The Demographic Basis of Population Regulation in Columbian Ground Squirrels

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Submitted May 17, 2000; Accepted April 18, 2001

abstract: Environmental factors influence the dynamics and regulation of biological populations through their influences on demographic variables, but demographic mechanisms of population regulation have received little attention. We investigated the demographic basis of regulation of Columbian ground squirrel (*Spermophilus columbianus*) populations under natural and experimentally food-supplemented conditions. Food supplementation caused substantial increases in population density, and population densities returned to pretreatment levels when the supplementation ended. Control (untreated) populations remained relatively stable throughout the study period (1981–1986). Because food resources regulated the size of the ground squirrel populations, we used life-table response experiment (LTRE) analyses to examine the demographic basis of changes in population growth rate and thus also demographic influences on population regulation. LTRE analyses of two food-manipulated populations revealed that changes in age at maturity and fertility rate of females generally made the largest contributions to observed changes in population growth rate. Thus, our results suggested that abundance of food resources regulated the size of our study populations through the effects of food resources on age at maturity and fertility rates. Our results also indicated that different demographic mechanisms can underlie population regulation under different environmental conditions, because lower juvenile survival substantially contributed to population decline, but in only one of the populations. Demographic analyses of experimental data, such as those presented here, offer a rigorous and unambiguous means to elucidate the demographic basis of population regulation and to help identify environmental factors that underlie dynamics and regulation of biological populations.

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Am. Nat. 2001. Vol. 158, pp. 236–247. 0003-0147/2001/15803-0003$03.00.

Keywords: demographic mechanisms, elasticity analysis, life-table response experiment (LTRE) analysis, partial life cycle model, population regulation, *Spermophilus columbianus*.

The study of population regulation, the means by which numbers of individuals are determined in populations, is a major topic in ecology (e.g., Murdoch 1970, 1994; Sinclair 1989, 1996; Krebs 1994). Because population regulation underlies many ecological as well as evolutionary processes (Murdoch 1994), this topic has been fervently debated during much of the past century (e.g., Andrewartha and Birch 1954; Lack 1954; Tamarin 1978; Turchin 1990, 1995, 1999; den Boer and Reddingius 1996; Murray 1999*a*). Although debates regarding mechanisms of population regulation continue, a general agreement exists among ecologists that most biological populations persist because of some regulatory mechanisms (Murdoch 1970, 1994; Royama 1992; Krebs 1994; Turchin 1995). However, the question of how to detect or quantify regulation has remained unresolved and controversial (Gaston and Lawton 1987; Murdoch and Walde 1989; Hanski et al. 1993; Holyoak and Lawton 1993; Wolda and Dennis 1993; Murray 1994, 1999*a*, 1999*b*).

Due to the interactive nature of organisms and their environments, studies of population regulation need to elucidate two closely linked topics: environmental influences on population size and the demographic mechanisms (defined here as changes in demographic parameters that underlie changes in the growth rate or size of a population) of a population's response to those environmental influences (Oli and Dobson 2001). When population size changes, the changes in demography that have occurred (i.e., that mechanistically underlie a change in numbers) are limited. Changes in population size are consequences of changes in reproduction, survival, or migration of individuals. In age- or stage-structured populations, individuals of different ages or life-cycle stages may differ in their responses to environmental change and in their influences on the subsequent dynamics of the overall population. Such age- or stage-specific differences can complicate the study of the demographic mechanisms of

population regulation. In addition, different environments may influence population size and demographic processes differently, so that the interplay of demographic mechanisms and population regulation becomes quite complex. Statistical analyses of time series data, the most commonly used method for quantifying density dependence and population regulation (e.g., Gaston and Lawton 1987; Murdoch and Walde 1989; Hanski et al. 1993; Holyoak and Lawton 1993; Wolda and Dennis 1993; Wolda 1995), are inadequate for elucidating such interplays. An unambiguous and robust approach to quantifying population regulation and to elucidating the interplay between the environment, demographic mechanisms, and population regulation is to perturb populations experimentally and analyze demographic data from the perturbed populations (Nicholson 1957; Murdoch 1970; Sinclair 1989; Harrison and Cappuccino 1995; Cappuccino and Harrison 1996).

Substantial progress has been made in demographic methods over the past decades, and analyses that allow investigations into demographic mechanisms of the dynamics and regulation of populations are now available (e.g., Tuljapurkar and Caswell 1997; Caswell 2001; Oli et al. 2001). Two classes of demographic tools are particularly useful: sensitivity analysis and analysis of life-table response experiments (Caswell 1989, 2001; Horvitz et al. 1997). Sensitivity analyses allow the potential influence of changes in demographic parameters on population growth to be quantified (Oli 1999; Caswell 2000, 2001; Oli and Zinner 2001). Sensitivity analyses, however, only reveal the potential influence of different demographic variables because they reflect the influence that would result from small absolute or proportional changes in demographic variables. Some demographic variables may not change when populations in natural environments grow or decline because the environment or life history of particular species may constrain the changes that are possible. We term changes in demographic variables under such constraints the environmental "scope" for change. For example, age at first reproduction may be relatively inflexible in annually breeding species of mammals in temperate environments, even under experimental conditions (Slade and Balph 1974; Oli et al. 2001).

When population growth rate changes, however, actual demographic influences can be analyzed via the analysis of a life-table response experiment (LTRE; after Caswell 1989, 2001; Oli et al. 2001). In LTRE analyses, observed changes in population growth rate are decomposed into contributions due to changes in underlying demographic variables. These contributions quantify the actual influence of changes in age- or stage-specific demographic parameters and thus reflect both the underlying potential of a parameter and its environmental scope. Furthermore, comparison of sensitivity of population growth rate to changes in a demographic parameter with its actual contribution to population change can indicate which demographic parameters have considerable environmental scope and which do not, under specific environmental circumstances (Oli et al. 2001). These demographic techniques, while informative, might not provide insight into environmental factors that regulate population size. Population size can change for a variety of reasons, and only some of these may be relevant to population regulation. For example, Darwin (1859) believed that predation most often determines population size. While predators obviously cause decrements in population size through the elimination of individuals, Lack (1954) concluded that most often it was food resources that regulate population size. For terrestrial vertebrates, it appears that food-resource limitation or regulation is a common occurrence (reviewed by Boutin 1990; Sinclair 1996). To elucidate demographic mechanisms of population regulation through the application of the above analyses, it is necessary to link population changes to a regulating environmental factor, preferably through experimentation, and then to the contributing demographic changes (Murdoch 1970; Sinclair 1989).

Using LTRE analyses of experimental data, our objective was to investigate the demographic mechanisms of population regulation in the Columbian ground squirrel (*Spermophilus columbianus*). The experimental manipulation of food resources used in our study allowed concurrent tests of the hypothesis that food resources regulate population size and of the demographic mechanisms that underlie increases and decreases in population size. Because the experiments were replicated (Dobson and Kjelgaard 1985*b*; Dobson 1995), we can also make a preliminary examination of whether the demographic mechanisms that underlie changes in population size were consistent in different environments. By comparison of sensitivity and LTRE analyses, we also identified the demographic processes that were most likely to produce changes in population size and the processes that actually did influence population changes, during the time when the populations were regulated to higher and lower densities in populations occupying montane habitats at two different elevations.

Methods

Study Sites and Animals

Six populations of Columbian ground squirrels were sampled by static life-table methods (Caughley 1977) in 1980 and 1981 by R. M. Zammuto (Zammuto 1983, 1987; Zammuto and Miller 1985*a*, 1985*b*). The populations occurred at different elevations in the Rocky Mountains of southwestern Alberta, from 1,300 to 2,200 m, and ranged over

a 183-km distance along the Continental Divide (map in Dobson 1994). All ground squirrels in these populations were kill trapped with Conibear traps, and individuals were aged from microscopic examination of layers of bone deposition in the periosteum of the lower jaw. Age distributions were used to estimate survival rates for these populations (Zammuto 1987) under the assumption of stable age distributions and stationary populations. Reproduction of females was estimated from the presence and number of embryos in utero or placental scars from recently born litters, and age-specific fecundities were estimated from these data (Zammuto 1987). Thus, fecundity may have been slightly overestimated if some pups were stillborn (Murie et al. 1980). Survival data included both sexes, but reproductive data were known only for females. Survivorship was smoothed to produce an age distribution that likely reflected typical life cycles for females in the different populations (Zammuto 1983; Zammuto and Miller 1985*b*).

We sampled four populations of ground squirrels by cohort life-table methods (sensu Caughley 1977) from 1981 to 1986 (Dobson and Kjelgaard 1985*a*, 1985*b*; Dobson and Murie 1987; Dobson 1988, 1992, 1995). Two populations occurred at an elevation of 1,580 m (1.2- and 3.5-ha sites, 50°25′N, 114°44′W) and two at 2,100 m (1.4- and 1.2-ha sites, 50°30′N, 114°57′W). Ground squirrels were livetrapped, individually marked for permanent (metal ear tags) and temporary visual (marks with fur dye) recognition, and monitored by livetrapping and observation every spring and summer. Adults were trapped as they emerged from hibernation and young as they emerged from natal burrows. Ages were estimated by following female cohorts from juvenile or yearling ages over subsequent years. Cohort and static life-table methods produced fairly consistent estimates of demographic variables in populations at different elevations (Dobson et al. 1986).

One population at each elevation received supplementation of ad lib. food (a mixture of oats, wheat, and barley) to a central 0.25 ha during the years 1981–1983. During 1983–1986, these populations were monitored without further supplementation. The other population at each elevation was monitored without manipulation to provide reference data for comparisons (details in Dobson 1995). Demographic variables were estimated under three treatments: for unmanipulated ("control") populations, for food-supplemented populations during increases due to the experimental treatment, and during the population declines that followed the end of the food supplementations.

Demographic Methods

Using survival and fecundity data, we constructed an age-classified projection matrix **A** for populations studied by Zammuto (1983, 1987). We estimated age-specific fertilities (F_i) and survival probabilities (P_i) using the birth-pulse, postbreeding census formulation of Caswell (2001):

$$P_i = \frac{l_i}{l_{i-1}}, \tag{1}$$

$$F_i = P_i m_i, \tag{2}$$

where l_i is the survivorship (probability at birth of surviving to age i) and m_i is the fecundity (the average number of daughters born to females of age i). Although Leslie matrix models incorporate age-specific demographic data, life-history variables of females, such as age at maturity (α) and age at last reproduction (ω), do not appear explicitly in these models. Consequently, the sensitivity of population growth rate to changes in α and ω cannot be calculated using the standard methods of these models. Therefore, we used a partial life-cycle model for this purpose (Oli 1999; Caswell 2001; Oli and Zinner 2001). In a partial life-cycle model, age-specific fertilities (F_i) are approximated by F, age-specific survival (P_i) prior to reproduction (i.e., juvenile survival) by P_j, and age-specific survival from α until ω by P_a. The characteristic equation for this type of two-stage life cycle is (Oli 1999; Oli and Zinner 2001)

$$1 = FP_j^{\alpha-1}\lambda^{-\alpha} - FP_j^{\alpha-1}P_a\lambda^{-\alpha-1} + FP_j^{\alpha}\lambda^{-\alpha-1} - FP_j^{\alpha}P_a^{\omega-\alpha}\lambda^{-\omega-1} + P_a\lambda^{-1}. \tag{3}$$

The population growth rate (λ) is the largest real root of equation (3) and was obtained numerically. For the partial life-cycle model for the static life-table populations (Zammuto 1987), α and ω were the first and last age classes with nonzero fertility, respectively. In the cohort-studied populations, age at maturity (α) was estimated from the average age of maturing (e.g., lactating) females under each treatment. Juvenile survival (P_j) was estimated from the survival of females from weaning (namely, when they were first captured and marked) until they began breeding, and this survival rate was annualized. Adult survival (P_a) was estimated from the survival of previously breeding females from one spring to the next. Since age at last reproduction (ω) was unknown, we estimated it by projecting the annual survival of females into the future until only one female was left alive. Finally, fertility (F) was estimated as the product of one-half of litter size, the proportion of breeders among mature females, and adult survival. To ensure maximum correspondence between results of age-classified and partial life-cycle models, F, P_j, and P_a were estimated from the age-classified projection matrix as

weighted averages, weighted according to the contribution of each age class to the stable age distribution (Oli 1999; Oli and Zinner 2001):

$$F = \frac{\sum_{i=\alpha}^{\omega} \mathbf{w}_i F_i}{\sum_{i=\alpha}^{\omega} \mathbf{w}_i}, \tag{4}$$

$$P_{\mathrm{j}} = \frac{\sum_{i=1}^{\alpha} \mathbf{w}_i P_i}{\sum_{i=1}^{\alpha} \mathbf{w}_i}, \tag{5}$$

$$P_{\mathrm{a}} = \frac{\sum_{i=\alpha+1}^{\omega-1} \mathbf{w}_i P_i}{\sum_{i=\alpha+1}^{\omega-1} \mathbf{w}_i}, \tag{6}$$

where $\mathbf{w}_i$ is the ith entry of the right eigenvector corresponding to the dominant eigenvalue of the age-classified projection matrix **A**.

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 equation (3) (for formulae, see Oli and Zinner 2001). Sensitivities of λ quantify how λ would change in response to small changes in demographic variables (Caswell 2001). However, sensitivity of λ to changes in various life-history variables may not be comparable because they are measured in different units (e.g., P_i are probabilities and may only take values between 0 and 1, whereas F_i are not under such a restriction). To address this problem, ecologists have introduced the concept of elasticity (de Kroon et al. 1986, 2000). Elasticities are proportional sensitivities and quantify potential changes in λ with respect to proportional changes in life-history variables (Caswell 1997, 2000, 2001; Horvitz et al. 1997). Elasticities are scaled, dimensionless quantities and are thus directly comparable among demographic variables and across populations (Caswell et al. 1984; Horvitz et al. 1997; Caswell 2001). Therefore, we used elasticities as measures of potential influence of demographic variables to λ. Elasticities, or proportional sensitivities of λ to changes in p, were calculated as $(\partial\lambda/\partial p) \times (p/\lambda)$ (de Kroon et al. 1986, 2000; Caswell 2000, 2001).

Absolute or proportional sensitivities quantify potential influences on population growth rate of changes in demographic variables, but sensitivities or elasticities do not consider actual changes in demographic variables. In contrast, LTRE analyses simultaneously consider sensitivities and observed changes in demographic variables and allow decomposition of the population-level response into contributions from individual demographic variables (Caswell 1989, 2001; Horvitz et al. 1997). Thus, we used LTRE analyses to discern the demographic mechanisms of changes in population growth rate under the experimental manipulation of food resources.

For each of the two pairs of populations in the food-supplementation experiment, we conducted two sets of two-sample comparisons using LTRE analyses. First, we compared food-supplemented populations with their paired "control" populations. Because food supplementation caused substantial increases in growth rate, these analyses should reveal the demographic mechanisms of population increases. Second, we compared the food-supplemented population when it was increasing with the same population after food supplementation was terminated. Because population growth rate at both study sites declined when food supplementation was terminated (Dobson 1995), this comparison should provide insights into demographic mechanisms of population declines relative to increases.

When comparing control populations with food-supplemented populations, we used demographic characteristics of control populations as a reference for each habitat to evaluate the population-level effect of food supplementation. To evaluate the population-level effect of food removal, we used demographic characteristics of populations when being supplemented as a reference and compared these with demographic characteristics of the population following the termination of food supplementation. In either case, a change in a demographic parameter p was calculated as $\Delta p = p^{\mathrm{treat\ 2}} - p^{\mathrm{treat\ 1}}$. Total change in λ in response to a treatment, that is, the effect of a treatment (e.g., food supplementation vs. decrementation) on the entire life table, was calculated as $\Delta\lambda = \lambda^{\mathrm{treat\ 2}} - \lambda^{\mathrm{treat\ 1}}$. We decomposed $\Delta\lambda$ into contributions from changes in a model parameter p (Caswell 1989, 2001; Levin et al. 1996; Oli et al., in press):

$$\Delta\lambda \approx \sum_{ij} \Delta p \frac{\partial\lambda}{\partial p}\bigg|_{\left(\frac{p^{\mathrm{treat\ 2}} + p^{\mathrm{treat\ 1}}}{2}\right)}, \tag{7}$$

where $\Delta\lambda$ is the total change in λ in response to food supplementation or decrementation and Δp is the change in a model parameter p (α, ω, P_{j}, P_{a}, or F) in response to a treatment. Sensitivities were calculated at the mean of the two treatments being compared (e.g., control and food supplementation, as recommended by Caswell [1989, 2001]).

Because we did not have complete reproductive histories of females for all elevation-treatment combinations, we could not employ resampling methods for statistical inference regarding changes in λ's in response to experimental treatment (Lenski and Service 1982; McPeek and Kalisz 1993; Caswell 2001). Instead, we calculated approximate estimates of variation in λ using the delta method (Seber 1973; Caswell 2001). We estimated the variance of the juvenile and adult survival rates with the

standard formula for the estimate of variance of a binomial parameter: $\mathrm{Var}(\hat{s}) = \hat{s}(1 - \hat{s})/n$. To estimate the variance of fertilities, we estimated separate fertility terms for each year and then calculated sample variance in these terms among years. Observed variation in the age at first reproduction of females was used as an estimate of variance of age at maturity. The variance of λ was then estimated (e.g., Seber 1973; Caswell 2001) as $\mathrm{Var}(\hat{\lambda}) = \sum (\partial\hat{\lambda}/\partial\hat{p})^2 \mathrm{Var}(\hat{p})$, where p is a demographic variable.

Results

The six populations that were studied by snap trapping exhibited a considerable range of survival and reproductive patterns (table 1). Juvenile survival was particularly variable among populations, and fertility varied by more than twofold. Population growth rate (λ) was close to 1.0 for these populations. Demographic variables with the highest and second highest elasticities, respectively, at different elevations were α and F at 1,300 m and 1,675 m, F and α at 1,360 m, P_j and α at 1,500 m, and α and P_j at 2,000 m and 2,200 m (fig. 1), suggesting that age at maturity, juvenile survival, and fertility were potentially the most influential demographic variables.

In cohort-sampled populations at both elevations, controls declined slightly in size during the study (fig. 2). Under experimental supplementation of food resources, however, population growth was substantial, at roughly 48%–74% per year (table 1). When food supplementation ended, population decline was relatively gradual, at 12%–19% per year. During food supplementation, manipulated populations nearly tripled and quadrupled and then, with food decrementation, declined over 3 yr to densities similar to those before food supplementation. Food supplementations caused improvements in most demographic variables. Consequently, growth rate of both experimental populations increased substantially. When the supplementations were ended, age at maturity of females increased and age at last reproduction, survival, and fertility decreased; these demographic changes caused substantial decline in population growth rates (table 1).

Patterns of elasticity differed slightly between elevations and between treatments within each elevation. In control and declining populations at both elevations, juvenile survival had high elasticities (table 2). In increasing populations at both elevations, age at maturity and fertility had high elasticities. Finally, the highest elasticity in the declining population at 1,580 m was for age at maturity, a pattern that was not repeated at 2,100 m. Adult survival and age at last reproduction had middling-to-low and very low elasticities, respectively, in all populations and treatments.

We analyzed two LTREs at each elevation. In the first experiment, we compared control populations to the growing populations under the supplementation treatment. The difference in λ between the two populations ($\Delta\lambda$) was 0.552 at 1,580 m and 0.874 at 2,100 m. The total LTRE contributions were 0.523 and 0.793, respectively, slightly less than the observed differences in population growth. LTRE contributions of the demographic variables were different in populations at different elevations (table 3). At 1,580 m, changes in age at maturity made the largest contributions to the observed increase in population growth rate, and fertility was almost as strong an influence. At 2,100 m, fertility contributed most to the observed

Table 1: Values of demographic characteristics (SD in parentheses) used to parameterize the partial life-cycle model for several populations of Columbian ground squirrels

Population/ treatment	Age at maturity (α)	Age at last reproduction (ω)	Juvenile survival (P_j)	Adult survival (P_a)	Fertility (F)	Population growth rate (λ)
1,300 m[a]	1	5	.250	.591	.650	1.00
1,360 m[a]	1	4	.453	.541	.534	.99
1,500 m[a]	2	7	.611	.617	.671	1.00
1,675 m[a]	1	5	.338	.685	.540	1.00
2,000 m[a]	2	5	.378	.770	1.259	.96
2,200 m[a]	2	5	.350	.765	1.382	.96
1,580 m (control)	2.111 (.323)	5.71[b]	.624 (.079)	.500 (.068)	.636 (.168)	.932 (.112)
1,580 m (+ food)	1.286 (.455)	11.60[b]	.711 (.049)	.710 (.055)	.955 (.127)	1.484 (.246)
1,580 m (− food)	1.941 (.243)	6.67[b]	.390 (.055)	.678 (.035)	.617 (.247)	.816 (.116)
2,100 m (control)	2.500 (.527)	8.99[b]	.711 (.131)	.644 (.062)	.308 (.196)	.864 (.148)
2,100 m (+ food)	1.375 (.500)	12.00[b]	.815 (.078)	.854 (.068)	1.201 (.240)	1.738 (.328)
2,100 m (− food)	2.333 (.488)	7.30[b]	.735 (.072)	.566 (.057)	.366 (.122)	.882 (.095)

Note: Population growth rates calculated using the partial life-cycle model are also given. See text for details.

[a] Data from Zammuto (1987) and R. M. Zammuto (unpublished data).

[b] Estimates of standard deviation not available for ω.

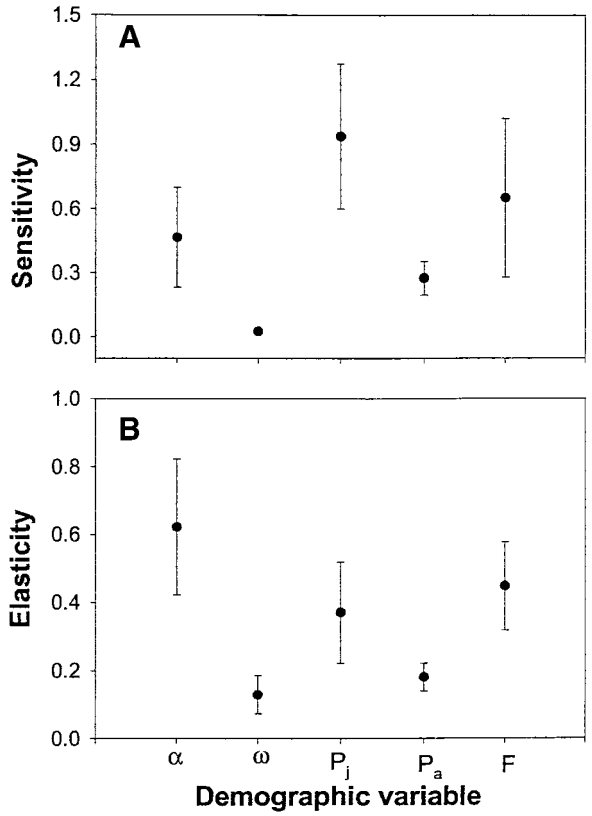

Figure 1: For six populations of Columbian ground squirrels, sampled by static life-table methods, sensitivities (*A*) and elasticities (*B*) of population growth rate (λ) to demographic parameters are shown: age at maturity (α), last age of reproduction (ω), juvenile survival (P_j), adult survival (P_a), and fertility (F). Means $\pm$ 1 standard deviation of the mean are shown for each variable.

increase in population growth rate, with age at maturity as a secondary influence.

Our second LTRE comparison was of experimental populations under conditions of increasing (food supplemented) versus decreasing (food decremented) population size. When food supplementation was terminated, population growth rates declined, with $\Delta\lambda = -0.668$ at 1,580 m and $\Delta\lambda = -0.856$ at 2,100 m. The total LTRE contributions were -0.638 and -0.792, respectively, again slightly lower than the actual changes in population growth rates. At 1,580 m, decrease in juvenile survival contributed most to the decline in population growth rate, and age at maturity and fertility were secondary influences (table 3). At 2,100 m, decreased fertility contributed most to the decline in population growth rate, with decreases in age at maturity and survival of adults playing secondary roles.

Discussion

Ever since Malthus (1798), the study of population regulation has been of critical importance in population ecology. Darwin (1859) made competition for environmental resources the focus of his theory of evolution, and he dealt with topics in population ecology explicitly in the third chapter of his opus. Lack (1954), while noting the paucity of interest in a topic of such importance to evolutionary theory, directed the attention of ecologists to the fundamental importance of the question of the regulation of population size. Since Nicholson's (1933), Lack's (1954), and Andrewartha and Birch's (1954) seminal reviews of population regulation, tremendous theoretical advances have been made, and numerous studies have examined empirical evidence on environmental factors that influence population size (e.g., Murdoch 1970, 1994; Watson and Moss 1970; Slade and Balph 1974; Sinclair 1989, 1996; Boutin 1990; Krebs 1994; Harrison and Cappuccino 1995; Cappuccino and Harrison 1996; Turchin 1999). However, population regulation remains a controversial topic, and the debate sparked by Nicholson's (1933) influential essay continues to date (Wolda and Dennis 1993; Wolda 1995; den Boer and Reddingius 1996; Murray 1999*a*, 1999*b*; Turchin 1999).

There are two primary approaches to quantifying population regulation, and both focus on identifying density dependence of population growth rate. The first approach (statistical analysis of time series data) looks for the presence of stabilizing density dependence in a time series of population densities (reviewed in Murdoch 1994 and Turchin 1995). Although statistical analysis of time series data is the most commonly used method of quantifying population regulation, this approach has many shortcomings, and the adequacy of this approach for studying population regulation has been controversial (Hanski et al. 1993; Holyoak and Lawton 1993; Wolda and Dennis 1993; Murdoch 1994; den Boer and Reddingius 1996). Moreover, this approach focuses on the detection of direct or delayed density dependence of population growth rate but provides no information on either the demographic mechanisms of regulation or the environmental factors that influence regulation. The second approach (density-perturbation experiments or the experimental approach) attempts to investigate the mechanism of population regulation directly by employing experimental perturbations of population density and examining density-dependent responses of population parameters (Murdoch 1970; Harrison and Cappuccino 1995; Cappuccino and Harrison 1996). This latter method has the advantage of both demonstrating density dependence of population growth rate and identifying environmental factors that regulate population size. The experimental approach also is, in general, more widely

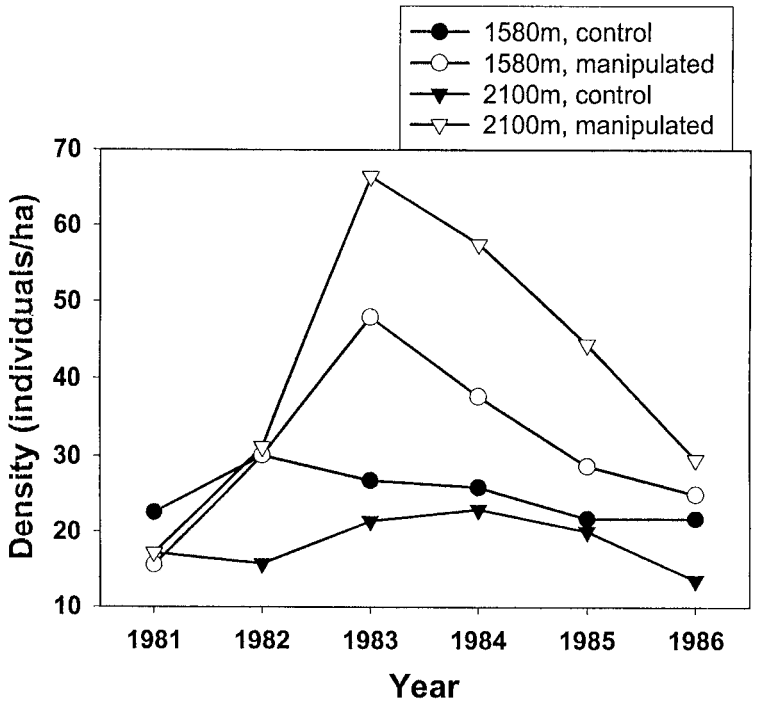

Figure 2: Population size over 6 yr for four populations of Columbian ground squirrels. At each elevation, two populations formed a block with a manipulated and a control population.

accepted and less controversial than statistical analysis of time series data (Murdoch 1970; Harrison and Cappuccino 1995).

Using the experimental approach, our study addressed three fundamental questions regarding population regulation of Columbian ground squirrels: Were our study populations regulated? What environmental factors underlay population regulation? And what were the demographic mechanisms of population regulation? First, the sizes of our study populations were regulated. Murdoch (1970) suggested that density-perturbation experiments are the only generally acceptable method for detecting population regulation. In our study populations, food supplementation caused substantial increases in squirrel densities at both elevations, and the densities in experimental plots converged to pretreatment levels following cessation of food supplementation (fig. 2; see also Dobson 1995). Meanwhile, untreated populations remained relatively stable. Using Murdoch's (1970) criterion, these results provide unambiguous evidence that our study populations were regulated.

Second, what environmental factors underlay the dynamics and regulation of our study populations? This question can best be addressed by manipulating an environmental factor and examining its effects on population densities (Murdoch 1970). Experimental evidence supported the role of food resources in both limiting and regulating the size of Columbian ground squirrel populations (sensu Sinclair 1989). Supplementation studies showed that additional food resources caused densities of ground squirrels to increase (fig. 2), thus demonstrating that food is a limiting resource (Murdoch 1970, 1994; Dobson and Kjelgaard 1985*b*; Sinclair 1989, 1996; Boag and Wiggett 1994; Dobson 1995; J. O. Murie, unpublished data). During the three years following cessation of supplementation, these populations returned to sizes that were not greatly different from their preexperimental levels. This latter part of the experiment followed the populations as they returned to the presumed equilibrium with the unmanipulated environment under stressful shortages of food, as indicated by significant declines in body condition of individuals (Dobson 1988, 1995). Experimental increases and decreases in population density thus indicated that food resources caused density-dependent changes in population growth rates, a condition that indicates population regulation (e.g., Murdoch 1970, 1994; Sinclair 1989).

Finally, what were the demographic mechanisms of the dynamics and regulation of the population? It is important to identify demographic mechanisms that underlie changes

Table 2: Sensitivities and elasticities of λ to changes in demographic parameters in Columbian ground squirrels

Population/ treatment	Sensitivities					Elasticities				
	α	ω	P_j	P_a	F	α	ω	P_j	P_a	F
1,580 m (control)	−.134	.013	.811	.248	.475	−.303	.077	.543	.133	.324
1,580 m (+ food)	−.496	.000	.725	.415	.706	−.430	.001	.348	.198	.454
1,580 m (− food)	−.190	.019	.929	.327	.376	−.452	.156	.444	.272	.284
2,100 m (control)	−.044	.007	.596	.388	.616	−.128	.074	.490	.290	.220
2,100 m (+ food)	−.568	.000	.787	.405	.625	−.450	.001	.369	.199	.432
2,100 m (− food)	−.051	.009	.634	.325	.634	−.135	.071	.528	.209	.263

Note: α is age at maturity in years, ω is age at last reproduction, P_j is survival to reproductive age on an annual basis, P_a is annual survival of adults, and F is fertility.

in population growth rates, especially when changes in growth rates reflect regulation of population size. This is because population growth rate is an emergent property of the underlying demography. Environmental influences on population size operate through their effects on reproduction, survival, and the timing of life-cycle events such as the onset and termination of reproductive life. Thus, a complete understanding of population regulation requires both identification of environmental influences that result in increases and decreases in population size and investigation of the demographic changes that cause population regulation (Murdoch 1970; Oli and Dobson 1999, 2001).

Among various demographic techniques, LTRE analyses are particularly useful in discerning the demographic bases of the dynamics and regulation of biological populations (Caswell 2001; Oli et al. 2001). We investigated demographic mechanisms of population regulation by examining LTRE contributions of demographic variables to observed changes in population growth rate. Elasticities suggested and LTRE analyses confirmed that improvements in age at maturity and fertility made the largest contributions to observed increases in population growth rate in response to experimental food supplementation at 1,580 m; adverse effects of food shortages on population dynamics were manifested through decreases in age at maturity, survival of juveniles, and fertility (fig. 1; table 3). At 2,100 m, however, changes in fertility made the largest contribution to an increase in population growth rate in response to supplemented food as well as to a decrease in population growth rate when the population was food stressed. Also at 2,100 m, changes in age at maturity (abetted by adult survival during population decline) played a secondary role in changes in population size. These results reflected consistency of two demographic influences (age at maturity and fertility) on growth and decline in population size but also suggested that the specific pattern of demographic mechanisms of population regulation may differ among populations under different environmental conditions.

Age at maturity has been suggested to be an influential life-history variable with substantial population dynamic consequences (e.g., Cole 1954; Lewontin 1965; Oli and Dobson 1999; Oli and Dobson 2001). Age at maturity had the highest elasticity in four of six populations sampled by static life-table methods (fig. 1) and the highest elasticity in two elevation-treatment combinations (table 2), and changes in mean age at maturity under experimental conditions appeared biologically meaningful (table 3). However, this variable may not always make the largest contributions to observed changes in population growth rates. In Uinta ground squirrels, age at maturity made no contribution to observed changes in population growth rate since age at maturity did not change at all under experimental density reductions (yearling females commonly reproduce in this species, and earlier reproduction is likely impossible; Slade and Balph 1974; Oli et al. 2001). Thus, Uinta ground squirrels lack environmental or genetic "scope" for changes in age at maturity. Because of the strong potential for changes and actual changes in age at maturity in Columbian ground squirrels, sufficient environmental scope was obviously available for influences on λ. However, most hibernating species of ground squirrels are annual breeders (Armitage 1981; Michener 1983), and perhaps population growth rate is more strongly influenced by changes in age at maturity in species with shorter generation times and higher reproductive rates (e.g., Stearns 1992; Oli and Dobson 1999).

The importance of environmental scope was highlighted by the influence of juvenile survival on changes in population growth rates. Although juvenile survival had consistently high elasticities (fig. 1; table 2), it generally made relatively low LTRE contributions, especially in increasing populations (table 3). This may have resulted from the ground squirrels exhibiting relatively high rates of juvenile survival, compared with adult survival, under most of the

Table 3: Analysis of life-table response experiments (LTRE) for populations of Columbian ground squirrels, comparing populations under different conditions of population regulation

Treatment comparison/ demographic parameter (p)	Change in parameter (Δp)	Sensitivity	LTRE contribution
Control vs. food supplementation at 1,580 m:			
α	−.825	−.237	.196
ω	5.890	.002	.012
P_j	.087	.780	.068
P_a	.210	.376	.079
F	.319	.529	.169
Supplemented food vs. decremented food at 1,580 m:			
α	.655	−.279	−.182
ω	−4.930	.003	−.015
P_j	−.321	.814	−.261
P_a	−.032	.427	−.014
F	−.338	.489	−.165
Control vs. food supplementation at 2,100 m:			
α	−1.125	−.174	.196
ω	3.010	.002	.006
P_j	.104	.731	.076
P_a	.210	.419	.088
F	.893	.478	.426
Supplemented food vs. decremented food at 2,100 m:			
α	.958	−.193	−.184
ω	−4.700	.002	−.009
P_j	−.080	.739	−.059
P_a	−.288	.398	−.115
F	−.835	.508	−.424

Note: Demographic parameters are described in table 2. The LTRE contributions were estimated as the product of the actual change in demographic parameters and the sensitivity of population growth rate to changes in a demographic parameter evaluated at the mean parameter value.

experimental treatments (table 1). Substantial improvements to juvenile survival may not have been possible regardless of improvements in food resources. Such high rates of juvenile survival may have been unusual since similar high rates of juvenile survival did not occur in the populations studied by static life-table methods. In any case, scope for change in demographic variables is likely to be specific to particular environmental conditions or locations. In the declining population at 1,580 m, decreased juvenile survival made a substantial contribution to the decline in λ, but a similar influence of declining juvenile survival was not evident at 2,100 m (table 3).

Most of the past discussion regarding population regulation has centered around the type (biotic or abiotic) and nature (density dependent or density independent) of regulating environmental factors (e.g., Andrewartha and Birch 1954; Tamarin 1978 and articles therein) or on the methods of quantifying regulation (e.g., Gaston and Lawton 1987; Murdoch and Walde 1989; Hanski et al. 1993; Holyoak and Lawton 1993; Wolda and Dennis 1993; Wolda 1995; Murray 1999*a*, 1999*b*). Despite the undisputable fact that dynamics and regulation of biological populations are essentially demographic processes, little has been said regarding the demographic processes that underlie changes in numbers. Environmental influences on population dynamics operate through their effects on demographic parameters. We suggest that a complete understanding of population regulation, essentially a demographic process, should necessarily involve an understanding of underlying demographic mechanisms, followed by the ascertainment of underlying environmental causes (the two-step approach of Oli and Dobson 2001).

Our results provide unambiguous evidence that abundance of food resources regulated the size of our study populations and that regulation occurred primarily through the effect of food resources on fertility rate and

age at maturity (table 3). Demographic analyses of experimental data, such as those presented here, will not only elucidate demographic basis of population regulation but also help identify environmental factors that underlie dynamics and regulation of biological populations. Three decades have elapsed since Murdoch (1970) persuasively articulated the importance of density-perturbation experiments to study population regulation, and we now have powerful demographic tools such as LTRE analysis at our disposal to analyze such experimental data. Enough has been said about whether populations are regulated or how to quantify regulation (e.g., Hanski et al. 1993; Wolda and Dennis 1993; Dennis and Taper 1994; Turchin 1995, 1999; Wolda 1995; den Boer and Reddingius 1996; Murray 1999*a*, 1999*b*). It is time for ecologists to move away from "largely futile arguments" (cf. Hanski et al. 1993) and focus on how best to study population regulation—a topic of tremendous ecological as well as evolutionary significance (Murdoch 1994).

Acknowledgments

Our greatest thanks go to M. J. Badry, R. Bonnah, C. Geddes, W. J. King, J. D. Kjelgaard, J. F. Kjelgaard, and L. Powell for excellent field assistance. We thank D. R. Broussard, C. Guyer, G. R. Michener, J. O. Murie, and N. A. Slade for critical comments on the manuscript. Fieldwork was facilitated by the Alberta Fish and Wildlife division (H. Carr, District Biologist), the Forest Service (I. Allen, Head District Ranger), and Recreation and Parks (K. Powell, Highwood Ranger). The Kananaskis Field Stations, University of Calgary, provided facilities during the fieldwork. R. M. Zammuto generously provided a copy of his data set, thus ensuring the accuracy of our analyses. The research was funded in 1984 and 1985 by a Canadian National Sportsman's Fund grant to J. O. Murie. The research was supported by a series of grants from the University of Michigan, the American Society of Mammalogists, the Arctic Institute, and Sigma Xi; a North Atlantic Treaty Organization postdoctoral fellowship at the Department of Zoology, University of Alberta; and a postdoctoral fellowship at the Department of Biological Sciences, University of Lethbridge. This research was supported by the Florida Agricultural Experiment Station and approved for publication as Journal Series R-08081.

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Associate Editor: Mark A. McPeek