A CONSIDERATION OF BET-HEDGING IN
SPERMOPHILUS COLUMBIANUS

RICHARD M. ZAMMUTO AND JOHN S. MILLAR

Department of Zoology, University of Western Ontario, London, Ontario, Canada N6A 5B7
Present address of RMZ: Kananaskis Centre for Environmental Research,
University of Calgary, Seebe, Alberta, Canada T0L 1X0

ABSTRACT.—We consider theoretical predictions of bet-hedging theory using life-history and environmental data from six populations of Columbian ground squirrels. Contrary to the pattern predicted by bet-hedging theory, juvenile survival, pre-reproductive survival, and the percentage of squirrels surviving to maturity were positively associated, whereas the adult/juvenile survival ratio and variance in reproductive output were negatively associated with the degree of iteroparity, generation length, and/or the age at maturity. Survival of immatures and the degree of iteroparity were lower, whereas the adult/juvenile survival ratio was higher, in environments with more variable daily temperatures. Survival of immatures was higher, adult survival was lower, and the adult/juvenile survival ratio was lower where the length of the growing season was most variable. Most of our data show ($P < 0.05$) a pattern reversed to that predicted by bet-hedging theory. The possible effect of variability in length of growing season on survival of immatures versus adults could have precluded bet-hedging from existing among these populations.

Several theoretical and empirical studies have focused upon life-history tactics (survival and reproduction) and the environmental factors that might shape them (see reviews by Parsons, 1982; Stearns, 1976, 1977, 1980). The first comprehensive theory of life-history evolution, r and K theory (MacArthur and Wilson, 1967), made specific predictions about the natural relationships among (mammalian) survival, reproduction, and various environmental conditions without regard to population age-structure (i.e., maturation is late and survival is high in stable environments). A subsequent theory, bet-hedging theory (Charnov and Schaffer, 1973; Murphy, 1968; Schaffer, 1974; Stearns, 1976), made predictions mostly contradictory to those of r and K theory and additionally it considers population age-structure (i.e., maturation is late, immature survival is low, and adult survival is high in variable environments). Specifically, the theory of bet-hedging predicts that mortality of immatures, variance in reproductive output, variance in mortality of immatures, and/or the ratio of adult survival to juvenile survival should be positively associated with the degree of iteroparity (extent of repeated reproduction; see Stearns, 1976), generation length, and/or age at maturity in natural, age-structured populations (Abrams, 1983; Bell, 1976; Charlesworth, 1980; Charnov and Schaffer, 1973; Goodman, 1984; Holgate, 1967; Murphy, 1968; Schaffer, 1974; Schaffer and Gadgil, 1975; Sibly and Calow, 1983; Young, 1981). Stearns (1976) coined the term bet-hedging theory and argued that variable environments which affect juvenile survival more than adult survival should lead to the above relationships. Conversely, Hastings and Caswell (1979) argued that the predictions of Schaffer (1974) and Schaffer and Gadgil (1975) (and therefore Stearns, 1976) can be completely reversed given different mathematical assumptions of their models and that environmental variability affecting juvenile survival should favor a decreased degree of iteroparity.

Quantitative attempts to test bet-hedging theory have been made in several studies. Stearns' (1976) test, using several vertebrates, has been considered invalid (Bell, 1980). Bell (1980) argued that interspecific comparisons should not be used to test the theory (after Charnov and Schaffer, 1973) and that Stearns' (1976) variables were autocorrelated. Murie (1985) suggested that one of the two populations of Columbian ground squirrels, *Spermophilus columbianus*, he studied could be bet-hedging but he also suggests other alternatives. Haukioja and Hakala (1978) claimed their results on mollusks supported bet-hedging on the assumption that high resource availability

was equivalent to a stable environment. Barclay and Gregory (1981, 1982), Tallamy and Denno (1981), and Hairston et al. (in press) claim support of bet-hedging from their studies of invertebrates.

Here we report our study of life-history variables important to bet-hedging theory (using the "strategic model" of Tuomi and Haukioja, 1979) for the Columbian ground squirrel, an abundant, montane/sub-alpine, herbivorous rodent which inhabits diverse environmental conditions in northwestern North America. As a result of our study, it became clear that some of the variables considered important to bet-hedging are autocorrelated and/or redundant. Here, we examine most relationships considered by various authors concerned with bet-hedging theory in an effort to better understand how this theory might apply to wild mammals in natural, undisturbed environments. We focus upon r-K theory in a forthcoming communication (Zammuto and Millar, in press).

Throughout this paper we assume the life-history traits we studied were molded by natural selection in relatively stationary, discrete populations within environments similar to those that existed during the past few decades. We feel this assumption is justified for the following reasons: (1) Powell and MacIver (1977) found that a 3–10-year period was as adequate as a long-term period (>30 years) for describing the summer temperature and precipitation at sites within and adjacent to our study region, and (2) Boag and Murie (1981), Bronson (1977, 1979), and Murie et al. (1980) found small or nonexistent interyear differences in ground squirrel life histories during several multi-year studies. One of these studies spanned 7 years (see Boag and Murie, 1981; Murie et al., 1980) and concerned two populations in our study region where litter size and its variance, adult survival, and age at maturity did not significantly change among years. Notwithstanding, juvenile survival within our study region may vary among years (Boag and Murie, 1981; Murie, 1985; Murie and Harris, 1982), so we examine several measures of immature survival to help compensate for possible biases. Some of our data will not represent long-term (evolutionary time) trends of life histories if our assumptions and methodology are unjustified, but they will represent natural, standing age-structures or life histories of at least a short-term (recent decade) nature.

METHODS

Collections of 268 females ($\geq$1-year-old) were made with Conibear traps from six relatively discrete (i.e., more than 25 linear km separated each studied population from another) populations of similar density (10–15 adults/ha) in southwestern Alberta during the birth-pulses (see Caughley, 1977:6) of 1980 and 1981 (range of elevation 1,300–2,200 m). Almost all females present within four of these populations were collected (we saw no activity for 2 days after collections; males were also collected but are not used in our analysis because they would bias some of our variables). Populations 2, 3, and 5 were studied in 1980 and populations 1, 4, and 6 were studied in 1981. Litter size (embryos or placental scars) was determined in the field for all collected adult females. Lower jawbones were histologically sectioned across the diastema (after Millar and Zwickel, 1972), and age was determined from annual adhesion lines in the periosteal zone. This technique correctly aged all 16 known-aged animals which had been ear-tagged during previous studies in population 3 (see Boag and Murie, 1981) and aged one of 14 minimum-aged animals younger than its known minimum age (6 versus 7 years).

Mean age at maturity (α) was calculated as:

$$\alpha = [(N_p)(a) + (N_q)(a + 1)]/(N_p + N_q),\tag{1}$$

where N_p was the number of females mature (pregnant or lactating) at a, the first age (whole years, since animals were studied at the birth-pulse, Caughley, 1977:6) at which more than one female (if only one female was mature at an early age it was ignored in this calculation) was mature in a population, and N_q was the number of females in the population not mature at age a (this assumes that females not mature at age a, would have matured at a + 1, an assumption which is supported by our data). This estimate of mean maturation-age preserved variation within populations and allowed more meaningful comparisons among populations than conventional estimates (see DeMaster, 1978).

Smoothed, time-specific life tables were constructed for females for each population (Caughley, 1977:96),

assuming (supported by Boag and Murie, 1981:2231; Bronson, 1977, 1979) that all populations approached a stationary age-structure (Charlesworth, 1980; Michod and Anderson, 1980; Pielou, 1974). Age-specific survival (l_x) was calculated after Caughley (1977), Deevey (1947), and Pielou (1974) as:

$$l_x = bl_x/bl_0, \tag{2}$$

where bl_0 was 0.5 times the total number of embryos or placental scars (assuming a 1:1 sex ratio at birth) produced by collected females and bl_x was the number of collected females living to age x. Juvenile survival (l_1) was the survival rate of females from birth (bl_0) to the end of their first year (i.e., bl_1/bl_0). Pre-reproductive survival (l_p) was the mean annual survival rate of pre-reproductive age-classes (i.e., age-classes previous to and at maturation inclusive, l_1 for population 1, $(l_1 + l_2)/2$ for populations 2, 4, 5, and 6, and $(l_1 + l_2 + l_3)/3$ for population 3). The percentage of squirrels surviving to maturity was l_α (where α was rounded to whole years). Adult survival (l_a) was the mean annual survival rate of adults (i.e., mean of all adult l_{x+1}/l_x, for each population). Age-specific fecundity (m_x) was calculated after Birch (1948) and Caughley (1977) as 0.5 times the mean number of embryos or placental scars for all collected females of age x, assuming a 1:1 primary sex ratio. Variance in reproductive output (a measure of variation in immature survival) was defined as the variance (S^2) of mean litter size for each population. The ratio of adult/juvenile survival was the adult survival rate divided by the juvenile survival rate for the population.

Generation length (T_c) was calculated after Birch (1948) and Caughley (1977) as:

$$T_c = \sum xl_xm_x/\sum l_xm_x, \tag{3}$$

where the denominator equalled one. The degree of iteroparity (DI) was calculated after Taylor and Condra (1980) as:

$$DI = -\sum_{x-\alpha}^{\omega} l_xm_x\log l_xm_x, \tag{4}$$

where α was the age at maturity (rounded to whole years), and ω was the last age of reproduction for our sample.

Environmental variability was defined as the statistical variance (S^2) of daily maximum, minimum, and mean temperatures, of daily precipitation, and of annual growing-season length during 10 vegetative growing seasons (May–September 1965–74; later years were not available, those used are exemplary of later years; see Powell and MacIver, 1977; Zammuto, 1983). Growing-season length was the number of days the mean daily temperature rose above 5.6°C (see Boughner, 1964). A climatic station was located within 10 km of each of the six ground squirrel populations (Atmospheric Environment Service, 1965–74; Water Survey of Canada, Calgary District, 1965–74, $n = 1,248$ for each temperature and 937 for precipitation for each population–site).

All proportions were arcsine-transformed before subsequent analysis. The distributions of all variables were checked for normality with Kolmogorov-Smirnov one-sample tests and interrelationships among variables were determined using path analysis (4 variable general model, standardized beta technique, Kerlinger and Pedhazur, 1973; Nie et al., 1975) and/or bivariate correlation analysis (Zar, 1984). Specifically, juvenile survival (l_1), pre-reproductive survival (l_p), the percentage of squirrels surviving to maturity (l_α), variance in reproductive output (variance of litter size), and the ratio of adult/juvenile survival (l_a/l_1) were each examined with respect to α, T_c, and DI (=15 tests). Similarly, variability of daily maximum, minimum, and mean temperatures, of daily precipitation, and of growing-season length were each examined with respect to all eight of the above life-history variables (=40 tests). Generally, only significant ($P < 0.05$, two-tailed) correlations among the variables presumably relevant to bet-hedging theory are discussed. Zammuto (1983) and Zammuto and Millar (in press) contain detailed background information on the study area and ground squirrel populations.

RESULTS

Significant ($P < 0.05$) differences existed among populations for most life-history and environmental variables (Zammuto, 1983; Zammuto and Millar, in press). Specifically, age at maturity ($\chi^2 = 52.1$, $d.f. = 5$, $P < 0.001$), age-specific survival ($D = 20.4$, $d.f. = 5$, $P < 0.001$, Lee and Desu (1972) D_{stat}), litter size ($H = 17.9$, $n = 174$, $P < 0.01$, Kruskal-Wallis ANOVA), variance of litter size ($P < 0.001$, Bartlett F), the degree of iteroparity ($z = -1.95$, $n = 6$, $P < 0.05$, Wald-Wolfowitz), growing-season length ($F = 11.8$, $d.f. = 59$, $P < 0.001$, ANOVA), and variance of all climatic variables (all $P < 0.001$, Bartlett F, Kolmogorov-Smirnov two-sample tests) varied among populations (Tables 1 and 2).

TABLE 1.—*Age-specific net fecundities ($l_x m_x$) for females from six populations of Columbian ground squirrels.*

Age	Population					
	1	2	3	4	5	6
1	0.343 (21)*	0.137 (28)	0.000 (19)	0.079 (9)	0.000 (14)	0.000 (5)
2	0.312 (12)	0.385 (12)	0.224 (17)	0.388 (16)	0.296 (9)	0.291 (7)
3	0.223 (15)	0.293 (6)	0.291 (6)	0.273 (14)	0.335 (17)	0.286 (9)
4	0.095 (1)	0.116 (4)	0.282 (3)	0.223 (4)	0.229 (10)	0.266 (4)
5	0.036 (2)	0.000 (1)	0.154 (1)	0.044 (1)	0.138 (4)	0.168 (3)
6	0.000 (0)	0.014 (2)	0.057 (1)	0.000 (0)	0.000 (0)	0.000 (1)
7	0.000 (0)	0.048 (1)	0.000 (1)	0.000 (0)	0.000 (0)	0.000 (0)
Degree of iteroparity[1]	0.61	0.63	0.65	0.61	0.58	0.59

* Sample size in parentheses.
[1] After Taylor and Condra (1980).

The ratio of adult/juvenile survival was inversely associated with the degree of iteroparity ($r = -0.87$, $n = 6$, $P < 0.05$; Tables 1 and 2). The percentage of squirrels surviving to maturity (l_a) was positively associated with the degree of iteroparity ($r = 0.82$, $n = 6$, $P < 0.05$; Tables 1 and 2). These relationships were probably caused by the positive correlation between juvenile survival and the degree of iteroparity ($r = 0.93$, $n = 6$, $P < 0.01$; Tables 1 and 2) since a path analysis (Kerlinger and Pedhazur, 1973; Nie et al., 1975) among the three variables correlated ($P < 0.05$) with DI (variability of maximum temperature, l_1 and l_a) indicated that 85% of the variance in DI was associated with l_1 when the effects of maximum temperature variability were controlled.

Pre-reproductive survival increased with generation length ($r = 0.90$, $n = 6$, $P < 0.05$) and with age at maturity ($r = 0.98$, $n = 6$, $P < 0.001$) (Table 2). Variance in litter size was inversely associated with generation length ($r = -0.85$, $n = 6$, $P < 0.05$) and with the age at maturity ($r = -0.95$, $n = 6$, $P < 0.01$) (Table 2). A path analysis among l_p, variance of litter size, α, and T_c indicated that 77% of the variance in T_c was associated with α when the effects of l_p were controlled.

The greater the variability of daily maximum, minimum, and mean temperatures, the greater the adult/juvenile survival ratio ($r = 0.88$, $n = 6$, $P < 0.05$; $r = 0.95$, $n = 6$, $P < 0.01$; $r = 0.94$, $n = 6$, $P < 0.01$, respectively). The greater the variability of daily maximum temperatures the lower the degree of iteroparity ($r = -0.84$, $n = 6$, $P < 0.05$) and the lower the juvenile survival ($r = -0.90$, $n = 6$, $P < 0.05$). A smaller percentage of squirrels survived to maturity as the variability of daily minimum and daily mean temperatures increased ($r = -0.89$, $n = 6$, $P < 0.05$, and $r = -0.91$, $n = 6$, $P < 0.05$, respectively, Table 2). The greater the variance of growing-season length, the larger the percentage of squirrels surviving to maturity ($r = 0.91$, $n = 6$, $P < 0.01$), the lower the adult survival ($r = -0.85$, $n = 6$, $P < 0.05$), and the lower the adult/juvenile survival ratio ($r = -0.87$, $n = 6$, $P < 0.05$).

DISCUSSION

Regardless of the definition of immature survival (juvenile survival, pre-reproductive survival, or percentage surviving to maturity), many bivariate comparisons (7 of 15) of life-history variables we investigated led to the same conclusion. Specifically, the greater and more invariable the recruitment of immatures, the greater the degree of iteroparity, the longer the generation length, and the later the age at maturity. Not a single significant ($P < 0.05$) reversal of this trend was found. Therefore, our data do not conform to the theory of bet-hedging. We conclude that bet-hedging does not explain the life histories of these populations because most of our data show ($P < 0.05$) a pattern diametrically opposed to that predicted by the theory.

Since we did not study the variance of immature versus adult mortality, our study does not fully address bet-hedging theory, and therefore our conclusions could be modified by an ap-

TABLE 2.—*Mean life-history variables and environmental variability for six populations of Columbian ground squirrels.*

Population (sample size)†	Percentage of squirrels surviving to maturity* (l_a)	Adult survival* (%) (l_a)	Pre-reproductive survival* (%) (l_p)	Juvenile survival* (%) (l_j)	Generation length* (years) (T_c)	Age at maturity (α)	Litter size ± SD@	Environmental variability (S^2)‡				
								Temperature (°C)			Precipitation	Growing season length ± SD
								Maximum	Mean	Minimum	(mm)	(Days)
1 (51)	30	46	30	30	2.2	1.14	3.88 ± 1.45	38.1	20.0	15.8	28.7	119 ± 19.08
2 (53)	27	63	49	40	2.7	1.79	3.75 ± 1.04	37.9	21.0	15.5	49.6	113 ± 18.44
3 (48)	33	52	65	69	3.6	2.59	2.94 ± 0.73	34.7	18.1	14.4	39.6	114 ± 19.17
4 (44)	29	46	58	36	2.8	2.22	4.22 ± 0.89	37.5	17.3	14.7	31.9	112 ± 19.25
5 (54)	22	72	61	22	3.2	2.13	3.44 ± 0.85	40.4	28.5	24.7	37.5	76 ± 16.78
6 (18)	23	63	57	27	3.3	2.25	3.71 ± 0.99	37.5	26.5	21.1	31.7	77 ± 16.45

† Almost all females present in populations 1, 4, 5, and 6 were collected.
* From life tables (see Methods).
@ Embryos or placental scars.
‡ Ten years of growing-season daily records.

proach using such variance data when they become available (i.e., see Lacey et al., 1983; Real, 1980). However, our study does include variation in fecundity (variance of litter size) which should vary in a manner similar to variance of immature mortality according to bet-hedging arguments (Goodman, 1984). Correlations among variance of litter size in our study are opposite ($P < 0.05$) to those predicted by bet-hedging theory.

Many of the life-history variables we analyzed were redundant and autocorrelated, but this choice of variables was due to the family of predictions generated by bet-hedging theorists and our attempts to measure immature survival. Pre-reproductive survival, variance of litter size, and age at maturity could be considered true independent variables. Since pre-reproductive survival was positively associated with the age at maturity, our data support the idea that when ground squirrels mature later pre-reproductive survival is higher than when maturation is early (see Crandall and Stearns, 1982; Sibly and Calow, 1983). In addition, variance of litter size was inversely associated with the age at maturity indicating that variance of litter size is higher when the age at maturity is early. This relationship would be expected if young breeding animals produced smaller litters than old breeding animals, and this seems to be the case in *S. columbianus* (Zammuto, 1983). Bet-hedging theory predicts opposite trends for both of these pairwise comparisons.

There were four significant ($P < 0.05$) trends indicating climatic variability was inversely associated with survival of immatures (juvenile survival, pre-reproductive survival, or the percentage surviving to maturity) and the degree of iteroparity. These relationships are supportive of Hastings and Caswell's (1979) prediction that if environmental variability affects juvenile survival more than adult survival, then a decreased degree of iteroparity should be favored. However, three significant ($P < 0.05$) correlations among the percentage surviving to maturity, adult survival, and the adult/juvenile survival ratio, and the variance of growing-season length indicated the relationships between environmental variability and life histories are paradoxical. The trend for variance in growing-season length diametrically opposes the trend for variance in climate. The more variable the length of the growing season, the more squirrels survived to maturity, the lower the adult survival, and the lower the adult/juvenile survival ratio. These relationships suggest that adult survival may be adversely affected by increased variability of growing-season length, whereas immature survival is enhanced. Theory predicts that bet-hedging should not be found where a variable environment affects mortality of adults more than mortality of immatures (Murphy, 1968; Schaffer, 1974; Stearns, 1976). Perhaps the possible effect of variability in length of growing season on immature versus adult survival could have prevented bet-hedging from existing among these populations.

Why has the pattern between age-specific life history and climatic variability emerged? Perhaps the differential abilities of non-adults and adults to succeed in thermoregulation (Hill, 1983) may explain the pattern. If thermoregulatory success increases with age (as in marmots, Webb, 1984), more variable weather may adversely affect immature survival more than it affects adult survival by causing more variable thermal history (above or below ground). In short, thermal history may be responsible for differential mortality rates between immatures and adults (see Webb, 1984). Why has the pattern between age-specific life history and variance of growing-season length emerged? Perhaps variability of food resources (via variability of growing-season length) adversely affects survival of litter-producing adult females more than it affects survival of immatures. Energy for reproductive processes is derived, in part, from food resources during the year preceding litter production (Kiell and Millar, 1980). Increased variation in the amount of food or in the time food is available to adult females may be causing increased mortality of adult females (see Andersen et al., 1976; Dobson, 1984; Zammuto and Millar, in press).

The survival patterns for immatures were usually opposite to the patterns for adults throughout our study. Perhaps competitive interactions between immature and adult age-classes caused these patterns (Brown, 1981; Tschumy, 1982). Perhaps a stable equilibrium between immature and adult survival rates evolved within these populations (by perhaps density-dependent feed-

back; see Tschumy, 1982). The inverse relationship between the percentage surviving to maturity and adult survival ($r = -0.82$, $n = 6$, $P < 0.05$) supports this idea.

Bell (1980) refuted Stearns' (1976) test for the existence of bet-hedging in 23 species by claiming that the expected number of breeding seasons (Stearns' [1976] measure of the degree of iteroparity) was equal to the reciprocal of adult mortality so that the positive relationship Stearns (1976) found between these variables was guaranteed. In Stearns' (1976) analysis this may be true, but our data indicate that other variables influence this relationship. The reciprocal of adult mortality ($1/(1 - l_a)$, Table 2) was not significantly correlated with the expected number of breeding seasons (defined as the difference between generation length and the age at maturity) in our study ($r = 0.46$, $n = 6$, $P = 0.35$). Nor was it associated with the measure we used for the degree of iteroparity ($r = -0.52$, $n = 6$, $P = 0.29$). Most important, adult survival (inverse of adult mortality) and the measure of iteroparity we used were not correlated ($P > 0.39$). We must conclude that other variables influence this relationship.

Since the juvenile component but not the adult component of the adult/juvenile survival ratio was related to the degree of iteroparity ($P < 0.01$), we have found supportive evidence for the idea that either increased juvenile survival may select for increased iteroparity, or increased iteroparity may create a better-adapted juvenile (perhaps because of increased breeding experience or better genes) and this leads to increased juvenile survival. The hypothesis that the more adept juveniles are in coping with environmental variation, the more apt they are to increase their degree of iteroparity needs to be tested. There is preliminary support for this hypothesis in our study since juvenile survival was inversely associated with one measure of environmental variation and positively associated with the degree of iteroparity (both $P < 0.05$).

Our study indicates that most of the predictions of bet-hedging fail to be found when mean life-history traits and environmental variabilities are considered for *S. columbianus*. Proponents of bet-hedging theory may focus on our failure to measure variance of age-specific mortality and suggest that our conclusions are invalid. However, for this and nearly all age-specific studies of mammals, evidence indicates that bet-hedging may not exist in mammals (*contra* Murie, 1985). Specifically, only one mammalian genus (*Antechinus*) occasionally displays semelparity and all others are iteroparous (Braithwaite and Lee, 1979). This may indicate that adult mortality almost never fluctuates more than immature mortality in mammals or more semelparous mammalian species would exist in nature. Further, life-history characteristics among most mammalian species are highly uniform and seem to be more dependent upon body size than age-specific mortality (Calder, 1983; Lindstedt and Calder, 1981; Millar and Zammuto, 1983; Tuomi 1980; Western and Ssemakula, 1982).

Proponents of bet-hedging argue that relatively high mortality of immatures should lead to later maturation because organisms should save energy for somatic development so their offspring may have a better chance at surviving to maturity. Our data indicate that saving energy for somatic development may not be meaningful for an endotherm with relatively determinate growth. Furthermore, breeding costs are usually assumed to cause decreased subsequent survival but this may be of minor importance to endotherms (Smith, 1981). If survival costs to breeders are low, "tradeoffs" may not occur and bet-hedging need not exist in wild endotherms.

LITERATURE CITED

ABRAMS, P. 1983. Life-history strategies of optimal foragers. Theor. Pop. Biol., 24:22–38.

ANDERSEN, D. C., K. B. ARMITAGE, AND R. S. HOFFMANN. 1976. Socioecology of marmots: female reproductive strategies. Ecology, 57:552–560.

ATMOSPHERIC ENVIRONMENT SERVICE. 1965–74. Monthly Record: meteorological observations in Canada. Environment Canada, Downsview, Ontario.

BARCLAY, H. J., AND P. T. GREGORY. 1981. An experimental test of models predicting life-history characteristics. Amer. Nat., 117:944–961.

———. 1982. An experimental test of life history evolution using *Drosophila melanogaster* and *Hyla regilla*. Amer. Nat., 120:26–40.

BELL, G. 1976. On breeding more than once. Amer. Nat., 110:57–77.

———. 1980. The costs of reproduction and their consequences. Amer. Nat., 116:45–76.

BIRCH, L. C. 1948. The intrinsic rate of natural increase of an insect population. J. Anim. Ecol., 17:15–26.

BOAG, D. A., AND J. O. MURIE. 1981. Population ecology of Columbian ground squirrels in southwestern Alberta. Canadian J. Zool., 59:2230–2240.

BOUGHNER, C. C. 1964. The distribution of growing-degree days in Canada. Canadian Meterol. Mem. No. 17, Meterol. Branch, Dept. Transportation, 40 pp.

BRAITHWAITE, R. W., AND A. K. LEE. 1979. A mammalian example of semelparity. Amer. Nat., 113:151–155.

BRONSON, M. T. 1977. Altitudinal variation in the annual cycle and life history of the Golden-mantled ground squirrel (*Spermophilus lateralis*). Unpubl. Ph.D. dissert., Univ. Calif., Berkeley, 134 pp.

———. 1979. Altitudinal variation in the life history of the Golden-mantled ground squirrel (*Spermophilus lateralis*). Ecology, 60:272–279.

BROWN, G. C. 1981. Theoretical consequences of competition between successive generations on population stability and life cycle evolution. Theor. Pop. Biol., 20:150–167.

CALDER, W. A. 1983. Ecological scaling:mammals and birds. Ann. Rev. Ecol. Syst., 14:213–230.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York, 234 pp.

CHARLESWORTH, B. 1980. Evolution in age-structured populations. Cambridge Univ. Press, Cambridge, Great Britain, 300 pp.

CHARNOV, E. L., AND W. M. SCHAFFER. 1973. Life-history consequences of natural selection: Cole's result revisited. Amer. Nat., 107:791–793.

CRANDALL, R. E., AND S. C. STEARNS. 1982. Variational models of life-histories: when do solutions exist? Theor. Pop. Biol., 21:11–23.

DEEVEY, E. S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol., 22:283–314.

DEMASTER, D. P. 1978. Calculation of the average age of sexual maturity in marine mammals. J. Fish. Res. Board Canada, 35:912–915.

DOBSON, F. S. 1984. Mating systems, population dynamics, and life history patterns in ground squirrels. Unpubl. Ph.D. dissert., Univ. Michigan, Ann Arbor, Michigan, U.S.A., 127 pp.

GOODMAN, D. 1984. Risk spreading as an adaptive strategy in iteroparous life histories. Theor. Pop. Biol., 25:1–20.

HAIRSTON, N. G., E. J. OLDS, AND W. R. MUNNS. In press. Bet-hedging and environmentally cued diapause strategies of Diaptomid copepods. Internat. Assoc. Theor. Appl. Limnol.

HAUKIOJA, E., AND T. HAKALA. 1978. Life-history evolution in *Anodonta piscinalis* (Mollusca, Pelecypoda): correlation of parameters. Oecologia, 35:253–266.

HASTINGS, A., AND H. CASWELL. 1979. Role of environmental variability in the evolution of life history strategies. Proc. Natl. Acad. Sci., 76:4700–4703.

HILL, R. W. 1983. Thermal physiology and energetics of *Peromyscus* ontogeny, body temperature, metabolism, insulation, and microclimatology. J. Mamm., 64:19–37.

HOLGATE, P. 1967. Population survival and life history phenomena. J. Theor. Biol., 14:1–10.

KERLINGER, F. N., AND E. J. PEDHAZUR. 1973. Multiple regression in behavioral research. Holt, Rinehart & Winston, New York, 534 pp.

KIELL, D. J., AND J. S. MILLAR. 1980. Reproduction and nutrient reserves of arctic ground squirrels. Canadian J. Zool., 58:416–421.

LACEY, E. P., L. REAL, J. ANTONOVICS, AND D. G. HECKEL. 1983. Variance models in the study of life histories. Amer. Nat., 122:114–131.

LEE, E., AND M. DESU. 1972. A computer program for comparing K samples with right-censored data. Computer Programs in Biomed., 2:315–321.

LINDSTEDT, S. L., AND W. A. CALDER. 1981. Body size, physiological time, and longevity of homeothermic animals. Quart. Rev. Biol., 56:1–16.

MACARTHUR, R. H. AND E. O. WILSON. 1967. The theory of island biogeography. Princeton Univ. Press, New Jersey, 203 pp.

MICHOD, R. E., AND W. W. ANDERSON. 1980. On calculating demographic parameters from age frequency data. Ecology, 61:265–269.

MILLAR, J. S., AND R. M. ZAMMUTO. 1983. Life histories of mammals. An analysis of life tables. Ecology, 64:631–635.

MILLAR, J. S., AND F. C. ZWICKEL. 1972. Determination of age, age structure, and mortality of the pika, *Ochotona princeps* (Richardson). Canadian Zool., 50:229–232.

MURIE, J. O. 1985. A comparison of life history traits in two populations of Columbian ground squirrels in Alberta, Canada. Ann. Zool. Fenn., 173:43–45.

MURIE, J. O., AND M. A. HARRIS. 1982. Annual variation of spring emergence and breeding in Columbian ground squirrels (*Spermophilus columbianus*). J. Mamm., 63:431–439.

MURIE, J. O., D. A. BOAG, AND V. K. KIVETT. 1980.

Litter size in Columbian ground squirrels (*Spermophilus columbianus*). J. Mamm., 61:237–244.

MURPHY, G. I. 1968. Pattern in life history and the environment. Amer. Nat., 102:391–403.

NIE, N. H., ET AL. 1975. Statistical package for the social sciences. McGraw-Hill, New York, 675 pp.

PARSONS, P. A. 1982. Adaptive strategies of colonizing animal species. Biol. Rev., 57:117–148.

PIELOU, E. C. 1974. Population and community ecology. Gordon & Breach, New York, 424 pp.

POWELL, J. M., AND D. C. MacIVER. 1977. A summer climate classification for the forested area of the prairie provinces using factor analysis. N. For. Res. Cnt. Info. Rep. NOR-X-177.

REAL, L. A. 1980. Fitness, uncertainty, and the role of diversification in evolution and behavior. Amer. Nat., 115:623–638.

SCHAFFER, W. M. 1974. Optimal reproductive effort in fluctuating environments. Amer. Nat., 108:783–790.

SCHAFFER, W. M., AND M. D. GADGIL. 1975. Selection for optimal life histories in plants. Pp. 142–157, *in* Ecology and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Harvard Univ. Press, Cambridge, Massachusetts, 545 pp.

SIBLY, R., AND P. CALOW. 1983. An integrated approach to life-cycle evolution using selective landscapes. J. Theor. Biol., 102:527–547.

SMITH, J. N. M. 1981. Does high fecundity reduce survival in Song Sparrows? Evolution, 35:1142–1148.

STEARNS, S. C. 1976. Life history tactics: A review of the ideas. Quart. Rev. Biol., 51:3–47.

———. 1977. The evolution of life history traits: A critique of the theory and a review of the data. Ann. Rev. Ecol. Syst., 8:145–171.

———. 1980. A new view of life-history evolution. Oikos, 35:266–281.

TALLAMY, D. W., AND R. F. DENNO. 1981. Alternative life history patterns in risky environments: An example from lacebugs. Pp. 129–147, *in* Insect life history patterns: Habitat and geographic variation (R. F. Denno and H. Dingle, eds.). Springer-Verlag, New York, 225 pp.

TAYLOR, C. E., AND C. CONDRA. 1980. r- and K-selection in *Drosophila pseudoobscura*. Evolution, 34:1183–1193.

TSCHUMY, W. O. 1982. Competition between juveniles and adults in age-structured populations. Theor. Pop. Biol., 21:255–268.

TUOMI, J. 1980. Mammalian reproductive strategies: A generalized relation of litter size to body size. Oecologia, 45:39–44.

TUOMI, J., AND E. HAUKIOJA. 1979. An analysis of natural selection in models of life-history theory. Savonia, 3:9–16.

WATER SURVEY OF CANADA, CALGARY DISTRICT. 1965–74. Compilation of hydrometeorological record—Marmot (vols. 1–10) and Streeter Creek Basins (vols. 1–10). Dept. Fish. and Environment, Calgary, Alberta.

WEBB, D. R. 1984. Age-specific energetics of yellow-bellied marmots. Ecology, 65:725–731.

WESTERN, D., AND J. SSEMAKULA. 1982. Life history patterns in birds and mammals and their evolutionary interpretation. Oecologia, 54:281–290.

YOUNG, T. P. 1981. A general model of comparative fecundity for semelparous and iteroparous life histories. Amer. Nat., 118:27–36.

ZAMMUTO, R. M. 1983. Effects of a climatic gradient on Columbian Ground Squirrel (*Spermophilus columbianus*) life history. Unpubl. Ph.D. dissert., Univ. Western Ontario, London, Ontario, Canada, 104 pp.

ZAMMUTO, R. M., AND J. S. MILLAR. In press. Environmental predictability, variability, and *Spermophilus columbianus* life history over an elevational gradient. Ecology.

ZAR, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, New Jersey, 718 pp.

ADDENDUM

F. S. Dobson has recently pointed out to us that if the coefficient of variation, instead of the raw variance, was used to determine both of the relationships between the variance of growing-season length and the percentage of squirrels surviving to maturity and between the former and the adult/juvenile survival ratio, the correlations would still be significant but they would be of opposite sign ($r = -0.85$, $n = 6$, $P < 0.05$ and $r = 0.84$, $n = 6$, $P < 0.05$, respectively). This would indicate that the variance of growing-season length was *positively* correlated with climatic variability. Therefore, the statement in the third paragraph of page 657, "The trend for variance in growing-season length diametrically opposes the trend for variance in climate," may be unnecessary. Since the coefficient of variation corrects for biases caused by unequal means and means here are not equal, it is probably the more correct statistic to use.