

BODY MASS, STRUCTURAL SIZE, AND LIFE-HISTORY PATTERNS OF THE COLUMBIAN GROUND SQUIRREL

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Abstract.—Columbian ground squirrels (*Spermophilus columbianus*) exhibit an elevational cline in several life-history traits and in body mass. Body mass is a trait that might interact with the elevational changes in life histories, but it could reflect either or both of two underlying factors: structural size and physiological condition. I studied these factors in several populations of ground squirrels. Structural size was estimated from first principal component scores in an analysis of postcranial bone lengths. Physiological condition was inferred from differences in body mass that were independent of structural size. Field body mass and structural size of yearlings decreased with increasing elevation, which indicates slower growth at higher elevations. For adults, physiological condition was not measured directly, but evidence suggested that it was reflected by changes in body mass: body mass declined with increasing elevation but structural size did not, residuals of body mass on structural size showed the same patterns of change as body mass, most of the variation in body mass was orthogonal to a "general size factor" in principal components analyses, and significant changes in body mass of individuals could be stimulated by experimental supplementation of food. Life-history traits and physiological condition covaried along the elevational cline and were phenotypically plastic, but the structural size of adult ground squirrels was not an extremely plastic trait.

Studies of life history often include the size of an organism as a trait. Early attempts to model the evolution of life histories, such as the *r*- and *K*-selection model, made specific predictions about body size (MacArthur and Wilson 1967; Pianka 1970; Boyce 1984). Subsequently, body size was used by physiological ecologists to explain other life-history traits as largely dependent on the size of the organism (see, e.g., Western 1979; Western and Ssemakula 1982; Calder 1983; but see Harvey and Zammuto 1985). Selection and scaling models of life history have been primarily applied to broad comparative studies of taxa, although they are occasionally examined in intraspecific studies (Taylor and Condra 1980; Barclay and Gregory 1981; Bergmans 1984; Harvey and Zammuto 1985; Zammuto and Millar 1985a; Bradshaw and Holzappel 1989). Body size in virtually all such studies has been equated with body mass, and recent work has even based life-history analysis on body mass as a more relevant variable than age for structuring populations (Sauer and Slade 1985, 1986, 1987a, 1987b).

A parallel but largely independent focus of research by morphologists and systematists has examined variation in body size of individuals among populations and species (Bookstein et al. 1985; Radinsky 1985; Patton and Brylski 1987;

Rohlf 1990). For the systematist, body size is a trait that might be entered into phylogenetic analysis. Size is often treated as a single character, estimated by some statistical combination of length measures of body parts, such as the skull, postcranial skeleton, or between landmarks along the outline of the body (Bookstein et al. 1985; Bookstein 1989, 1990). Often, attempts are made to "remove" the influence of size on morphology so that independent aspects of shape of morphological structures are revealed (Bookstein et al. 1985; Rohlf 1990). If size is strongly influenced by the environment, then size could be a confounding influence in systematic analysis (Patton and Brylski 1987).

The purpose of this study is to examine variation in life-history patterns and body size within several populations of Columbian ground squirrels, *Spermophilus columbianus*. These ground squirrels live along an elevational gradient and exhibit a cline (sensu Endler 1977) in life-history traits (Zammuto and Millar 1985a, 1985b; Dobson et al. 1986; Dobson and Murie 1987). One of the traits that changes over elevation is body mass, which declines significantly as elevation increases (reviewed in Dobson et al. 1986; Dobson and Murie 1987). It is difficult to interpret changes in body mass, however, because either or both of two underlying factors might be reflected.

First, ground squirrels could differ in the size of the supporting tissues of the body form. These supporting tissues, primarily bone of the skull and postcranial skeleton, reflect the overall size of the body structure (termed "structural size" below; see also Campbell and Dobson 1992). Patton and Brylski (1987) found that structural size exhibited remarkable phenotypic plasticity in pocket gophers (*Thomomys bottae*) and that this was associated with considerable plasticity in life-history traits. Thus, I expected that, since other life-history traits of the ground squirrels changed over the elevational gradient, structural size might also change with elevation. Similar phenotypic plasticity of structural size and at least some life-history traits occurs in several vertebrate species (Bervin 1982; Stearns 1983; Stearns and Koella 1986; Newman 1989; Trexler and Travis 1990; Trexler et al. 1990).

Second, ground squirrels could differ in body condition, that is, in the energy reserves that are stored as fat or other easily metabolizable tissues. This aspect of size might be termed "physiological condition," because energy reserves are closely associated with the physiological processes involved in reproduction and survival (Ritchie 1988, 1990; Campbell and Dobson 1992). Ground squirrels hibernate and go through an annual cycle of fat deposition during the active season and fat metabolism during hibernation (Davis 1976; Armitage 1981; Young 1988, 1990). Physiological condition fluctuates dramatically during the course of the year; thus, I expected changes over the elevational gradient, with ground squirrels at higher elevations in poorer condition. Phenotypic plasticity of physiological condition and some life-history traits occurs in at least a few species of vertebrates (Dunham 1980; Stearns 1983; Ford and Seigel 1989).

I considered these two aspects of size, structural size and physiological condition, as hypotheses to account for the significant elevational changes in body mass of the ground squirrels. Of course, changes in body mass could reflect both aspects of size, and the two aspects of size might be interdependent. My study

simply examined the extent to which each aspect of size contributed to changes in body mass, because different components of size might be expected to have different associations with life histories. If different aspects of size do differ in their associations with life-history traits, then studies of life histories that attempt to design or test theoretical models, whether applied to intraspecific or interspecific populations, should indicate which aspect of size is under examination.

METHODS

Columbian ground squirrels were studied from 1980 to 1986 in the Rocky Mountains of southwestern Alberta, Canada. Populations of ground squirrels occur in alpine and subalpine meadows and grasslands, from about 1,200 to 2,400 m in elevation. Results for the present study were drawn from two field research programs. The first source of data was from ground squirrels that I studied at two elevations (25 km apart) in the Highwood River drainage of southwestern Alberta (fig. 1). At each elevation, one population was monitored without manipulation and a second population was provided with an experimental supplementation of food resources. An enriched mixture of grains was supplied in excess to a 0.25-ha plot in the center of each of the two replicate experimental populations whenever the ground squirrels were active above ground, from 1981 to 1983. From 1983 to 1986, all four populations were monitored without further manipulation.

These populations were studied by live-trapping and observation. Details of data collection on life-history traits appear elsewhere (Dobson and Kjelgaard 1985*a*, 1985*b*; Dobson and Murie 1987; Dobson 1988). Adult ground squirrels were trapped in the spring, shortly after emergence from hibernation, and weighed (to estimate mass) with a Pesola spring balance to the nearest 5 g. In the spring, ground squirrels are at or near the lowest body mass in their annual cycle (Boag and Murie 1981).

The second source of data was R. M. Zammuto's research program (Zammuto 1983; Zammuto and Millar 1985*a*, 1985*b*; Dobson et al. 1986). Zammuto collected 506 ground squirrels from six discrete populations (>25 km between the closest pair of populations). These populations were at six different elevations and spanned a range of 182 km (fig. 1). Fieldwork at each population was conducted 3–4 wk after spring emergence, when females were at the end of pregnancy or early in lactation. Collections were made with Conibear snap traps, and virtually all ground squirrels in each population were caught. "Field body mass" of these ground squirrels was estimated to the nearest 5 g with a Pesola spring balance. Litter size was estimated from counts of embryos or placental scars. The carcasses of the ground squirrels were preserved in formalin. Half of each lower jaw was taken from each specimen and used for aging by the examination of annual adhesion lines in the periosteum of the diastema. Further details of methods appear in Zammuto (1983) and Zammuto and Millar (1985*a*).

In 1983, I obtained the preserved specimens and their accompanying data from Zammuto. At the Museum of Zoology, University of Michigan, the specimens were prepared as complete skeletons. Because many of the skulls had been crushed by traps, I chose five measurements that were most likely to reflect the

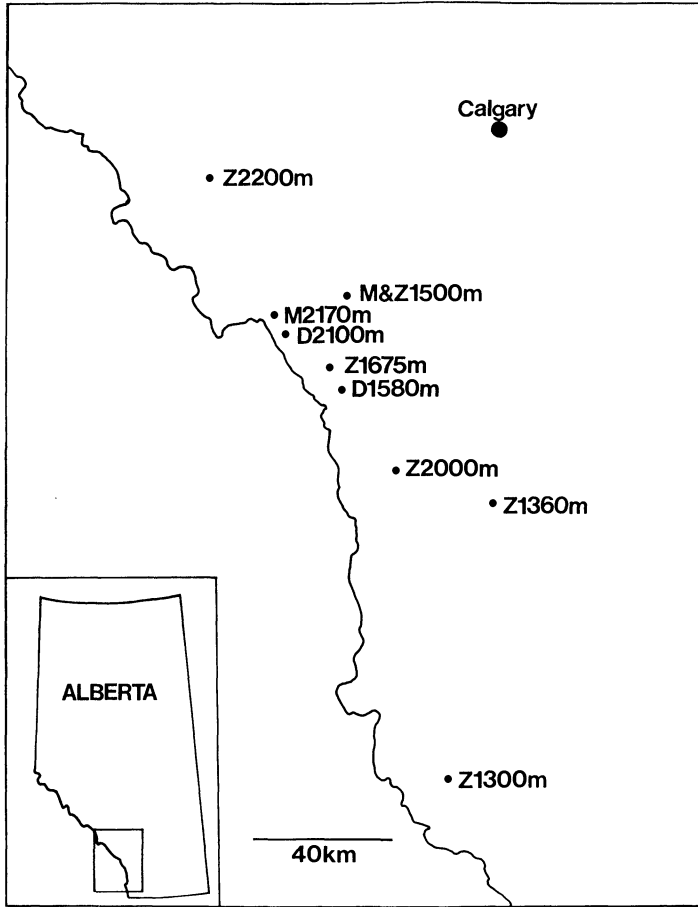


FIG. 1.—Location and elevation of study sites of Columbian ground squirrel populations in southwestern Alberta; sites indicated with a *D* are the experimental and associated unmanipulated populations that I studied, sites indicated with a *Z* are sources of the museum specimens (after R. M. Zammuto), and sites indicated with an *M* were studied by J. O. Murie (used for information on life-history traits; Dobson and Murie 1987).

structural size of individuals: femur length, tibia length, humerus length, ulna length, and ischium-iliac length. Measurements were taken with digital calipers and recorded to the nearest 0.1 mm.

Principal components analysis (PCA) was performed on logarithmically transformed skeletal measurements under the assumption of linear relationships among variables (after Bookstein et al. 1985; James and McCulloch 1990). Some pooling of age groups was necessary so that sample sizes would be adequate for the PCA. Rank correlations were calculated for measures on different age groups and populations at different elevations, which resulted in numerous “ties” in the data analysis. Adjustments were made for ties (Kendall 1962), but they may have been

insufficient to remove this source of bias. Thus, rank correlations are presented mainly for comparative purposes, and significance levels near .05 must be viewed askance.

RESULTS

Experimental Populations

Reference populations were used to document further patterns of life history with elevation that had been described earlier (Murie et al. 1980; Murie and Harris 1982; Zammuto 1983; Murie 1985; Zammuto and Millar 1985*a*, 1985*b*). The elevational cline in life history is well documented, with a total of 14 populations studied over 13 yr (1974–1986; reviewed by Dobson et al. [1986], Dobson and Murie [1987], and Dobson [1988]).

As elevation increased in the mountains, populations of ground squirrels had significantly smaller litters, later age at maturity of females (as indicated by the proportion of yearling females that bred), a lower proportion of adult females breeding in a given year, higher survival of both adults and juveniles, and lower body mass of adult males and females (Dobson et al. 1986; Dobson and Murie 1987). In populations at 1,580 and 2,100 m, the range of mean values of most life-history traits during and after food supplementation was similar to the range of values over the elevational gradient (Dobson and Kjelgaard 1985*b*; Dobson 1988). Under food supplementation, annual changes in mean adult body mass within populations were about 20%–25% greater for males and about 250%–300% greater for females than differences between populations at different elevations (Dobson 1988).

The changes in mean body mass within the experimental populations partially reflected year-to-year changes in mass of individuals. In the food-supplemented population at 1,580 and 2,100 m, individual adult males and females that survived from 1981 (before the supplementations began) to 1982 or 1983 (during food supplementation) had significantly increased spring body mass (table 1). After the food supplementation ended, individual males and females at both elevations that were already adults in 1983 and survived into the postexperimental period of 1984 to 1986 decreased in body mass significantly (table 1).

Museum Specimens

Body mass of males and females, measured in the field, could have been influenced by when the ground squirrels were captured (Michener 1990). A biologically defined point in time, such as first emergence from hibernation in the spring, can occur over a period of 3 wk in a population. The museum specimens, however, were collected over 3 or 4 d (R. M. Zammuto, personal communication). Thus, individuals in a population could be at different points in the annual cycle of weight change. In addition, some of the adult females were pregnant when captured, and some had already given birth or were not breeding. These sources of bias probably increased the variation in field body mass among ground squirrels.

TABLE 1

MEAN MASS ($g \pm 1$ SE) AT SPRING EMERGENCE FOR ADULT COLUMBIAN GROUND SQUIRRELS BEFORE AND UNDER EXPERIMENTAL CONDITIONS: FOOD SUPPLEMENTATION (1982–1983) AND ARTIFICIAL FOOD SHORTAGE (1984–1986)

	1981	1982–1983	<i>N</i>	<i>t</i>	<i>P</i>
1,580 m:					
Males	459 \pm 15	556 \pm 19	7	3.53	<.01
Females	393 \pm 12	481 \pm 14	19	6.88	<.001
2,100 m:					
Males	416 \pm 11	470 \pm 18	3	3.61	= .04
Females	382 \pm 17	499 \pm 10	9	4.06	<.01
	1983	1984–1986	<i>N</i>	<i>t</i>	<i>P</i>
1,580 m:					
Males	532 \pm 13	484 \pm 9	20	4.89	<.01
Females	472 \pm 10	381 \pm 10	30	9.58	<.001
2,100 m:					
Males	485 \pm 14	446 \pm 13	11	3.40	<.01
Females	510 \pm 14	416 \pm 17	12	7.88	<.001

NOTE.—Significance of comparisons from paired one-tailed *t*-tests ($df = N - 1$).

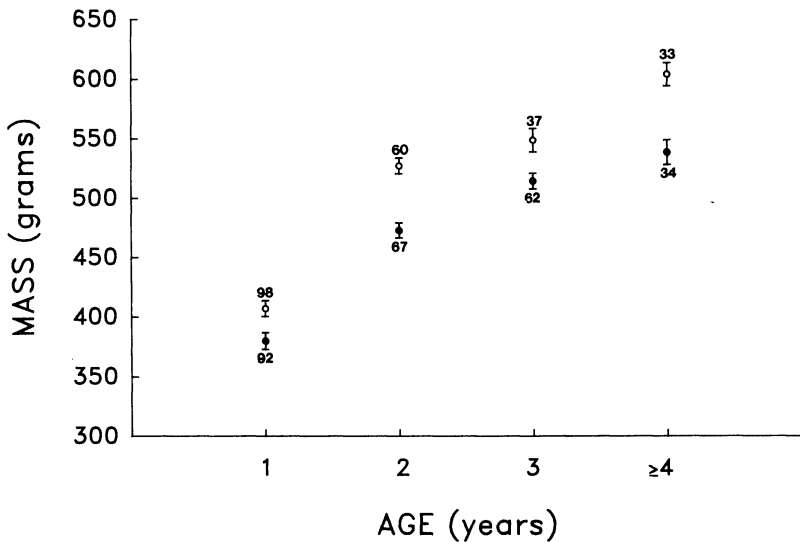


FIG. 2.—Field body mass of male (*open circles*) and female (*solid circles*) Columbian ground squirrels of different ages, ± 1 SE. Age class 4 includes all individuals 4 yr old or older. Sample sizes are given above and below the SE bars.

Field body mass of male and female ground squirrels was significantly heterogeneous among age classes (fig. 2; ANOVAs, $F = 115.1$ and 92.0 , $df = 3, 224$ and $3, 251$, respectively, both $P < .0001$). Comparisons among age classes could account for 68.3% and 59.7% of the variation in field mass of males and females, respectively. Male and female ground squirrels increased in body mass significantly with increases in age class (rank $r = 0.793$ and 0.738 , $n = 228$ and 255 , respectively, both $P < .0001$). In addition, males were significantly heavier than females in every age class (ANOVAs, all $P < .01$). In the population at 1,300 m, several yearling females reproduced, but in most populations ground squirrels are not reproductively mature until they are at least 2 yr old (Dobson and Murie 1987). Although body mass differed among age groups, the proportional annual change for ground squirrels 2 yr old and older was small (range, 4%–11%), and similar age-structured increases in mass were evident in all populations. Thus, I pooled ground squirrels 2 yr old and older to increase sample sizes in further analyses.

Field body mass of yearling male and female ground squirrels exhibited significant heterogeneity among populations (fig. 3A and B; ANOVAs, $F = 15.5$ and 15.7 , $df = 5, 92$ and $5, 86$, respectively, both $P < .0001$). Differences among populations could account for 48.8% and 50.5% of the variation in body mass of yearling males and females, respectively. The body masses of yearling males and females were significantly negatively associated with elevation (rank $r = -0.508$ and -0.576 , $n = 98$ and 92 , respectively, both $P < .0001$). When breeding yearling females were excluded from the analysis, the association of body mass of yearling females and elevation was improved slightly (rank $r = -0.653$, $n = 67$, $P < .0001$).

Field body mass of adult males and females also exhibited significant heterogeneity among populations (fig. 3A and B; ANOVAs, $F = 11.4$ and 8.1 , $df = 5, 124$, and $5, 157$, respectively, both $P < .0001$). Comparison among populations could account for 33.4% and 21.2% of the variation in body mass of adult males and females, respectively. Associations of body mass of adult males and females with elevation were lower than those for yearlings, but they were still negative (rank $r = -0.188$ and -0.317 , $n = 130$ and 163 , $P = .03$ and $< .0001$, respectively). As expected, the negative associations of field body mass with elevation were relatively low compared to those found for body mass when the stomachs and reproductive tracts of males and females were removed and age was held "constant" by partial correlation (Zammuto and Millar 1985a; $r = -0.40$ and -0.46 , respectively).

Principal components analyses of postcranial bone measurements were used to examine structural size of the ground squirrels (table 2). Because the measurements were chosen a priori for this purpose, the first component of the analysis (PC1) of the covariance matrix was interpreted as structural size. Scores for the specimens on PC1 were used as a single size variable. Body mass and structural size were significantly correlated for all sex and age classes of ground squirrels (yearling males, $r = 0.851$, $n = 80$, $P < .0001$; yearling females, $r = 0.789$, $n = 72$, $P < .0001$; adult males, $r = 0.593$, $n = 124$, $P < .0001$; adult females, $r = 0.543$, $n = 152$, $P < .0001$).

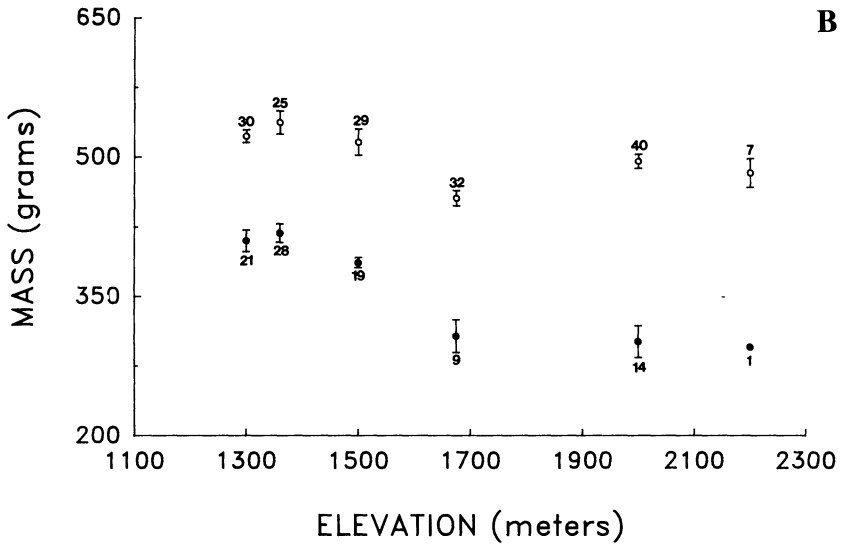
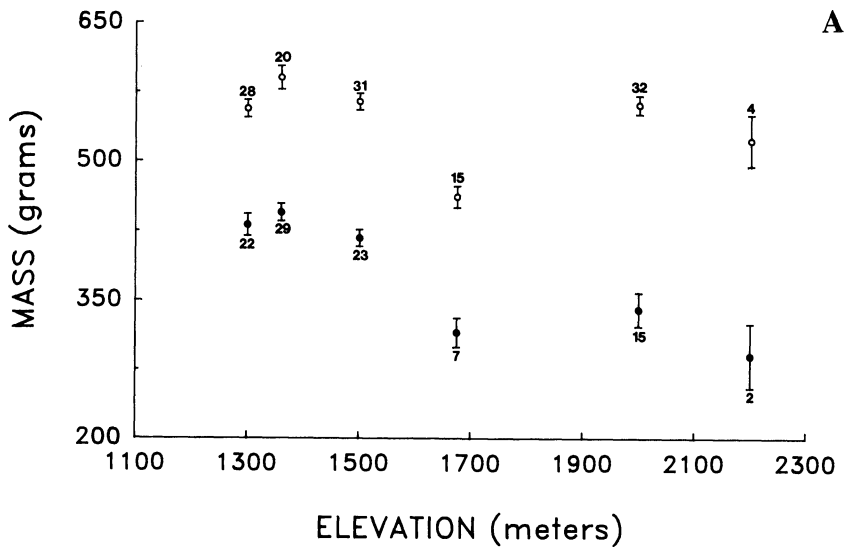


FIG. 3.—Field body mass of (A) male and (B) female Columbian ground squirrels in populations at different elevations. Adults (*open circles*) and yearlings (*solid circles*) are plotted separately, ± 1 SE. Sample sizes are given above and below the SE bars.

TABLE 2

FACTOR LOADINGS FOR PRINCIPAL COMPONENTS ANALYSES OF MASS AND STRUCTURAL SIZE

Variable	Skeleton Only PC1	Skeleton + Mass PC1	Skeleton + Mass PC2
Yearling males:			
Femur length	.47	.42***	.21
Tibia length	.42	.42***	.19
Humerus length	.43	.41***	.21
Ulna length	.38	.41***	.30**
Ischium-iliun length	.52	.41***	-.10
Mass (<i>a</i>)		.38***	-.88***
Eigenvalue (<i>k</i>)		5.45	.25
a^2k		.80 ^a	.20 ^a
% Variance explained ^b	94		
Significance	0	0	.017
Yearling females:			
Femur length	.47	.43***	.05
Tibia length	.44	.42***	.30**
Humerus length	.42	.42***	.05
Ulna length	.37	.41***	.40***
Ischium-iliun length	.52	.41***	-.05
Mass (<i>a</i>)		.36**	-.86***
Eigenvalue (<i>k</i>)		5.28	.40
a^2k		.69 ^a	.30 ^a
% Variance explained ^b	93		
Significance	0	0	0
Adult males:			
Femur length	.44	.44***	.23
Tibia length	.48	.44***	.26**
Humerus length	.44	.41***	.27**
Ulna length	.41	.42***	.13
Ischium-iliun length	.46	.40***	.24**
Mass (<i>a</i>)		.33***	-.86***
Eigenvalue (<i>k</i>)		4.40	.65
a^2k		.47 ^a	.48 ^a
% Variance explained ^b	80		
Significance	0	0	0
Adult females:			
Femur length	.48	.43***	.22
Tibia length	.45	.43***	.16
Humerus length	.42	.42***	.20
Ulna length	.39	.44***	.06
Ischium-iliun length	.50	.41***	.02
Mass (<i>a</i>)		.30***	-.94***
Eigenvalue (<i>k</i>)		4.55	.65
a^2k		.42 ^a	.58 ^a
% Variance explained ^b	84		
Significance	0	0	0

^a The correlation between factor scores for mass and the first and second principal components (i.e., the factor loadings) was squared and multiplied by the eigenvalue to yield the proportion of the variance in mass that was retained on each principal component.

^b The percentage of variance explained was not calculated for analyses based on the correlation matrices because variances of variables were standardized (see James and McCulloch 1990).

** $P < .01$; significance test described by Child (1970).

*** $P < .001$; significance test described by Child (1970).

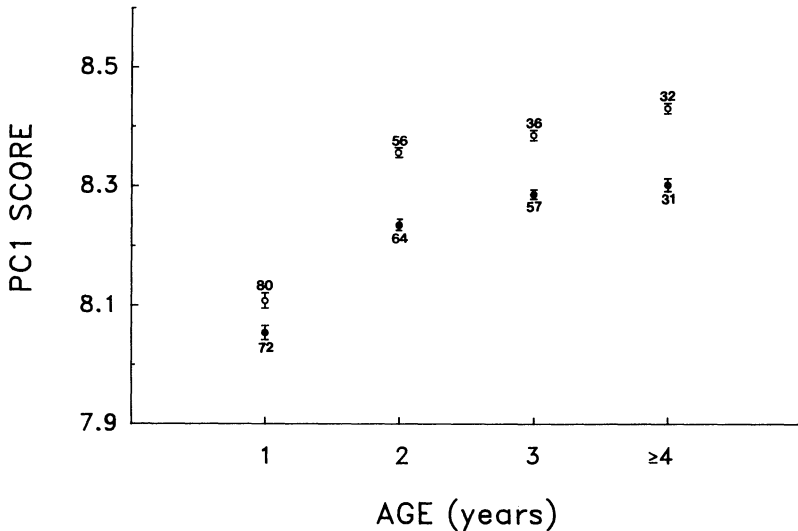


FIG. 4.—Structural size (PC1 score) of male (*open circles*) and female (*solid circles*) Columbian ground squirrels of different ages, ± 1 SE. Age class 4 includes all individuals 4 yr old or older. Sample sizes are given above and below the SE bars.

Structural size was significantly heterogeneous among age groups for both male and female ground squirrels (fig. 4; ANOVAs, $F = 189.4$ and 145.0 , $df = 3, 300$ and $3, 220$, respectively, both $P < .0001$). Differences in structural size among age groups could account for 79.4% of the variation in males and 72.5% of the variation in females. Structural size increased with age class for both males and females (rank $r = 0.847$ and 0.774 , $n = 204$ and 224 , respectively, both $P < .0001$). Two-year-olds were 99% of the structural size of older ground squirrels, however, so ground squirrels aged 2 yr and older were pooled for further analyses.

The structural size of yearling males and females exhibited significant heterogeneity among populations (fig. 5A and B; ANOVAs, $F = 16.4$ and 6.8 , $df = 5, 74$ and $5, 66$, respectively, $P < .0001$). The comparisons among populations could account for 55.4% and 34.6% of the variation in structural size of yearling males and females, respectively. Structural size of yearling males and females was significantly negatively associated with elevation (rank $r = -0.599$ and -0.482 , $n = 80$ and 72 , respectively, both $P < .0001$). Excluding breeding yearling females from the analysis still resulted in a negative association for yearling females (rank $r = -0.340$, $n = 49$, $P < .05$). Mean structural sizes of yearling males and females were not significantly negatively associated with elevation, but associations were fairly high, and the sample of populations was low (rank $r = -0.771$ and -0.829 , $n = 6$ and 6 , $P = .10$ and $.06$, respectively).

Structural size of adult males exhibited significant heterogeneity among populations, but for adult females the among-population comparison was not significant (fig. 5A and B; ANOVAs, $F = 4.62$ and 2.03 , $df = 5, 118$ and $5, 146$, $P < .001$

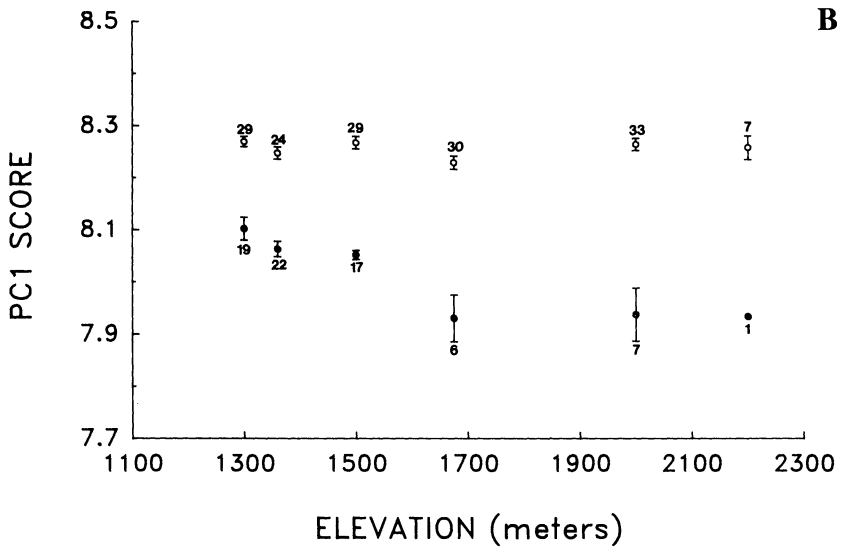
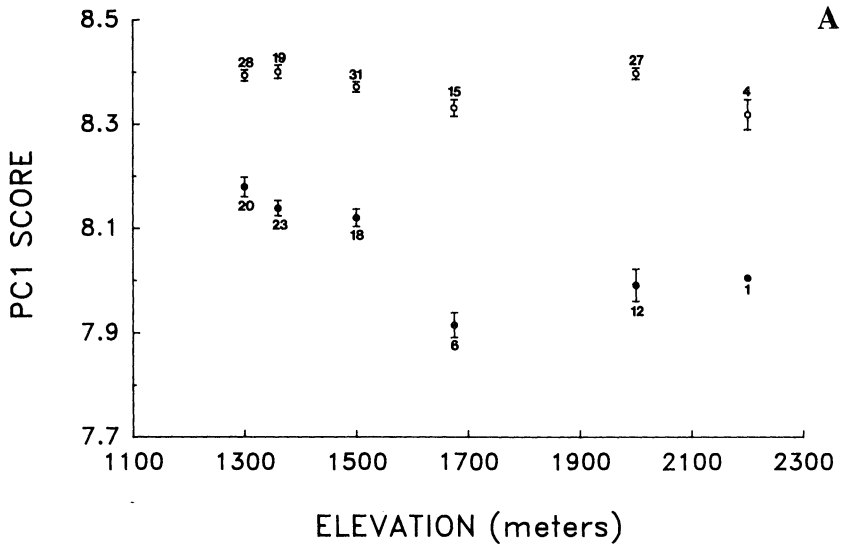


FIG. 5.—Structural size (PC1 score) of (A) male and (B) female Columbian ground squirrels in populations at different elevations. Adults (*open circles*) and yearlings (*solid circles*) are plotted separately, ± 1 SE. Sample sizes are given above and below the SE bars.

and = .08, respectively). The comparisons of adult males and females among populations could account for only 15.4% and 4.0% of the variation in structural size, respectively. For adult males and females, structural size was not significantly associated with elevation (rank $r = -0.149$ and -0.139 , $n = 124$ and 152 , $P = .10$ and $.09$, respectively).

Among populations at different elevations, mean litter size was not significantly associated with mean structural size of adult females (rank $r = 0.030$, $n = 6$ populations, $P > .50$). In the total sample of adult ground squirrels, structural size was weakly associated with litter size (rank $r = 0.174$, $n = 129$, $P = .05$). Field body mass of adult females, however, was more strongly associated with litter size (rank $r = 0.268$, $n = 139$, $P = .003$), as has been previously documented (Zammuto and Millar 1985a; Murie and Dobson 1987).

Physiological condition might be estimated as the residual of field body mass on structural size in a regression analysis. This procedure would "adjust" body mass for structural size, and thus the remaining variation might result from physiological condition plus an "error" term. I predicted that if differences in body mass among elevations were primarily due to changes in physiological condition, then the association of field body mass and elevation would be similar to the association of adjusted field body mass and elevation. For yearling males and females, adjusted body mass had significantly lower associations with elevation than did field body mass and elevation (for males, compare rank $r = -0.508$ and -0.040 , $n = 98$ and 80 , $P < .001$; for females, compare rank $r = -0.576$ and -0.230 , $n = 92$ and 72 , $P < .01$). The negative correlation of adjusted body mass with elevation was not significantly greater than zero for males or for females ($P > .50$ and $P = .06$, respectively). For adult males and females, adjusted body mass did not have a significantly different association with elevation than that of field body mass and elevation (for males, compare rank $r = -0.130$ and -0.188 , $n = 124$ and 130 , $P > .50$; for females, compare rank $r = -0.372$ and -0.317 , $n = 152$ and 163 , $P = .50$). The negative correlation of adjusted body mass with elevation was not significantly greater than zero for males but was highly significant for females ($P = .15$ and $< .0001$, respectively).

Field body mass was about twice as variable as any of the skeletal measures in comparisons of coefficients of variation (F -tests by the method of Lewontin [1966], sex and age groupings examined separately, all P s $< .001$). Because mass is in different units than linear measures, I used the correlation matrix to compute a PCA that included field body mass and the skeletal measurements. An alternative method is to transform body mass by taking its cube root (to obtain the dimensional equivalent of a linear measurement) and multiplying by five (to obtain a magnitude comparable to the linear measures). The covariance matrix of transformed body mass and skeletal measurements can then be subjected to PCA. Since both methods yielded very similar results, I present the PCA of the correlation matrix below.

Both body mass and measurements that were used to estimate structural size loaded significantly on PC1 (table 2). The strongest and most noteworthy contribution of body mass, however, was a negative loading on PC2. Skeletal measurements either loaded positively or were not significant on PC2. I multiplied the

squared correlation of the natural log of mass with PC1 and PC2 by the eigenvalue for each axis (table 2). The resulting value estimates the proportion of the variation in mass that is retained on each principal component. For yearlings, most of the variation in mass is associated with PC1. For adults, however, the majority of the variation in mass is associated with PC2.

DISCUSSION

Patterns of Body Mass and Life History

The gradual decline of body mass of yearling and adult males and females with increasing elevation (fig. 3A and B) follows a general pattern of change in life-history traits: litter size decreases, age at maturity increases, the proportion of females that breed decreases, and adult and juvenile survival increases with increasing elevation (reviewed in Dobson and Murie 1987). Changes in body mass might reflect changes in energy balance of the ground squirrels (Ritchie and Belovsky 1990), which would thus influence the cline in life-history traits over elevation and accompanying environments. Before the role of changes in body mass with elevation can be examined, however, an understanding of the factors that underlie mass is needed.

Factors Underlying Body Mass

Two factors might contribute to changes in body mass (Campbell and Dobson 1992). First, changes in body mass could reflect differences in structural size of the ground squirrels. Differences in structural size could be due to plasticity in structural growth of the ground squirrels, as Patton and Brylski (1987) found for pocket gophers in different environments. This seems a reasonable expectation for Columbian ground squirrels because many aspects of their life histories are extremely plastic (Dobson and Kjelgaard 1985*b*; Dobson and Murie 1987; Dobson 1988).

The second factor that might be reflected by changes in body mass is changes in body condition, or energy reserves that are stored as fat or other tissues. Ground squirrels have an annual cycle of change in physiological condition, with fat deposition during the active season and subsequent weight loss during hibernation (Davis 1976; Armitage 1981; Young 1988). It is reasonable to predict that changes in mass with elevation should reflect changes in physiological condition.

Yearling males and females exhibited a significant negative association of structural size with elevation, which indicates slower structural growth at higher elevations (fig. 5A and B). Structural growth was determinant, however, with older ground squirrels exhibiting a marked "plateau" in size (fig. 4). Among adult ground squirrels, there were no significant associations of structural size with elevation (fig. 5A and B). Thus, I found support for the hypothesis that changes in body mass among elevations were due to changes in structural size for yearlings but not for adults.

Three lines of evidence were used to test the hypothesis that changes in body mass of yearling ground squirrels among elevations were due to changes in physi-

ological condition. First, there was a significant negative association of structural size and elevation (fig. 5A and B), which suggests that the changes in structural size with elevation might provide an adequate explanation of changes in body mass. Second, when the influence of structural size was removed from field body mass of yearlings by analysis of regression residuals, the associations of "adjusted" body mass and elevation were not significantly different from zero but were significantly lower than the associations of body mass and elevation. Third, field body mass was most strongly associated with PC1 of a PCA of field body mass and skeletal measurements for both males and females, which indicates an association of body mass with structural size (table 2). Thus, the weight of evidence indicated that elevational differences in body mass of yearling ground squirrels did not reflect differences in physiological condition.

Three lines of evidence were used to test the hypothesis that changes in body mass of adult ground squirrels among elevations were due to changes in physiological condition. First, the lack of a significant negative association of structural size with elevation (fig. 5A and B) might suggest that the negative association of body mass over elevation reflects changes in nonstructural aspects of size. Second, when the influence of structural size was removed from field body mass of adults by analysis of regression residuals, the associations of "adjusted" body mass and elevation were similar to the associations of body mass and elevation. Third, field body mass was most strongly associated with PC2 of a PCA of field body mass and skeletal measurements for both males and females, which indicated variation in body mass that was orthogonal to structural size (table 2). Thus, the weight of evidence indicated that elevational differences in body mass of adult ground squirrels reflected differences in physiological condition over the elevational gradient.

During and after food supplementation of two experimental populations, significant increases and decreases in spring body mass occurred for adult ground squirrels (table 1). These ground squirrels were adults throughout the years covered by the comparisons, so they should have already plateaued in structural growth (fig. 4). The changes in spring body mass, therefore, were likely a plastic response of energy reserves, such as stored fat tissue, to the experimental supplementations and their aftermath. The changes within populations were as great in magnitude as differences in mass among populations. Thus, the experimental results indirectly supported the hypothesis that changes in body mass with elevation were due to differences in physiological condition by showing that such changes can be stimulated experimentally under field conditions.

Field body mass and structural size were strongly correlated for all sex and age classes, but the variation in field mass did not clearly coincide with structural size. In the PCA of structural size measures and body mass, PC1 had significant loadings for all variables, which reflects the strong correlation among variables (table 2). Also, PC1 appeared to be a "general size factor" (sensu Bookstein et al. 1985); PC2, however, had a strong negative loading for body mass and either positive or nonsignificant loadings for measures of structural size. Although body mass may partially reflect structural size, it may also reflect aspects of physiological condition that vary differently (orthogonally) from structural size.

Conclusions

The interpretation of changes in the size of ground squirrels over the elevational gradient was clarified through an examination of the potential factors that underlie changes in body mass. The rate of structural growth differs over the elevational gradient, with slower growth at higher elevations. The "plateau" structural size of adult ground squirrels, however, does not follow either the elevational gradient or the concurrent cline in life-history traits (e.g., litter size). Rather, changes in body mass of adults with elevation may have been primarily due to changes in physiological condition that were associated with life-history traits and with changes in elevation. Structural size of adults was not a highly plastic aspect of the ground squirrels. This result contrasts with the considerable plasticity of structural size of adults that Patton and Brylski (1987) found in pocket gophers.

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