

ENVIRONMENTAL PREDICTABILITY, VARIABILITY, AND *SPERMOPHILUS COLUMBIANUS* LIFE HISTORY OVER AN ELEVATIONAL GRADIENT¹

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Abstract. We quantitatively tested various aspects of the theory of *r*- and *K*-selection for six populations of Columbian ground squirrels from Alberta, Canada. Three measures of environmental predictability (maximum and minimum temperatures, precipitation) and a presumed measure of food resource levels supported the prediction that environments at lower elevations were less predictable, and had greater, more variable food resource levels than environments at higher elevations. Columbian ground squirrels in more predictable environments (i.e., at higher elevations) had higher adult survival rates, later ages at maturity, and possibly lower genetic variabilities than did squirrels in less predictable environments (at lower elevations). Body mass was greater at lower elevations than at higher elevations. Litter size showed no trend with respect to elevation, but it tended to be most variable in unpredictable environments at lower elevations. Although they were more predictable, the daily minimum temperatures at higher elevations tended ($P = .06$) to show wider variation than the minimum temperatures at lower elevations. Previous apparent problems with *r*-*K* theory may be attributable in part to the assumption that predictability and stability should covary. The major difference between the pattern emerging from our study and that predicted by traditional theory is that predictability of environments, and concomitantly the occurrence of *K*-strategists, was found to increase with movement up an elevational gradient. Portions of *r*-*K* theory may be found to be useful once all of its parameters are consistently measured.

Key words: age at maturity; body mass; Columbian ground squirrel; elevation; environmental predictability; environmental variability; genetics; life history; litter size; mammal; *r*-*K* theory; *Spermophilus columbianus*; survival.

INTRODUCTION

Recent arguments suggest that patterns in life-history variation should no longer be examined within the context of *r* and *K* theory (MacArthur and Wilson 1967, Pianka 1970), but should be examined within the context of bet-hedging theory and/or another (as yet undefined) age-specific theory (Charnov and Schaffer 1973, Stearns 1976, 1983, 1984). However, proponents of this new view of life-history evolution have had cogent arguments raised against their positions (e.g., Hastings and Caswell 1979, Etges 1982, Parsons 1982, Boyce 1984). Through perusal of life-history literature (see Stearns 1976, 1977, 1980, Parsons 1982, Boyce 1984), we conclude that none of these theories has been consistently tested enough to allow us to choose among them. We surmise that if such theories are to be rigorously tested, we must first develop a consistent methodology to measure interactions among life-history traits and patterns of environmental variation (Stearns 1976, 1977; but see Stearns 1980). Proponents of each view of life-history evolution admit that this methodology has not yet been developed (Charlesworth 1980, Stearns 1981, Etges 1982). Here we at-

tempt to develop a comprehensive methodology to measure interactions among life-history traits and environmental variation. Our focus here is on *r*-*K* theory; it is on bet-hedging theory (age-specific interactions) in Zammuto and Millar (1985).

The theory of *r*- and *K*-selection predicts that variable, unpredictable environments should be associated with smaller somatic size, increased mortality, earlier ages at maturity, increased reproduction, and higher genetic variabilities in plants and animals, whereas stable, predictable environments should be associated with the opposite attributes (Dobzhansky 1950, Cody 1966, MacArthur and Wilson 1967:149-152, 157; Pianka 1970, 1978:122). The portion of this theory dealing with reproduction has been tested and/or supported by some studies on birds (Cody 1966), mammals (Dunmire 1960, Lord 1960, Smith and McGinnis 1968, Kirkland and Kirkland 1979), and insects (Price 1975: 151), under the assumption that variable, unpredictable environments occur at higher elevations and latitudes (Cody 1966, Pianka 1970, 1978:135, Price 1975, Stearns 1976, 1977). The portion of the theory dealing with mortality and genetic variability has received some theoretical and empirical support (MacArthur and Wilson 1967, Levins 1968, Hedrick et al. 1976, Nevo 1978). However, considerable data exist which indicate that higher elevations or latitudes are not necessarily more *r*-selecting. For example, few annual plants are found in alpine and arctic regions (Billings and Mooney

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1968, Teeri 1973), body size of homeotherms usually increases with latitude (Bergmann 1847), lizards are more *K*-selected with increasing latitude and elevation (Andrews and Rand 1974, Ballinger 1979), marmots mature later at higher elevations than at lower elevations (Barash 1974), and some mammals have smaller litter sizes at higher elevations or latitudes than at lower elevations or latitudes (Chapman and Lind 1973, Bronson 1979, Murie et al. 1980).

Several reasons have been advanced to explain discrepancies between *r-K* theory and empirical data. Bet-hedging theory (Charnov and Schaffer 1973, Stearns 1976) has been proposed to explain life-history patterns. Others have argued that annual and/or semelparous organisms may not have enough time to grow and reproduce in the short growing season at higher elevations and latitudes (Billings and Mooney 1968, Spencer and Steinhoff 1968), that high elevations and latitudes may be more stable and more predictable than lower elevations and latitudes (Wolda 1978, Myers and Pitelka 1979), that observed differences may represent sampling biases for relatively old animals (Fleming and Rauscher 1978), that food resource levels and energetics may directly influence life-history patterns (McNab 1980), or that life histories may be influenced by social organization (Armitage 1981).

Stearns (1976, 1977; but see Stearns 1980, 1983 for an alternative view) reviewed current knowledge of life-history phenomena and concluded that to make meaningful progress with life-history theory, one must study several populations of a species in different environments, measuring life-history, genetic, and environmental variables at each population site. Here we report our studies of these factors for six populations of Columbian ground squirrels, *Spermophilus columbianus*. This is an abundant, colonial, montane/subalpine rodent of northwestern North America whose range includes a variety of environmental conditions. Age at maturity (Festa-Bianchet 1981), litter size, and survival (Murie et al. 1980), vary among populations, and weather may affect activity (Elliott and Flinders 1980). However, no studies have dealt in depth with the association of life-history or genetic parameters with environmental parameters for this species.

Hypotheses

Explicitly stated, *r-K* theory predicts that to facilitate ongoing or repeated colonization of a habitat and exploitation of food resources, animals living in unstable, unpredictable environments (e.g., high latitudes or high elevations; Cody 1966:182) are expected to have smaller body sizes, earlier ages at maturity, lower survival rates, larger litter sizes, and higher genetic variabilities (i.e., be more *r*-selected) than those (more *K*-selected) animals living in stable, predictable environments (e.g., low latitudes or low elevations) (Cody 1966, MacArthur and Wilson 1967:149–152, 157; Spencer and Steinhoff 1968, Pianka 1970). We at-

tempted to falsify this prediction by examining life-history and environmental variables with respect to elevation. Our specific predictions were that: (1) Columbian ground squirrels at low elevations have smaller body masses, earlier ages at maturity, lower adult survival rates, larger litter sizes, and higher genetic variabilities than squirrels at high elevations, and (2) environments at low elevations are less stable (more variable) and less predictable than environments at higher elevations. We expected reversed locations of stable/unstable, predictable/unpredictable environments (with respect to Cody 1966:182) and *r/K*-strategists because high elevations are usually subjected to temperature inversions, which may cause daily temperatures to remain more stable and predictable than those at lower elevations (Trewartha 1968:46), and we expected ground squirrels to tend towards *K*-strategies in stable, predictable environments. Each component of these predictions was examined separately.

METHODS

Ground squirrels

A total of 506 Columbian ground squirrels (≥ 1 yr old) were collected with Conibear traps from six relatively discrete populations (i.e., >25 km separated each studied population from another) of similar density (10–15 adults/ha) in the Rocky Mountains of southwestern Alberta (population 1 occurred at 1300 m elevation, 2 at 1360 m, 3 at 1500 m, 4 at 1675 m, 5 at 2000 m, 6 at 2200 m). Almost all animals present in populations 1, 4, 5, and 6 were collected. Each population was studied at the birth-pulse (see Caughley 1977:6) within 4 wk of female emergence from hibernation (during May), after copulation had ceased and females were 2–3 wk pregnant or lactating. Populations 2, 3, and 5 were studied in 1980 and populations 1, 4, and 6 were studied in 1981. Body mass (mass without stomach and reproductive tract), age (number of annual adhesion lines in diastema of lower jawbone, checked against animals of known ages, following Millar and Zwickel 1972), male reproductive condition (males with pigmented scrota or scrotal testes were considered mature), female maturity (females with embryos or placental scars were considered mature), approximate breeding date (by back-dating from embryo size; Tomich 1962), litter size (number of embryos or placental scars), and gene frequencies (at 30 loci in the liver, following Selander et al. 1971), were determined in the field or the laboratory.

Time-specific life tables were constructed under the assumptions (supported by Bronson 1979, Boag and Murie 1981*b*) that age structures were stable and the populations stationary (see Caughley 1977:90, Michod and Anderson 1980). Age-specific survival (the proportion of animals living to age x ; Caughley 1977:86) was calculated as:

$$l_x = n_x/n_0 \quad (1)$$

where n_0 was the number born and n_x the number of collected females living to age x . Age-specific life expectancy (e_x , expectation of further life, based on mean death age of a cohort; Pianka 1978:103) was calculated as:

$$e_x = \frac{\sum_{y=x}^{\infty} l_y}{l_x} \quad (2)$$

Adult survival was defined as the life expectancy at maturity (age at which >50% of the females in a population were mature) from each life table. Gene frequencies within populations were checked for Hardy-Weinberg equilibrium with chi-square analysis for each polymorphic locus (each locus at which the frequency of the most common allele was $\leq 95\%$).

Environmental measurements

Elliott and Flinders (1980) and Boag and Murie (1981a) found temporal and spatial differences in activity, growth, and reproduction of *S. columbianus* to be associated with differences in ambient temperature and precipitation. Therefore, relative variabilities (total variation) or predictabilities (proportion of variation explained) for these variables may affect the life history and genetics of this species.

Powell and MacIver (1977) found that a 3–10 yr period was as adequate as a long-term period (>30 yr) for describing the summer temperature and precipitation at sites within and adjacent to our study region. We obtained 10-yr (1965–1974; later years unavailable) daily weather records (maximum and minimum temperatures and precipitation) spanning the approximate vegetative growing season (late May through late September, the period when daily maximum temperatures exceeded 10°C), from weather stations within 10 km of each population (Atmospheric Environment Service 1965–1974, Water Survey of Canada, Calgary District 1965–1974). Environmental variability at each population site was defined as the statistical variance (S^2) of the 10-yr raw data for each of the three meteorological variables ($n = 1248$ for maximum temperature and for minimum temperature, $n = 937$ for precipitation for each population site; see Zammuto 1983 for dates). Environmental stability was defined as the inverse of variability ($1/S^2$). Variability (10-yr) of each meteorological variable at each population site was examined in relation to elevation. The z score (standard deviate; Steel and Torrie 1960:40) was calculated for each raw datum of each meteorological variable, and the scores were combined within each population site to create a single data set of z scores for each site. This transformation provided a total of six data sets (one for each population site); each datum in each of these sets was the number of standard deviations from the grand mean (mean of each meteorological variable for all population sites combined) of each combined

variable (Nie et al. 1975:187). The statistical variance of these z scores at each population site was examined in relation to elevation. This allowed us to simultaneously use the information contained in all three meteorological variables to test the prediction that environments at lower elevations are less stable (more variable) than environments at higher elevations.

Environmental predictability was defined as the probability of correctly predicting the daily temperature or daily amount of precipitation from knowledge of the time of year, and vice versa. Since ecologists have not yet determined which statistical measures of predictability should best be used to determine environmental predictability (Stearns 1981), we used most measures of predictability offered in the literature (see Appendix). We calculated predictability (values ranged between 0 = unpredictable and 1 = predictable) for each meteorological variable for each population site using 18 equations derived from either nonparametric statistical considerations (Goodman and Kruskal 1954), information theory (Kullback 1959), or conventional parametric statistics (Zar 1974). The mean of the arcsine-transformed predictability values for each variable for each population site was examined with respect to elevation. To use simultaneously the information contained in predictability values of all three meteorological variables, a pooled mean predictability value was calculated for each site by combining all 54 (3 variables \times 18 equations) arcsine-transformed (already standardized; see Appendix) predictability values. This mean value was correlated with elevation to test the prediction that environments at lower elevations are less predictable than environments at higher elevations. The arcsine-transformed predictability values of each equation for each variable were correlated with elevation to provide background information on how each predictability equation varied with elevation.

Food resources

According to r - K theory, r -selected populations should exist where food resource levels are high and variable, whereas K -selected populations should be present where food resource levels are low and stable (MacArthur and Wilson 1967:149–150). If our two major predictions are supported, an auxiliary prediction in this study might state that food resource levels of Columbian ground squirrels are greater and more variable at lower elevations than at higher elevations. Since Columbian ground squirrels eat grasses and forbs (Shaw 1925), and since McGinnies (1967) and Davis et al. (1972) found that annual growth of grasses and forbs is positively correlated with the width of the annual growth ring in neighboring woody plants, annual growth rings of trees were used to index food resource levels (presumably primary productivity) of grasses and forbs at each population site.

Two cores were taken with an increment borer from each of 14–20 lodgepole pines (of similar age, micro-

topography, soil, slope aspect, height, width, density, etc.; see Fritts 1976:247) within 2 km of each sampled ground squirrel population. The mean distance between annual rings (ring width) was determined for each tree using an ocular micrometer. Each value for annual ring width was divided by the tree's mean ring width for standardization (or filtering; Fritts 1976:266) with respect to age. The standardized variance and grand mean (all trees at each population site combined) annual ring width for 1965–1973 at each population site was compared to elevation.

Statistical analysis

All proportions were arcsine-transformed before subsequent analysis. Nonparametric tests were used whenever the raw and ln-transformed data were non-normally distributed within populations ($P < .01$, Kolmogorov-Smirnov one-sample tests) or variances were heterogeneous among populations ($P < .01$, Bartlett-Box F test).

RESULTS

Body mass

Body mass differed between sexes ($t = 5.6$, $df = 493$, $P < .001$; overall, males were heavier than females; Table 1), and increased with age for each sex ($r = 0.66$, $n = 236$, $P < .001$ for males; $r = 0.59$, $n = 259$, $P < .001$ for females). ANCOVA indicated that a higher percentage (44% for males, 35% for females) of the total variance in body mass was explained by age (covariate) than by population (17% for males, 19% for females).

Body mass was negatively correlated with elevation for each sex when the effects of age were held constant by partial correlation analysis ($r = -0.40$, $n = 233$, $P < .001$ for males; $r = -0.46$, $n = 256$, $P < .001$ for females). The prediction that squirrels at lower elevations should have smaller body masses than squirrels at higher elevations was not supported.

Age at maturity

Most (>70%) 2-yr-olds (and almost all older animals) were mature in all populations, except in population 3, where only 47% of the 2-yr-olds were mature. More than 60% of the yearlings were mature in population 1, whereas <12% of the yearlings were mature in populations 2–6 (Table 1). Higher proportions of yearling females (86%, 18/21) and males (36%, 8/22) were mature in population 1 than in all other populations ($\chi^2 > 10.8$, $df = 1$, $P < .001$), and a higher proportion of yearling females were mature in population 2 (21%, 6/28) than in populations 3–6 ($\chi^2 > 10.8$, $df = 1$, $P < .001$) (Table 1). The prediction that squirrels at lower elevations should have earlier ages at maturity than squirrels at higher elevations was supported.

Age structure and survival

Standing age structures did not differ between sexes within any population ($P > .05$ for all populations; Lee

and Desu [1972] D_{stat}), so males and females were combined for life-table calculations. Mean age varied among populations ($H = 33.9$, $df = 5$, $P < .001$, Kruskal-Wallis ANOVA), and age was greater at higher elevations than at lower elevations ($r = 0.20$, $n = 506$, $P < .001$; Table 1). Adult survival was also greater at higher elevations than at lower elevations ($r = 0.92$, $n = 6$, $P < .01$; Table 1). The prediction that squirrels at lower elevations should have lower adult survival rates than squirrels at higher elevations was supported.

Litter size and breeding synchrony

Variance in litter size varied among populations ($P < .001$, Bartlett F); the variance in population 1 was higher ($P < .05$, F ratio; no age effects) than that for populations 3, 4, or 5 (Table 1). Females in populations 2–6 displayed relatively synchronous conception (as dated qualitatively by embryo size), but those in population 1 were relatively asynchronous, with many females lactating while others had recently (1 wk previous to capture) conceived (Table 1).

Litter size increased with age ($r = 0.32$, $n = 174$, $P < .001$) and body mass ($r = 0.30$, $n = 174$, $P < .001$), and varied among populations ($H = 17.9$, $df = 5$, $P < .01$, Kruskal-Wallis ANOVA), but it was not correlated with elevation when the effects of age and body mass were held constant by partial correlation analysis ($r = -0.10$, $df = 165$, $P = .20$). The prediction that squirrels at lower elevations should have larger litter sizes than squirrels at higher elevations was not supported.

Genetics

Seven of the 30 loci were polymorphic in at least one population (Table 2). All loci in each population were in Hardy-Weinberg equilibrium (all $\chi^2 < 3.8$, $P > .05$). The number of heterozygous loci per individual (direct counts of heterozygous loci) did not differ between sexes within any of the six populations (all $P > .05$, t tests) or all of the populations combined ($t = 0.37$, $df = 431$, $P > .05$). It did not vary with body mass ($F = 1.82$, $df = 1$, $P > .05$, ANCOVA), or with age ($F = 0.84$, $df = 1$, $P > .05$, ANCOVA), but did vary among populations ($F = 9.80$, $df = 5$, $P < .001$, ANCOVA). The number of heterozygous loci per individual was inversely associated with elevation ($r = -0.14$, $n = 433$, $P < .01$; Table 1). However, nearly all the variation remained unexplained, and therefore these results give only weak support to the prediction that squirrels at higher elevations should have lower genetic variabilities than squirrels at lower elevations.

Environmental measurements and elevation

None of the raw or ln-transformed meteorological variables within population sites was normally distributed (all $P < .001$), and variances were heterogeneous (all $P < .001$). Kolmogorov-Smirnov two-sample tests indicated that most population sites, tested pairwise, differed in the raw (10-yr) distributions of meteorological variables (Tables 3 and 4).

TABLE 1. Life history and genetic variables for each population of Columbian ground squirrels.

Popu- lation	Eleva- tion (m)	Sample size		Body mass† (g, $\bar{X} \pm SE$)		Adult sur- vival‡ (yr)	Mean age of popula- tion (yr)	Proportion of yearlings reproductive§				Litter size $\bar{X} \pm SD$
		♂♂	♀♀	♂♂	♀♀			♂♂	n	♀♀	n	
1	1300	50	51	480 ± 11**	440 ± 9	2.27	2.07	0.4	22	0.9	21	3.88 ± 1.45
2	1360	51	53	485 ± 12**	445 ± 10	2.00	1.85	0.0	30	0.2	28	3.75 ± 1.04
3	1500	54	48	477 ± 14**	431 ± 11	2.31	2.16	0.0	23	0.0	19	2.94 ± 0.73
4	1675	25	44	385 ± 16	384 ± 10	2.21	2.33	0.1	8	0.1	9	4.22 ± 0.89
5	2000	47	54	445 ± 19*	396 ± 12	2.73	2.54	0.0	15	0.0	14	3.44 ± 0.85
6	2200	11	18	456 ± 37	423 ± 18	3.00	2.86	0.0	3	0.0	2	3.71 ± 0.99

† Mass after reproductive tract and stomach removed.

‡ Life expectancy at maturity, from life tables.

§ Males with scrotal testes or pigmented scrotum; pregnant or lactating females.

|| Embryos or placental scars.

¶ Frequency of most common allele $\leq 95\%$.

Direct counts of heterozygous loci.

†† Determined qualitatively by visual examination of embryo size.

* $P < .05$, ** $P < .01$, males significantly heavier than females, t tests.

Population sites were ranked from least to most variable in environmental conditions as follows: $3 < 4 = 6 < 2 < 1 < 5$ for maximum temperature, $3 < 4 < 2 < 1 < 6 < 5$ for minimum temperature, and $1 < 6 < 4 < 5 < 3 < 2$ for precipitation (Table 5). The positive association between (10-yr) variability of minimum daily temperature and elevation approached significance ($r = 0.79$, $n = 6$, $P = .06$; Table 5) but there was no relationship between z -transformed (pooled) variability and elevation ($r = 0.59$, $n = 6$, $P = .22$; Table 5). Furthermore, no relationships existed between (10-yr) maximum temperature ($P = .52$) or precipitation ($P = .58$) variability and elevation (Table 5). Therefore, our prediction that physical environments at lower elevations should be less stable (more variable) than environments at higher elevations was not supported.

There were no differences in predictabilities among population sites for daily maximum temperature ($F = 0.30$, $df = 1$, $P > .05$, ANCOVA) although differences existed for precipitation ($F = 20.4$, $df = 1$, $P < .001$, ANCOVA) and minimum temperature ($F = 93.4$, $df = 1$, $P < .001$, ANCOVA) (Table 6). Mean (of arcsines) predictability of maximum temperatures ($P = .77$) and precipitation ($P = .29$) showed no relationship with elevation, although mean predictability of minimum temperatures increased with elevation ($r = 0.97$, $n = 6$, $P < .001$). A positive correlation existed between elevation and the pooled mean predictability values derived from combining all standardized arcsine-transformed predictability values ($n = 54$; 18 values \times 3 variables) for each population site ($r = 0.85$, $n = 6$, $P < .05$). In addition, positive correlations (one-tailed, $P < .05$) existed for 12 of the 54 analyses (18 equations \times 3 variables) in which arcsine-transformed predictability values of each equation were examined with respect to elevation, whereas only 1 negative correlation ($P < .05$) existed. From these results, we concluded

that the prediction that environments at lower elevations should be less predictable than environments at higher elevations was supported.

Food resources

Variability of ring widths and mean ring widths were greater at lower elevations than at higher elevations ($r = -0.34$, $n = 54$, $P < .05$ and $r = -0.83$, $n = 6$, $P < .05$, respectively). From these results we concluded that the auxiliary prediction that food resource levels of Columbian ground squirrels should be greater and more variable at lower elevations than at higher elevations was supported.

DISCUSSION

Our data indicate that Columbian ground squirrels exhibit K -strategies (later maturity, higher adult survival, possibly lower genetic variability) in high-elevation environments, which tend to have more predictable temperatures and precipitation levels and smaller, less variable food resource levels than low-elevation environments. Squirrels exhibit r -strategies (earlier maturity, lower adult survival, possibly higher genetic variability) in low-elevation environments, which tend to have less predictable temperatures and precipitation levels and larger, more variable food resource levels than high-elevation environments. Body mass and litter size did not conform with this pattern. Body mass decreased ($P < .001$) with elevation; litter size (after controlling for age and body mass) was not correlated ($P = .20$) with elevation. Nevertheless, these data indicate that, in general, K -strategies occur in more predictable environments at higher elevations.

Our results require modification of the original theory of r - and K -selection as implied by Cody (1966) and treated in detail by Pianka (1970), since the locations of predictable/unpredictable environments and r/K -strategists in our study are reversed. However, lat-

TABLE 1. Continued.

Litter size		Polymorphism (P)†	Heterozygous loci per individual#		Approximate range of conception dates†† (d)
n	Range		$\bar{X} \pm SD$	n	
48	2-7	0.23	1.33 ± 0.19	85	30
28	2-6	0.20	1.21 ± 0.16	88	10
18	2-4	0.20	1.19 ± 0.15	86	10
27	3-6	0.17	1.18 ± 0.18	69	10
39	1-5	0.20	1.23 ± 0.16	91	10
14	2-5	0.10	1.12 ± 0.10	14	10

er maturity, higher adult survival, and possibly lower genetic variability were associated with more predictable environments and perhaps with smaller food-resource levels, so that a portion of *r-K* theory was supported (MacArthur and Wilson 1967). Perhaps some of the theoretical framework concerning the interface between life history and the environment that MacArthur and Wilson (1967) proposed was correct,

TABLE 2. Allelic frequencies for each population.†

Loci Alleles	Populations					
	1	2	3	4	5	6
Leucylglycyl-glycine 1						
A	0.62	0.72	0.71	0.80	0.76	0.86
B	0.38	0.28	0.29	0.20	0.24	0.14
Nucleoside phosphorylase						
A	0.56	0.85	0.80	0.70	0.70	0.64
B	0.44	0.13	0.20	0.30	0.29	0.36
C	0.00	0.02	0.00	0.00	0.01	0.00
6-phosphogluconate dehydrogenase						
A	0.91	1.00	0.99	0.99	1.00	1.00
B	0.09	0.00	0.01	0.01	0.00	0.00
Adenosine deaminase 1‡						
A	0.85	0.87	0.85	0.74	0.73	1.00
B	0.15	0.13	0.15	0.26	0.27	0.00
Adenosine deaminase 2						
A	0.86	0.95	0.95	0.85	0.90	0.75
B	0.14	0.05	0.05	0.15	0.10	0.25
Alcohol dehydrogenase						
A	0.78	0.89	0.95	0.98	0.85	1.00
B	0.22	0.11	0.05	0.02	0.15	0.00
Esterase 3						
A	0.86	0.88	0.94	0.92	0.95	1.00
B	0.05	0.06	0.01	0.01	0.01	0.00
C	0.09	0.06	0.05	0.07	0.04	0.00
n	90	90	87	69	91	14

† Monomorphic loci were: superoxide dismutase 1, 2; isocitrate dehydrogenase 1, 2; glucose phosphate isomerase 1, 2; phosphoglucomutase 1, 2, 3; lactate dehydrogenase; malic enzyme 1, 3; hemoglobin; aspartate aminotransferase 1, 2; glutamate pyruvate transaminase; leucyl alanine peptidase 1, 3; phenylalanyl-proline peptidase; phosphomannose isomerase; leucylglycyl-glycine peptidase 2; glucuronidase; guanine deaminase.

‡ Sample size decreased because of inconsistent scoring.

TABLE 3. Pairwise differences† in the 10-yr distributions of daily maximum temperature (°C) (upper matrix) and daily minimum temperature (°C) (lower matrix) between population sites.

Population site	Population site					
	1	2	3	4	5	6
1		***	***	***	***	***
2	***		NS	NS	***	***
3	***	**		NS	***	***
4	***	***	***		***	***
5	***	***	***	***		NS
6	***	***	***	***	*	

† Kolmogorov-Smirnov two-sample tests; significance levels: * *P* < .05, ** *P* < .01, *** *P* < .001, NS *P* > .05.

but Cody (1966) was wrong to assume (as many others have) that environmental conditions on mountaintops could be equated with those at higher latitudes.

Levins (1968:90) suggested that a mixed strategy (no optimum) for litter size will be adaptive where environmental conditions are unpredictable. In our study, litter size and conception dates were most variable at the lowest elevations (populations 1 and 2), where environmental conditions were least predictable. Since environmental predictability tended to be lower at lower elevations, our results are consistent with Giesel's (1976) prediction that populations living in unpredictable environments should be polymorphic for reproductive characteristics. Variability in conception date and litter size at lower elevations may have been selected for (or not selected against) because no one date or litter size was always advantageous.

Why has the observed pattern emerged? Three main possibilities come to mind. First, hibernating Columbian ground squirrels may experience higher rates of winter mortality at low elevations than at high elevations due to deeper frost lines resulting from reduced snow cover (Atmospheric Environment Service 1965-1974, Water Survey of Canada, Calgary District 1965-1974, Geiger 1966:178, 445; Barash 1974). Second, food resources may be more limiting at higher elevations than at low elevations because of the shorter vegetative growing season (Zammuto 1983), and this may lead to delayed maturity (Dobson 1984), and smaller litters (Murie et al. 1980, Dobson 1984), which in turn

TABLE 4. Pairwise differences† in the 10-yr distributions of daily precipitation (mm) between population sites.

Population site	Population site					
	1	2	3	4	5	6
1						
2	NS					
3	***	NS				
4	NS	NS	NS			
5	***	***	*	***		
6	***	***	***	***	*	

† Kolmogorov-Smirnov two-sample tests; significance levels: * *P* < .05, *** *P* < .001, NS *P* > .05.

TABLE 5. Variabilities (over 10 yr) for the three meteorological variables.*

Population site	Temperature		Precip.	z-transformed pooled variability
	Maximum	Minimum		
1	38.1	15.8	28.7	0.87
2	37.9	15.5	49.6	0.94
3	34.7	14.4	39.6	0.84
4	37.5	14.7	31.9	0.82
5	40.4	24.7	37.5	1.10
6	37.5	21.1	31.7	0.97

* Sample size per population site: 1248 for temperatures, 937 for precipitation, 3433 for z scores (see Methods: Environmental Measurements).

may lead to increased adult survival (Murdoch 1966, Kohn 1978:191). Third, litter size and conception date may be less variable (Levins 1968, Giesel 1976), genetic variability may be unnecessary to individuals (Soule 1971), and mortality may be reduced (and in turn maturation delayed) where climatic variability is temporally predictable (Roughgarden 1979:259, 347, 373).

Two of the variables we studied (body mass and variability of minimum temperature) exhibited trends opposite to the overall pattern. Squirrels had greater body mass at lower elevations than at higher elevations even though they were younger and thus should have been lighter because body mass increased with age. MacArthur (1968) predicted that larger body size should be found where food supplies are more variable, and our data indicate food supplies may be more variable at lower elevations than at higher elevations. Variability of minimum temperature was marginally greater ($P = .06$), even though predictability of this variable was also greater ($P < .001$), at higher elevations than at lower elevations. It may be said that higher elevations exhibited a pattern of predictable variability

(Vannote and Sweeney 1980) with respect to minimum temperatures. This trend is opposite to the conventional assumption that variable environments are unpredictable environments, an assumption that has become prevalent over the last 15 yr (references summarized in Stearns 1976, 1977, 1980). It is possible that some problems with r - K theory in the past may have been caused by a failure to detect the apparent paradox that a variable environment can be predictable. Much of the theory is supported by this study if the predictabilities of high- and low-elevation environments are reversed from Cody's (1966) original placement. Intuitively, there is no reason to assume that a variable environment cannot be predictable. All that is necessary is that the variability is predictable. We propose that environmental predictability may be more important to the evolution of Columbian ground squirrel life history than environmental variability.

The adjectives variable, unpredictable, harsh, unstable, and uncertain have been used interchangeably to describe environments associated with r -strategists (references summarized in Stearns 1976, 1977, 1980). Our results indicate that these five adjectives cannot be interchangeably used for our study area. Clearly, we need consistent quantitative methodologies for measuring the extent to which each of these adjectives applies, because they may not signify similar environmental conditions.

One might argue that we should have chosen the best predictability equation and used it alone throughout our analyses. However, the accuracy with which some of these equations measure predictability has only recently been studied (Stearns 1981). It is presently impossible to choose the best equations. Our objective at this time is to introduce these equations to ecologists for future use or rejection once the equations' accuracies and inaccuracies are better understood. At present, the mean of the 18 arcsine-transformed values of

TABLE 6. Predictability values† (0 = unpredictable; 1 = predictable) for maximum and minimum daily temperatures and daily (natural logarithmic) precipitation with respect to month for each population site.

Variable	Population site					
	1	2	3	4	5	6
	Predictability values					
Maximum temperature ($n = 18$)						
Means	0.132	0.127	0.130	0.131	0.128	0.132
Means of arcsines	20.124	20.022	20.284	20.285	20.091	20.325
Precipitation ($n = 18$)						
Means	0.184	0.134	0.146	0.148	0.147	0.132
Means of arcsines	23.173	18.378	19.706	20.064	19.624	18.378
Minimum temperature ($n = 18$)						
Means	0.098	0.115	0.131	0.113	0.152	0.167
Means of arcsines	15.310	16.657	18.916	18.236	22.031	23.413
Pooled variables ($n = 54$)						
Means	0.112	0.099	0.113	0.112	0.124	0.125
Means of arcsines	19.536	18.352	19.635	19.528	20.582	20.705

† All means statistically greater than 0 ($P < .01$); see Appendix for the $n = 18$ equations for each variable.

these equations at each population site is probably the best estimate of environmental predictability at each site.

The trends we found relating ground squirrel life history and elevation are not entirely new. Bronson (1979) and Murie et al. (1980) indicated that survival increased and litter size decreased at higher elevations for some ground squirrel populations. However, these authors did not identify patterns of predictability or variability, but assumed that conventional descriptions of environmental patterns were true; thus they concluded that r - K theory was of little predictive value. If the findings of these authors and our findings are repeatable, r - K theory may become more useful for natural populations than has recently been proposed (Stearns 1976, 1980, 1983, 1984). This body of theory may be false for many populations only because Cody (1966) and many others incorrectly assumed that mountaintops are r -selecting habitats.

In conclusion, we have two suggestions for future life-history studies. First, the interrelationships between body mass, age, and litter size should be investigated before examining relationships among life-history traits and environmental predictability or variability. Knowing the pattern for some of these variables without the others could confound conclusions. Second, both variability and predictability should have consistent, quantitative definitions from study to study. Portions of r - K theory may be found useful once all of its parameters are consistently measured.

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APPENDIX

EQUATIONS USED FOR ENVIRONMENTAL PREDICTABILITY

The environmental predictability analyses progressed as follows. Daily records were cast into joint frequency distribution matrices where Celsius temperature was classified into one of 10-14 classes (rows), with 2.8° per class, and columns were approximate months of the growing season: May = 5 to October = 10. Precipitation (in millimetres) was classified into one of eight logarithmic (naperian or natural) classes (rows), with 0.5 units per class (Colwell 1974), and columns were months: June = 6 to September = 9. The elements of the matrices represented the number of times a given temperature or logarithmic precipitation class occurred in a given month during the approximate growing season over 10 yr. Some matrices differed by one or two rows for a given variable, but all six populations were otherwise identically analyzed for a given variable (i.e., same days per year, same number of columns, same sample size, etc.). The absolute values of the predictability equations were inherently standardized to vary from 0 to 1, where 0 was totally unpredictable and 1 was completely predictable (Goodman and Kruskal 1954). The first of the 18 equations was:

$$\text{Cramer's } V = \left\{ \frac{\chi^2/n}{\min[(r-1), (c-1)]} \right\}^n, \quad (\text{A.1})$$

where χ^2 = chi-square value of matrix (= contingency table), r = the number of rows (= temperature or logarithmic precipitation states), c = the number of columns (= months), and n = the sample size (at each population site for each temperature variable, $n = 1248$; for precipitation, $n = 937$) (Cramer 1946, Goodman and Kruskal 1954, Bishop et al. 1975). For the 18 matrices (6 populations by 3 variables) analyzed, $c - 1$ was always 5 for temperature and always 4 for precipitation and therefore always less than $r - 1$ (range: 7-13).

The next equation was:

$$\text{Lambda}_{\text{AsymTP}} = \frac{\left(\sum_k \max_j f_{jk} \right) - \max f_{.k}}{n - \max f_{.k}}, \quad (\text{A.2})$$

where $\sum_k \max_j f_{jk}$ = the sum of the maximum values in each column, $\max f_{.k}$ = the maximum value of the row totals, and

n is as above (Goodman and Kruskal 1954, Garson 1971, Bishop et al. 1975, Mueller et al. 1977, Stearns 1981). This measures how well we can predict the temperature/logarithmic precipitation class given the month. We used the same equation to determine how well we can predict the month knowing the temperature or logarithmic precipitation class, by simply transposing the matrix ($\text{Lambda}_{\text{AsymM}}$, Eq. A.3). The fourth equation used determines overall prediction, making no assumption about which variable is dependent or independent (as Eqs. A.2 and A.3 do). It merely averages prediction in both directions at the same time and thus is symmetric:

$$\text{Lambda}_{\text{Sym}} = \frac{\sum_k \max_j f_{jk} + \sum_j \max_k f_{jk} - \max f_{.k} - \max f_{.j}}{2n - \max f_{.k} - \max f_{.j}}, \quad (\text{A.4})$$

where $\sum_k \max_j f_{jk}$ and $\max f_{.k}$ are as defined for Eq. A.2, $\max f_{.j}$ is the maximum column total, and $\sum_j \max_k f_{jk}$ is the sum of the maximum values in each row (Goodman and Kruskal 1954, Garson 1971, Bishop et al. 1975, Mueller et al. 1977, Stearns 1981).

The fifth equation used was the uncertainty coefficient:

$$\text{Uncert}_{\text{AsymTP}} = \frac{\left[-\sum_j p(Y_j) \log p(Y_j) \right] - \left[-\sum_k \sum_j p(Y_j, X_k) \log p(Y_j | X_k) \right]}{-\sum_j p(Y_j) \log p(Y_j)}, \quad (\text{A.5})$$

where $p(Y_j)$ = the probability of a certain temperature/logarithmic precipitation class occurring, and $p(X_k)$ = the probability of a certain month occurring. This equation determines the proportion by which the uncertainty in the temperature/precipitation class is reduced by knowing the month (Kullback 1959, Theil 1967, Nie et al. 1975); it is similar to the lambda equations, but here the entire frequency distribution instead of just the mode is used. A similar equation was used for determining the proportion by which uncertainty in the month is reduced by knowing the temperature or logarithmic precipitation state (Kullback 1959, Theil 1967, Nie et al. 1975, Legendre et al. 1981):

$$\text{Uncert}_{\text{AsymM}} = \frac{\left[-\sum_k p(X_k) \log p(X_k) \right] - \left[-\sum_j \sum_k p(X_k, Y_j) \log p(X_k | Y_j) \right]}{-\sum_k p(X_k) \log p(X_k)}, \quad (\text{A.6})$$

The seventh equation is similar to Eq. A.4 but does not use the mode; it measures the proportional reduction in uncertainty when the joint distribution of months and temperatures/precipitation are known (Kullback 1959, Theil 1967, Nie et al. 1975):

$$\text{Uncert}_{\text{Sym}} = \left\{ \left[-\sum_j p(Y_j) \log p(Y_j) \right] + \left[-\sum_k p(X_k) \log p(X_k) \right] \right\}$$

$$\begin{aligned}
 & - \left[- \sum_j \sum_k p(Y_j, X_k) \log p(Y_j | X_k) \right] \\
 & + \left\{ - \sum_j p(Y_j) \log p(Y_j) \right\} \\
 & + \left[- \sum_k p(X_k) \log p(X_k) \right].
 \end{aligned} \tag{A.7}$$

Eqs. A.8–A.15 each determines if the relative ordering on one variable is the same (concordant) as the relative ordering of another variable (Bishop et al. 1975, Mueller et al. 1977). Eq. A.8 was:

$$\text{Tau}_b = \frac{P - Q}{[\frac{1}{2}(n^2 - \sum T_1^2) \frac{1}{2}(n^2 - \sum T_2^2)]^{1/2}}, \tag{A.8}$$

where P = the number of times the dependent (row) variable is in the same order as the independent (column) variable; Q = the number of times the dependent variable is not in the same order as the independent; T_1 is the number of ties on the row variable, T_2 is the number of ties in the column variable, and n = sample size (Goodman and Kruskal 1954, Garson 1971, Bishop et al. 1975, Mueller et al. 1977, Stearns 1981). This measure of association is similar to Spearman's rank correlation (r_s).

Eqs. A.9 and A.10 utilize information derived from the P and Q values of Eq. A.8. Eq. A.9 was:

$$\text{Tau}_c = \frac{2m(P - Q)}{n^2(m - 1)}, \tag{A.9}$$

where m = the number of columns. The interpretation is similar to that of Eq. A.8 but Eq. A.9 adjusts for the number of rows and columns (Stuart 1953, Goodman and Kruskal 1954, Bishop et al. 1975, Mueller et al. 1977, Stearns 1981). Eq. A.10,

$$\text{Gamma} = \frac{P - Q}{P + Q}, \tag{A.10}$$

indicates, as Eqs. A.8 and A.9 do, the probability of determining the ordering of a pair of values in one variable once the ordering in the other variable is known, but here there is no adjustment for ties (Goodman and Kruskal 1954, Garson 1971, Mueller et al. 1977, Stearns 1981).

Eqs. A.11–A.13 are similar to Eqs. A.8 and A.9 but the adjustment for ties is different (Somers 1962a, b, Garson 1971). Eq. A.11 was:

$$\text{Somers's } D_{\text{AsymTP}} = \frac{P - Q}{P + Q + T_1}, \tag{A.11}$$

when temperature or logarithmic precipitation was the dependent variable. Eq. A.12 was:

$$\text{Somers's } D_{\text{AsymM}} = \frac{P - Q}{P + Q + T_2}, \tag{A.12}$$

when month was the dependent variable, and Eq. A.13 was:

$$\text{Somers's } D_{\text{Sym}} = \frac{P - Q}{P + Q + \frac{1}{2}(T_1 + T_2)}, \tag{A.13}$$

a kind of averaging (Somers 1962a, b).

The 14th and 15th equations indicate how dissimilar means on one variable are within the categories of the other (Nie et al. 1975). The two formulas are identical but for A.15 the matrix is transposed from A.14:

$$\text{Eta} = \left(1 - \frac{\sum_{i=\text{low}}^{\text{high}} \left\{ \sum_{j=\text{low}}^{\text{high}} f_{ij}^2 - \left[\left(\sum_{j=\text{low}}^{\text{high}} f_{ij} \right)^2 / \left(\sum_{j=\text{low}}^{\text{high}} f_{ij} \right) \right] \right\}}{\sum_{i=\text{low}}^{\text{high}} \sum_{j=\text{low}}^{\text{high}} f_{ij}^2 - \left[\left(\sum_{i=\text{low}}^{\text{high}} \sum_{j=\text{low}}^{\text{high}} f_{ij} \right)^2 / n \right]} \right)^{1/2}, \tag{A.14, A.15}$$

where i = rows, j = columns, f_{ij} = the value of element ij , "low" is the lowest element value, and "high" is the highest element value (Nie et al. 1975, Mueller et al. 1977).

Eq. A.16 is a simple correlation coefficient from a frequency matrix (Orlaci 1978:15), with temperature or logarithmic precipitation class as the dependent variable and month as the independent.

Eq. A.17 was:

$$P = 1 - \left\{ \frac{\left[- \sum_i \sum_j \left(\frac{n_{ij}}{Z} \right) \log \left(\frac{n_{ij}}{Z} \right) \right] - \left[- \sum_j \left(\frac{X_j}{Z} \right) \log \left(\frac{X_j}{Z} \right) \right]}{\log_{10} 5} \right\}, \tag{A.17}$$

where i = a temperature or precipitation state (row), j = a month (column), n_{ij} = the value of element ij , s = the number of temperature or logarithmic precipitation states, $Z = \sum_i \sum_j n_{ij}$ or simply the total number of days sampled, and $X_j = \sum_i n_{ij}$ or simply the total for column j (Kullback 1959, Colwell 1974, Stearns 1981).

The final equation was:

$$P = \frac{(R)(\bar{Q}) - 1}{R - 1}, \tag{A.18}$$

where R = the number of temperature or logarithmic precipitation states (rows) and \bar{Q} = the summation of the highest values in each column divided by the average number of data points expected for each column, this quotient being divided by the number of columns (Raveh and Tapiero 1980).