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# Effects Of A Climatic Gradient On Columbian Ground Squirrel (*spermophilus Columbianus*) Life History

Richard Michael Zammuto

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EFFECTS OF A CLIMATIC  
GRADIENT ON COLUMBIAN GROUND SQUIRREL  
(SPERMOPHILUS COLUMBIANUS)  
LIFE HISTORY

by

Richard Michael Zamuto

Department of Zoology

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Submitted in partial fulfillment  
of the requirements for the degree of  
Doctor of Philosophy

Faculty of Graduate Studies  
The University of Western Ontario

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## ABSTRACT

Relationships among Columbian ground squirrel life history traits and environmental parameters were determined in order to test r-K theory over an elevational gradient in the Rocky Mountains of southwestern Alberta. The hypotheses tested were: 1) Columbian ground squirrels at lower elevations have smaller body sizes, earlier ages at maturity, lower adult survival rates, and larger litter sizes than squirrels at higher elevations, and 2) environments at lower elevations are less stable/more variable and less predictable than environments at higher elevations.

Over 500 ground squirrels were collected from 6 populations at different elevations (1300-2200m). Body weight, head-body length, reproductive condition, and litter size were determined. Ages were determined by examination of annual adhesion lines in the lower jawbone. Six life tables were constructed.

Variability and predictability of 3 meteorological variables were studied with respect to elevation. Other environmental factors were studied at the location of each population.

Body size (weight, length) was greater at lower elevations than at higher elevations. On average, squirrels matured later and lived longer at higher elevations than at lower elevations. Litter size did not vary ( $P > 0.05$ ) with elevation.

Variabilities and predictabilities of maximum temperatures and precipitation did not vary ( $P > 0.05$ ) with elevation. Minimum

temperatures at higher elevations tended to be more predictable, but more variable ( $P=0.06$ ), than minimum temperatures at lower elevations. Standardized pooled predictabilities and variabilities of the 3 meteorological variables indicated that environments at higher elevations were more predictable than environments at lower elevations whereas variabilities of environments did not vary ( $P>0.05$ ) with elevation. Growing seasons were shorter, primary productivity (as indicated by tree-ring width) was lower, and winter soil temperatures below 50 cm were warmer at higher elevations than at lower elevations.

A variable environment may not necessarily be an unpredictable environment. Populations at higher elevations seemed to be limited by the summer environment while lower elevation populations seemed to be limited by the winter environment.

Contingent upon several assumptions, the original theory of r and K-selection was falsified by this empirical research. However, a number of the original predictions of the theory would have been supported if the locations of the predictable/unpredictable environments and r/K-strategists were reversed with respect to elevation.

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## INTRODUCTION

Most semelparous organisms (e.g. annual plants, insects) exhibit smaller somatic size, earlier maturation, lower survival rates, shorter life spans, and produce more, smaller progeny than iteroparous organisms (e.g. mammals, birds) (Cole 1954, Tinkle 1969, Planka 1970, 1978, Gadgil and Solbrig 1972, French et al. 1975, Hirshfield and Tinkle 1975, Price 1975, Stearns 1976). Organisms with life history traits similar to those found in semelparous organisms have been termed r-strategists while those with traits similar to those found in iteroparous organisms have been termed K-strategists (MacArthur 1962, MacArthur and Wilson 1967). Organisms are thought to exhibit a life history which exists somewhere on a continuum, the r-K-continuum, where r-selection on the one hand and K-selection on the other are at opposite extremes (Planka 1970). Life histories (and positions on the continuum) are expected to vary with selective pressures from an organism's environment (Cody 1966, Gadgil and Bossert 1970, Planka 1970, 1978, Tinkle et al. 1970, Wiens 1976, Lackey 1978, Nevo 1978). For example, harsh, unstable, unpredictable environments are assumed to cause higher mortality rates than placid, stable, predictable environments (Cody 1966, Planka 1970, 1978, Lackey 1978). The arctic has been termed harsh, unpredictable, and unstable whereas the tropics have been termed predictable and stable (Dobzhansky 1950). Therefore, theoretical studies have proposed that organisms should have larger clutch or litter sizes (be more r-selected) in the arctic than in the tropics, as an adaptation to the harsh, unstable, unpredictable

environmental conditions that cause high mortality (Dobzhansky 1950, Planka 1970). Similar arguments have been used for high and low elevations (Johnson and Cook 1968, Ehrlich et al. 1972). Selective pressures at higher elevations are thought to parallel arctic conditions and those at lower elevations are thought to parallel more austral conditions.

These theories have been tested and supported by some studies on birds (Cody 1966, Ricklefs 1972), mammals (Jackson 1965, Blus 1966, Chapman and Lind 1973, Dunmire 1960, Lord 1960, Smith and McGinnis 1968, Kirkland and Kirkland 1979), and insects (Price 1974, 1975). However, several studies show conflicting patterns. For example, only a few annual plants are found in alpine and arctic regions (Billings and Mooney 1968, Teerl 1973), lizards are more K-selected with increasing latitude and elevation (Andrews and Rand 1974, Ballinger 1979), marmots mature later in more harsh than in less harsh environments (Barash 1973, 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 can be advanced to explain these discrepancies between r-K theory and empirical data. One reason is that annual and/or semelparous organisms may not have enough time to grow and reproduce in the short growing seasons at higher elevations and latitudes (Spencer and Steinoff 1968). Alternatively, bet-hedging, an alternative theory of life history phenomena alluded to by Murphy (1968), Charnov and Schaffer (1973), and synthesized by Stearns (1976), may explain life history patterns. This theory proposes that when juvenile mortality is



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more variable than adult mortality, the life history traits usually associated with unstable, unpredictable environments should be found in stable, predictable environments.

A brief survey of the literature concerning r-K theory reveals that some researchers have accepted correlates of r-K theory without questioning their validity. For example, Lord (1960), Gody (1966), Smith and McGinnis (1968), and Pulliam (1971) found animals with larger clutch or litter sizes at higher elevations and latitudes and assumed that environmental harshness, unpredictability and instability, causing high levels of mortality, were responsible. However, these researchers did not study age-specific fecundity and this could lead to biased conclusions. If clutch and litter size increased with animal age, one would have to determine the animals' ages before concluding that the higher production was associated with the environment and not merely a by-product of age structure (see Fleming and Rauscher 1978). Few researchers have studied age-specific fecundity or survival when considering r-K theory. As well, few researchers have quantitatively determined if higher elevations and latitudes really are more harsh, more unpredictable, and more unstable than lower elevations or latitudes (Wolda 1978, Myers and Pitelka 1979). Most ecologists assume that such research has been done but a close look at the literature reveals that it has not. Stearns (1976) felt that to make meaningful progress with life history theory one must study more than one population of a species, preferably in different environments, measuring life history and environmental variables at each study site (but see Stearns 1980).

• Some life history traits have been examined among ground squirrel populations and Boag and Murie (1981b), Bronson (1977, 1979), and Murie et al. (1980) found some aspects of ground squirrel life history to vary with elevation. They found that litter size was sometimes lower and survival rates were sometimes higher at higher elevations. At first impression this opposes conventional r-K theory. However, it is possible that the most predictable, stable environments occur at the highest elevations and these squirrels' life histories were "correct" with respect to many of the premises of the r-K theory originally proposed by MacArthur and Wilson (1967). Neither Boag and Murie (1981b), Bronson (1977, 1979), nor Murie et al. (1980) measured enough environmental variables to identify patterns of environmental variability and predictability.

This study examined life history patterns among six populations of Columbian ground squirrels Spermophilus columbianus. This is an abundant, colonial, montane/sub-alpine ground squirrel. Its range is relatively allopatric with other ground squirrels and it occurs over a wide range of elevations. Numerous aspects of its ecology have been studied (Moore 1937, Manville 1959, Michener 1977, Murie and Harris 1978, Murie et al. 1980, Boag and Murie 1981a,b). Age at maturity (Festa-Blanchet 1981), litter size and survival (Murie et al. 1980) vary among populations, and weather may have an effect on activity (Betts 1976, Michener 1977, Elliott and Flinders 1980). However, no researcher has dealt in depth with life tables or the association of elevation and/or environmental variables with life history parameters of Columbian ground squirrels. Thus my objective was to study these

aspects in detail.

Hypotheses

I hypothesized that environmental conditions, from the viewpoint of Columbian ground squirrels, are more predictable and stable at higher than at lower elevations and this leads to a K-strategy at higher elevations.

Environments at high elevations may be more predictable than those at low elevations because they usually have winter snow-cover and as a result, unfrozen ground (Pruitt 1970; Marchand 1982, Z. Fisera pers. comm.). They almost never experience winter or early-spring rainfall, snow-melt or surface soil thaw severe enough to cause destruction of normal hibernacula conditions (Shaw 1926, Potter 1956, Geiger 1966, Quanstrom 1966, Atmospheric Environment Service 1965-1974, Calgary District, Water Survey of Canada, Marmot Basin 1965-1974). Low elevation environments may or may not have snow-cover; ground freezing is common during winter (Atmospheric Environment Service 1965-1981, Calgary District, Water Survey of Canada, Streefer Creek Basin 1965-1968). Therefore, conditions could lead to greater winter mortality at low elevations than at high elevations. Environmental conditions may also be more stable/predictable at high elevations than at low elevations during other seasons. For example, high elevations are usually subjected to temperature inversions in summer which may cause daily temperatures to remain more stable at high elevations than at low elevations (Trewartha 1968, Dabberdt 1981). Since varying ambient temperatures differentially affect metabolic energy loss by mammals through varying radiation, convection, conduction and evaporation rates

(Moen, 1973), they may also affect ground squirrel life history.

Explicitly stated r-K theory predicts that to facilitate on-going or repeated colonization of a habitat, and exploitation of food-resources, animals living in unpredictable, unstable environments at high elevations (mountain-tops were considered islands) are expected to have smaller body sizes, earlier ages at maturity, lower survival rates, larger litter sizes and higher dispersal rates (i.e. be more r-selected) than those (more K-selected animals) living in predictable, stable environments at low elevations (MacArthur and Wilson 1967, Spencer and Steinhoff 1968, Planka 1970). I attempted to falsify (Popper 1959:86) this prediction by hypothesizing reversed locations of the r-selected/K-selected animals and the predictable/unpredictable, stable/unstable environments with respect to elevation. My specific predictions were that: (1) Columbian ground squirrels at low elevations have smaller body sizes, earlier ages at maturity, lower adult survival rates, and larger litter sizes than squirrels at high elevations, and (2) environments at low elevations are less stable/more variable and less predictable than environments at high elevations. Each component of these predictions is considered separately.

#### STUDY REGION

The study was conducted on the Eastern slopes of the Rocky Mountains in southwestern Alberta (Fig. 1). This region was forested, dominated by 30-70 year-old lodgepole pine, Pinus contorta, white



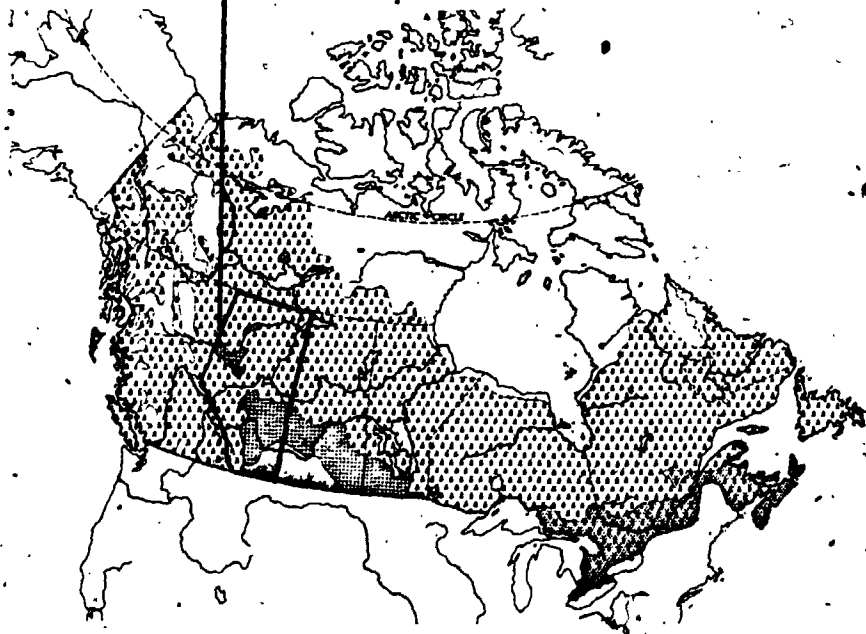
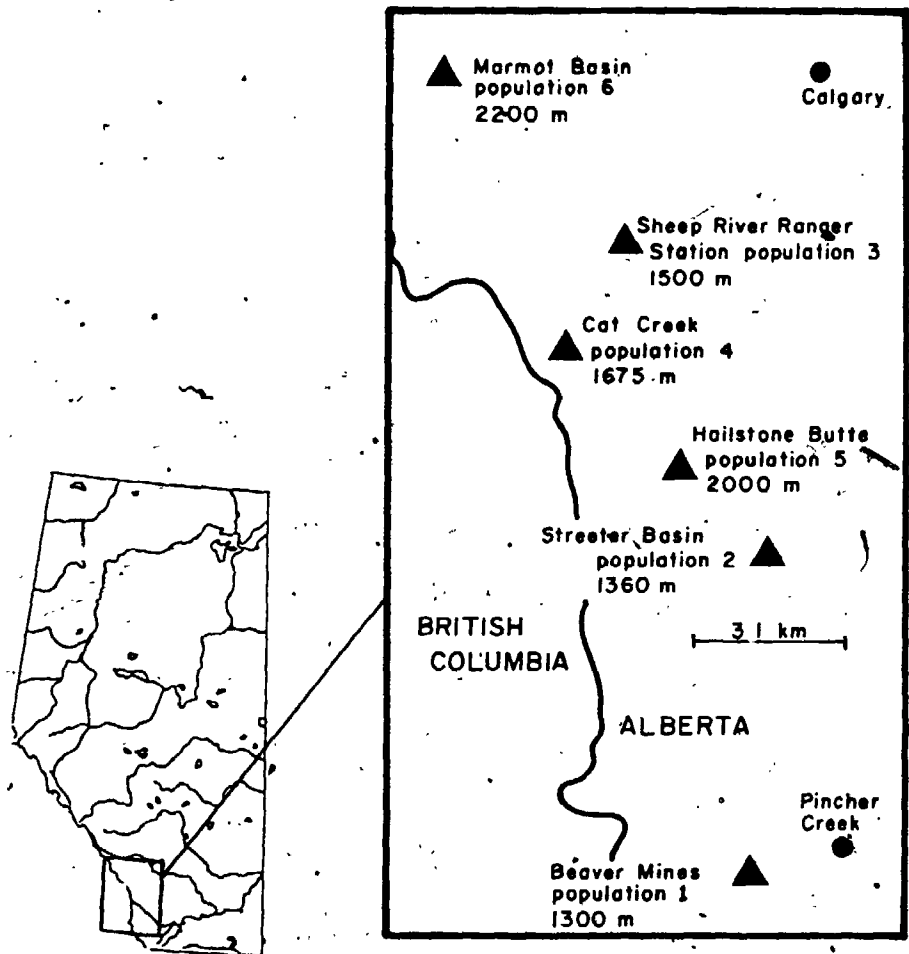


Figure 1. Locations of the six populations.

spruce, Picea glauca, engelmann spruce, P. engelmannii, subalpine fir Abies lasiocarpa, quaking aspen, Populus tremuloides, and balsam poplar, P. balsamifera (Scoggan 1978). The forest was broken by occasional grassy clearings, alpine meadows, and/or rock outcrops. The topography was mountainous with 1000 - 1800 m local relief; the highest peaks rose to 3000 m above mean sea level.

Six ground squirrel populations were located between 1300 and 2200 m above mean sea level (Fig. 1). The six populations were relatively discrete, separated by several km from other populations. Population-sites were: Beaver Mines (population 1, elevation 1300 m), 49°26'N. latitude, 114°13'W. longitude; Streeter Basin (population 2, 1360 m) 50°03'N. latitude, 114°10'W. longitude; Sheep River Ranger Station (population 3, 1500 m) 50°39'N. latitude, 114°38'W. longitude; Cat Creek (population 4, 1675 m) 50°26'N. latitude, 114°44'W. longitude; Hallstone Butte (population 5, 2000 m) 50°12'N. latitude, 114°27'W. longitude and Marmot Basin (population 6, 2200 m) 50°57'N. latitude, 115°11'W. longitude. The distance between the two most distant population-sites (Beaver Mines-Marmot Basin) was 180 km.

## METHODS

### Ground Squirrels

The six populations were located after ground squirrels had emerged from hibernation in spring. Populations 2, 3, and 5 were studied in 1980 and populations 1, 4, and 6 were studied in 1981 (Fig.

1). Within 3 weeks of spring emergence, active burrows were marked with survey flags. Conibear traps (Victor, No. 110 mink, muskrat size) were set at active burrow entrances from 0800 - 1200 hr and checked every hour until 1800 hr. Each collected animal was sexed, weighed to 5 g (total weight, Pesola Spring Scale) and assessed for reproductive condition (lactating, pregnant, scrotal testes, pigmented scrotum) in the field. Litter size was determined for each female by counting whole embryos or placental scars. To gain a qualitative idea of breeding synchrony within each population, embryo-sac size was visually examined for each female (see Litter Size in DISCUSSION). To correct for possible biases caused by litter and stomach weight, the stomach and reproductive tract were removed and each animal was reweighed (=corrected weight). Head-body lengths were measured to the closest mm in the laboratory. Some statistics for total weights are reported for researchers working with living animals but corrected weights were used in most analyses where possible biases caused by varying stomach or litter weights could affect results and/or conclusions.

One ramus of the lower jaw was removed from each animal, stored in 10% formalin for several months, washed for 24 hrs in water, decalcified 24 hrs in RDO (Rapid Bone Decalcifier, Maynard Scientific, Toronto, Ontario), and cut at the proximal edge of the diastema. The diastema and incisor were washed for 24 hrs in water, dehydrated in a series of alcohols, embedded in paraffin, sectioned at 10-20 microns, subserially mounted on slides (12-20 sections, 1 slide/animal) and stained with Harris' or Erlich's haematoxylin. A cover slip was added

before microscopic examination of the ventro-labial surface for annual adhesion lines in the periosteal zone (following Millar and Zwickel 1972). Thirty known-aged or minimum-aged Columbian ground squirrels (ear-tagged during previous studies, Boag and Murie 1981b) were captured at Sheep Ranger Station and analyzed as above to test the accuracy of this aging method for this species. The aging method correctly aged all known-aged animals ( $n=16$ ) and aged only one of 14 minimum-aged animals younger than its known minimum-age (6 vs. 7 yr).

Males with pigmented scrota or scrotal testes were considered to be mature whereas males with non-pigmented scrota and non-scrotal testes were considered to be immature. Pregnant or lactating females or those with resorbing litters were considered to be mature whereas non-pregnant or non-lactating females were considered to be immature. Approximately 10 "immature" females may have been incorrectly classified since previous breeding history (ovulation, pregnancies in past years) was not studied. Age at maturity for a population was defined as the first age (whole years) at which more than 50% of the animals in an age-class were mature.

Ground squirrel data were analyzed with respect to age, body weight, population, elevation, and in some cases sex and body length using SPSS (version 8.0b) (Nie et al. 1975, Hull and Nie 1981). Standing age structures were compared between sexes within each population with Lee and Desu (1972) D statistics. Life tables (smoothed, Caughley 1977: 96) (see Appendix A, Page 77) were constructed for each population (Deevey 1947, Birch 1948, Caughley 1966, Pianka 1974, 1978, Pielou 1974). These were tested for

significant differences between populations using D statistics (Gehan 1965, Lee and Desu 1972, Hull and Nie 1981). Life expectancy of adults (adult survival) was defined as the life expectancy at maturity in each population.

#### Environmental Variability/Stability and Predictability

Betts (1976), Elliott and Finders (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, see below) and predictabilities (proportion of variation explained, see below) for these variables could proximally, as well as ultimately, affect the life history of this species.

Daily weather records (maximum and minimum temperatures, precipitation) spanning the approximate growing season for 10 years (1965-74) were obtained from weather stations (Atmospheric Environment Service Monthly Meteorological Summaries, Downsview, Ontario; Calgary District, Water Survey of Canada, Calgary, Alberta) within 1-10 km from each sampled population (=population-site). All stations recorded the environmental variables at the same time each day. Dispersion statistics for daily maximum and minimum temperatures and precipitation during the approximate growing season were calculated for each year for each population-site (see Appendix B, page 79). Kolmogorov-Smirnov Two-Sample Tests were used to test for significant differences in raw 10-year distributions between population-sites for the 3 meteorological variables.

Environmental variability was defined as the statistical variance ( $S^2$ ) of the raw data for each of the 3 meteorological variables. Environmental stability was defined as the inverse of variability ( $1/S^2$ ). Variability (10-year) of each meteorological variable at each population-site was examined in relation to elevation. To combine variabilities of the 3 meteorological variables within population-sites, z-scores (standard deviate, Steel and Torrie 1960, Nie et al. 1975) were calculated for each raw datum of each meteorological variable. These z-scores were combined within each population-site, creating a single data set composed of z-scores of all 3 meteorological variables for each population-site. This transformation provided a total of 6 data sets (one for each population-site), where each datum was the number of standard deviations that each raw datum deviated from the grand mean (mean of each meteorological variable for all population-sites combined) of each meteorological variable (Nie et al. 1975:187). The statistical variance of these z-scores was calculated for each population-site and was examined in relation to elevation. This allowed me to simultaneously utilize the information contained in all 3 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 discerning the daily maximum or minimum temperature class or precipitation class for a given time of year and vice-versa. Since ecologists have not yet determined which measures of predictability should be used to best determine environmental predictability (Stearns

1981), I used most measures of predictability offered in the literature (see Appendix C, Page 91). I calculated predictability for each meteorological variable for each population-site using 18 equations derived from either non-parametric statistical considerations (Goodman and Kruskal 1954, 1959, 1963), information theory (Shannon 1948, Kullback 1959), or conventional parametric statistics (Zar 1974). Three ANCOVA's were used to determine the amount of variance in predictability accounted for by elevation of the population-site (Green pers. comm.). For each meteorological variable, the 18 arcsine transformed predictability values were considered dependent variables, each of the 18 equations was considered a group and elevation the covariate (Green pers. comm.). The mean of the arcsine transformed predictability values for each variable for each population-site was examined in relation to elevation. To simultaneously utilize the information contained in predictability values of all 3 meteorological variables, a pooled mean predictability value was calculated for each population-site by combining all 54 (3 variables by 18 equations) arcsine transformed (already standardized, see Appendix C) predictability values. This mean value was correlated to elevation to test the prediction that environments at lower elevations are less predictable than environments at higher elevations.

#### Other Environmental Measures

According to r-K theory, r-selected populations should exist where food-resource levels are high, whereas K-selected populations should be present where food-resource levels are low (MacArthur and Wilson 1967). An auxiliary hypothesis or prediction in this study might state that:

food-resource levels of Columbian ground squirrels are greater at lower elevations than at higher elevations. Food-resource use by Columbian ground squirrels has not been studied in great detail, but it is known that a large variety of grasses and forbs is eaten, depending upon availability (Shaw 1925a). Since McGinnies (1967) and Davis et al. (1972) found that annual growth of grasses and forbs was positively correlated to widths of annual growth-rings in many species of 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 14-20 lodgepole pines (of similar age, microtopography, soil, slope aspect, height, width, density, etc., see Fritts 1976:247) within 2 km from each sampled ground squirrel population. The mean distance between each annual ring (ring-width) for 1963-1979 (the youngest trees in my sample were seedlings in 1963) was determined for each tree using an ocular micrometer. The 1963-64 and 1974-79 climatic data were incomplete, but since a better ring-width standardization is calculated by using as many ring-widths as possible (Fritts 1976), each annual ring-width was divided by the tree's 17-year mean ring-width for standardization (or filtering, Fritts 1976) with respect to age (Davis et al. 1972, Orloci 1978). The standardized grand mean (all trees at each population-site combined) annual ring-width for 1965-73 at each population-site was compared to annual precipitation and annual growing season length (see below) for 1965-73 at each population-site, to determine if this index of primary productivity was related to meteorological parameters in a



fashion expected for such an index (Fritts 1976). For each population-site, the 9-year mean ring-width for 1965-73 was compared to elevation.

To further index primary productivity, growing season length was calculated as the number of days the mean daily temperature rose above 5.6°C (Boughner 1964). Differences among population-sites and years were determined by ANOVAS and multiple range tests (Student-Newman-Keuls). The 9-year (1974 data incomplete) mean growing season length for each population-site was examined in relation to elevation.

Weekly soil temperatures at depths of 3 - 183 cm were obtained from weather records (Calgary District, Water Survey of Canada, Marmot Basin, 1965-69, Streeter Basin, 1965-68) for one low (population-site 2, 1360 m) and one high (population-site 6, 2200 m) elevation (data from the other 4 population-sites were not available). In addition, soil temperatures at a depth of 50 cm were recorded daily at another low elevation site (1375 m) during 1980-82.

#### Statistical Analysis

All proportions were arcsine transformed before subsequent analysis. All raw data were first checked for normality within groups (Kolmogorov-Smirnov one sample tests) and then for homogeneity of variances among groups (Bartlett-Box F test) before subsequent analysis. In cases where raw and ln transformed data were non-normally distributed ( $P < 0.01$ ) and/or variances were heterogenous ( $P < 0.01$ ), non-parametric ANOVA (Kruskal-Wallis one-way), Mann-Whitney U tests, or Dunn's (1964) range test for multiple comparisons were used in lieu of conventional parametric ANOVA's, t-tests, or multiple range tests (Student-Newman-Keuls).

Many statistical tests are used throughout this report. Since the probability of committing one Type I error is 92% when 20 tests are performed on a data set with an alpha of 0.05 (Zar 1974), it is obvious that some Type I errors exist in this report. However, since I collected nearly all resident ground squirrels living in populations 1,4,5, and 6, my "sample statistics" may approximate true "population parameters" for these populations, effecting a decrease in the possible number of Type I errors (Sokal and Rohlf 1981). To further decrease Type I errors, I used a two-tailed probability level regardless of the hypothesis being tested, thus reducing my accepted significance level by 1/2 in some cases. I accepted a significance level of 0.05 to avoid committing too many type II errors (see Miller 1966, Zar 1974, Sokal and Rohlf 1981). For reader convenience, Bonferroni's P (= 0.05/number of comparisons) is provided as the probability level that may be necessary to accept an alpha-level of 0.05 for multiple pairwise comparisons on the same data (see Wallenstein et al. 1980). I did not use Bonferroni's P for reasons outlined in Miller (1966). All means are reported with  $\pm 1$  SE unless otherwise noted.

## RESULTS

A total of 506 ground squirrels (238 males, 268 females) was collected from the six populations (Table 1). Of these, 124 were mature males and 173 were mature females (Table 2). Mature females in populations 2-6 were relatively synchronous (i.e. a range of about 10

Table 1. Number of ground squirrels captured  
from each of the six populations.

Population	Males	Females	Total
	Collected	Collected	
1	50	51	101
2	51	53	104
3	54	48	102
4*	25	44	69
5	47	54	101
6	11	18	29
Totals	238	268	506

\* Significantly different from 1:1 sex ratio

( $\chi^2 = 5.23$ ,  $df = 1$ ,  $P < 0.05$ ).

Table 2. Number of mature<sup>1</sup> ground squirrels captured from each of the six populations.

Population	Mature <sup>1</sup>	Mature <sup>1</sup>	Total
	Males Collected	Females Collected	
1	36	48	84
2	19	28	47
3	24	18	42
4	16	28	44
5	25	39	64
6	4*	12*	16
Totals	124	173	297

<sup>1</sup> Males with pigmented scrota and/or scrotal testes; pregnant or lactating females and/or those resorbing litters.

\* Significantly different from 1:1 sex ratio ( $\chi^2 = 4.00$ ,  $df = 1$ ,  $P < 0.05$ ).

days) for breeding dates (as seen qualitatively by embryo size) whereas those in population 1 were relatively asynchronous (i.e. a range of about 30 days).

### Body Size

As expected, correlations between total weight and corrected weight were high among all squirrels ( $r = 0.97$ ,  $n = 495$ ,  $P < 0.001$ ) and within populations (range of  $r = 0.94-0.98$ ,  $P < 0.001$  for all populations). Not enough data were obtained for body length (carcasses stiffened by preservation for populations 1, 4, and 6) to analyze the variable in detail, but this variable was strongly correlated with both total weight ( $r = 0.85$ ,  $n = 306$ ,  $P < 0.001$ ) and corrected weight ( $r = 0.87$ ,  $n = 306$ ,  $P < 0.001$ ) among populations 2, 3 and 5.

The mean corrected weight of mature animals was greater than that of immature animals (Table 3; combined  $\bar{x} = 478$  vs. 385 g,  $\pm = 13.6$ ,  $df = 493$ ,  $P < 0.001$ ). Mean corrected weights of mature and immature animals varied among populations ( $F = 20.0$ ,  $df = 293$ ,  $P < 0.001$ ;  $F = 11.6$ ,  $df = 200$ ,  $P < 0.001$ , respectively) and between the sexes ( $\pm = 9.3$ ,  $df = 292$ ,  $P < 0.001$ ; for mature;  $\pm = 3.5$ ,  $df = 199$ ,  $P < 0.001$ , for immature) (Table 3). Corrected weight increased with age for each sex within each population (all  $P < 0.001$ , range of  $r = 0.62-0.82$ ) except 6 (both  $P > 0.05$ ) (Table 4). Analysis of covariance indicated that population and age accounted for a significant ( $P < 0.001$ ) proportion of the variance in corrected weight for both males and females and that a much higher percentage (44% for males, 35% for females) of the total variance in corrected weight (dependent variable) was explained by age (covariate) than by population (17% for males, 19% for females).

Table 3. Mean corrected<sup>1</sup> weights (g) of mature<sup>2</sup> and immature<sup>3</sup> animals from each of the six populations.

Popula- tion	Mature	Mature	Immature	Immature
	Male	Female	Male	Female
	Mean	Mean	Mean	Mean
	Corrected	Corrected	Corrected	Corrected
	Weights	Weights	Weights	Weights
	±SE	±SE	±SE	±SE
1	508±12***	441± 9	408±16	395± 0
2	568±11***	489± 9	436±11*	397±12
3	551±10***	497±12	417±11	391±10
4	431±12	411± 8	303±21	336±17
5	516± 9***	441± 6	365±23**	279±16
6	490±23	435±16	428±65	368±83

<sup>1</sup> Weight after stomach and reproductive tract removed.

<sup>2</sup> Males with pigmented scrota or scrotal testes; pregnant or lactating females or those resorbing litters.

<sup>3</sup> Males with non-pigmented scrota and non-scrotal testes; non-pregnant, non-lactating females. Approximately 10 "immature" females may have been incorrectly classified since previous breeding history (ovulation, pregnancies in the past) was not studied.

\* Male mean weight significantly (\*P<0.05, \*\*P<0.01, \*\*\*P<0.001) greater than female mean weight (t-tests, Mann-Whitney U Tests). Bonferroni's P = .0.004.

Table 3

(Continued)

Homogeneous ( $P > 0.05$ ) subsets of means (means are homogeneous when bars under population numbers are on same horizontal plane, Student-Newman-Keuls) and variation among populations (in parentheses):

	Population					
	1	2	3	4	5	6
corrected weight mature males ( $F = 13.4$ , $df = 123$ , $P < 0.001$ )	_____			_____	_____	
corrected weight immature males ( $F = 5.8$ , $df = 111$ , $P < 0.001$ )	_____	_____		_____	_____	
corrected weight mature females ( $F = 10.6$ , $df = 169$ , $P < 0.001$ )	_____	_____			_____	
corrected weight immature females ( $F = 9.3$ , $df = 88$ , $P < 0.001$ )	_____	_____		_____		

Table 4. Mean corrected weight<sup>1</sup> with respect to age for each population<sup>2</sup>.

Age (yr)	Population						Pooled
	1	2	3	4	5	6	
1	394±8 (40)	414±7 (58)	381±6 (42)	285±10 (17)	287±11 (29)	278±23 (3)	369±5 (189)
2	500±7*** (26)	505±13*** (23)	469±9*** (32)	397±7*** (23)	452±11*** (19)	453±16*** (7)	466±5*** (130)
3	484±10 (19)	553±15* (12)	536±9*** (15)	430±8** (21)	470±9 (30)	483±16 (8)	484±6* (105)
4	561±16*** (8)	557±19 (7)	565±23 (7)	436±23 (5)	494±11 (16)		522±10*** (44)
5	537±37 (5)			442±28 (3)	492±29 (7)		490±20 (18)

All

Populations



Table 4  
(Cont Inued)

6									541±35
									(4)
7									564±16
									(3)
All	460±8	465±9	452±8	384±9	419±10	437±19	440±4		
Ages	(98)	(104)	(100)	(69)	(101)	(21)	(493)		
Pooled									

1 Weight after stomach and reproductive tract removed.

2 Sample size is in parentheses. Mean not included in Table if n < 3 for age-class.

\* Mean significantly higher (none lower) than that of preceding age class (t-tests),  
#P<0.05, \*\*P<0.01, \*\*\*P<0.001, Bonferroni's P=0.002.

Corrected weight was negatively correlated with elevation for each sex with the effects of age held constant by partial correlation analysis ( $r = -0.40$ ,  $n = 233$ ,  $P < 0.001$ , for males;  $r = -0.46$ ,  $n = 256$ ,  $P < 0.001$  for females).

Although most of the variation remained unexplained, these results indicated that the prediction that squirrels at lower elevations have smaller body sizes than squirrels at higher elevations was not supported. Conversely, the opposite trend was indicated.

#### Age at Maturity

Most (>70%) of the 2-year-olds were mature in all populations, but only 41% (7/17) of the 2-year-old females and only 53% (8/15) of the 2-year-old males were mature in population 3. Age at maturity was 1 year of age in population 1 (60%, 26/43 yearlings mature), 2 years of age in populations 2, 4, 5 and 6 (87%, 20/23; 78%, 18/23; 84%, 16/19 and 71%, 5/7 of the two-year-olds mature, respectively), and 3 years of age in population 3 (93%, 14/15 three-year-olds mature). One yearling male in populations 2 (3%, 1/30) and 4 (13%, 1/8), and one yearling female in population 4 (11%, 1/9) was mature. No yearlings were mature in populations 3, 5 or 6. A higher proportion of yearling females (86%, 18/21) and males (36%, 8/22) were mature in population 1 than in each other population (all  $\chi^2 > 10.8$ ,  $df = 1$ ,  $P < 0.001$ ) and a higher proportion of yearling females were mature in population 2 (21%, 6/28) than in each other population (except population 1, all  $\chi^2 > 10.8$ ,  $df = 1$ ,  $P < 0.001$ ). These results indicated that the prediction that squirrels at lower elevations have earlier ages at maturity than squirrels at higher elevations was supported.

### Age Structure and Survival

Standing age structures did not vary between sexes within any population ( $P > 0.05$  for all  $D_{stat}$ ) so males and females were combined for life table calculations (Tables 5-10). Standing age structures differed (Table 11) and mean age (range 1.9-2.9 yr) varied ( $\chi^2 = 33.9$ ,  $n = 506$ ,  $P < 0.001$ ) among populations. Juvenile survival rates were low at both highest and lowest elevations (Tables 5-10).

Life expectancy of adults (range 2.0-3.0 yr, Tables 5-10) was greater at higher elevations than at lower elevations ( $r = 0.92$ ,  $n = 6$ ,  $P < 0.01$ ) (life expectancy within age classes 1 and 2 also increased ( $P < 0.01$ ) with elevation). These results indicated that the prediction that squirrels at lower elevations have lower adult survival rates than squirrels at higher elevations was supported.

### Litter Size

Frequency distributions of litter size differed between populations 3 and 4 (Table 12) and heterogeneity of variances existed among populations ( $P < 0.001$ , Table 13). The variance of litter size in population 1 was higher ( $P < 0.05$ ; no age effects,  $P > 0.05$ ) than that for populations 3, 4, and 5 (Table 13). Mean litter size varied among populations ( $\chi^2 = 17.9$ ,  $n = 174$ ,  $P < 0.01$ , Table 13).

The degree of association varied within populations but overall, litter size increased with age ( $r = 0.32$ ,  $n = 174$ ,  $P < 0.001$ , Table 14) and corrected weight ( $r = 0.30$ ,  $n = 174$ ,  $P < 0.001$ ). Litter size was not significantly correlated with elevation when the effects of age and corrected weight were held constant by partial correlation analysis ( $r = -0.10$ ,  $df = 165$ ,  $P > 0.05$ ).

Table 5. Time-specific life table<sup>1</sup> for population 1 (1300 m).

Age (yr)	Number Captured	Smoothed Frequency <sup>2</sup>	$l_x$	$m_x$	$l_x m_x$	$e_x$
0	186 <sup>3</sup>	180 <sup>4</sup>	1.000	0.000	0.000	1.567
1	43	45	0.250	1.143	0.286	2.268
2	26	27	0.150	1.917	0.288	2.113
3	19	16	0.089	2.533	0.225	1.876
4	8	9	0.050	2.500	0.125	1.560
5	5	5	0.028	2.750	0.077	1.000
$R_0 =$					1.00	
.life expectancy at maturity ( $e_1$ ) = 2.268.						

<sup>1</sup> Equations in Appendix A.

<sup>2</sup> See Caughley (1977:96).

<sup>3</sup> Sum of all litters in population (=number born).

<sup>4</sup> The product of the number born and  $\sum l_x m_x$  when  $l_x$  was calculated using the number born.

Table 6. Time-specific life table<sup>1</sup> for population 2 (1360 m).

Age (yr)	Number Captured	Smoothed Frequency <sup>2</sup>	$l_x$	$m_x$	$l_x m_x$	$e_x$
0	105 <sup>3</sup>	95 <sup>4</sup>	1.000	0.000	0.000	1.960
1	58	43	0.453	0.339	0.154	2.119
2	23	24	0.253	1.667	0.422	2.004
3	12	13	0.137	2.167	0.297	1.854
4	7	7	0.074	1.500	0.111	1.581
5	1	3	0.032	0.000	0.000	1.344
6	2	1	0.011	1.500	0.017	1.000
7	1	0	0.000	2.500	0.000	0.000

$$R_0 = 1.00$$

Life expectancy at maturity ( $e_2$ ) = 2.004.

<sup>1</sup> Equations in Appendix A.

<sup>2</sup> See Caughley (1977:96).

<sup>3</sup> Sum of all litters in population. (=number born).

<sup>4</sup> The product of the number born and  $\sum l_x m_x$  when  $l_x$  was calculated using the number born.

Table 7. Time-specific life table<sup>1</sup> for population 3 (1500 m).

Age (yr)	Number Captured	Smoothed Frequency <sup>2</sup>	$l_x$	$m_x$	$l_x m_x$	$e_x$
0	53 <sup>3</sup>	56 <sup>4</sup>	1.000	0.000	0.000	2.518
1	42	34	0.607	0.000	0.000	2.501
2	32	21	0.375	0.529	0.198	2.429
3	15	13	0.232	1.083	0.251	2.310
4	7	8	0.143	1.833	0.262	2.126
5	1	5	0.089	2.000	0.178	1.809
6	1	3	0.054	1.500	0.081	1.333
7	2	1	0.018	2.000	0.036	1.000
8	2	0	0.000	0.000	0.000	0.000

$$R_0 = 1.01$$

life expectancy at maturity ( $e_3$ ) = 2.310.

<sup>1</sup> Equations in Appendix A.

<sup>2</sup> See Caughley (1977:96).

<sup>3</sup> Sum of all litters in population (=number born).

<sup>4</sup> The product of the number born and  $\sum l_x m_x$  when  $l_x$  was calculated using the number born.

Table 8. Time-specific life table<sup>1</sup> for population 4 (1675 m).

Age (yr)	Number Captured	Smoothed Frequency <sup>2</sup>	$l_x$	$m_x$	$l_x m_x$	$e_x$
0	114 <sup>3</sup>	74 <sup>4</sup>	1.000	0.000	0.000	1.907
1	17	25	0.338	0.222	0.075	2.683
2	23	19	0.257	1.344	0.345	2.214
3	21	13	0.176	1.536	0.270	1.773
4	5	7	0.095	2.500	0.238	1.432
5	3	3	0.041	2.000	0.082	1.000

$$R_0 = 1.01$$

life expectancy at maturity ( $e_2$ ) = 2.214.

<sup>1</sup> Equations in Appendix A.

<sup>2</sup> See Caughley (1977:96).

<sup>3</sup> Sum of all litters in population (=number born).

<sup>4</sup> The product of the number born and  $\sum l_x m_x$  when  $l_x$  was calculated using the number born.

Table 9. Time-specific life table<sup>1</sup> for population 5 (2000 m).

Age (yr)	Number Captured	Smoothed Frequency <sup>2</sup>	$l_x$	$m_x$	$f_x m_x$	$e_x$
0	134 <sup>3</sup>	115 <sup>4</sup>	1.000	0.000	0.000	1.860
1	29	28	0.243	0.000	0.000	3.539
2	19	26	0.226	1.333	0.301	2.730
3	30	22	0.191	1.765	0.337	2.047
4	16	15	0.130	1.800	0.234	1.538
5	7	8	0.070	1.750	0.123	1.000

$$R_0 = 1.00$$

Life expectancy at maturity ( $e_2$ ) = 2.730.

<sup>1</sup> Equations in Appendix A.

<sup>2</sup> See Caughley (1977:96).

<sup>3</sup> Sum of all litters in population (=number born).

<sup>4</sup> The product of the number born and  $\sum l_x m_x$  when  $l_x$  was calculated using the number born.



Table 10. Time-specific life table<sup>1</sup> for population 6 (2200 m).

Age (yr)	Number Captured	Smoothed Frequency <sup>2</sup>	$l_x$	$m_x$	$l_x m_x$	$e_x$
0	52 <sup>3</sup>	35 <sup>4</sup>	1.000	0.000	0.000	1.829
1	5	8	0.229	0.000	0.000	3.620
2	7	7	0.200	1.250	0.250	3.000
3	9	6	0.171	1.714	0.293	2.339
4	4	4	0.114	2.000	0.228	2.009
5	3	3	0.086	2.500	0.215	1.337
6	1	1	0.029	0.000	0.000	1.000

$$R_0 = 0.99$$

life expectancy at maturity ( $e_2$ ) = 3.000.

<sup>1</sup> Equations in Appendix A.

<sup>2</sup> See Caughley (1977:96).

<sup>3</sup> Sum of all litters in population (=number born).

<sup>4</sup> The product of the number born and  $\sum l_x m_x$  when  $l_x$  was calculated using the number born.

Table 11. Differences<sup>1</sup> between standing age structures of the six populations.

		Population					
Population	1	2	3	4	5	6	
1		N.S.	N.S.	N.S.	***	**	
2			N.S.	***	***	***	
3				*	**	**	
4					N.S.	N.S.	
5						N.S.	

<sup>1</sup> Lee and Desu (1972)  $D_{stat}$ , significance levels: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , N.S.  $P > 0.05$ , Bonferroni's  $P = 0.003$ .

Table 12. Frequencies of litter sizes for each population.

Litter Size	Population					
	1	2	3*	4*	5	6
1					1	
2	9	2	5		3	2
3	13	12	9	6	16	3
4	12	6	4	11	16	6
5	5	7		8	3	3
6	7	1		2		
7	2					
Totals	48	28	18	27	39	14

\* Non-homogeneous distributions for litter size, Kolmogorov-Smirnov two sample test ( $z = 1.83$ ,  $P < 0.01$ ).

Table 13. Dispersion statistics for litter size.

Popula- tion <sup>1</sup>	Mode	Mean <sup>2</sup> ±SE	Variance <sup>3</sup>	Range
1	3	3.88±0.21	2.11	2-7
2	3	3.75±0.20	1.08	2-6
3	3	2.94±0.17	0.53	2-4
4	4	4.22±0.17	0.80	3-6
5	3	3.44±0.14	0.73	1-5
6	4	3.71±0.27	0.99	2-5

<sup>1</sup> Sample size in Table 12.

<sup>2</sup> Homogeneous ( $P > 0.05$ ) subsets of means (means are homogeneous when bars under population numbers are on same horizontal plane, Dunn's range test):

Populations

1	2	3	4	5	6
	_____			_____	
_____				_____	_____
_____			_____		_____

<sup>3</sup> Differences among population variances ( $P < 0.001$ ). Differences between population variances (variance ratio tests): 1 vs. 3 ( $P < 0.01$ ), 4 ( $P < 0.01$ ), and 5 ( $P < 0.001$ ), Bonferroni's  $P = 0.008$ .

Table 14. Mean litter sizes with respect to age for each population<sup>1</sup>.

Age (yr)	Population						All Populations Pooled
	1	2	3	4	5	6	
1	2.67±0.2 (18)	3.17±0.2 (6)					2.84±0.15 (25)
2	3.83±0.3** (12)	3.64±0.3 (11)	2.57±0.2 (7)	3.91±0.3 (11)	3.00±0.4 (8)	3.33±0.9 (3)	3.48±0.15** (52)
3	5.07±0.3** (15)	4.33±0.5 (6)	2.60±0.2 (5)	4.30±0.3 (10)	3.53±0.2 (17)	3.43±0.3 (7)	4.03±0.15** (60)
4		4.00±1.0 (3)	3.67±0.3* (3)	5.00±0.6 (4)	3.60±0.3 (10)		4.00±0.22 (23)
5					3.50±0.3 (4)		4.30±0.30 (10)

<sup>1</sup> Sample size is in parentheses. Mean not included in Table if  $n \leq 3$  for age-class.

\* Mean significantly higher (none lower) than that of preceding age class  
( $\pm$ -tests, Mann-Whitney U Tests), \* $P < 0.05$ , \*\* $P < 0.01$ , Bonferroni's  $P = 0.003$ .

These results indicated that the prediction that squirrels at lower elevations have larger litter sizes than squirrels at higher elevations was not supported.

#### Environmental Variability/Stability and Elevation

A total of 1248 daily temperature and 937 daily precipitation records was analyzed for each population-site (Table 15). All raw and ln-transformed meteorological variables within population-sites were not normally distributed (all  $P < 0.001$ ) and variances were heterogenous (all  $P < 0.001$ ). The distribution-free Kolmogorov-Smirnov two sample test indicated that raw 10-year distributions of meteorological variables differed between most population-sites (Tables 20 and 21, Appendix B, pages 80 and 81).

Environmental conditions at population-sites were arranged from least to most variable 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 (Tables 22-30, Appendix B, page 82). The positive association between variability (10-year) of minimum daily temperature and elevation approached significance ( $r = 0.79$ ,  $n = 6$ ,  $P = 0.06$ , Tables 22-30) but there was no relationship between z-transformed (pooled) variability and elevation ( $r = 0.59$ ,  $n = 6$ ,  $P > 0.05$ ) and no relationships ( $P > 0.05$ ) existed between (10-year) maximum temperature or precipitation variability/stability and elevation. From these results, I concluded that the prediction that environments at lower elevations are less stable/more variable than environments at higher elevations was not supported.

Table 15. The inclusive dates<sup>1</sup> used for analysis of climatic variables for each year.

Year	Dates		Dates	
	Analyzed For Temperatures	No. Days	Analyzed For Precipitation	No. Days
1965	1 June-30 Sept.	122	1 July-31 Aug.	62
1966	24 May -30 Sept.	130	1 June-31 Aug.	92
1967	1 June-20 Oct.	142	1 June-30 Sept.	122
1968	21 May -30 Sept.	133	29 May -15 Sept.	122
1969	20 May -28 Sept.	132	1 June-31 Aug.	110
1970	25 May -16 Sept.	115	1 June-14 Sept.	92
1971	17 May -26 Sept.	133	1 June-31 Aug.	92
1972	1 June-22 Sept.	114	1 June-31 Aug.	92
1973	10 May -27 Sept.	141	1 June-31 Aug.	92
1974	7 May -31 July	86	1 June-31 Aug.	61
Totals		1248		937

<sup>1</sup> Dates were chosen on the basis of availability of data from higher elevations. Weather stations usually collect daily data at higher elevations only during the "snow-free" season.

### Environmental Predictability and Elevation

There were no differences in predictabilities among population-sites for daily maximum temperature ( $F = 0.30$ ,  $df = 1$ ,  $P > 0.05$ ) although differences existed for precipitation ( $F = 20.4$ ,  $df = 1$ ,  $P < 0.001$ ) and minimum temperatures ( $F = 93.4$ ,  $df = 1$ ,  $P < 0.001$ ) (Tables 16-18, generally, a predictability value exceeding 0.03 is significantly ( $P < 0.05$ ) greater than zero). Mean (of arcsines) predictability of maximum temperatures and precipitation showed no ( $P > 0.05$ ) relationship with elevation although mean predictability of minimum temperatures increased with elevation ( $r = 0.97$ ,  $n = 6$ ,  $P < 0.001$ ; Tables 16-18). In addition, a positive correlation existed between elevation and the pooled mean predictability values derived from combining all (already standardized) arcsine transformed predictability values ( $n = 54$ ; 18 values by 3 variables) for each population-site ( $r = 0.85$ ,  $n = 6$ ,  $P < 0.05$ , Tables 16-18). From these results, I concluded that the prediction that environments at lower elevations are less predictable than environments at higher elevations was supported.

### Other Environmental Measures

Growing season length varied among population-sites ( $F = 11.8$ ,  $df = 53$ ,  $P < 0.001$ , Table 19). Variance explained by the between-populations component was 52% ( $P < 0.001$ ) and no significant ( $P > 0.05$ ) proportion of variance was accounted for by year effects (1965-73). Homogeneous subsets (Student-Newman-Keuls) for growing season length existed as: (1) subset 1 = populations 5 and 6, and (2) subset 2 = populations 1-4 (Table 19). Growing season length was longer at lower elevations than at higher elevations ( $r = -0.94$ ,  $n = 6$ ,  $P < 0.01$ ).



Table 16. Relative predictability values (0 = unpredictable; 1 = predictable) for maximum daily temperature with respect to month for each population-site.

Equation (from Appendix C)	Population-Site					
	1	2	3	4	5	6
1	0.27	0.24	0.25	0.26	0.25	0.26
2	0.05	0.04	0.04	0.03	0.04	0.05
3	0.16	0.16	0.14	0.15	0.14	0.16
4	0.10	0.10	0.09	0.09	0.09	0.11
5	0.08	0.06	0.07	0.08	0.07	0.08
6	0.11	0.09	0.10	0.10	0.10	0.11
7	0.09	0.07	0.08	0.09	0.09	0.09
8	0.06	0.08	0.08	0.08	0.08	0.07
9	0.06	0.08	0.08	0.08	0.08	0.07
10	0.08	0.10	0.10	0.09	0.09	0.08
11	0.07	0.09	0.09	0.08	0.08	0.07
12	0.06	0.08	0.08	0.07	0.07	0.07
13	0.06	0.08	0.08	0.08	0.08	0.07
14	0.49	0.44	0.46	0.46	0.49	0.50
15	0.19	0.16	0.17	0.18	0.16	0.18
16	0.03	0.06	0.07	0.05	0.06	0.05
17	0.24	0.20	0.22	0.23	0.20	0.21
18	0.15	0.15	0.14	0.14	0.13	0.14
Mean	0.132	0.127	0.130	0.131	0.128	0.132
Mean of arcsines	20.124	20.022	20.284	20.285	20.091	20.325

Table 17. Relative predictability values (0 = unpredictable; 1 = predictable) for logarithmic precipitation classes with respect to month for each population-site.

Equation (from Appendix C)	Population-Site					
	1	2	3	4	5	6
1	0.17	0.12	0.12	0.13	0.11	0.11
2	0.01	0.00	0.00	0.01	0.00	0.00
3	0.07	0.03	0.05	0.05	0.04	0.03
4	0.06	0.03	0.04	0.04	0.03	0.02
5	0.05	0.03	0.03	0.03	0.02	0.02
6	0.03	0.02	0.02	0.02	0.02	0.02
7	0.03	0.02	0.02	0.02	0.02	0.02
8	0.14	0.07	0.10	0.09	0.10	0.09
9	0.08	0.04	0.06	0.06	0.06	0.06
10	0.29	0.14	0.19	0.18	0.20	0.16
11	0.09	0.05	0.07	0.07	0.07	0.07
12	0.21	0.10	0.14	0.13	0.14	0.11
13	0.13	0.06	0.09	0.09	0.09	0.08
14	0.19	0.12	0.14	0.16	0.15	0.11
15	0.19	0.12	0.14	0.13	0.12	0.13
16	0.13	0.08	0.10	0.11	0.10	0.09
17	0.64	0.61	0.57	0.58	0.60	0.54
18	0.80	0.78	0.76	0.77	0.78	0.72
Mean	0.184	0.134	0.146	0.148	0.147	0.132
Mean of arcsines	23.173	18.378	19.706	20.064	19.624	18.378

Table 18. Relative predictability values (0 = unpredictable; 1 = predictable) for minimum daily temperatures with respect to month for each population-site.

Equation (from Appendix C)	Population-Site					
	1	2	3	4	5	6
1	0.22	0.25	0.28	0.22	0.30	0.30
2	0.00	0.04	0.07	0.04	0.08	0.08
3	0.10	0.12	0.13	0.10	0.17	0.19
4	0.05	0.08	0.10	0.07	0.13	0.13
5	0.07	0.09	0.10	0.07	0.11	0.11
6	0.07	0.10	0.11	0.08	0.13	0.13
7	0.07	0.09	0.10	0.07	0.12	0.12
8	0.01	0.00	0.02	0.04	0.08	0.10
9	0.01	0.00	0.02	0.04	0.08	0.10
10	0.01	0.01	0.02	0.05	0.10	0.13
11	0.01	0.00	0.02	0.04	0.08	0.10
12	0.01	0.00	0.02	0.04	0.08	0.10
13	0.01	0.00	0.02	0.04	0.08	0.10
14	0.39	0.49	0.52	0.43	0.54	0.52
15	0.17	0.16	0.18	0.12	0.15	0.19
16	0.04	0.04	0.06	0.06	0.05	0.09
17	0.31	0.33	0.35	0.29	0.26	0.29
18	0.23	0.24	0.25	0.23	0.22	0.24
Mean	0.098	0.115	0.131	0.113	0.152	0.167
Mean of arcsines	15.310	16.657	18.916	18.236	22.031	23.413

Table 19. Growing season length<sup>1</sup> for each population-site over the 10 years.

Year	Population-Site					
	1	2	3	4	5	6
1965	105	100	105	95	67	73
1966	130	119	129	126	86	91
1967	138	129	132	132	100	103
1968	128	125	124	118	58	60
1969	130	123	122	122	85	76
1970	111	107	107	107	86	83
1971	125	122	121	119	80	75
1972	113	109	108	105	68	74
1973	137	127	127	125	89	88
1974	75	68	67	67	44	44
Total	1192	1129	1142	1116	763	767

<sup>1</sup> Number of days average daily temperature was above 5.6°C (Boughner 1964).

Homogeneous ( $P > 0.05$ ) subsets of means (means are homogeneous when bars under population numbers are on same horizontal plane, Student-Newman-Keuls):

Population-Site					
1	2	3	4	5	6

Greater annual ring-widths occurred with longer growing seasons ( $r = 0.28$ ,  $n = 54$ ,  $P < 0.05$ ) and with larger amounts of precipitation during the growing season ( $r = 0.27$ ,  $n = 54$ ,  $P < 0.05$ ). These relationships show that tree-ring widths may indicate annual primary productivity at my population-sites (Currie and Peterson 1966, McGinnies 1967, Davis et al. 1972, Fritts 1976). Variability of annual ring-widths decreased with elevation ( $r = -0.34$ ,  $n = 54$ ,  $P < 0.05$ ). Nine-year mean ring-widths were larger at lower elevations than at higher elevations ( $r = -0.83$ ,  $n = 6$ ,  $P < 0.05$ ).

From these results, I concluded that the auxiliary hypothesis or prediction that food-resource levels of Columbian ground squirrels are greater at lower elevations than at higher elevations was supported.

Frozen soils under grassland at one low elevation site (population-site 2) exceeded depths of 91 cm in 1966, 61 cm in 1967, and only 15 cm in 1968 while squirrels were hibernating. Frozen soils under grassland at another low elevation site (1375 m), exceeded depths of 50 cm for several months during 1980-82 while squirrels were hibernating. Frozen soils under grassland at a high elevation site (population-site 6) exceeded a depth of 46 cm only once (one week maximum) during 1964-69 while squirrels were hibernating.

#### DISCUSSION

My data indicated that ground squirrels exhibited ( $P < 0.05$ ) K-strategies (later maturity, increased adult survival) in high elevation

environments that tended ( $P < 0.05$ ) to be more predictable and tended to have smaller food-resource levels than low elevation environments, and squirrels exhibited ( $P < 0.05$ ) r-strategies (earlier maturity, decreased adult survival) in low elevation environments, that tended ( $P < 0.05$ ) to be less predictable and tended to have larger food-resource levels than high elevation environments. Body weight and litter size did not conform ( $P > 0.05$ ) with this pattern. Body weight decreased ( $P < 0.001$ ) with elevation. Litter size (controlling for age and body weight) was not correlated ( $P = 0.20$ ) with elevation. These results falsify (Popper 1959:86) the original theory of r and K-selection as proposed by MacArthur and Wilson (1967) since they predicted reversed locations of predictable/unpredictable environments and r/K-strategists. However, since increased age at maturity and increased survival were associated with more predictable environments and smaller food-resource levels, 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 but they were wrong to assume (as many others have) that environmental conditions on mountain-tops could be equated with those on islands.

Why has this pattern emerged? Three main thoughts come to mind: First, hibernating squirrels may experience winter mortality more often at low elevations than at high elevations due to deeper frost lines resulting from reduced snow-cover (Potter 1956, Atmospheric Environment Service 1964-74, Calgary District, Water Survey of Canada 1965-74, Gelger 1966, Carl 1971, Barash 1973, 1974). Secondly, food-resources

may be more limiting and/or less nutritious at high elevations than at low elevations because of the shorter growing season and this may lead to delayed maturity (Frisch 1975), which in turn may lead to increased adult survival (Murdoch 1966, Tinkle 1969, Tilley 1973, Kohn 1978, Boyce 1979a) at high elevations. Thirdly, mortality may be reduced and maturation delayed where climatic variability is temporally predictable (Roughgarden 1979). One overall finding seemed to have emerged from this research. That is, the coevolved complex of traits predicted by original r-K theory (MacArthur and Wilson 1967) seemed to be lacking. Perhaps a consideration of individual traits may best explain the results.

#### Body Size

Lower elevation animals tended to have larger body sizes than higher elevation animals even though they were younger and thus should have been smaller because body size increased with age. This indicates partial support of original r-K theory which explicitly predicts a larger body size at lower elevations (MacArthur and Wilson 1967). However, none of the phenomena (later maturity, higher survival rates, greater environmental predictability, lower food-resource levels) that MacArthur and Wilson (1967) felt would accompany a large body size at low elevations were prevalent at low elevations in this study.

Population 4 had the lightest animals and the largest mean litter size among populations. r-K theory is partly supported because the smallest body size was associated with the largest litter size, but the location of this population is incorrect with respect to original r-K theory. r-K theory predicts that this population should be at the

highest elevation (MacArthur and Wilson 1967) .

On average, primiparous animals from population 1 matured earlier and had a smaller body size than primiparous animals from most other populations ( $P < 0.05$  for all except population 4, Student-Newman-Keuls). According to r-K theory, animals should breed earlier and at a smaller body size in less predictable than in more predictable environments (MacArthur and Wilson 1967). Less predictable environments tended to occur at low elevations in this study so the original theory of r and K-selection is supported for primiparous animals at low elevations (MacArthur and Wilson 1967).

My data support MacArthur's (1968) prediction that larger body size should be found where food supplies are more variable. A positive relationship existed between corrected weight of immature animals and variability of primary productivity (as determined by tree-rings,  $r = 0.87$ ,  $n = 6$ ,  $P < 0.05$ ). Case (1979) predicted that a variable food supply will affect the body weight of inexperienced young more than it will affect the body weight of adults. My data support Case (1979) since adult body weight was not associated ( $P > 0.05$ ) whereas immature body weight was associated with variability in primary productivity (as determined by tree-rings).

#### Age at Maturity

The prediction that squirrels at lower elevations have earlier ages at maturity than those at higher elevations was supported. Many squirrels in population 1 and some in population 2 matured as yearlings while those in populations 3-6 generally matured as 2- or 3-year-olds. The original prediction of r-K theory that animals should mature



earlier at higher elevations than at lower elevations was not supported by these data (MacArthur and Wilson 1967). Schaffer and Gadgil (1975) proposed that the shorter growing season at higher elevations causes plants to delay maturity and adopt a biennial habit there. Barash (1973, 1974) found delayed maturity in marmots (Marmota sp.) at high elevations and Frisch (1975) indicated that delayed maturity was associated with increasing elevation and reduced food-resources in mammals. The same phenomena appears to occur in Columbian ground squirrels.

Lower elevations had the greatest tree growth in this study. Since yield of grass was positively correlated with growth of woody vegetation in some cases (McGinnies 1967, Davis et al. 1972), there was support for the prediction that primary productivity of grasses may have been greater at lower elevations. F.S. Dobson (pers. comm.) found some yearlings breeding where he experimentally supplemented food whereas reference populations in the same region had no breeding yearlings for two years. Since Columbian ground/squirrels largely feed upon grass (Shaw 1925a), higher productivity of grass at lower elevations may have led to the early age at maturity in population 1.

#### Survival

Adult life expectancy increased almost monotonically with elevation contrary to the original predictions of r-K theory (MacArthur and Wilson 1967).

Decreased nutrition caused by low primary productivity at higher elevations should inhibit aging processes and increase life expectancy (see Kohn 1978). As Tinkle (1969) and Tilley (1973) found for lizards

and salamanders, ground squirrel life expectancy also was higher at higher elevations--the environments with lower primary productivity as indicated by tree-ring-width.

Murdoch (1966) found that low food supplies led to increased survival of adult insects. Boyce (1979a) simulated a resource-poor environment and found that a hypothetical K-strategist had superior fitness over an r-strategist there. The r-strategist had higher fitness where resources were abundant. This same pattern may occur in the Columbian ground squirrel. Squirrels in the presumably resource-poor, higher elevation environment, tended towards a K-strategy because they lived longer and matured later than the r-strategists who lived shorter lives, and matured earlier in the presumably resource-rich, lower elevation environment. Further studies may elucidate if any causal relationships exist among these variables. I speculate that low food supplies prevent early maturity which selects for increased survival.

Barash (1973, 1974) found that winter kill was the primary source of death in marmots and that winter kill was greater for juveniles than adults. In most ground squirrel species studied, hibernation chambers of adults were better constructed, built in better-drained soils, and/or were found deeper in the ground than those of juveniles (Shaw 1925b, 1926, Alcorn 1940, Carl 1971). For example, the average depth of hibernation cells for Columbian ground squirrels in Washington was 95 (range 75-113) cm for 9 adults and 46 (range 15-100) cm for 9 juveniles (Shaw 1926). Since soil temperatures at lower elevations in my study dropped below freezing at depths exceeding 91 cm in 1966, 61

cm in 1967, and 50 cm in 1980-82 for weeks at a time, it is possible that squirrels hibernating above these depths at lower elevations froze to death. If the same age-class-specific depths of hibernacula used in Washington are used in Alberta, then proportionately more juveniles than adults should freeze to death in hibernation at lower elevations. In contrast, squirrels hibernating at higher elevations were subjected to freezing temperatures deeper than 46 cm only once (one week maximum) in 6 years. Therefore, squirrels at higher elevations might freeze to death during hibernation due to ground freezing much less often than those at lower elevations.

Potter (1956) found that 4 cm of snow-cover prevented the ground from freezing deeper than 30 cm and Geiger (1966) showed that 5-20 cm of snow may keep all parts of the ground from freezing depending on soil texture. Soil under grasslands froze to 1 m depths without snow-cover but adjacent fields with snow-cover did not freeze (Potter 1956). In southwestern Alberta, snow usually covers the ground for the entire winter at higher elevations (Z. Eisera, pers. comm., pers. obs.) while at lower elevations snow-cover is highly variable (Atmospheric Environment Service 1965-81, Calgary District, Water Survey of Canada 1965-74, Longley 1967, pers. obs.). The main reasons for this are that an additional 56 cm of snow falls during the winter for every 300 m increase in elevation in the study area (Golding 1972). Also, the frequency of winter chinooks is greater at lower elevations than at higher elevations (9 of 10 years at lower elevations, relatively non-existent at higher elevations, Longley 1967). Barash (1973, 1974) and Svendsen (1974) found that winter mortality in marmots was inversely

related to snow-cover and Carl (1971) found that all perennially-used burrow systems of Arctic ground squirrels were covered by snow-drifts even when only 10% of the ground in an area was snow-covered. Without snow-cover, Carl (1971) found that hibernation burrows were useless to Arctic ground squirrels. From these data it seems probable that snow-cover may influence winter mortality rates of hibernating Columbian ground squirrels. Although I collected no direct evidence in this study, it seems likely that overwinter mortality by freezing is greater at lower elevations than at higher elevations. I expect that the shorter growing seasons and lower primary productivity (as indicated by tree-rings) at higher elevations may not allow juveniles to gain enough fat (energy) reserves to survive the winter while frozen ground at lower elevations kills many (fat) juveniles. This could explain the very low juvenile survival rates at both highest and lowest elevations (Tables 5-10).

In conclusion, lower primary productivity and shorter growing seasons may limit juvenile survival at higher elevations while poor snow-cover may limit juvenile survival at lower elevations. Therefore these data indicate that eventual reproductive success and survival may be limited by the summer environment at higher elevations and by the winter environment at lower elevations.

#### Litter Size

Levins (1968) suggested that a mixed strategy (no optimum) for litter size will be adaptive where environmental conditions are unpredictable. Litter size in this study was most variable at the lowest elevations (populations 1 and 2; low sample size from population

6 is probably responsible for its high variability for litter size, Table 13) where environmental conditions were least predictable. Females in populations 2-6 were relatively synchronous (i.e. ranged  $\pm 10$  days) for breeding dates (as seen qualitatively by embryo size) but those in population 1 were relatively asynchronous (i.e. range  $\pm 30$  days) since many there were lactating while others were only a few days pregnant. Since litter size and date of breeding was most variable at the lower elevations, and environmental predictability tended to be lower at lower elevations, there is supportive evidence for Gleesell's (1976) prediction that populations living in unpredictable environments should be polymorphic for reproductive characteristics. Variability in date of breeding and litter size was probably selected for (or not selected against) because no one date or litter size was always advantageous and thus higher variability was maintained in lower elevation populations.

#### Environmental Predictability, Variability and Elevation

The prediction that environments at lower elevations are less predictable than environments at higher elevations was supported for minimum temperatures and pooled mean predictabilities. Because of this, and because predictability of maximum temperature and precipitation showed no relationship ( $P > 0.05$ ) with elevation, the conventionally accepted idea that environments at higher elevations are less predictable than environments at lower elevations seems falsified in this study. In short, the original prediction of r-K theory that unpredictable environments should occur at higher elevations (MacArthur and Wilson 1967) was not supported. Although none of the six sites was

highly predictable, given the month, the weather tended to be more predictable at higher elevations than at lower elevations and vice-versa. Since Powell and MacIver (1977) found that a 3-10-year period is as adequate as a 30-yr period for describing the summer temperature and precipitation in an area, it is expected that the environmental trends I have found are not influenced by temporal phenomena.

One might argue that I should have chosen the best predictability equation and only used it throughout. 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. My objective at this time is to introduce these equations to ecologists for their future use and/or rejection once the equations' accuracies and/or inaccuracies are better understood. At the present time, the mean of the 18 arcsine-transformed values of these equations at each population-site is probably the best estimate of environmental predictability at each population-site.

The prediction that environments at lower elevations are less stable/more variable than environments at higher elevations was not supported. Conversely, variability (10-year) of minimum temperature approached positive significance with elevation ( $P = 0.06$ ).  $Z$ -transformed pooled variability, formed by combining variabilities of the 3 meteorological variables, and variabilities (10-year) of maximum temperature and precipitation, were not associated with elevation. The only trend, if any, that these data indicated, was that higher elevations exhibited a pattern of predictable variability (Vannote and Sweeney 1980) with respect to minimum temperature since predictability

and variability tended to be greater at higher elevations for this variable. The finding that minimum temperatures at higher elevations tended ( $P < 0.001$ ) to be more predictable, but perhaps ( $P = 0.06$ ) more variable than minimum temperatures at lower elevations opposes the conventional assumption that variable environments are unpredictable environments--an assumption that has become prevalent over the last 15 years (references summarized in Stearns 1976, 1977, 1980). It is possible that problems with r-K theory in the past (see Stearns 1976, 1977 for summary) may have been caused by this apparent paradox (i.e. some of the theory is supported by this study when the locations of predictable/unpredictable environments are reversed from MacArthur and Wilson's (1967) 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.

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). Here, it is suggested that these 5 adjectives cannot be used interchangeably. Indeed, the terms variable ( $S^2$  of minimum temperature) and Barash's (1973, 1974) harsh (shorter growing seasons, less primary productivity), tended ( $P \leq 0.06$ ) to define the higher elevations in this study, but at higher elevations environments were predictable and animals were found tending towards a K-strategy (as in Barash's studies 1973, 1974). The locations of the predictable/unpredictable environments tended to be reversed with respect to original r-K theory, but ground squirrel life history tended

to fit expected trends with respect to environmental predictability (i.e. more K-selected in predictable environments) as MacArthur and Wilson (1967) originally proposed. The data for minimum temperature variability tended ( $P=0.06$ ) to support Barclay's (1975) prediction that environmental variability may promote K-selection, and Boyce's (1979a) simulations which showed that a hypothetical K-strategist had superior fitness over an r-strategist in a variable environment. Clearly, we need consistent quantitative methodologies for measuring the 5 adjectives (and their converses) because they may not signify similar environmental conditions.

Since definitive analyses concerning predictable environments over elevational gradients have to my knowledge not been done, the first quantitative test performed here should be considered tentative evidence for the geographic locations of predictable/unpredictable environments over an elevational gradient. Perhaps future researchers should strive to refine the techniques presented here using other data.

In the only other work I know of that used a quantitative measure of environmental predictability for mammals, variance in litter size was positively correlated with environmental predictability of precipitation for muskrats (Boyce 1979b). The relationship between these two variables approached significance in my study ( $r = 0.75$ ,  $n = 6$ ,  $P = 0.08$ ), suggesting that variance in litter size may be adaptive where precipitation tends to be predictable. This is supportive of Boyce (1979b) but contrary to Gillespie (1977) who argued that variance in litter size should rarely be adaptive, especially in predictable environments, because it should reduce fitness in predictable



environments.

### Epilog

This study associated instantaneous (time-specific) life history traits with recent environmental conditions in an effort to understand long-term trends. The time-specific life tables in this report are presented under the assumption that the age structures of these populations were relatively stable (=net reproductive rate,  $R_0 = 1$ ) and stationary (intrinsic rate of increase,  $r = 0$ ) (sensu Caughley 1977). If this assumption is proven incorrect, the life tables may still be accurate since: (1) even when the intrinsic rate of increase ( $r$ ) is not zero the net reproductive rate ( $R_0$ ) is still usually close to unity (Charlesworth 1980), (2) the idea that a population must be stationary ( $r = 0$ ) before a proper life table can be calculated may be incorrect (Michod and Anderson 1980), (3) it takes a serious perturbation to severely disrupt a stable age distribution (Goodman 1981), and (4) even with serious perturbations in a life table, convergence to a stable age distribution usually occurs within three generations (Charlesworth 1980) (i.e.  $\pm 6$  years for Columbian ground squirrels). However, the possibility exists that these life tables were not representative of Columbian ground squirrel demography. Further research on this subject will be needed before a definitive conclusion can be made one way or the other.

Throughout this report it was assumed that the ground squirrel life histories I studied were moulded by natural selection in relatively discrete, stationary populations over recent decades within environments similar to those that existed during 1965-82 (thus inter-

year sampling of squirrels should not affect results). I feel this assumption was justified since: (1) Balph (pers. comm.), Boag and Murie (1981b), Bronson (1977, 1979), Murie et al. (1980), and Slade and Balph (1974) did not find large, permanent, inter-year differences in mountain ground squirrel life histories during multi-year studies, and (2) Powell and MacIver (1977) found that a 3-10-year period was as adequate as a long-term period (> 30 yr) for describing the summer temperature and precipitation at sites within and near my study region. If this assumption is proven unjustified then it is possible that the life history traits I observed may only be time-specific and thus associations with the environment may only represent instantaneous relationships (and/or phenotypic plasticity). Even if the relationships are only instantaneous (and/or phenotypically plastic) it may be necessary to explain why they existed at all.

The true relationships among environmental predictability, stability/variability and life history will be unknown until the interaction among these parameters is better understood. Even if statistical relationships among life history and environmental parameters are documented, we do not know if the life history traits have a genetic basis or if they are merely due to phenotypic plasticity. Once we know which genes are responsible for specific life history traits, we may be able to determine the true relationships among phenotypes, genotypes, life histories and environmental parameters. This study did not specifically define cause and effect and/or interactive relationships among these parameters but suggested the possibility of life history/environmental relationships (that could

be cause and effect) with statistical associations among some of the presumably relevant variables. Only by repeating this study with the same and other species will we be able to test the mettle of my approach and perhaps explain the causes of the relationships.

### CONCLUSIONS

Contingent upon several assumptions, the original theory of  $r$  and  $K$ -selection, proposed by MacArthur and Wilson (1967) and treated in detail by Planka (1970), was falsified (Popper 1959:86). Ground squirrels tended to be  $K$ -strategists (later maturity, greater adult survival), environments tended to be more predictable, and a presumed index of the food-resource was lower at higher elevations than at lower elevations. Ground squirrels tended to be  $r$ -strategists (earlier maturity, lower adult survival), environments tended to be less predictable, and a presumed index of the food-resource was greater at lower elevations than at higher elevations. A portion of  $r$ - $K$  theory was supported since increasing survival, age at maturity, and environmental predictability were associated with decreasing food-resource levels and growing season length, but the coevolved complex of traits predicted by original  $r$ - $K$  theory (MacArthur and Wilson 1967) seemed to be lacking. The major difference between the trends from this empirical research and expected trends of  $r$ - $K$  theory was the reversal of the locations of predictable/unpredictable environments and  $r$ / $K$ -strategists.

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APPENDIX A

Equations Used to Construct Life Tables

- 1) Age specific survival, or proportion living to age  $x$  (Deevey 1947, Pielou 1974, Caughley 1977):

$$l_x = bl_x / bl_0$$

where  $bl_0$  was the number born and  $bl_x$  was the number living to age  $x$ .

- 2) Age specific fecundity, number of females born to a female of age  $x$  (Birch 1948):

$$m_x = \frac{\text{Number of female embryos}}{\text{Number of females sampled}}$$

- 3) Age specific life expectancy, expectation of further life, mean death age of a cohort (Deevey 1947, Pianka 1974, 1978):

$$e_x = \frac{\sum_{y=x}^{\infty} l_y}{l_x}$$

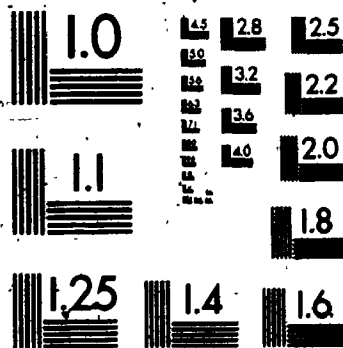
- 4) Net reproductive rate, mean number of daughters produced in a female's lifetime (Birch 1948):

$$R_0 = \sum_{x=0}^{\infty} l_x m_x$$



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APPENDIX B

Dispersion Statistics and Differences Among Population-Sites for  
Climatic Variables.

Table 20. Differences<sup>1</sup> between the 10-year distributions of daily maximum temperature (°C) (upper matrix) and daily minimum temperature (mm) (lower matrix) between population-sites.

Population-Site	Population-Site					
	1	2	3	4	5	6
1		***	***	***	***	***
2	***		N.S.	N.S.	***	***
3	***	**		N.S.	***	***
4	***	***	***		***	***
5	***	***	***	***		N.S.
6	***	***	***	***	*	

<sup>1</sup> Kolmogorov-Smirnov two-sample tests, significance levels: \*P<0.05, \*\*P<0.01, \*\*\*P<0.001, N.S. P>0.05, Bonferroni's P = 0.003.

Table 21. Differences<sup>1</sup> between the 10-year distributions of daily precipitation (mm) between population-sites.

Population-Site	Population-Site					
	1	2	3	4	5	6
1						
2	N.S.					
3	***	N.S.				
4	N.S.	N.S.	N.S.			
5	***	***	*	***		
6	***	***	***	***	*	

<sup>1</sup>Kolmogorov-Smirnov two-sample tests, significance levels: \*P<0.05, \*\*\*P<0.001, N.S. P>0.05, Bonferroni's P = 0.003.

Table 22. Dispersion statistics for maximum and minimum daily temperatures ( $^{\circ}\text{C}$ ) for population-site 1, Beaver Mines (1300 m).

Year	Maximum Temperature			Minimum Temperature		
	$\bar{X} \pm \text{SE}$	$S^2$	Max-Min <sup>1</sup>	$\bar{X} \pm \text{SE}$	$S^2$	Max-Min <sup>1</sup>
1965	18.1 $\pm$ 0.67	54.3	31 to -4	5.9 $\pm$ 0.42	21.2	15 to -6
1966	20.3 $\pm$ 0.43	23.9	30 to 9	6.8 $\pm$ 0.29	10.6	18 to -2
1967	21.8 $\pm$ 0.50	35.0	32 to 7	6.6 $\pm$ 0.34	16.8	17 to -3
1968	18.4 $\pm$ 0.47	29.6	30 to 1	6.4 $\pm$ 0.27	9.7	14 to -2
1969	20.4 $\pm$ 0.46	27.4	33 to 7	6.4 $\pm$ 0.32	13.6	18 to -4
1970	22.2 $\pm$ 0.61	43.2	31 to -1	8.0 $\pm$ 0.42	20.4	18 to -11
1971	20.6 $\pm$ 0.58	44.9	34 to 4	7.1 $\pm$ 0.34	15.7	17 to -4
1972	19.6 $\pm$ 0.50	27.9	29 to 4	6.8 $\pm$ 0.34	12.9	14 to -3
1973	20.9 $\pm$ 0.53	39.3	33 to 0	6.7 $\pm$ 0.36	18.6	16 to -5
1974	18.8 $\pm$ 0.73	45.5	31 to 3	6.4 $\pm$ 0.46	18.0	15 to -2
Pooled	20.2 $\pm$ 0.18	38.1		6.7 $\pm$ 0.11	15.8	

<sup>1</sup> The maximum and minimum temperature in category rounded for easier interpretation.

Table 23. Dispersion statistics for maximum and minimum daily temperatures ( $^{\circ}\text{C}$ ) for population-site 2, Streeter Basin (1360 m).

Year	Maximum Temperature			Minimum Temperature		
	$\bar{X} \pm \text{SE}$	$S^2$	Max-Min <sup>1</sup>	$\bar{X} \pm \text{SE}$	$S^2$	Max-Min <sup>1</sup>
1965	17.2 $\pm$ 0.65	50.8	31 to -5	4.2 $\pm$ 0.40	19.8	16 to -7
1966	18.0 $\pm$ 0.46	27.8	29 to 4	4.3 $\pm$ 0.29	10.6	12 to -3
1967	20.1 $\pm$ 0.48	32.2	31 to 3	4.4 $\pm$ 0.31	13.4	13 to -5
1968	16.9 $\pm$ 0.50	32.6	31 to -1	4.0 $\pm$ 0.26	9.1	12 to -3
1969	18.9 $\pm$ 0.50	32.6	31 to 4	3.1 $\pm$ 0.29	11.0	12 to -5
1970	20.6 $\pm$ 0.62	44.8	31 to -3	5.0 $\pm$ 0.42	20.4	13 to -12
1971	19.3 $\pm$ 0.54	39.4	32 to 4	4.0 $\pm$ 0.34	15.8	15 to -6
1972	17.9 $\pm$ 0.50	28.1	28 to 1	5.0 $\pm$ 0.33	12.4	12 to -4
1973	18.8 $\pm$ 0.50	35.0	31 to -1	3.8 $\pm$ 0.33	15.0	12 to -7
1974	16.7 $\pm$ 0.75	48.8	28 to 2	5.5 $\pm$ 0.60	31.2	17 to -5
Pooled	18.5 $\pm$ 0.17	37.9		4.3 $\pm$ 0.11	15.5	

<sup>1</sup> The maximum and minimum temperature in category rounded for easier interpretation.

Table 24. Dispersion statistics for maximum and minimum daily temperatures ( $^{\circ}\text{C}$ ) for population-site 3, Sheep Ranger Station (1500 m).

Year	Maximum Temperature			Minimum Temperature		
	$\bar{X} \pm \text{SE}$	$S^2$	Max-Min <sup>1</sup>	$\bar{X} \pm \text{SE}$	$S^2$	Max-Min <sup>1</sup>
1965	18.0 $\pm$ 0.52	32.7	29 to -1	3.6 $\pm$ 0.44	23.3	14 to -12
1966	18.5 $\pm$ 0.41	22.0	28 to 7	4.1 $\pm$ 0.26	8.5	11 to -4
1967	21.4 $\pm$ 0.48	32.8	33 to 6	3.8 $\pm$ 0.34	16.0	12 to -7
1968	18.9 $\pm$ 0.53	37.9	32 to -1	3.1 $\pm$ 0.27	9.7	11 to -3
1969	18.5 $\pm$ 0.50	32.5	29 to 3	3.3 $\pm$ 0.26	8.8	12 to -3
1970	20.4 $\pm$ 0.57	37.1	31 to -1	4.7 $\pm$ 0.38	17.0	12 to -11
1971	19.1 $\pm$ 0.55	39.7	32 to 2	4.1 $\pm$ 0.35	15.8	18 to -6
1972	17.9 $\pm$ 0.48	26.2	28 to 2	4.2 $\pm$ 0.31	11.1	11 to -4
1973	18.4 $\pm$ 0.50	34.5	29 to 0	3.0 $\pm$ 0.32	14.0	13 to -6
1974	17.6 $\pm$ 0.72	44.9	28 to 3	3.0 $\pm$ 0.48	20.2	14 to -5
Pooled	18.9 $\pm$ 0.17	34.7		3.7 $\pm$ 0.11	14.4	

<sup>1</sup> The maximum and minimum temperature in category rounded for easier interpretation.

Table 25. Dispersion statistics for maximum and minimum daily temperatures ( $^{\circ}\text{C}$ ) for population-site 4, Caj Creek (1675 m).

Year	Maximum Temperature			Minimum Temperature		
	$\bar{X} \pm \text{SE}$	$S^2$	Max-Min <sup>1</sup>	$\bar{X} \pm \text{SE}$	$S^2$	Max-Min <sup>1</sup>
1965	16.8 $\pm$ 0.65	52.0	29 to -4	2.6 $\pm$ 0.40	19.0	11 to -11
1966	18.4 $\pm$ 0.42	22.5	28 to 6	3.5 $\pm$ 0.32	13.0	12 to -4
1967	20.4 $\pm$ 0.51	36.7	34 to 4	2.6 $\pm$ 0.30	12.4	13 to -6
1968	16.7 $\pm$ 0.47	28.9	29 to 0	3.0 $\pm$ 0.30	11.6	13 to -7
1969	18.5 $\pm$ 0.51	33.9	33 to 2	2.7 $\pm$ 0.27	9.9	13 to -5
1970	20.3 $\pm$ 0.58	39.2	31 to -1	3.8 $\pm$ 0.41	19.6	14 to -12
1971	18.9 $\pm$ 0.57	43.0	32 to 2	3.6 $\pm$ 0.35	15.9	14 to -8
1972	17.9 $\pm$ 0.48	26.3	29 to 1	3.7 $\pm$ 0.34	13.1	14 to -6
1973	18.4 $\pm$ 0.51	36.1	29 to -1	2.6 $\pm$ 0.32	14.0	12 to -7
1974	18.0 $\pm$ 0.76	49.3	30 to 3	2.2 $\pm$ 0.46	18.5	13 to -7
Pooled	18.5 $\pm$ 0.17	37.5		3.0 $\pm$ 0.11	14.7	

<sup>1</sup> The maximum and minimum temperature in category rounded for easier interpretation.



Table 26. Dispersion statistics for maximum and minimum daily temperatures ( $^{\circ}\text{C}$ ) for population-site 5, Halistone Butte (2000 m).

Year	Maximum Temperature			Minimum Temperature		
	$\bar{X} \pm \text{SE}$	$S^2$	Max-Min <sup>1</sup>	$\bar{X} \pm \text{SE}$	$S^2$	Max-Min <sup>1</sup>
1965	9.7 $\pm$ 0.68	56.0	23 to -11	1.5 $\pm$ 0.57	39.7	13 to -14
1966	11.5 $\pm$ 0.46	27.6	22 to -1	3.1 $\pm$ 0.32	13.2	13 to -5
1967	12.9 $\pm$ 0.52	37.8	24 to -2	3.1 $\pm$ 0.41	24.0	15 to -7
1968	9.8 $\pm$ 0.49	32.2	23 to -6	0.6 $\pm$ 0.33	14.4	12 to -9
1969	12.4 $\pm$ 0.48	30.7	24 to -2	3.0 $\pm$ 0.40	21.2	11 to -10
1970	14.3 $\pm$ 0.57	37.3	23 to -1	3.5 $\pm$ 0.54	33.4	13 to -12
1971	13.5 $\pm$ 0.56	41.6	25 to -1	1.6 $\pm$ 0.44	25.5	12 to -12
1972	11.4 $\pm$ 0.55	34.6	23 to -2	2.0 $\pm$ 0.38	16.4	12 to -8
1973	11.9 $\pm$ 0.50	35.0	23 to -8	2.0 $\pm$ 0.40	22.8	14 to -9
1974	10.2 $\pm$ 0.84	60.9	24 to -4	0.3 $\pm$ 0.62	32.7	9 to -14
Pooled	11.8 $\pm$ 0.18	40.4		2.1 $\pm$ 0.14	24.7	

<sup>1</sup> The maximum and minimum temperature in category rounded for easier interpretation.

Table 27. Dispersion statistics for maximum and minimum daily temperatures ( $^{\circ}\text{C}$ ) for population-site 6, Marmot Basin (2200 m).

Year	Maximum Temperature			Minimum Temperature,		
	$\bar{X} \pm \text{SE}$	$S^2$	Max-Min <sup>1</sup>	$\bar{X} \pm \text{SE}$	$S^2$	Max-Min <sup>1</sup>
1965	12.6 $\pm$ 0.70	59.4	28 to -7	1.9 $\pm$ 0.48	28.2	13 to -12
1966	12.0 $\pm$ 0.40	20.7	23 to 1	2.9 $\pm$ 0.30	11.8	13 to -5
1967	13.2 $\pm$ 0.44	27.3	23 to 0	3.6 $\pm$ 0.40	21.7	14 to -5
1968	9.7 $\pm$ 0.44	26.0	22 to -4	1.8 $\pm$ 0.32	13.5	13 to -7
1969	11.0 $\pm$ 0.50	32.6	26 to -3	2.5 $\pm$ 0.36	16.9	12 to -8
1970	13.1 $\pm$ 0.61	43.2	23 to -8	3.9 $\pm$ 0.49	27.4	14 to -13
1971	11.9 $\pm$ 0.55	40.1	25 to -2	2.8 $\pm$ 0.45	27.0	17 to -8
1972	12.6 $\pm$ 0.60	40.1	23 to -1	2.7 $\pm$ 0.38	16.6	13 to -6
1973	12.1 $\pm$ 0.54	40.4	24 to -6	2.6 $\pm$ 0.39	21.9	12 to -8
1974	10.9 $\pm$ 0.69	41.5	26 to -2	1.0 $\pm$ 0.51	22.7	9 to -8
Pooled	11.9 $\pm$ 0.17	37.5		2.6 $\pm$ 0.13	21.1	

<sup>1</sup> The maximum and minimum temperature in category rounded for easier interpretation.

Table 28. Dispersion statistics for daily precipitation (mm) for population-sites 1, Beaver Mines (1300 m) and 2, Streeter Basin (1360 m).

Year	Population-Site 1			Population-Site 2		
	$\bar{X} \pm SE$	$S^2$	Max	$\bar{X} \pm SE$	$S^2$	Max
1965	1.85±0.74	33.5	31.2	2.59±0.95	55.4	48.0
1966	2.76±0.67	41.7	29.5	2.82±0.48	21.4	23.6
1967	1.08±0.37	16.9	35.3	1.26±0.45	24.7	34.0
1968	2.72±0.55	36.2	32.0	3.43±0.62	46.4	37.3
1969	2.39±0.72	57.2	49.3	2.71±0.77	64.6	49.3
1970	1.40±0.54	26.3	35.3	2.10±1.10	110.7	84.1
1971	1.23±0.41	15.5	23.6	1.76±0.76	53.7	63.0
1972	2.21±0.58	30.4	33.0	2.66±0.91	76.7	66.0
1973	0.88±0.32	9.3	18.3	1.87±0.55	27.5	32.5
1974	1.20±0.38	8.8	16.5	1.20±0.39	9.2	14.7
Pooled	1.81±0.18	28.7		2.27±0.23	49.6	

Table 29. Dispersion statistics for daily precipitation (mm) for population-sites 3, Sheep Ranger Station (1500 m) and 4, Cat Creek (1675 m).

Year	Population-Site 3			Population-Site 4		
	$\bar{X} \pm SE$	$S^2$	Max	$\bar{X} \pm SE$	$S^2$	Max
1965	2.56±0.76	36.2	28.2	1.84±0.69	29.6	34.8
1966	2.75±0.69	43.5	35.1	2.30±0.63	36.5	34.5
1967	1.12±0.32	12.6	17.5	0.96±0.25	7.7	15.7
1968	3.21±0.62	46.7	30.2	2.64±0.48	27.9	26.4
1969	3.13±0.74	60.3	51.3	2.64±0.64	44.7	45.5
1970	2.23±0.80	58.5	54.1	2.58±0.84	65.4	53.3
1971	1.80±0.52	25.2	30.0	1.44±0.43	17.2	27.2
1972	1.95±0.54	26.5	27.4	2.11±0.49	22.3	24.9
1973	2.90±0.72	47.7	37.3	2.33±0.66	39.9	36.6
1974	1.95±0.80	39.4	35.1	1.33±0.75	34.1	38.1
Pooled	2.37±0.21	39.6		2.04±0.19	31.9	

Table 30. Dispersion statistics for daily precipitation (mm) for population-sites 5, Hallstone Butte (2000 m) and 6, Marmot Basin (2200 m).

Year	Population-Site 5			Population-Site 6		
	$\bar{X} \pm SE$	$s^2$	Max	$\bar{X} \pm SE$	$s^2$	Max
1965	1.50±0.56	19.6	27.7	3.20±0.96	57.1	36.6
1966	2.79±0.76	52.8	38.1	2.19±0.53	25.9	26.2
1967	0.97±0.26	8.0	15.2	1.49±0.35	14.8	20.8
1968	2.62±0.50	30.5	33.8	2.52±0.40	19.1	19.8
1969	3.23±0.91	90.5	63.0	2.35±0.49	26.8	30.7
1970	1.62±0.49	21.8	28.2	2.56±1.00	91.1	80.3
1971	1.78±0.59	32.1	37.3	1.82±0.62	35.7	49.5
1972	2.86±0.82	62.1	50.3	2.10±0.45	18.2	26.9
1973	2.04±0.60	33.5	34.3	2.26±0.58	31.2	33.0
1974	0.92±0.32	6.3	14.5	1.18±0.38	8.9	17.8
Pooled	2.10±0.20	37.5		2.16±0.18	31.7	

APPENDIX C

Equations Used for Environmental Predictability

The environmental predictability analyses progressed as follows. Daily records were cast into joint frequency distribution matrices where temperature was classified into 10-14 classes (rows) with 2.8°C per class and approximate growing season months (columns) were categorized as 5=May-October=10. Precipitation (mm) was classified into 8 logarithmic (napierian) classes (rows) with 0.5 units per class (Colwell, 1974) and months were categorized as 5 = June-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 years. Some matrices differed by 1 or 2 rows for a given variable, but all 6 stations 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:

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

where  $\chi^2$  = 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 station for each temperature variable  $N = 1248$ , for precipitation  $N = 937$ ) (Cramer 1946, Goodman and Kruskal 1954, Bishop et al. 1975). Thus  $\min(r-1), (c-1)$  simply means the denominator is the value of one less than the number of rows or one less than the number of columns,

whichever is less. Cramer's V indicates the degree of association between temperature or precipitation classes and months. For the 24 matrices (6 populations by 4 variables) built and 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 Lambda AsymTP:

$$\text{Lambda}_{\text{AsymTP}} = \frac{\sum_k \max.f_{jk} - \max.f_k}{N - \max.f_k} \quad (2)$$

where  $\sum_k \max.f_{jk}$  = 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. I used the same equation to determine how well we can predict the month knowing the temperature or logarithmic precipitation class by simply inverting the matrix (Lambda<sub>AsymM</sub> equation 3). The 4th equation determines overall prediction making no assumption about which variable is dependent or independent (as (2) and (3) do). It merely averages prediction in both directions at the same time and thus is symmetric:

$$\text{Lambda}_{\text{Sym}} = \frac{\sum_k \max.f_{jk} + \sum_j \max.f_{jk} - \max.f_k - \max.f_j}{2N - \max.f_k - \max.f_j} \quad (4)$$

where  $\sum_k \max.f_{jk}$  and  $\sum_j \max.f_{jk}$  are as defined for (2) above,  $\max.f_j$  is the maximum column total, and  $\sum \max.f_{jk}$  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 5th equation used was the uncertainty coefficient:

$$\text{Uncert}_{\text{AsymTP}} = \frac{-\sum_j p(Y_j) \log p(Y_j) - \sum_{kj} \sum p(Y_j, X_k) \log p(Y_j | X_k)}{-\sum_j p(Y_j) \log p(Y_j)} \quad (5)$$

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) similar to the lambda values but here the entire frequency distribution instead of just the mode is used. A similar equation was used for determining the proportion by which the 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):

$$\text{Uncert}_{\text{AsymM}} = \frac{-\sum_k p(X_k) \log p(X_k) - \sum_{jk} \sum p(X_k, Y_j) \log p(X_k | Y_j)}{-\sum_k p(X_k) \log p(X_k)} \quad (6)$$

The 7th equation is similar to (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):

$$\text{Uncert}_{\text{sym}} = \frac{(-\sum_j p(Y_j) \log p(Y_j)) + (-\sum_k p(X_k) \log p(X_k)) - (-\sum_{jk} p(Y_j, X_k) \log p(Y_j, X_k))}{(-\sum_j p(Y_j) \log p(Y_j)) + (-\sum_k p(X_k) \log p(X_k))} \quad (7)$$

Equations 8-15 determine if the relative ordering on one variable is the same (concordant) as the relative ordering of the other variable (Bishop et al. 1975, Mueller et al. 1977). Equation 8 was:

$$\tau_b = \frac{P-Q}{\left[ \frac{1}{2}(N^2 - \sum_1 T_1^2) \frac{1}{2}(N^2 - \sum_2 T_2^2) \right]^{\frac{1}{2}}} \quad (8)$$

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,  $N$  = 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 ( $r_s$ ).

Equations 9 and 10 utilize information derived from the  $P$  and  $Q$  values of (8):

$$\tau_c = \frac{2m(P-Q)}{N^2(m-1)} \quad (9)$$

where  $m$  = the number of rows. Equation 9's interpretation is similar

to that of (8) but it adjusts for the number of rows and columns (Stuart 1953, Goodman and Kruskal 1954, Bishop et al. 1975, Mueller et al. 1977, Stearns 1981). Equation 10,

$$\text{gamma} = \frac{P-Q}{P+Q} \quad (10)$$

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

Equations 11-13 are similar to the tau's but the adjustment for ties is different (Somers 1962a, b, Garson 1971). Equation 11 was:

$$\text{Somers's } D_{\text{AsymTP}} = \frac{P-Q}{P+Q+T_1} \quad (11)$$

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

$$\text{Somers's } D_{\text{AsymM}} = \frac{P-Q_1}{P+Q+T_2} \quad (12)$$

when month was the dependent variable, and equation 13 was:

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

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 2 formulas are identical but the matrix is inverted:

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

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

Equation 16 is a simple correlation coefficient. (Orlaci, 1978:15) with temperature or logarithmic precipitation classes as the dependent variable and months the independent.

Equation 17:

$$P = 1 - \left\{ \frac{\left( -\sum \frac{N_{ij}}{Z} \log \frac{N_{ij}}{Z} \right) - \left( -\sum \frac{X_j}{Z} \log \frac{X_j}{Z} \right)}{\log_{10} s} \right\}, \quad (17)$$

where  $i$  = a temperature or precipitation state (row),  $j$  = a month (column),  $N_{ij}$  = the value of the  $ij$  element,  $s$  = the number of temperature or logarithmic precipitation states,  $Z = \sum_{ij} N_{ij}$  or simply the total number of days sampled, and  $X_j = \sum_{i=1}^R N_{ij}$  or simply each row total (Kullback 1959, Colwell 1974, Stearns 1981).

The final equation was:

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

where  $R$  = the number of temperature or logarithmic precipitation states (rows),  $\bar{Q}$  = 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).



**END**

1 | 5 | 0 | 9 | 8 | 3

**FIN**