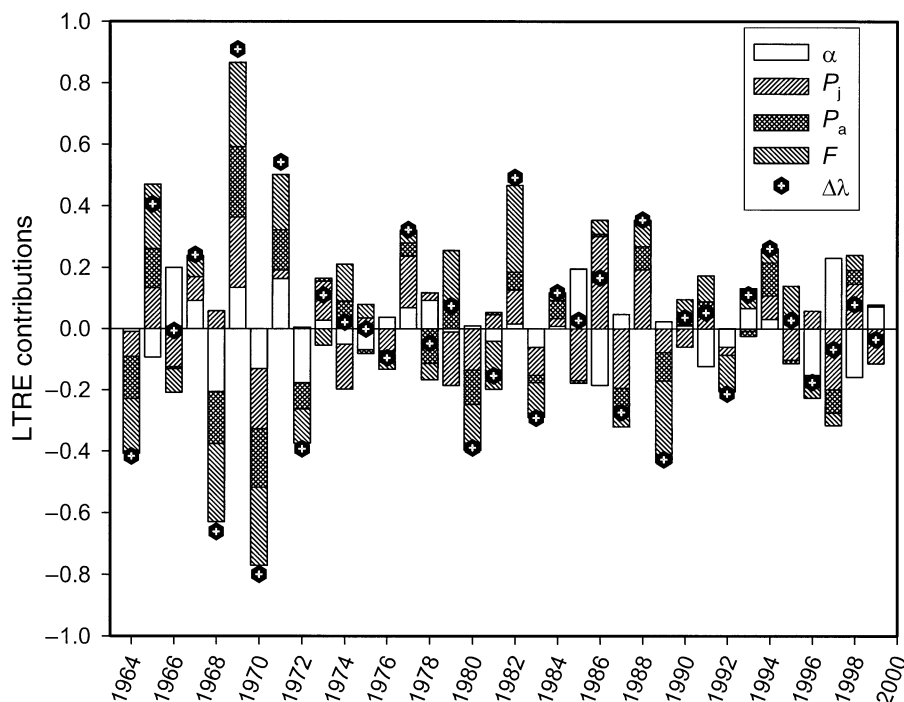


FIG. 3. Life-table response experiment (LTRE) contribution of age of first reproduction (α), juvenile survival (P_j), adult survival (P_a), and fertility (F) to annual changes in projected population growth rate ($\Delta\lambda$). LTRE contributions are given for successive years from 1964 to 2000. Note that the year in x-axis represents the first of the two successive years being compared (e.g., 1964 indicates LTRE comparison of changes in λ from 1964 to 1965).

onies. In River colony, λ ranged from 0.59 ± 0.28 (period 2) to 1.28 ± 0.30 (period 4), and averaged 0.91 ± 0.10 . In Marmot Meadow colony, λ ranged from 0.85 ± 0.13 (period 4) to 1.15 ± 0.35 (period 6), and averaged 1.0 ± 0.05 . In Picnic colony, λ ranged from 0.84 ± 0.11 (period 5) to 1.13 ± 0.12 (period 4), and averaged 0.95 ± 0.04 . In River colony, mean $e(\alpha)$; absolute values), $e(\omega)$, $e(P_j)$, $e(P_a)$, and $e(F)$ was 0.28 ± 0.06 , 0.04 ± 0.01 , 0.55 ± 0.02 , 0.25 ± 0.01 , and 0.20 ± 0.02 , respectively. In Marmot Meadow colony, mean $e(\alpha)$; absolute values), $e(\omega)$, $e(P_j)$, $e(P_a)$, and $e(F)$ was 0.44 ± 0.07 , 0.03 ± 0.01 , 0.55 ± 0.03 , 0.23 ± 0.02 , and 0.22 ± 0.02 , respectively. In Picnic colony, mean $e(\alpha)$; absolute values), $e(\omega)$, $e(P_j)$, $e(P_a)$, and $e(F)$ was 0.33 ± 0.03 , 0.06 ± 0.01 , 0.54 ± 0.02 , 0.28 ± 0.02 , and 0.19 ± 0.01 . The magnitude of $e(P_j)$ was the largest most frequently, in 6, 5, and 4 periods in Picnic, River, and Marmot Meadow colony, respectively; $e(\alpha)$ was highest in all other periods (Fig. 4).

Retrospective analyses.—Within temporal periods, some pairs of colonies had substantially different λ . Thus, we applied LTRE analyses to decompose within-period, between-colony differences in λ . A total of 18 LTRE comparisons were made. α contributed most to differences in λ in seven comparisons (River and Picnic, three comparisons; River and Marmot Meadow, two comparisons; and Marmot Meadow and Picnic, two comparisons). P_j made the largest contributions in a total of six comparisons (River and Picnic, two com-

parisons; River and Marmot Meadow, one comparison; Marmot Meadow and Picnic, three comparisons). F made the largest contributions in a total of four comparisons (River and Marmot Meadow, two comparisons; River and Picnic, one comparison; and Marmot Meadow and Picnic, one comparison). Contribution of ΔP_a to $\Delta\lambda$ was minimal (Fig. 5).

DISCUSSION

Beyond doubt, dynamics of biological populations are governed by changes in the environment, but environmental factors influence population dynamics through their influences on demographic variables (Oli and Dobson 1999, Dobson and Oli 2001). This must be so, because changes in population size are consequences of changes in population growth rates, which in turn are functions of demographic variables. Thus, a complete understanding of the dynamics and regulation of biological populations requires an understanding of demographic changes that underlie population fluctuations. Short-term experimental studies of population dynamics have proved useful in testing specific hypotheses, but such studies fail to capture the complexity of the synergistic effects of multiple environmental factors on the dynamics of biological populations because simultaneous manipulation of multiple environmental factors over a long period is generally not possible. Short-term observational studies are even less informative because they do not capture the range

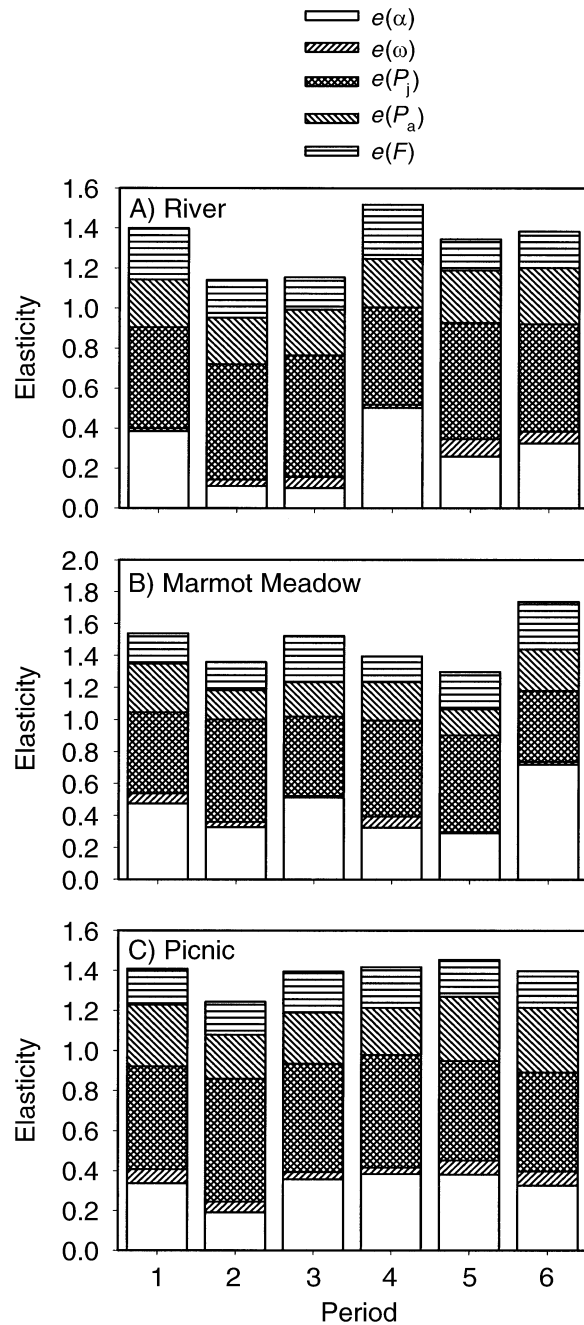


FIG. 4. Elasticity (proportional sensitivity) of the projected population growth rate (λ) to changes in demographic variables, $e(p)$, for three colonies: (A) River, (B) Marmot Meadow, and (C) Picnic of yellow-bellied marmots in the East River Valley, Colorado. Elasticities are given for each of the six temporal periods: period 1 (1970 and before), period 2 (1971–1976), period 3 (1977–1982), period 4 (1983–1988), period 5 (1989–1994), and period 6 (1995–2000). Demographic variables are: α , age of first reproduction; P_j , juvenile survival; P_a , adult survival; and F , fertility.

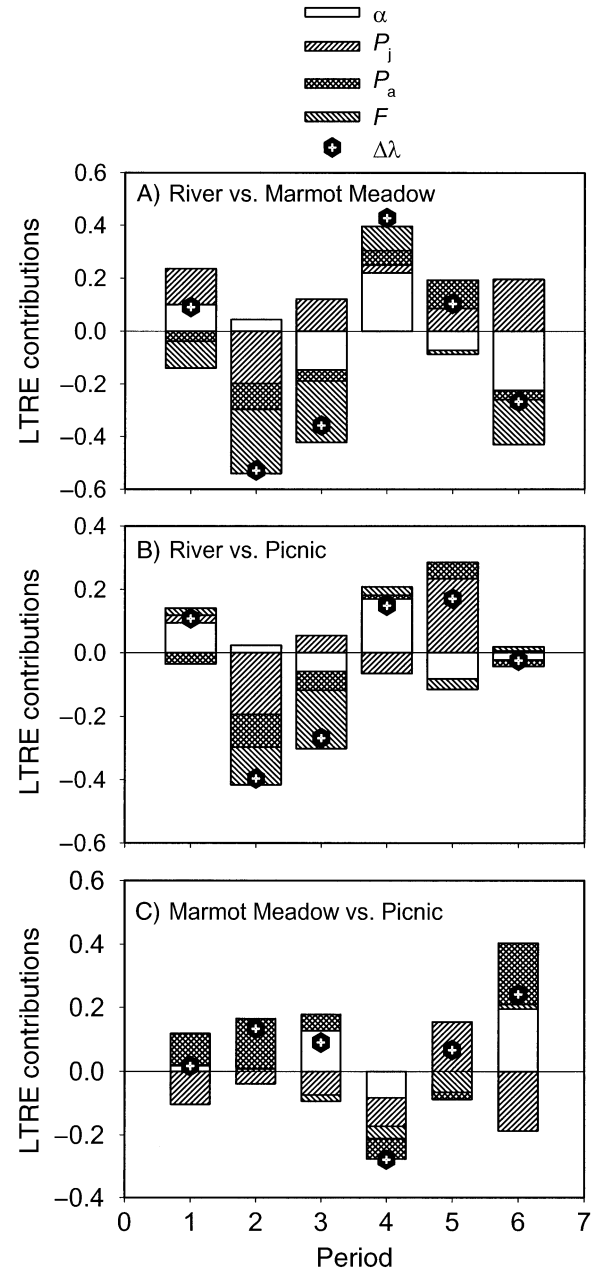


FIG. 5. Life-table response experiment (LTRE) analysis of spatial variation in projected population growth rate (λ). Contributions of spatial differences in demographic variables to within-period, between-colony differences in λ are given for: (A) River and Marmot Meadow colony, (B) River and Picnic colony, and (C) Marmot Meadow and Picnic colony. Demographic variables are: α , age of first reproduction; P_j , juvenile survival; P_a , adult survival; and F , fertility. The six temporal “periods” are: period 1 (1970 and before), period 2 (1971–1976), period 3 (1977–1982), period 4 (1983–1988), period 5 (1989–1994), and period 6 (1995–2000). Observed between-colony differences in λ ($\Delta\lambda$) also are given for each period.

of environmental variability experienced by biological populations. Given that natural populations are subjected to the synergistic effects of multiple environmental factors that can change over time and space unpredictably, only long-term demographic studies allow demographic mechanisms of population dynamics to be discerned under natural conditions.

Our long-term study of individually marked animals provided data necessary for discerning the demographic mechanisms of yellow-bellied marmot population dynamics. During the study period, our study population was exposed to the synergistic effects of multiple environmental factors, which undoubtedly changed over time. Effects of temporal environmental changes were naturally translated into temporal fluctuations in demographic variables, and size and projected growth rate of our study population. Given these changes, our goal was to investigate the demographic mechanisms that underlay temporal changes in λ . Elasticity analyses indicated that changes in P_j would make the largest contribution to temporal changes in λ if it changed, because $e(P_j)$ was the largest in 32 out of 37 years of study. Potential influences on λ of changes in P_a and F were rather insubstantial. These patterns did not substantially change when analyses were conducted at the colony level. Furthermore, the pattern of elasticities did not differ between years characterized by population increases ($\lambda > 1$) and those characterized by population declines ($\lambda < 1$), corroborating recent findings that the actual values of λ have little influence on the pattern of elasticities (Oli and Dobson 2003).

The pattern of LTRE contributions of demographic variables to observed annual changes in λ was quite different than that of elasticities. Overall, F , followed by α , made the largest contributions to $\Delta\lambda$ most frequently. However, when data were analyzed based on whether λ increased ($\Delta\lambda > 0$) or declined ($\Delta\lambda < 0$) between years being compared, a clear pattern emerged. F , followed by α made the largest contributions to decreases in λ most frequently, whereas F , P_j , and α made almost equal contributions to increases in λ . Moreover, we point out that $\lambda \gg 1$ were generally observed only in years characterized by early reproductive maturity (i.e., less than the mean value of α), and that large increases or declines in λ were frequently associated with substantial changes in α . These results suggest that the temporal dynamics of our study population are driven primarily by changes in reproductive parameters (α and F), with changes in juvenile survival playing an important secondary role, and that survival of adults, although quite variable over time, had insignificant potential or actual influence on temporal changes in λ . Moreover, decreases in λ of our study population were primarily a consequence of delayed age of first reproduction and reduced reproductive rates, whereas improvements in P_j also played an important role to cause increases in λ . These findings are consistent with the results of earlier studies investi-

gating demographic mechanisms underlying population dynamics of other ground-dwelling sciurids (Dobson and Oli 2001, Oli et al. 2001), but our study is one of the first to empirically demonstrate that demographic changes that underlie population increases may differ from those underlying population declines. These findings highlight the importance of the retrospective analysis of the long-term demographic data in population ecological studies. If we had focused only on prospective analyses, we would have erroneously concluded that changes in juvenile survival drives the dynamics of our study population; analyses of a subsample of our data for a short period could have led to similarly erroneous conclusions.

Local differences in environmental factors can engender demographic differences over space at any given time, and these differences can have potentially important consequences (Kareiva 1990, Tilman and Kareiva 1997). The pattern of elasticities was similar in the three colonies, but LTRE analyses revealed interesting patterns of spatial differences. For example, in periods 2 (1971–1976) and 3 (1977–1982), River colony was characterized by demographic rates that yielded $\lambda \ll 1$; in Marmot Meadow, however, the projected population growth rate was >1 during the same periods. LTRE analyses further revealed that among-colony differences in λ were primarily a consequence of differences in age of first reproduction and survival of the juveniles. Differences in the quality of habitat patches and predation pressure, and spatial variation in the effects of weather factors (Schwartz and Armitage 2002) may, at least in part, explain the observed spatial variation in demography and population dynamics. The role of spatial demographic variations in the overall temporal dynamics deserves further investigation.

Because dynamics and regulation of biological populations are essentially demographic processes, a complete understanding of population dynamics must necessarily involve two steps (Oli and Dobson 1999, Dobson and Oli 2001). The first step in the study of population regulation should be to understand the demographic machinery that underlies changes in size or growth rate of a population. This can be achieved by LTRE analyses of experimental or long-term demographic data (Brault and Caswell 1993, Levin et al. 1996, Cooch et al. 2001, Dobson and Oli 2001, Oli et al. 2001). Once the demographic mechanisms are discerned and the key demographic variables identified, the second step is to ascertain environmental factors or ecological processes that cause changes in the key demographic variables. The second step usually requires manipulation of the environmental factors hypothesized to influence the key demographic variables. The present study represents the first of the two steps necessary for explaining why yellow-bellied marmot populations fluctuate the way they do.

Precise mechanisms underlying changes in the key demographic variables remain to be ascertained, but

current evidence suggests that the primary cause of changes in age of first reproduction in our study population is social suppression of reproduction in young females (Oli and Armitage 2003). In particular, age of first reproduction of young females is substantially delayed when older, reproductive females are present (Armitage 1996, 2003b, Armitage and Schwartz 2000, Oli and Armitage 2003). Thus, it seems possible that density-dependent influences on yellow-bellied marmot population dynamics may be mediated via the influence of adult female density on age of first reproduction. Weather factors appeared to be the primary determinants of reproductive rate in yellow-bellied marmots (Schwartz and Armitage 2002, Armitage 2003a). Low summer precipitation combined with a long winter (late snow cover) apparently results in more females being in poor condition when they emerge from hibernation. Poor condition is expressed as insufficient fat to both survive the hibernation and reproduce (Andersen et al. 1976). Finally, the major causes of yellow-bellied marmot mortality are predation and failure to survive hibernation (Schwartz et al. 1998, Schwartz and Armitage 2002). Low survival in 1981 was the consequence of heavy badger predation that resulted in the disappearance of at least 25 young and three adults (Armitage 2004). Overwinter survival is poor for young hibernating at lower mass (Lenihan and Van Vuren 1996). Poor growth is associated with weather factors, especially low summer rainfall and long winters (Armitage 1994, Schwartz and Armitage 2002) or with late weaning, which does not provide sufficient time for adequate mass gain before the vegetation senesces (Armitage et al. 1976, Van Vuren and Armitage 1991). Poor juvenile survival in 1967 resulted from poor growth of young and yearlings (Salsbury and Armitage 2003) and in 1969, resulted from late weaning of litters.

In conclusion, our prospective and retrospective analyses of long-term demographic data revealed that the dynamics of our study population were driven primarily by changes in reproductive parameters but that demographic mechanisms of population dynamics may vary over space or time, that changes in juvenile survival played only a secondary role even though this variable generally had the largest potential influence on λ , and that demographic mechanisms underlying population increases were somewhat different from those underlying population declines. Our results highlight the importance of the retrospective analysis of long-term demographic data in population ecological studies, and suggest that only retrospective analyses of long-term demographic data can reveal demographic mechanisms of population dynamics and help identify intrinsic and extrinsic environmental influences on population dynamics. Future studies of yellow-bellied marmot population dynamics should focus on factors or processes that influence the key demographic variables, age of first reproduction and fertility rate.

ACKNOWLEDGMENTS

We thank Dan Blumstein, and several graduate students and technicians; this work would not have been possible without their dedicated field work. Brent Danielson and two anonymous reviewers provided many helpful comments on the manuscript. This research was supported in part by National Science Foundation grants G16354, GB-1980, GB-6123, GB-32494, BMS74-21193, DEB78-07327, BSR-8121231, BSR-8614690, BSR-9006772 (K. B. Armitage), and DEB-0224953 (M. K. Oli), and by Florida Agricultural Experiment Station, and approved for publication as Journal Series No. R-09903.

LITERATURE CITED

- Andersen, D. C., K. B. Armitage, and R. S. Hoffmann. 1976. Socioecology of marmots: female reproductive strategies. *Ecology* 57:552–560.
- Armitage, K. B. 1986. Individuality, social behavior, and reproductive success in yellow-bellied marmots. *Ecology* 67:1186–1193.
- Armitage, K. B. 1991. Social and population dynamics of yellow-bellied marmots—results from long-term research. *Annual Review of Ecology and Systematics* 22:379–407.
- Armitage, K. B. 1994. Unusual mortality in a yellow-bellied marmot population. Pages 5–13 in V. Rumiantsev, editor. *Actual problems of marmots investigation*. ABF Publishing House, Moscow, Russia.
- Armitage, K. B. 1996. Social dynamics, kinship, and population dynamics of marmots. Pages 113–128 in M. Le Berre, R. Ramousse, and L. Le Guelte, editors. *Biodiversity in marmots*. International Marmot Network, Moscow-Lyon, Russia.
- Armitage, K. B. 1998. Reproductive strategies of yellow-bellied marmots: energy conservation and differences between the sexes. *Journal of Mammalogy* 79:385–393.
- Armitage, K. B. 2003a. Recovery of a yellow-bellied marmot population following a weather-induced decline. Pages 217–224 in R. Ramousse, D. Allaine, and M. LeBerre, editors. *Adaptive strategies and diversity in marmots*. International Network on Marmots, Lyon, France.
- Armitage, K. B. 2003b. Reproductive competition in female yellow-bellied marmots. Pages 133–142 in R. Ramousse, D. Allaine, and M. LeBerre, editors. *Adaptive strategies and diversity in marmots*. International Network on Marmots, Lyon, France.
- Armitage, K. B. 2004. Badger predation on yellow-bellied marmots. *American Midland Naturalist* 151:378–387.
- Armitage, K. B., J. F. Downhower, and G. E. Svendsen. 1976. Seasonal changes in weights of marmots. *American Midland Naturalist* 96:36–51.
- Armitage, K. B., and O. A. Schwartz. 2000. Social enhancement of fitness in yellow-bellied marmots. *Proceedings of the National Academy of Sciences (USA)* 97:12149–12152.
- Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (*Orcinus orca*). *Ecology* 74:1444–1454.
- Caswell, H. 1989. Analysis of life table response experiments. I. Decomposition of effects on population growth rate. *Ecological Modelling* 46:221–237.
- Caswell, H. 1996. Analysis of life table response experiments. II. Alternative parameterizations for size- and stage-structured models. *Ecological Modelling* 88:73–82.
- Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* 81:619–627.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Cole, L. 1954. The population consequences of life-history phenomena. *Quarterly Review of Biology* 29:103–137.

- Cooch, E., R. F. Rockwell, and S. Brault. 2001. Retrospective analysis of demographic responses to environmental change: a lesser snow geese example. *Ecological Monographs* **71**:377–400.
- de Kroon, H., A. Plaisier, J. van Groenendaal, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* **67**:1427–1431.
- de Kroon, H., J. van Groenendaal, and J. Ehrlén. 2000. Elasticities: a review of methods and model limitations. *Ecology* **81**:607–618.
- Dobson, F. S., and M. K. Oli. 2001. The demographic basis of population regulation in Columbian ground squirrels. *American Naturalist* **158**:236–247.
- Frase, B. A., and R. S. Hoffmann. 1980. *Marmota flaviventris*. *Mammalian Species* **135**:1–8.
- Harrison, S., and N. Cappuccino. 1995. Using density-manipulation experiments to study population regulation. Pages 131–147 in N. Cappuccino and P. W. Price, editors. *Population dynamics: novel approaches and synthesis*. Academic Press, San Diego, California, USA.
- Heppell, S. S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* **81**:654–665.
- Horvitz, C., D. W. Schemske, and H. Caswell. 1997. The relative “importance” of life-history stages to population growth: prospective and retrospective analyses. Pages 247–271 in S. Tuljapourkar and H. Caswell, editors. *Structured population models in marine, terrestrial, and freshwater systems*. Chapman and Hall, New York, New York, USA.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. *Proceedings of the Royal Society of London, Series B* **330**:175–190.
- Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* **75**:601–607.
- Lenihan, C., and D. Van Vuren. 1996. Growth and survival of juvenile yellow-bellied marmots (*Marmota flaviventris*). *Canadian Journal of Zoology* **74**:297–302.
- Levin, L. A., H. Caswell, T. Bridges, D. Cabera, G. Plaia, and C. DiBacco. 1996. Demographic responses of estuarine polychaetes to pollutants: life table response experiments. *Ecological Applications* **6**:1295–1313.
- Murdoch, W. W. 1970. Population regulation and population inertia. *Ecology* **51**:497–502.
- Oli, M. K. 2003. Partial life-cycle models: how good are they? *Ecological Modelling* **169**:313–325.
- Oli, M. K., and K. B. Armitage. 2003. Sociality and individual fitness in yellow-bellied marmots: insights from a long-term study (1962–2001). *Oecologia* **136**:543–550.
- Oli, M. K., and F. S. Dobson. 1999. Population cycles in small mammals: the role of age at sexual maturity. *Oikos* **86**:557–566.
- Oli, M. K., and F. S. Dobson. 2003. The relative importance of life-history variables to population growth rate: Cole's prediction revisited. *American Naturalist* **161**:422–440.
- Oli, M. K., G. R. Hepp, and R. A. Kenamer. 2002. Fitness consequences of delayed maturity in female wood ducks. *Evolutionary Ecology Research* **4**:563–576.
- Oli, M. K., N. A. Slade, and F. S. Dobson. 2001. Effect of density reduction on Uinta ground squirrels: analysis of life table response experiments. *Ecology* **82**:1921–1929.
- Oli, M. K., and B. Zinner. 2001a. Partial life-cycle analysis: a model for birth-pulse populations. *Ecology* **82**:1180–1190.
- Oli, M. K., and B. Zinner. 2001b. Partial life-cycle analysis: a model for pre-breeding census data. *Oikos* **93**:376–387.
- Podoler, H., and D. Rogers. 1975. A new method for the identification of key factors from life-table data. *Journal of Animal Ecology* **44**:85–114.
- Royama, T. 1992. *Analytical population dynamics*. Chapman and Hall, London, UK.
- Royama, T. 1996. A fundamental problem in key factor analysis. *Ecology* **77**:87–93.
- Salsbury, C. M., and K. B. Armitage. 2003. Variation in growth rates of yellow-bellied marmots (*Marmota flaviventris*). Pages 197–206 in R. Ramousse, D. Allaine, and M. LeBerre, editors. *Adaptive strategies and diversity in marmots*. International Network on Marmots, Lyon, France.
- Schwartz, O. A., and K. B. Armitage. 2002. Correlations between weather factors and life-history traits of yellow-bellied marmots. Pages 345–351 in K. B. Armitage and V. Y. Rumiantsev, editors. *Holarctic marmots as a factor of biodiversity*. ABF Publishing House, Moscow, Russia.
- Schwartz, O. A., K. B. Armitage, and D. Van Vuren. 1998. A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). *Journal of Zoology (London)* **246**:337–346.
- Sibly, R. M., and R. H. Smith. 1998. Identifying key factors using lambda contribution analysis. *Journal of Animal Ecology* **67**:17–24.
- Smith, R. H. 1973. The analysis of intra-generation change in animal populations. *Journal of Animal Ecology* **42**:611–622.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, UK.
- Svendsen, G. E. 1974. Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. *Ecology* **55**:760–771.
- Tilman, D., and P. Kareiva, editors. 1997. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, New Jersey, USA.
- Tuljapourkar, S., and H. Caswell, editors. 1997. *Structured-population models in marine, terrestrial, and freshwater systems*. Chapman and Hall, New York, New York, USA.
- Van Vuren, D., and K. B. Armitage. 1991. Duration of snow cover and its influence on life-history variation in yellow-bellied marmots. *Canadian Journal of Zoology* **69**:1755–1758.
- Van Vuren, D., and K. B. Armitage. 1994. Survival of dispersing and philopatric yellow-bellied marmots—what is the cost of dispersal. *Oikos* **69**:179–181.
- Varley, G. C., and G. R. Gradwell. 1960. Key factors in population studies. *Journal of Animal Ecology* **29**:399–401.