# LIFE HISTORIES OF MAMMALS: ANALYSES AMONG AND WITHIN *SPERMOPHILUS COLUMBIANUS* LIFE TABLES[1]

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*Abstract.* Eleven theoretical predictions (or assumptions) of life history evolution are considered for the montane Columbian ground squirrel, *Spermophilus columbianus,* using age-specific survival and fecundity from six life tables of natural populations. The following statements are supported among age classes among populations, among age classes within populations, and (or) within age classes among populations: (1) mortality rates are high after birth, drop to a minimum by age 1 yr, and then rise with age; (2) fecundity increases with age and seldom decreases at the last age of reproduction; (3) reproductive value and residual reproductive value rise to a peak and then fall with age; (4) age-specific mortality rates and age-specific mortality rates covary inversely with reproductive value; (5) residual reproductive value, survival, and survival rates covary inversely with fecundity; (6) residual reproductive value is positively correlated with adult survival; (7) no relationships were found between fecundity and successive survival probabilities in the life table; (8) no relationship was found between age at maturity and life expectancy; (9) no relationship was found between litter size and generation length; (10) future fecundity is positively correlated with present fecundity; and (11) age-specific fecundity varies inversely with modified reproductive value. Life history patterns among populations, within populations, within age classes, and among species are not always similar, so that theoretical predictions should explicitly delineate the level of organization to which they pertain.

*Key words: age at maturity; age-specific; Columbian ground squirrel; demography; fecundity; life history; life tables; mammal; mortality; reproductive value; residual reproductive value; Spermophilus columbianus; survival.*

## INTRODUCTION

Mammalian life history traits of natural populations have been examined in the light of life history theory in several interspecific studies (Millar 1977, Blueweiss et al. 1978, Western 1979, Tuomi 1980, Millar and Zammuto 1983, Stearns 1983a). However, few studies have examined life history traits in several populations of one species (Smith 1978, Bronson 1979, Zammuto and Millar 1985a, b, Dobson et al. 1986). One reason for the lack of such studies is the difficulty of obtaining life-table data. Accurate aging techniques and tests of assumptions (net reproductive rate, $R_o = 1$; intrinsic rate of increase, $r = 0$; no year effects) needed to construct time-specific life tables have only recently begun development (Zammuto and Sherman 1986), so they are not available for many mammals. Therefore, zero age class cohorts must be followed throughout their lives before life tables can be constructed for most mammals. This vastly increases study logistics for long-lived mammals. Even when multiple life tables are available for a mammal, they have seldom been analyzed in light of life history theory (see Caughley 1977: 86, Millar and Zammuto 1983).

Recent arguments suggest that intraspecific life his-

tory patterns should consider bet-hedging theory (Murphy 1968, Charnov and Schaffer 1973, Stearns 1976), or another as yet unarticulated theory that considers age structure (Charlesworth 1980, Stearns 1983b). Nevertheless, most predictions of bet-hedging theory were contradicted by age-specific survival and fecundity patterns in different populations of Columbian ground squirrels, *Spermophilus columbianus* (Zammuto and Millar 1985b). Perhaps other age-specific, theoretical predictions are important for the evolution of intraspecific life history patterns. The life history literature contains a number of such predictions. The purpose of this study is to evaluate the importance of several of these predictions for the evolution of mammalian life histories.

I consider age-specific, theoretical predictions of life history evolution that do not directly pertain to *r–K* or bet-hedging theory, using six life tables for the herbivorous, montane Columbian ground squirrel. This species is relatively long lived (>3 yr), allowing examination of several age classes, and abundant, so that removed animals are quickly replaced. In addition, litter size and survival within populations are relatively stable from year to year when compared with many rodents (Murie et al. 1980, Boag and Murie 1981), and the influence of differing environmental conditions on the life history and population genetics among popu-

lations of this species has been documented (Dobson and Kjelgaard 1985a, b, Zammuto and Millar 1985a, b, Dobson et al. 1986).

Most of the life-table predictions appearing in the literature that were not directly related to r–k or bet-hedging theories and were testable by the data presented here were considered. Relationships among traits for entire age classes were examined under the assumption, supported by Lande (1982), that life history characteristics of age classes many times depict the summation of life history characteristics of individuals. No doubt some of these predictions may be examined using individuals or species instead of age classes, and conclusions from such studies may differ from conclusions made here. Heretofore, some of these predictions have been examined for individual Columbian ground squirrels, with results similar to those presented here (J. O. Murie and F. S. Dobson, *personal communication*). The predictions considered here are: (1) the age-specific mortality rate should be high after birth, should drop to a minimum prior to the age at maturation, and then should rise with age (Emlen 1970: 591, Preston 1972:168); (2) age-specific fecundity should rise to a peak and then should fall with age (Emlen 1970:593, Preston 1972:168); (3) reproductive value and residual reproductive value should rise to a peak and then should fall with age (Fisher 1958:28, Pianka and Parker 1975:457, Pianka 1976:779); (4) age-specific mortality and (or) mortality rates should be inversely related to reproductive value (Fisher 1958:29, Caughley 1966:917, Michod 1979:546); (5) residual reproductive value should vary inversely with age-specific fecundity (Pianka and Parker 1975:454, Snell and King 1977:886); (6) residual reproductive value should be positively correlated with adult survival (Williams 1966:689); (7) age-specific survival, survival rates, and (or) successive survival probabilities in the life table should vary inversely with age-specific fecundity (Snell and King 1977:887, Caswell 1980:20, 1982:521); (8) age at maturity should be positively correlated with life expectancy (Tinkle 1969:502, Wittenberger 1979: 442); (9) litter size should be inversely related to generation length (Hirshfield and Tinkle 1975:2229); (10) future fecundity should vary inversely with present fecundity (Caswell 1982:521); and (11) age-specific fecundity should vary inversely with modified reproductive value (Charlesworth 1980:242). Although some sample sizes for older age classes (age 4+) within populations are small (<5), the number of animals in younger age classes allows examination of most predictions (see Conley 1984:117).

Millar and Zammuto (1983) concluded that life-table characteristics of one population of a given mammal may be representative of many species. Hence, an intra- and (or) interpopulational consideration of these 11 predictions for six populations could help elucidate general relationships between age-specific survival and fecundity for other populations. The approach here is to determine correlations among life history traits—an approach termed the "strategic life history model" (Tuomi and Haukioja 1979:11).

## METHODS

I collected 506 Columbian ground squirrels ($\geq 1$ yr old) with Conibear traps from six undisturbed populations of similar adult density (10–15 individuals/ha), at elevations of 1300–2200 m, in the Rocky Mountains of southwestern Alberta during 1980 and 1981. Most of the animals present in four populations were collected so that statistics for these populations should approach real population parameters. Two populations were larger (>200 individuals) than the others so individuals were sampled as randomly as possible from these populations until $\approx 100$ were captured. Each population was studied at the birth-pulse (see Caughley 1977:6) within 4 wk of female emergence from hibernation. Age (annual adhesion lines in diastema of lower jawbone, checked against known-aged animals, following Millar and Zwickel (1972)), male maturity (males with pigmented scrota or scrotal testes were considered mature), female maturity (females with embryos or placental scars were considered mature), and litter size (embryos or placental scars) were determined.

Time-specific life tables were constructed under the assumption that stationary age-distributions were approached in these populations (see Caughley 1977:90, Charlesworth 1980:31, 42, 62, 78, Michod and Anderson 1980). The assumption of nearly stationary age-distributions for these populations was indirectly supported during long-term studies on four Columbian ground squirrel populations in the same region and on other populations of montane ground squirrels living under similar undisturbed conditions (Bronson 1979, Murie et al. 1980, Boag and Murie 1981, Dobson et al. 1986, Zammuto and Sherman 1986). The life tables were smoothed using the log-polynomial method described by Caughley (1977:96) to produce the greatest similarity possible between the time-specific life tables and the long-term age structures of the populations.

Age-specific survival, $l_x$, the proportion of animals living to age $x$, and the age-specific survival rate, $p_x$, the proportion of animals alive at age $x$ that survive to age $x + 1$, were calculated after Caughley (1977:85) as:

$$l_x = n_x/n_0, \qquad (1)$$

where $n_0$ was the number born and $n_x$ was the number living to age $x$, and as:

$$p_x = l_{x+1}/l_x, \qquad (2)$$

respectively. Age-specific mortality, $d_x$, the probability of dying between ages $x$ and $x + 1$, and the age-specific mortality rate, $q_x$, the proportion of animals alive at age $x$ that die before age $x + 1$, were calculated after Caughley (1966, 1977:85) as:

$$d_x = l_x - l_{x+1}, \qquad (3)$$

TABLE 1. Time-specific life table for population 1 (1300 m).

| Age (yr) | Number captured | Smoothed frequency[†] | $l_x$ | $m_x$ | $l_x m_x$ | $e_x$ | $v_x$ | $v_x{}^*$ | $d_x$ |
|---|---|---|---|---|---|---|---|---|---|
| 0 | 186[‡] | 180[§] | 1.000 | 0.000 | 0.000 | 1.567 | 1.00 | 1.00 | 0.750 |
| 1 | 43 | 45 | 0.250 | 1.143 | 0.286 | 2.268 | 4.00 | 2.86 | 0.100 |
| 2 | 26 | 27 | 0.150 | 1.917 | 0.288 | 2.113 | 4.77 | 2.85 | 0.061 |
| 3 | 19 | 16 | 0.089 | 2.533 | 0.225 | 1.876 | 4.80 | 2.27 | 0.039 |
| 4 | 8 | 9 | 0.050 | 2.500 | 0.125 | 1.560 | 4.04 | 1.54 | 0.022 |
| 5 | 5 | 5 | 0.028 | 2.750 | 0.077 | 1.000 | 2.75 | 0.00 | 0.028 |
| Total | 287 | | | | $R_0 = 1.00$[‖] | | | | |

$\bar{X}$ litter size $= 3.88 \pm 1.45$; $\alpha = 1.14$; $T_c = 2.42$

† See Caughley (1977:96).
‡ Sum of all litter sizes of collected females in population (=number born).
§ The product of the number born, $n_0$, and $\Sigma\, l_x m_x$ when $l_x$ was calculated using the number born.
‖ Net reproductive rate, $\Sigma\, l_x m_x$ (Pielou 1974:17).

and as:

$$q_x = d_x/l_x = l_x - l_{x+1}/l_x, \qquad (4)$$

respectively. Age-specific fecundity ($m_x$) was calculated after Caughley (1966:912, 1977:84) as one-half the mean number of embryos or placental scars for collected females of age $x$, assuming a 1:1 primary sex ratio. Therefore, $m_x$ values were weighted means and barren females reduced several $m_x$ values (see Caughley 1966: 912, 1977:82). Age-specific reproductive value, $v_x$, expectation of future offspring (Pianka 1978:106), was calculated as:

$$v_x = \sum (l_t/l_x)m_t, \qquad (5)$$

where $l_t/l_x$ was the probability of living from age $x$ to age $t$, and $m_t$ was the average number of females born to a female of age $t$. Age-specific residual reproductive value, $v_x{}^*$, reproductive value in the next age-interval with respect to the probability of surviving to that interval (Williams 1966), was calculated as:

$$v_x{}^* = (l_{x+1}/l_x)v_{x+1}. \qquad (6)$$

Mean age at maturity ($\alpha$) was calculated as:

$$\alpha = [(N_p)(a) + (N_q)(a + 1)]/(N_p + N_q), \qquad (7)$$

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) that more than one female was mature in a population, and $N_q$ was the number of females in the population not mature at age $a$. The calculation assumes that females not mature at age $a$ would have matured at age $a + 1$, an assumption that is supported by these data. This estimate of mean maturation-age preserved variation within populations and allowed more meaningful comparisons among populations than conventional estimates that state maturation-age as whole numbers. Generation length, $T_c$, the average age of females giving birth to all offspring or the turnover rate of the population (Pianka 1978:104), was calculated as:

$$T_c = \sum xl_x m_x / \sum l_x m_x, \qquad (8)$$

where the denominator equalled one. Age-specific life expectancy, $e_x$, expectation of further life (Pianka 1978: 103), was calculated as:

$$e_x = \sum l_y/l_x. \qquad (9)$$

The accuracy with which these terms describe the life history of a species depends on how closely a stationary age-distribution is approached (see Pielou 1974:29). The calculated life tables should accurately reflect population dynamics over the last decade because adult survival and litter size have been relatively stable in the study region during this time (Murie et al. 1980, Boag and Murie 1981, Dobson et al. 1986).

All proportions ($l_x$, $p_x$, $d_x$, $q_x$) were arcsine-transformed before parametric statistical analysis (Zar 1984: 239). Nonparametric tests were used whenever the raw, arcsine-transformed, and ln-transformed data were non-normally distributed within populations ($P < .05$, Kolmogorov-Smirnov one-sample tests) and (or) variances were heterogeneous among populations ($P < .05$, Bartlett-Box $F$). Relationships among life-table variables were examined among age classes among populations (=among populations), among age classes within populations (=within populations), and (or) within each age class (1–5 yr) among populations (=within age-classes) with correlation analyses (Nie et al. 1975). Age-specific life-table values were usually not analyzed when they were constant among populations because analyzing them unjustly weighted correlations. For example, $l_0$, $m_0$, $v_0$, $v_0{}^*$, and the last $p_x$, $q_x$ and $v_x{}^*$ of all life tables always approach 1.0 or 0.0 by definition, and thus these values were usually dropped from analyses. For predictions 3 and 4, $v_0$ or $v_0{}^*$ were exceptions to this method, since information was lost by their elimination from analyses. In addition, the oldest age classes in two populations were composed only of males, so they are not used in any fecundity analyses, and the age classes previous to these were treated as the last age classes of these life tables. All data appear in the tables and (or) figures for completeness.

TABLE 2. Time-specific life table for population 2 (1360 m). All Table 1 footnotes apply.

| Age (yr) | Number captured | Smoothed frequency | $l_x$ | $m_x$ | $l_x m_x$ | $e_x$ | $v_x$ | $v_x^*$ | $d_x$ |
|---|---|---|---|---|---|---|---|---|---|
| 0 | 105 | 95 | 1.000 | 0.000 | 0.000 | 1.960 | 1.00 | 1.00 | 0.547 |
| 1 | 58 | 43 | 0.453 | 0.339 | 0.154 | 2.119 | 2.21 | 1.87 | 0.200 |
| 2 | 23 | 24 | 0.253 | 1.667 | 0.422 | 2.004 | 3.34 | 1.68 | 0.116 |
| 3 | 12 | 13 | 0.137 | 2.167 | 0.297 | 1.854 | 3.10 | 0.93 | 0.063 |
| 4 | 7 | 7 | 0.074 | 1.500 | 0.111 | 1.581 | 1.72 | 0.22 | 0.042 |
| 5 | 1 | 3 | 0.032 | 0.000 | 0.000 | 1.344 | 0.52 | 0.52 | 0.021 |
| 6 | 2 | 1 | 0.011 | 1.500 | 0.017 | 1.000 | 1.50 | 0.00 | 0.011 |
| 7 | 1 | 0 | 0.000 | 2.500 | 0.000 | 0.000 | 2.50 | 0.00 | 0.000 |
| | | | | | $R_0 = 1.00$ | | | | |
| Total | 209 | | | $\bar{X}$ litter size $= 3.75 \pm 1.04$; $\alpha = 1.79$; $T_c = 2.44$ | | | | | |

## RESULTS AND DISCUSSION

Standing age structures did not differ between sexes for any population ($P > .05$, for all Lee and Desu [1972] $D_{stat}$), so males and females were combined for life-table calculations (Tables 1–6). Age structures (Table 7, $D = 34.2$, df $= 5$, $P < .001$, Lee-Desu $D_{stat}$) and litter sizes ($H = 17.9$, df $= 5$, $P < .01$, Kruskal-Wallis ANOVA) varied among populations.

### Prediction 1

The age-specific mortality rate ($q_x$) is the life-table parameter that is least affected by sampling biases, contains the most direct information about the mortality pattern, and is the most efficient parameter for comparing life tables among populations (Caughley 1966, 1977:87). Emlen (1970:591) predicted that $q_x$ should be high after birth, should drop to a minimum prior to the age at maturation, and then should rise with age after maturation (also see Caughley 1966). That is, maximum resistance to mortality should occur during the pre-reproductive period and resistance should decrease thereafter (Williams 1957, Hamilton 1966, Emlen 1970).

Overall, $q_x$ (for $x = 0, 1$) was high after birth, dropped to a minimum by 1 yr ($r = -0.79$, $n = 12$, $P < .01$; see Fig. 1A), and then increased with age (for $x \geq 1$ and $q_x > 0$) among populations ($r = 0.66$, $n = 28$, $P <$

.001), supporting Emlen's (1970) prediction. In populations 2, 4, and 5, $q_x$ (for $x \geq 1$ and $q_x > 0$) increased ($P < .05$) with age; in populations 1 and 6, it marginally increased ($P = .06$) with age; but did not ($P = .14$) increase with age in population 3 until later in life (Fig. 1A). $q_x$ remained relatively constant until age 5 in population 3 and then increased for two age classes (Fig. 1A). A constant $q_x$ from birth to age 5 may indicate that animals in population 3 may possess the same ability to respond to selective pressure from birth to age 5 yr (Emlen 1970). Alternatively, the pattern in population 3 may be a result of the higher juvenile survival coupled with the lower litter size (both $P < .05$) that population 3 possessed when compared to the other populations (Tables 1–6).

$q_x$ usually rose with age after age 1 yr, even though maturation did not occur until ages 2 or 3 yr in five populations. Therefore, high $q_x$ usually occurred after birth and then fell as predicted, but it usually began to rise after the juvenile year, even though maturation had not occurred by then in five populations. Overall, these data indicate moderate support of Emlen's (1970) prediction, since $q_x$ usually was high after birth, decreased during the pre-reproductive period, and then increased with age as he predicted, but variation existed with regard to the age that $q_x$ increased with respect to maturation-age, and population 3 did not follow the prediction.

TABLE 3. Time-specific life table for population 3 (1500 m). All Table 1 footnotes apply.

| Age (yr) | Number captured | Smoothed frequency | $l_x$ | $m_x$ | $l_x m_x$ | $e_x$ | $v_x$ | $v_x^*$ | $d_x$ |
|---|---|---|---|---|---|---|---|---|---|
| 0 | 53 | 56 | 1.000 | 0.000 | 0.000 | 2.518 | 1.01 | 1.00 | 0.393 |
| 1 | 42 | 34 | 0.607 | 0.000 | 0.000 | 2.501 | 1.66 | 1.66 | 0.232 |
| 2 | 32 | 21 | 0.375 | 0.529 | 0.198 | 2.429 | 2.68 | 2.15 | 0.143 |
| 3 | 15 | 13 | 0.232 | 1.083 | 0.251 | 2.310 | 3.48 | 2.40 | 0.089 |
| 4 | 7 | 8 | 0.143 | 1.833 | 0.262 | 2.126 | 3.90 | 2.06 | 0.054 |
| 5 | 1 | 5 | 0.089 | 2.000 | 0.178 | 1.809 | 3.31 | 1.32 | 0.035 |
| 6 | 1 | 3 | 0.054 | 1.500 | 0.081 | 1.333 | 2.17 | 0.67 | 0.036 |
| 7 | 2 | 1 | 0.018 | 2.000 | 0.036 | 1.000 | 2.00 | 0.00 | 0.018 |
| 8† | 2 | 0 | 0.000 | 0.000 | 0.000 | 0.000 | 0.00 | 0.00 | 0.000 |
| | | | | | $R_0 = 1.01$ | | | | |
| Total | 155 | | | $\bar{X}$ litter size $= 2.94 \pm 0.73$; $\alpha = 2.59$; $T_c = 3.83$ | | | | | |

† Age class composed only of males so not used in fecundity analyses.

TABLE 4. Time-specific life table for population 4 (1675 m). All Table 1 footnotes apply.

| Age (yr) | Number captured | Smoothed frequency | $l_x$ | $m_x$ | $l_x m_x$ | $e_x$ | $v_x$ | $v_x{}^*$ | $d_x$ |
|---|---|---|---|---|---|---|---|---|---|
| 0 | 114 | 74 | 1.000 | 0.000 | 0.000 | 1.907 | 1.01 | 1.01 | 0.662 |
| 1 | 17 | 25 | 0.338 | 0.222 | 0.075 | 2.683 | 2.99 | 2.77 | 0.081 |
| 2 | 23 | 19 | 0.257 | 1.344 | 0.345 | 2.214 | 3.64 | 2.29 | 0.081 |
| 3 | 21 | 13 | 0.176 | 1.536 | 0.270 | 1.773 | 3.35 | 1.81 | 0.081 |
| 4 | 5 | 7 | 0.095 | 2.500 | 0.238 | 1.432 | 3.36 | 0.86 | 0.054 |
| 5 | 3 | 3 | 0.041 | 2.000 | 0.082 | 1.000 | 2.00 | 0.00 | 0.041 |
| | | | | | $R_0 = 1.01$ | | | | |
| Total | 183 | | | $\bar{X}$ litter size = 4.22 ± 0.89; $\alpha$ = 2.22; $T_c$ = 2.94 | | | | | |

These results indicate that selective intensity to decrease $q_x$ should be highest between birth and age 1 yr in all populations except population 3, if selective intensity to decrease $q_x$ is highest where $q_x$ falls with age (Williams 1957, Emlen 1970:590). Perhaps selection operates most intensively on the juvenile age classes in populations 1, 2, 4, 5, and 6. Poor survival in juvenile age classes compared with other age classes supports this idea (Tables 1, 2, 4–6).

### Prediction 2

Emlen (1970:593) predicted age-specific fecundity ($m_x$) should rise to a peak and then should fall with age. That is, it is thought that natural selection should push the highest possible fecundity towards earlier and earlier age classes until opposing forces keep fecundity from further increasing and (or) opposing forces keep fecundity from occurring at earlier ages. After this, selection for fecundity should decrease with increasing age because selective forces no longer exist for high fecundity after high, early, successful fecundity occurs (Emlen 1970).

Overall, $m_x$ (for $x > 0$) increased with age among populations ($r = 0.60$, $n = 34$, $P < .001$; Tables 1–6, Fig. 1B), and increased with age within populations 1, 3, 4, and 6 (all $P < .05$), whereas the positive trends in populations 2 and 5 were not significant (both $P > .06$) (Tables 1–6, Fig. 1B). $m_x$ peaked at the last reproductive age in population 2 after a fall at age 5, whereas $m_x$ remained relatively stable for ages 3–5 yr within population 5 (Tables 2 and 5, Fig. 1B). $m_x$ dropped with age for one age class after peaking within popu-

lation 4, the only population where the predicted pattern could be considered to have been followed (Table 4, Fig. 1B).

Overall, these results indicate that $m_x$ increases with age as Emlen (1970) predicted, but it seldom decreases after peaking. Laboratory populations have displayed the predicted decrease after a peak for $m_x$ (Myers and Master 1983). Perhaps the predicted decrease of $m_x$ with age was not observed in natural populations because most individuals died before this "aging" effect could be observed. Alternatively, selection for fecundity may not decrease after peaking as Emlen (1970) predicted.

### Prediction 3

Fisher (1958:28), Pianka and Parker (1975:457), and Pianka (1976:779) predicted that reproductive value ($v_x$) and (or) residual reproductive value ($v_x{}^*$) should rise to a peak and then should fall with age. The arguments for this prediction relate to those for Prediction 2, but here $v_x$ and $v_x{}^*$ combine survival with $m_x$. The following is a synthesis of arguments advanced by Williams (1957, 1966), Emlen (1970), Pianka and Parker (1975), Pianka (1976), and Rose (1984). It is argued that individuals risk subsequent survival by reproducing. The youngest age class that reproduces has a greater survival risk caused by reproduction than older age classes, because of their relative inexperience at obtaining resources and producing offspring. This pattern causes each individual in younger age classes to contribute fewer offspring to future generations than those in older age classes. As individuals grow older, larger,

TABLE 5. Time-specific life table for population 5 (2000 m). All Table 1 footnotes apply.

| Age (yr) | Number captured | Smoothed frequency | $l_x$ | $m_x$ | $l_x m_x$ | $e_x$ | $v_x$ | $v_x{}^*$ | $d_x$ |
|---|---|---|---|---|---|---|---|---|---|
| 0 | 134 | 115 | 1.000 | 0.000 | 0.000 | 1.860 | 1.00 | 1.00 | 0.757 |
| 1 | 29 | 28 | 0.243 | 0.000 | 0.000 | 3.539 | 4.09 | 4.09 | 0.017 |
| 2 | 19 | 26 | 0.226 | 1.333 | 0.301 | 2.730 | 4.40 | 3.07 | 0.035 |
| 3 | 30 | 22 | 0.191 | 1.765 | 0.337 | 2.047 | 3.63 | 1.87 | 0.061 |
| 4 | 16 | 15 | 0.130 | 1.800 | 0.234 | 1.538 | 2.74 | 0.94 | 0.060 |
| 5 | 7 | 8 | 0.070 | 1.750 | 0.123 | 1.000 | 1.75 | 0.00 | 0.070 |
| | | | | | $R_0 = 1.00$ | | | | |
| Total | 235 | | | $\bar{X}$ litter size = 3.44 ± 0.85; $\alpha$ = 2.13; $T_c$ = 3.16 | | | | | |

TABLE 6.    Time-specific life table for population 6 (2200 m). All Table 1 footnotes apply.

| Age (yr) | Number captured | Smoothed frequency | $l_x$ | $m_x$ | $l_x m_x$ | $e_x$ | $v_x$ | $v_x{}^*$ | $d_x$ |
|---|---|---|---|---|---|---|---|---|---|
| 0 | 52 | 35 | 1.000 | 0.000 | 0.000 | 1.829 | 0.99 | 0.99 | 0.771 |
| 1 | 5 | 8 | 0.229 | 0.000 | 0.000 | 3.620 | 4.31 | 4.31 | 0.029 |
| 2 | 7 | 7 | 0.200 | 1.250 | 0.250 | 3.000 | 4.93 | 3.68 | 0.029 |
| 3 | 9 | 6 | 0.171 | 1.714 | 0.293 | 2.339 | 4.30 | 2.59 | 0.057 |
| 4 | 4 | 4 | 0.114 | 2.000 | 0.228 | 2.009 | 3.89 | 1.89 | 0.028 |
| 5 | 3 | 3 | 0.086 | 2.500 | 0.215 | 1.337 | 2.50 | 0.00 | 0.057 |
| 6† | 1 | 1 | 0.029 | 0.000 | 0.000 | 1.000 | 0.00 | 0.00 | 0.029 |
| Total | 81 | | | | | | | | |

$R_0 = 0.99$

$\bar{X}$ litter size $= 3.71 \pm 0.99$; $\alpha = 2.25$; $T_c = 3.37$

† Age class composed only of males so not used in fecundity analyses.

and more experienced, they obtain more resources and possess lower survival risks for each offspring produced than when they first bred. Thus, older animals contribute more offspring to future generations at a lower cost to survival than younger animals, and therefore $v_x$ and $v_x{}^*$ should increase with advancing age. After the maximum number of offspring are contributed to future generations (peaks of $v_x$ and $v_x{}^*$), it is argued that selective pressure to survive and reproduce is relaxed, senescence leads to decreased reproduction and survival with increasing age, and therefore $v_x$ and $v_x{}^*$ decrease with age (Williams 1957, 1966, Rose 1984).

$v_x$ (for $x \leq v_{max}$) rose to its maximum value with increasing age among populations ($r = 0.75$, $n = 21$, $P < .001$) and within populations 2 and 3 (both $P < .05$) (Tables 1–6, Fig. 1C). Similarly, $v_x{}^*$ (for $x \leq v_{max}{}^*$) marginally rose to its maximum value with increasing age among populations ($r = 0.52$, $n = 14$, $P = .06$) (Tables 1–6, Fig. 1D). The predicted fall of $v_x$ (for $x \geq v_{max}$) and $v_x{}^*$ (for $x \geq v_{max}{}^*$) with increasing age after each peaked was strongly supported among populations ($r = -0.69$, $n = 25$, $P < .001$, and $r = -0.77$, $n = 25$, $P < .001$, respectively; Tables 1–6, Fig. 1C, D). The predicted fall of $v_x$ (for $x \geq v_{max}$) with increasing age was supported within populations 3, 5, and 6 (all $P < .05$), and the fall of $v_x{}^*$ (for $x \geq v_{max}{}^*$) with increasing age was supported within populations 2–6 (all $P < .05$), and marginally within population 1 ($P = .06$) (Tables 1–6, Fig. 1C, D). The general rise and fall pattern between $v_x$ and age and $v_x{}^*$ and age has been found for six other mammals.

Animals of the age class where $v_x$ peaks contribute the most offspring to future generations (Fisher 1958: 27). $v_x$ peaked for age classes 2 or 3 yr in all populations except population 3 where it peaked at age 4 yr, whereas $v_x{}^*$ peaked at age 1 yr in all populations except population 3 where it peaked at age 3 yr (Tables 1–6, Fig. 1C, D). The pattern for $v_x{}^*$ within population 2 may be noteworthy. Population 2 displayed a semibimodal peak, probably caused by a nonreproductive 5-yr-old (Table 2, Fig. 1C, D). This pattern of $v_x$ indicates that, contrary to Pianka and Parker (1975:455), $v_x{}^*$ does not always maximize when $m_x = 0$.

All data indicate that $v_x$ and $v_x{}^*$ usually increase to

a peak and then fall with age among populations, among species, and within most populations of mammals. Therefore, these results are consistent with arguments that young animals have a greater survival risk attached to reproduction than older animals and that selective pressure to survive and reproduce is relaxed with increasing age in mammals (Williams 1957, 1966, Rose 1984).

### Prediction 4

Fisher (1958:29), Caughley (1966:917), and Michod (1979:546) predicted that age-specific mortality ($d_x$) and (or) age-specific mortality rates ($q_x$) should covary inversely with reproductive value ($v_x$). That is, high current mortality should reduce the average contribution of offspring to future generations. Michod (1979) and Charlesworth (1980:265) questioned the biological significance of such a relationship on mathematical grounds of autocorrelation. For example, this prediction may simply indicate that if animals die they will not produce offspring. However, this prediction may also indicate that age classes that are adept at resisting mortality are also adept at successful reproduction.

$q_x$ and $v_x$, and $d_x$ and $v_x$ were correlated inversely among populations ($r = -0.72$, $n = 34$, $P < .001$ and $r = -0.60$, $n = 39$, $P < .001$, respectively; Tables 1–6, Fig. 2A, B). $q_x$ and $v_x$ were correlated inversely within populations 1, 2, 5, and 6, and $d_x$ and $v_x$ were correlated inversely within populations 1 and 6 (all $P < .05$) (Tables 1–6). $d_x$ and $v_x$ were correlated inversely within

TABLE 7.    Differences† between standing age structures of the six populations.

| Popu-lation | Population | | | | | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| 1 | | NS | NS | NS | *** | ** |
| 2 | | | NS | *** | *** | *** |
| 3 | | | | * | ** | ** |
| 4 | | | | | NS | NS |
| 5 | | | | | | NS |

† Lee and Desu (1972) $D_{stat}$, significance levels: * $P < .05$, ** $P < .01$, *** $P < .001$, NS $= P > .05$, overall $D = 34.2$, df $= 5$, $P < .001$.
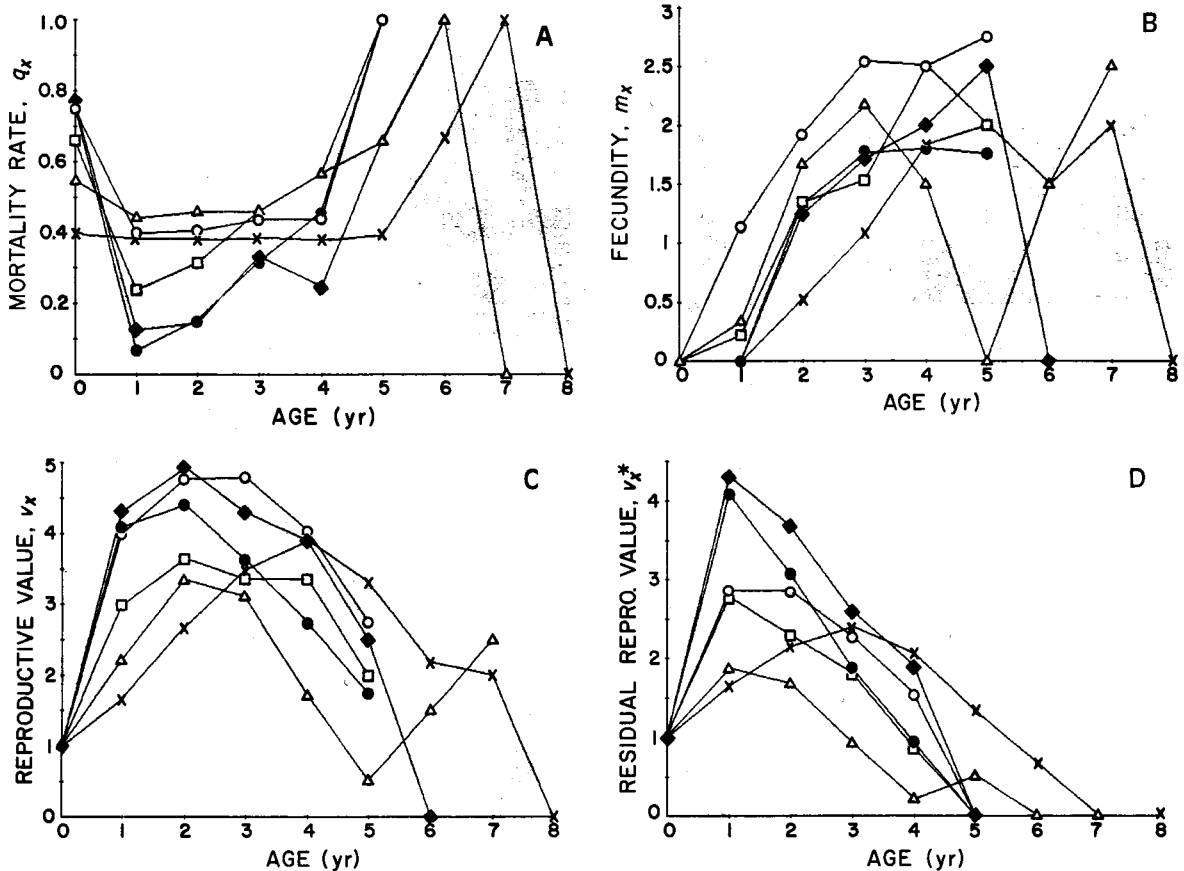
FIG. 1. Relationships of age vs.: (A) mortality rate, $q_x$; (B) fecundity, $m_x$ ($r = 0.60$, $n = 34$, $P < .001$); (C) reproductive value, $v_x$; and (D) residual reproductive value, $v_x^*$ for six populations of Columbian ground squirrels. Population 1 (O), 2 (△), 3 (X), 4 (□), 5 (●), and 6 (◆).

age classes 1 and 2 yr ($r = -0.91$, $n = 6$, $P < .05$ and $r = -0.93$, $n = 6$, $P < .01$, respectively), whereas $q_x$ and $v_x$ were not correlated (all $P > .05$) within any age class. Therefore the prediction that $q_x$ or $d_x$ should covary inversely with $v_x$ is supported among populations, within the majority of populations, and within two age classes.

These results moderately support the hypothesis that mortality-resistant age classes are more adept at contributing offspring to future generations than age classes not resistant to mortality, and they are also consistent with an autocorrelative cause for these inverse relationships. Perhaps other predictions will help shed light on this apparent theoretical and empirical underpinning (see Michod 1979 and Conclusions).

## Prediction 5

Pianka and Parker (1975) and Snell and King (1977) predicted that residual reproductive value ($v_x^*$) should vary inversely with age-specific fecundity ($m_x$). That is, if high fecundity has a greater cost in terms of decreased future fecundity than low fecundity, then high

fecundity in an age class should diminish the contribution of offspring to future generations by future age classes.

$v_x^*$ and $m_x$ (for $x > 0$) were marginally correlated inversely among populations ($r = -0.36$, $n = 28$, $P = .06$, Tables 1–6, Fig. 2C). $v_x^*$ and $m_x$ were correlated only within population 4 ($r = -0.96$, $n = 4$, $P < .05$) and they were not correlated within any age class (all $P > .50$, Tables 1–6). These results suggest that present levels of fecundity ($m_x$) may slightly ($P = .06$) reduce residual reproductive value ($v_x^*$) among populations and within one population, whereas $m_x$ does not seem to reduce $v_x^*$ within any age class. Therefore there is only weak support for the prediction that high fecundity in one age class diminishes the contribution of offspring to future generations by future age classes.

$m_x$ is a measure of reproductive effort (Williams 1966: 689, Hirshfield and Tinkle 1975:2228). Therefore, these results weakly ($P = .06$) support Willliams' (1966) prediction that reproductive effort should vary inversely with $v_x^*$ (contra Tuomi et al. 1983). However, Williams (1966) suggested this relationship should be found for interspecific comparisons, but it does not seem to exist
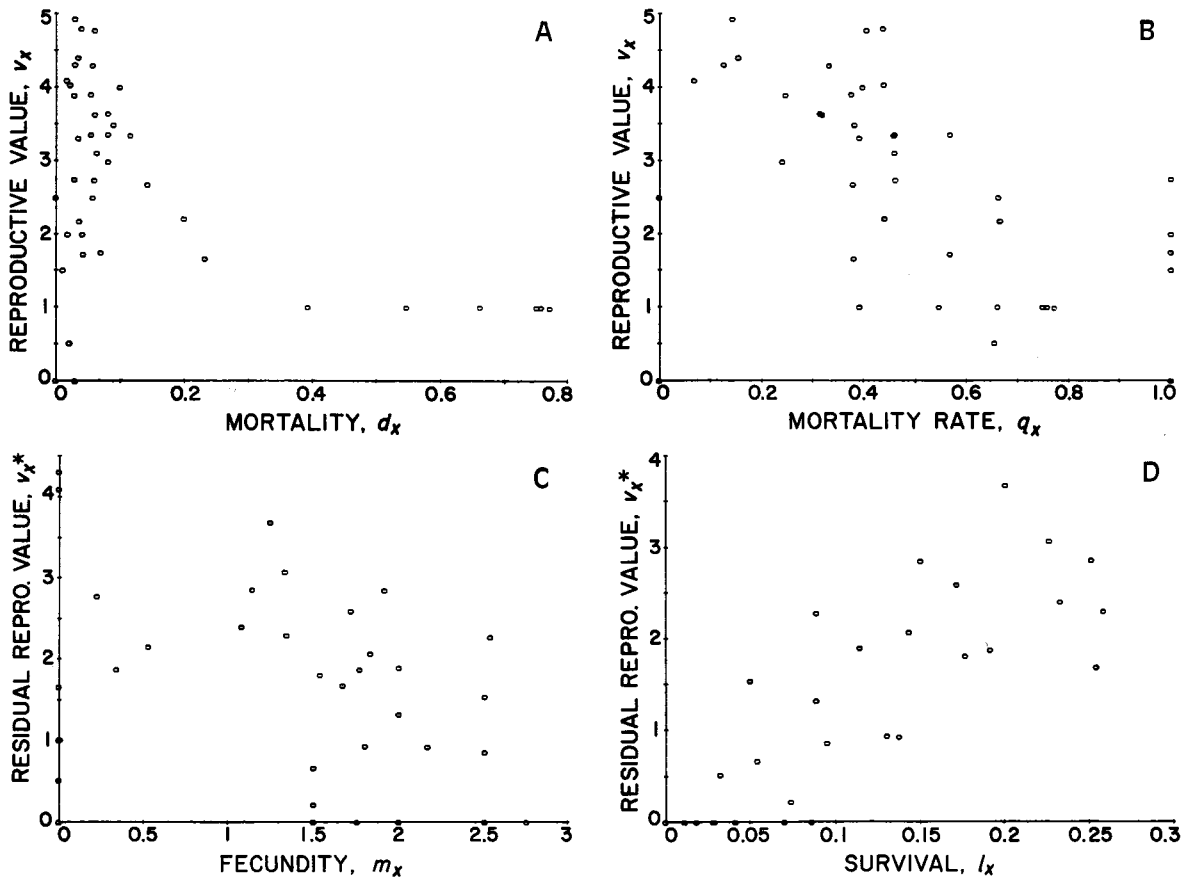
FIG. 2. Relationships of reproductive value, $v_x$ vs.: (A) mortality, $d_x$ ($r = -0.60$, $n = 39$, $P < .001$); and (B) mortality rate, $q_x$ ($r = -0.72$, $n = 34$, $P < .001$); and relationships of residual reproductive value, $v_x^*$ vs.: (C) fecundity, $m_x$ ($r = -0.36$, $n = 28$, $P = .06$); and (D) survival, $l_x$ ($r = 0.69$, $n = 21$, $P < .001$) for six populations of Columbian ground squirrels.

for interspecific studies of mammals (Millar and Zammuto 1983).

### Prediction 6

Williams (1966:689) predicted that residual reproductive value ($v_x^*$) should be positively correlated with adult survival ($l_x$, for $x \geq \alpha$). That is, age classes (or species) with low mortality rates should channel resources for reproduction into later life instead of during the present, since this allows low mortality to continue by the avoidance of increased stress from breeding. Channeling resources for reproduction into later life also maximizes reproductive output over a lifetime and best represents animals in future generations. High reproductive output in the present reduces future reproductive output because it shortens lifespan and thus reduces the average number of offspring contributed to future generations (Williams 1966). This evolutionary reason for a correlation between $v_x^*$ and $l_x$ may be real, but $v_x^*$ and $l_x$ may be correlated simply because both generally decrease with age and (or) $v_x$ is calculated using $l_x$ values. Nonetheless, the prediction is examined here because the degree of autocorrelation is not nec-

essarily high, and $v_x^*$ does not uniformly decrease with age (Tables 2 and 3).

$v_x^*$ and $l_x$ (for $x \geq \alpha$) were positively correlated among populations ($r = 0.69$, $n = 21$, $P < .001$), but not within any adult ($x \geq 2$) age class (all $P > .25$; Tables 1–6, Fig. 2D). $v_x^*$ and $l_x$ ($x \geq \alpha$) were significantly correlated only within population 3 ($r = 0.97$, $n = 4$, $P < .05$). However, all correlation coefficients between $v_x^*$ and $l_x$ within populations exceeded 0.89, but with only 1 or 2 df, they were insignificant, suggesting that this prediction needs further study within populations that possess >3–4 adult age classes.

Overall, these results support Williams' (1966) prediction among populations and are suggestive of support within populations. However, contrary to Williams (1966), this positive relationship may pertain only to intra- and interpopulational comparisons, since it does not appear to exist for interspecific comparisons among mammals (Millar and Zammuto 1983).

### Prediction 7

Williams (1966), Snell and King (1977), and Caswell (1980, 1982) predicted that age-specific survival rates

$(p_x)$, and (or) survival $(l_x)$, and (or) successive survival probabilities in the life table $(l_{x+2}/l_x, l_{x+3}/l_x$, see Caswell 1980), should vary inversely with age-specific fecundity $(m_x)$ (contra Gadgil and Bossert 1970:19). That is, costs of reproduction for a given age class should be manifested as reduced survival for the current and subsequent age classes (Caswell 1980, 1982). Schaffer (1981) and Yodzis (1981) argue Caswell's (1980) mathematics incorrectly assert that fecundity at age $x$ can affect fecundity or survival at age $x - 1$. Schaffer (1981) argues that this is only possible in the case of extended parental care. However, Caswell (1981) and Ricklefs (1981) maintain Caswell's (1980) original assertion was correct. Notwithstanding, the social structure of Columbian ground squirrel populations may involve extended parental care, since daughters either acquire their mother's nest site or maintain nest sites adjacent to their mother's throughout life (Harris and Murie 1984, King and Murie 1985). Therefore, there is empirical support indicating that Caswell's (1980, 1981) ideas could refer to Columbian ground squirrels, so his prediction is examined here.

$p_x$ ($=l_{x+1}/l_x$) and $m_x$ (for $x$ and $p_x > 0$), and $l_x$ and $m_x$ (for $x > 0$) were correlated inversely among populations ($r = -0.38$, $n = 28$, $P < .05$ and $r = -0.63$, $n = 33$, $P < .001$, respectively; Tables 1–6, Fig. 3A, B) supporting the first part of Prediction 7 and falsifying Gadgil and Bossert's (1970) opposing prediction. $p_x$ and $m_x$ (for $x$ and $p_x > 0$) were marginally correlated inversely only within population 4 ($P = .06$), whereas $l_x$ and $m_x$ were correlated inversely (all $P < .05$) within populations 1, 3, and 6, and they were marginally ($P = .06$) correlated inversely within population 4 (Tables 1–6). $l_x$ and $m_x$ were correlated inversely within age classes 2 and 3 yr (both $P < .05$), whereas $p_x$ and $m_x$ were not correlated within any age class (all $P > .25$). $l_{x+2}/l_x$ and $m_x$, and $l_{x+3}/l_x$ and $m_x$ were not correlated among populations, within populations, or within any age class (all $P > .05$, Tables 1–6, Fig. 3C, D).

These results indicate that current reproduction $(m_x)$ may be manifested as reduced current survival $(l_x)$, or reduced current survival rates $p_x$ among populations, within some populations, and within some age classes, whereas current reproduction does not appear to reduce subsequent survival $(l_{x+n}/l_x$, for $n > 1)$ among populations, within populations, or within age classes.
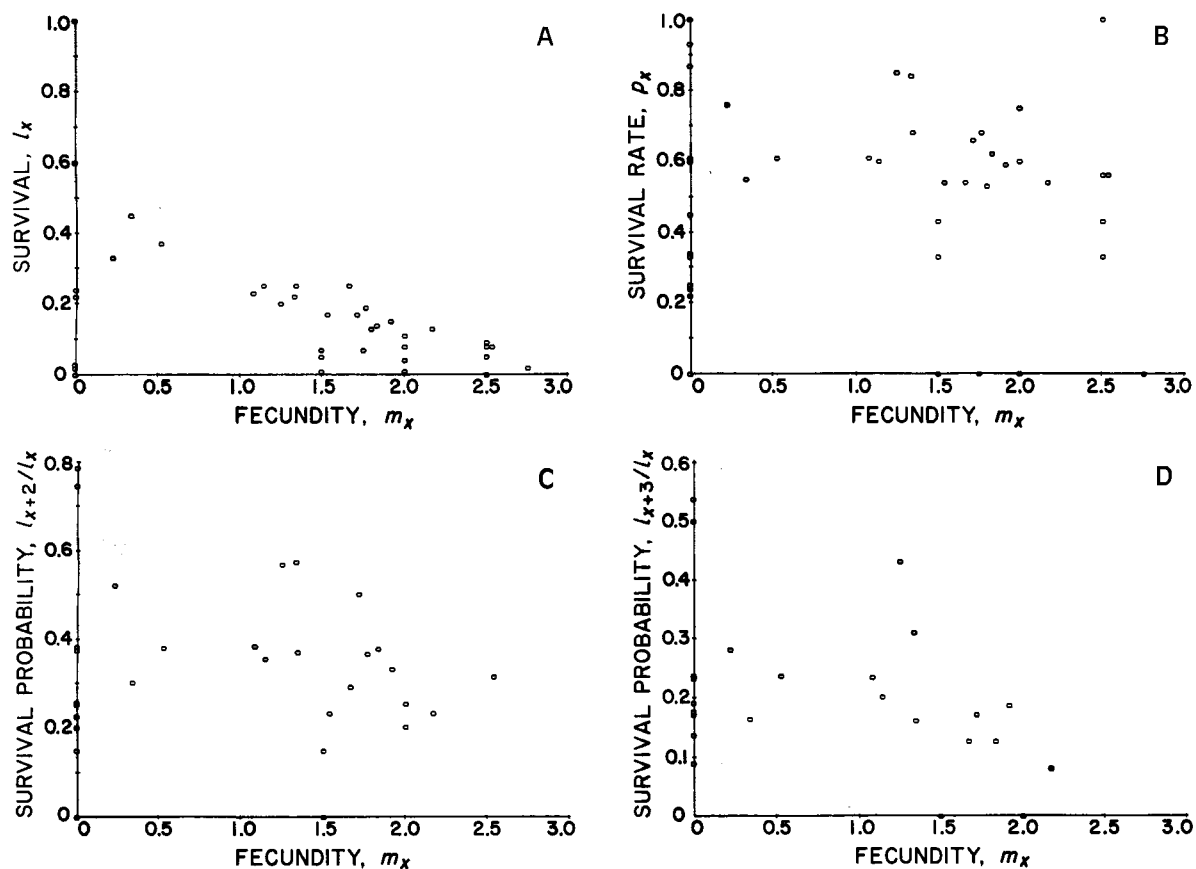


FIG. 3. Relationships of fecundity, $m_x$ vs.: (A) survival, $l_x$ ($r = -0.63$, $n = 33$, $P < .001$); (B) survival rates, $p_x = l_{x+1}/l_x$ ($r = -0.38$, $n = 28$, $P < .05$); and successive survival probabilities in the life table (C) $l_{x+2}/l_x$ ($r = -0.38$, $n = 19$, $P = .11$); and (D) $l_{x+3}/l_x$ ($r = -0.46$, $n = 13$, $P = .11$) for six populations of Columbian ground squirrels.
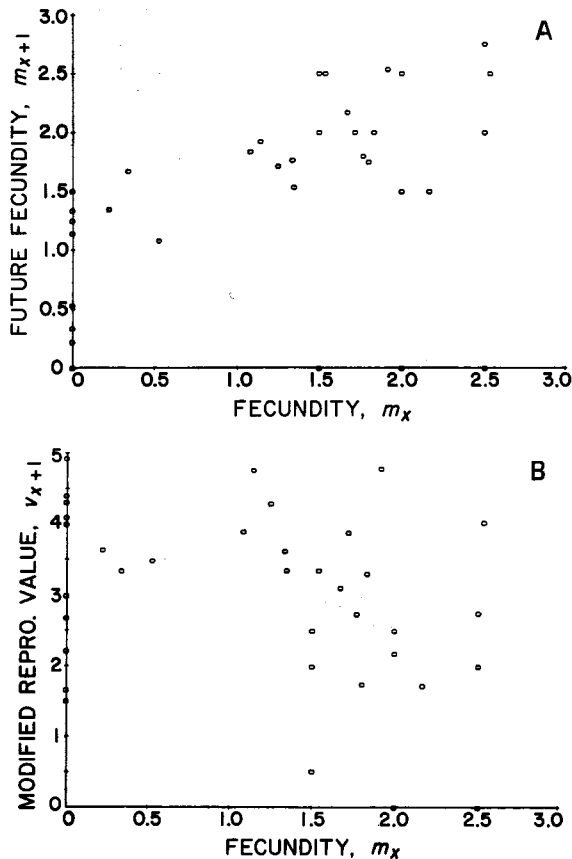
FIG. 4. Relationships of fecundity, $m_x$ vs.: (A) future fecundity, $m_{x+1}$ ($r = 0.59$, $n = 23$, $P < .01$); and (B) modified reproductive value, $v_{x+1}$ ($r = -0.40$, $n = 26$, $P < .05$) for six populations of Columbian ground squirrels.

Part of the reason that successive survival probabilities ($l_{x+n}/l_x$ for $n > 1$) were not significantly correlated with $m_x$ could have been caused by the automatic reduction of sample size as $n$ increased, but in general correlation coefficients were usually small between these traits. Further study with more age classes may be needed to test this portion of Prediction 7 sufficiently.

### Prediction 8

Tinkle (1969) and Wittenberger (1979) predicted age at maturity ($\alpha$) should be positively correlated with life expectancy ($e_x$). That is, high survival rates should favor delayed breeding. To elaborate, it is argued that the benefits of early breeding by young animals are drastically reduced when survival is high because breeding habitats are more often saturated by older animals than when survival is low, and this pattern leads to reduced reproductive success in young breeding animals. The pattern causes young animals to delay breeding, to reduce survival costs attached to breeding, and to increase their survival, which in turn leads to a positive correlation between age at maturity and life expectancy (Wittenberger 1979).

Neither life expectancy at birth ($e_0$) or maturity ($e_m$) were correlated with $\alpha$ among populations ($r = 0.78$, $n = 6$, $P = .07$ and $r = 0.32$, $n = 6$, $P = .54$, respectively, Tables 1–6), even though $\alpha$ is contained within $e_0$ (see Sutherland et al. 1986). Interspecific comparisons have indicated strong correlations among $\alpha$, $e_0$, and $e_m$ for mammals (see Millar and Zammuto 1983, Harvey and Zammuto 1985, but see Sutherland et al. 1986).

### Prediction 9

Hirshfield and Tinkle (1975) predicted that mean litter size ($\bar{m}_x$) should be inversely related to generation length ($T_c$). That is, shortening the generation time increases the rate at which alleles leading to high fecundity increase within the gene pool of the population (Hirshfield and Tinkle 1975). $\bar{m}_x$ and $T_c$ were not correlated among these populations ($r = -0.70$, $n = 6$, $P = .13$, Tables 1–6), even though $m_x$ is contained within $T_c$. Perhaps this correlation exists only among mammalian species (Millar and Zammuto 1983).

### Prediction 10

Caswell (1982) predicted that future fecundity ($m_{x+1}$) should vary inversely with present fecundity $m_x$. That is, a cost of high fecundity in any current age class is manifested as a reduction of fecundity in the next age class because, it is argued, there is a limited amount of energy available for reproduction during the lifetime of an animal, and using this energy at young ages reduces its availability at future ages (Caswell 1982). Conversely, $m_x$ (for $m_x > 0$) and $m_{x+1}$ were positively correlated among populations ($r = 0.59$, $n = 23$, $P < .01$; Tables 1–6, Fig. 4A). $m_x$ and $m_{x+1}$ were not correlated (all $P > .10$) within any population, whereas they were correlated between adjacent age classes 2 yr ($=m_x$) and 3 yr ($=m_{x+1}$) among populations ($r = 0.96$, $n = 6$, $P < .01$; Tables 1–6).

These results suggest that high fecundity in one age class is not costly in terms of future fecundity. One might ask how $m_x$ can increase with age, as Prediction 2 demonstrates, if the costs of high fecundity are manifested as reduced fecundity in the next age class. Clearly, Emlen's (1970) and Caswell's (1982) predictions are contradictory. The present study suggests that Columbian ground squirrel life tables do not follow Caswell's (1982) prediction when the costs of high fecundity are measured in terms of reduced fecundity in the subsequent age class.

### Prediction 11

Charlesworth (1980:242) predicted that age-specific fecundity ($m_x$) should vary inversely with modified reproductive value ($v_{x+1}$). That is, the costs of current reproduction should reduce the contribution of offspring to future generations by the next age class. $m_x$ and $v_{x+1}$ (for $m_x > 0$) were correlated inversely among populations ($r = -0.40$, $n = 26$, $P < .05$, Fig. 4B) and within population 6 ($r = -0.95$, $n = 4$, $P < .05$),

TABLE 8. Summary of results for each of 11 theoretical predictions (or assumptions) of life history evolution examined for six life tables of the Columbian ground squirrel.

| Prediction number | Predicted pattern of variables | Do results support prediction? | | |
|---|---|---|---|---|
| | | Among populations | Within populations | Within age classes |
| 1 | $q_x$ drops, then increases with age | drop: strong, ** increase: strong, *** | 3 strong§ 2 marginal§ 1 no support§ | ⋯ ⋯ ⋯ |
| 2 | $m_x$ increases, then drops with age | increase: strong, *** drop: no support, NS† | 1 strong 4 marginal 1 no support | ⋯ ⋯ ⋯ |
| 3 | $v_x$ increases, then drops with age | increase: strong, *** drop: strong, *** | 2–3 strong 2–3 marginal 1 no support | ⋯ ⋯ ⋯ |
| | $v_x^*$ increases, then drops with age | increase: marginal, AS‡ drop: strong, *** | 5 strong 1 marginal | ⋯ ⋯ |
| 4 | $q_x$ varies inversely with $v_x$ | strong, *** | 4 strong 2 no support | 5 no support |
| | $d_x$ varies inversely with $v_x$ | strong, *** | 2 strong 4 no support | 2 strong 3 no support |
| 5 | $v_x^*$ varies inversely with $m_x$ | marginal, AS | 1 strong 5 no support | 5 no support |
| 6 | $v_x^*$ increases with adult $l_x$ | strong, *** | 1 strong 5? (see text) | 4 no support |
| 7 | $p_x$ varies inversely with $m_x$ | strong, * | 1 marginal 5 no support | 4 no support |
| | $l_x$ varies inversely with $m_x$ | strong, *** | 3 strong 1 marginal 2 no support | 2 strong 3 no support |
| | $l_{x+2}/l_x$ varies inversely with $m_x$ | no support, NS | 6 no support | 3 no support |
| | $l_{x+3}/l_x$ varies inversely with $m_x$ | no support, NS | 6 no support | 2 no support |
| 8 | $\alpha$ increases with $e_0$ | no support, NS | ⋯ | ⋯ |
| | $\alpha$ increases with $e_m$ | no support, NS | ⋯ | ⋯ |
| 9 | $m_x$ varies inversely with $T_c$ | no support, NS | ⋯ | ⋯ |
| 10 | $m_{x+1}$ varies inversely with $m_x$ | converse strongly supported, ** | 6 no support | 1 converse strong 2 no support |
| 11 | $v_{x+1}$ varies inversely with $m_x$ | strong, * | 1 strong 5 no support | 3 no support |

* $P < .05$, ** $P < .01$, *** $P < .001$.
† NS = not significant.
‡ AS = approaches significance as $P \leq .06$.
§ Strong = significant; marginal = AS; no support = NS.

whereas no correlations existed within the other five populations (all $P > .10$), and no correlations (all $P > .20$) were found between any two adjacent age classes among populations (Tables 1–6).

These results indicate that current reproduction ($m_x$) may reduce reproductive value in the next age class ($v_{x+1}$) among populations, whereas the relationship seldom exists within populations or between adjacent age classes. I conclude that the costs of current reproduction may reduce the contribution of offspring to future generations by the next age class, but that this pattern is detected only when a large number of age classes or populations are examined.

CONCLUSIONS

The following statements pertain to life history patterns among populations, within populations, and (or)

within age classes of the Columbian ground squirrel: (1) maximum resistance to mortality usually occurs during the 1st yr of life, and resistance usually decreases thereafter (Prediction 1); (2) fecundity increases with age and seldom decreases at the last reproductive age (Prediction 2); (3) reproductive value and residual reproductive value rise to a peak, then fall with age, resulting in peak numbers of offspring being contributed to future generations by 2- or 3-yr-olds (Prediction 3); (4) high current mortality rates and current mortality may reduce the contribution of offspring to future generations by the current age class (Prediction 4); (5) high current fecundity may reduce current survival, current survival rates, and current residual reproductive value, whereas it probably does not reduce future survival (Predictions 5 and 7); (6) high adult survival may lead to high residual reproductive value through-

out life (Prediction 6); (7) delayed maturity does not clearly ($P = .07$) lead to increased life expectancy (Prediction 8); (8) high fecundity does not seem to lead to reduced generation time (Prediction 9); and (9) current fecundity does not seem to reduce future fecundity, whereas it may reduce the contribution of offspring to future generations by the next age class (Predictions 10 and 11) (see Table 8 for summary).

Why have the above patterns emerged for the Columbian ground squirrel? First, maximum resistance to mortality (Emlen 1970) and high age-specific mortality rates ($q_x$) usually occurred during the 1st yr of life, preceding the age at maturity, when most (>50%) squirrels died (Prediction 1; Tables 1–6, Fig. 1A). After squirrels reached maturity, the maximum number of offspring were contributed to future generations (Predictions 2–3; Tables 1–6, Fig. 1C, D). A relatively low mortality rate during midlife, after resistance to mortality had developed, was associated with the maximum number of offspring being contributed to future generations in most populations (Predictions 1–4). Thus, the highest numbers of offspring were contributed to future generations by squirrels with low mortality rates. This pattern supports the hypothesis that the most adapted (mortality resistant) squirrels produce the most offspring and these offspring constitute most of the animals in an average population of Columbian ground squirrels (also see Preston 1972:168). These considerations are consistent with the idea that the inverse relationship between mortality rates and reproductive value may have a biological reason, as well as a possible autocorrelative reason, for being prevalent in nature (also see Charlesworth 1980:265 and Michod 1979). Perhaps mortality and reproductive patterns simply follow the mathematical path of least resistance in nature (see Brooks and Wiley 1985: 89 for a similar phenomenon). Second, there is some support for the hypothesis that a trade-off exists between fecundity and survival, since survival patterns usually covaried inversely with fecundity patterns (Predictions 5 and 7), and high survival early in life was usually followed by high fecundity later in life (Prediction 6). Finally, there seemed to be conflicting answers as to whether high fecundity early in life always leads to reduced fecundity later in life, since some fecundity traits ($m_{x+1}$, $v_x^*$, $v_{x+1}$) were either positively (Prediction 10) or inversely (Predictions 5 and 11) correlated with current fecundity ($m_x$). However, these conflicts disappear when it is realized that residual reproductive value ($v_x^*$) and modified reproductive value ($v_{x+1}$) contain measures of survival as well as measures of fecundity. This realization allows one to interpret the inverse correlations between $m_x$ and $v_x^*$ and $m_x$ and $v_{x+1}$ as possibly being influenced by the survival portions of these fecundity/survival traits. Therefore, relationships between $m_x$ and $v_x^*$ and $m_x$ and $v_{x+1}$ may support the fecundity/survival trade-off hypothesis after all.

In sum, decreased mortality and increased survival seem to lead to increased fecundity, and increased fecundity seems to lead to decreased survival in the Columbian ground squirrel. Further studies on other mammals should be carried out when data become available to see if this intraspecific pattern is general for other mammals. Presently, data indicate that life cycle patterns for one mammal may be representative of many mammals, because design constraints may preclude significant differences in life history patterns among mammals (Millar and Zammuto 1983). This study indicated that patterns among populations, within populations, within age classes, and among species of mammals are not always similar, so that theoretical predictions should explicitly delineate the level of organization to which they pertain.

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