# WILEY

Is Mean Litter Size the Most Productive? A Test in Columbian Ground Squirrels
Author(s): Thomas S. Risch, F. Stephen Dobson and  Jan O. Murie
Source: *Ecology*, Vol. 76, No. 5 (Jul., 1995), pp. 1643-1654
Published by: Wiley
Stable URL: http://www.jstor.org/stable/1938165
Accessed: 27-06-2016 02:58 UTC

## REFERENCES
Linked references are available on JSTOR for this article:
http://www.jstor.org/stable/1938165?seq=1&cid=pdf-reference#references_tab_contents
You may need to log in to JSTOR to access the linked references.

*Wiley* is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*

# IS MEAN LITTER SIZE THE MOST PRODUCTIVE? A TEST IN COLUMBIAN GROUND SQUIRRELS[1]

Thomas S. Risch

*Department of Zoology and Wildlife Science, Auburn University, Auburn, Alabama 36849-5414 USA and Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802 USA*

F. Stephen Dobson

*Department of Zoology and Wildlife Science, and Alabama Agricultural Experiment Station, Auburn University, Auburn, Alabama 36849-5414 USA*

Jan O. Murie

*Department of Zoology, University of Alberta, Edmonton, Alberta Canada T6G 2E9*

*Abstract.* We studied the evolution of litter size in natural and experimentally manipulated populations of Columbian ground squirrels (*Spermophilus columbianus*) in eastern Washington state and southwest Alberta. Litter size at weaning in a large natural population (mean = 3.51 pups/litter, 248 litters) was significantly lower than the litter size (6 pups) that produced the most offspring surviving to yearling age class. This evidence contradicted Lack's "optimal litter size" hypothesis, which predicts that the most productive litter size should approximate the mean. Litter size had no significant effect on the subsequent survival or reproduction of mothers, contrary to the negative effects predicted by the "cost of reproduction" hypothesis. Litter success varied among years, and good and bad years for reproduction could be experimentally simulated with food supplementations. However, small samples of the largest litters rendered the "bad-years" hypothesis inappropriate for application to our data. Proportional survival of offspring was relatively constant among different litter sizes, contrary to the necessary condition of the "cliff edge" hypothesis of a dramatic decrease in survival of young from the largest litters. The data supported the "individual optimization" hypothesis most strongly. As predicted, the number of surviving offspring increased with litter size, although in one population the six largest litters (2.4% of 248 litters) suffered reduced success. In natural and food-supplemented populations, changes in maternal body mass were associated with changes in litter size ($r = 0.205$ to 0.926). Because survival of young remained relatively constant as litter size increased, these correlations resulted in greater offspring success for mothers in better body condition.

*Key words:* bad-years effect; cliff edge effect; costs of reproduction; individual optimization; Lack's hypothesis; life history; litter size; Spermophilus.

## INTRODUCTION

Lack's (1947, 1948a, 1954, 1966) seminal work on clutch size in birds stimulated a great deal of research on how the number of a female's offspring affects her reproductive success and the survival of her nestlings (see reviews by Klomp 1970, Winkler and Walters 1983, Murphy and Haukioja 1986, Godfray et al. 1991, VanderWerf 1992). Lack proposed that natural selection favors the clutch size that on average produces the most young that survive to reproductive age. He referred to the most productive clutch size as the "optimal clutch size." Lack predicted that the optimal clutch should equal the "average" or "most frequent" clutch size in a population. We defined the Lack clutch as the mean clutch, choosing the mean as the measure of central tendency.

According to Lack (1947, 1954), parents should have more young survive to reproductive age per nesting

attempt as clutch size increases, up to some critical clutch size (the "optimal clutch size"). When considering birds that feed their young, Lack argued that parents with clutch sizes larger than the optimal size were limited in their ability to provide adequate food for all individuals in the brood. At high clutch sizes, each nestling received less food as compared to nestlings in a smaller brood, resulting in lower survival of nestlings in broods that were too large.

Lack suggested brood manipulation experiments to test the relationship of offspring survival to clutch size. If eggs or hatchlings were transferred between nests, resulting in numerous broods smaller or larger than the mean, differences in subsequent offspring survival between the manipulated and control broods could be predicted. Contrary to Lack's prediction of low individual offspring survival from broods larger than the mean, brood manipulation studies often demonstrate that the most productive clutch size exceeds mean clutch size (for reviews see Lessells 1986, Ydenberg and Bertram 1989, VanderWerf 1992).

To explain the deviation between the most productive

and the mean clutch sizes, several modifications of Lack's hypothesis have been proposed. The "individual optimization" hypothesis (Perrins and Moss 1975, Högstedt 1980, Pettifor et al. 1988) suggests that each female lays a clutch size that is appropriate for her specific breeding situation, which is affected by body condition of parents and territorial quality. The clutch size laid by each female represents the one that will be the most productive for that female in terms of producing young that survive to reproductive age. One outcome of individual optimization may be the maintenance of mean clutch size below the most productive (Pettifor et al. 1988, Price and Liou 1989). Results of brood manipulation experiments showed that the clutch size originally laid by females was more productive than altered clutches (Högstedt 1980, Gustafsson and Sutherland 1988, Pettifor et al. 1988, Pettifor 1993). In clear contrast to Lack's hypothesis, which predicts low offspring survival of young from broods larger than the most productive, the individual-optimization hypothesis implies that survival of individual offspring is independent of clutch size (Högstedt 1981, Morris 1992).

The "cliff edge" hypothesis attributes reduced mean clutch size to interaction of the frequency distribution of litter size with the distribution of success among brood sizes (Mountford 1968). This hypothesis assumes that each genotype has a phenotypic distribution of clutch sizes. When these distributions are normal or skewed to the right (positive skew), and the proportion of surviving offspring by brood size is truncated to the right (negative skew), then the resulting mean clutch is smaller than the most productive.

The "bad-years" hypothesis predicts that when the most productive clutch is characterized by the geometric mean of number of offspring surviving, rather than the arithmetic mean, then the most productive clutch will equal mean clutch size (Boyce and Perrins 1987). When environmental variables related to fitness vary among years, the geometric mean number of offspring surviving is a more accurate fitness estimate than the arithmetic mean (Gillespie 1977, Ritland and Jain 1984, Bulmer 1985, Boyce and Perrins 1987). The bad-years hypothesis requires that variance in offspring survival increase with clutch size. Although some empirical evidence exists for this hypothesis (Boyce and Perrins 1987), small sample sizes at extreme clutch sizes may make the effect difficult to discern (Liou et al. 1993). Also, it may be difficult to determine the precise effect of a bad year, since over the duration of a field study under natural conditions most years may be intermediate between "bad" and "good" years.

Models of life history evolution often assume a "trade-off" between current reproductive effort and subsequent reproduction and/or survival (Lack 1966, Williams 1966, Stearns 1976, Bell 1980, Partridge and Harvey 1985). This trade-off has been articulated as the cost-of-reproduction hypothesis, which predicts

that increased reproductive effort results in costs such as reduced life span or reduced reproductive success later in life. Therefore, the clutch size that results in the most offspring produced within a lifetime could be smaller than the most productive clutch size in a single season, when parental mortality increases or subsequent fecundity decreases with clutch size (Charnov and Krebs 1974). The result would be a mean clutch size that is lower than the most productive clutch.

Lack (1948b) did not limit his ideas on optimal family size and offspring survival to birds. He hypothesized that mammalian populations have an "optimal" litter size at birth that on average produces the most offspring that survive to reproduce. Lack outlined mechanisms to explain limits in litter size (Lack 1948b) similar to those he had previously suggested for limits in clutch size for birds (Lack 1947). He proposed that mothers raising litters larger than the optimal were unable to provide adequate care for the young (viz., milk resources during lactation). As litter size increased beyond the mean, mortality of individual offspring should increase.

Despite the abundance of studies on birds, remarkably few studies have addressed offspring survival in relation to litter size in natural populations of mammals (but see Morris 1986, Boutin et al. 1988, Rieger 1991, Morris 1992, Hoogland 1995). The most productive litter was larger than mean litter size in white-footed mice (*Peromyscus leucopus*; Morris 1992). Morris rejected the cost of reproduction and the bad-years hypotheses as explanations for this pattern. The majority of evidence for white-footed mice supported the cliff-edge hypothesis as an explanation for the distribution of litter size. Like all studies that have examined these hypotheses to date, Morris' (1992) data were insufficient to offer a compelling rejection of all the alternative hypotheses, as some results supported individual optimization.

Columbian ground squirrels (*Spermophilus columbianus*) provide an excellent opportunity for examining hypotheses about litter size because their reproductive ecology and life histories have been well studied. Research has addressed phenotypic plasticity of life history traits (Dobson and Kjelgaard 1985a, Dobson and Murie 1987, Dobson 1988), classical models of life history evolution (Zammuto and Millar 1985a, b), the effect of food availability on reproduction and recruitment (Dobson and Kjelgaard 1985a, b, Dobson 1995), effects of litter size on population dynamics (Festa-Bianchet and King 1991), juvenile mortality due to infanticide (Balfour 1983, Waterman 1984, Dobson 1990), and the effect of body size on life history patterns (Dobson 1992, Dobson et al. 1992).

Columbian ground squirrels do not pay short-term phenotypic "costs" for larger litters, in terms of decreased parental survival or smaller subsequent litters (Murie and Dobson 1987, Hare and Murie 1992), although we should point out that the latter study lacked

sufficient sample sizes. To date, however, Lack's ideas about number of offspring and subsequent modifications have not been specifically examined in these hibernating, ground-dwelling rodents. The aim of our study was to evaluate the hypotheses outlined above as they apply to the relationship between litter size and juvenile survival in Columbian ground squirrels.

## METHODS

Columbian ground squirrels were studied from 1983 to 1990 on a 9-ha area in the Turnbull National Wildlife Refuge (hereafter called "Turnbull") in Washington State, USA (47°26' N, 117°36' W; elevation 695 m; Murie 1992), and in southwestern Alberta, Canada from 1981 to 1986 (Dobson and Kjelgaard 1985a, b, Dobson 1988, 1995). In Alberta, two low-elevation populations (50°30' N, 114°44' W; elevation 1580 m) and two high-elevation populations (50°30' N, 114°57' W; elevation 2100 m) were monitored. The populations at low elevation (3.5 and 1.2 ha) were 1 km apart on opposite sides of the Highwood River, while the populations at high elevation (1.4 and 1.2 ha) were 2 km apart on opposite sides of Mt. Lipsett.

Life history data were collected in a similar manner in all populations. Ground squirrels were trapped after first emergence from hibernation in early to mid-March, late April to early May, and late May to early June, respectively, at the three sites described above. All squirrels were ear tagged with a numbered metal tag in each ear and given a unique mark on the dorsal pelage with hair dye. Ear tags and/or dye marks were renewed as needed on recapture.

To ensure that litters were assigned to the appropriate females, and to gain precise counts of litter size, juvenile emergence dates were estimated when possible by adding 24 d for gestation (Shaw 1925, Murie and Harris 1982) and 27 d for lactation (Murie 1992) to the date of female breeding. Date of female breeding was recorded by observing aboveground copulations, documenting behavioral evidence associated with underground copulation, or by noting the presence of copulatory plugs or observing sperm in vaginal smears. Date of breeding was approximated for other females from the appearance of the vulva (Murie and Harris 1982). Near the calculated time of emergence, each nest burrow was checked 1–3 times per day for appearance of juveniles. It was, therefore, possible to capture most juveniles within 1–3 d of emergence using standard live traps or wire traps placed over nest burrows. Data on litter size excludes females for which we were uncertain that all juveniles had been captured or seen.

Females were considered successful at raising a litter to weaning if juveniles appeared above ground, or, in a few cases in which nest burrows were unknown, females were assigned a litter when they were observed with juveniles not attributed to neighboring females. Females were considered unsuccessful if no juveniles emerged from their burrows and nipples appeared flat-tened and dried after previously being swollen and surrounded by matted hair.

In Alberta, all populations were monitored for reference in the spring of 1981. Five days after juvenile emergence began, high protein horse feed (an enriched mixture of grains) was provided ad libitum in the center of two populations (one low and one high). The second population at each elevation was monitored without food supplementation for reference. Food supplementation on experimental sites continued throughout the active seasons of ground squirrels until 5 d after the first juvenile emergence in 1983. At that time food supplementation was stopped, and all populations were monitored through the summer of 1986 (for more details, see Dobson and Kjelgaard 1985b, Dobson 1988). Since density of food-supplemented populations increased and then decreased dramatically after supplementation (Dobson and Kjelgaard 1985b, Dobson 1995), years subsequent to feeding can be considered "bad years" in terms of reproduction and offspring survival, while years during supplementation can be considered "good years." Although food supplementation did not occur throughout the entire reproductive period in 1981, we conservatively designated 1981 as a good year because offspring survival was universally high throughout 1981 to 1983. This assumption was further supported because offspring survival by litter size varied significantly between good years and bad years (see *Results: Bad-year effect*).

Ground squirrels give birth in burrows, so litter size cannot be determined easily at birth. Young can be counted as they emerge from natal burrows, however, to accurately enumerate litter size near time of weaning. Differences in litter size from time of birth in the laboratory to weaning after being returned to the field are not dramatically different in Columbian ground squirrels. Murie et al. (1980) investigated the decrease in litter size from birth to weaning in three populations of Columbian ground squirrels that had different mean litter sizes. Despite a different range of litter sizes among the populations, the decrease in litter size from birth to weaning was similar (14–17%) among the populations. This decrease in litter size from birth to weaning was similar to the 12% decrease found in Uinta ground squirrels (*Spermophilus armatus*; Slade and Balph 1974), which exhibit no significant difference between litter size at birth and litter size at weaning.

Survival to subadult (yearling) age can also be accurately measured for these ground squirrels, since yearlings remain in close proximity to their natal areas, and dispersal ordinarily does not occur until the summer after yearlings emerge from hibernation (Boag and Murie 1981, Murie and Harris 1984).

## RESULTS

Litter size of Columbian ground squirrels at Turnbull ranged from 1 to 8 young (Table 1). We first considered the potentially confounding effects of female age and

TABLE 1. Distribution and performance of litters for Columbian ground squirrels at Turnbull, 1983–1990.

| Variable | Litter size (no. young) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Frequency (no. litters) | 26 | 41 | 49 | 75 | 32 | 19 | 4 | 2 |
| % Litter failure | 0.58 | 0.43 | 0.42 | 0.24 | 0.09 | 0.11 | 0.0 | 0.0 |
| Proportional survival | 0.42 | 0.32 | 0.28 | 0.36 | 0.33 | 0.32 | 0.17* | |
| Variance in offspring survival | 0.71 | 0.79 | 0.96 | 1.06 | 0.97 | 1.12 | ⋯† | ⋯ |

  \* Value for litter sizes of 7 and 8 combined.
  † Not computed due to low sample size.

yearly variation on the relationship between juvenile survival and litter size. Litter size at Turnbull varied among years (Table 2), and with age of females (Fig. 1; ANOVA $F$ = 5.45, df = 6, 246, $P$ < 0.0001). Therefore, an analysis of covariance was performed, which considered the effects of year and female age on the relationship between litter size and number of offspring surviving (with litter sizes of 7 and 8 young pooled due to low sample size). None of the interaction terms in this analysis were significant (all $Ps$ > 0.39). Without consideration of interactions the analysis of covariance revealed no significant age effect ($F$ = 0.87, df = 6, 244, $P$ > 0.53), and the effect of year only approached significance ($F$ = 1.79, df = 7, 244, $P$ > 0.09). Therefore, litter size data from Turnbull were pooled among ages of females and years in subsequent analyses. The sample included females that gave birth to litters in more than one year, which violated the assumption of independence. However, a female's litter size in one year was found to have no significant influence on her litter size in the following year (see *Results: Costs of reproduction*). This result was similar to that reported for Columbian ground squirrels in Alberta (Murie and Dobson 1987). We therefore retained all observations in our analyses.

We investigated whether our measure of productivity should be adjusted for variation in breeding date. Date of juvenile emergence was used as a measure of breeding date. Date of juvenile emergence varied among years (Table 3). Breeding date had no significant interaction with litter size (ANCOVA $F$ = 0.90, df = 7, 207, $P$ > 0.51), and no significant effect on the number of recruits from each litter size ($F$ = 2.34, df = 1, 207, $P$ > 0.13). To correct for variation in breeding date among years we repeated the above analysis of covariance using a measure of breeding date adjusted by the mean of each year, where the date of each litter emergence was subtracted from the mean of that year (Table 3). This analysis also revealed no significant influence of date of juvenile emergence on the number of recruits from each litter size ($F$ = 0.09, df = 1, 207, $P$ > 0.76). Date of juvenile emergence was recently reported to have no effect on females' annual reproductive success in another population of Columbian ground squirrels in Alberta (King et al. 1991). Thus, our estimates of productivity did not include a correction for breeding date.

Our measure of litter size at Turnbull included litters that may have been affected by badger predation before emergence. However, exclusion of litters emerging from natal burrows that showed badger activity had no effect on any of our conclusions.

Number of young surviving increased linearly with litter size at Turnbull except the largest litters, which exhibited an apparent decline in production (Fig. 2). Reference populations in Alberta, at both low and high elevation, were not significantly different in production of surviving offspring by litter size from the pattern evident at Turnbull (Fig. 2). In contrast to Turnbull however, the Alberta reference populations had a smaller range of litter sizes (low elevation 1–4 young; high elevation 1–3 young), and did not show the decrease in recruitment with litter size for the largest litters. Due to lower sample sizes in Alberta (Fig. 2), we pooled

TABLE 2. Litter size of Columbian ground squirrels and number of offspring surviving to 1 yr of age per litter at Turnbull (means ± 1 SE).*

| Variable | 1983 | 1984 | 1985 | 1986 |
|---|---|---|---|---|
| Litter size | 3.62 ± 0.315 | 3.19 ± 0.168 | 2.62 ± 0.329 | 4.37 ± 0.220 |
| Number surviving | 1.81 ± 0.344 | 0.83 ± 0.146 | 1.00 ± 0.170 | 1.35 ± 0.149 |
| Sample size | 16 | 36 | 24 | 40 |

| Variable | 1987 | 1988 | 1989 | 1990 |
|---|---|---|---|---|
| Litter size | 2.96 ± 0.260 | 4.00 ± 0.241 | 3.39 ± 0.288 | 3.47 ± 0.277 |
| Number surviving | 1.18 ± 0.206 | 1.23 ± 0.193 | 0.85 ± 0.169 | 1.19 ± 0.170 |
| Sample size | 28 | 39 | 33 | 32 |

  \* Litter size varies among years (ANOVA: $F$ = 4.89, df = 7, 247, $P$ < 0.0001), as does the number of offspring surviving (ANOVA: $F$ = 2.22, df = 7, 245, $P$ < 0.033). Mean litter size by year is correlated with mean number of offspring surviving by year (Spearman rank correlation: $r_s$ = 0.738, $n$ = 8 years, $P$ < 0.036).
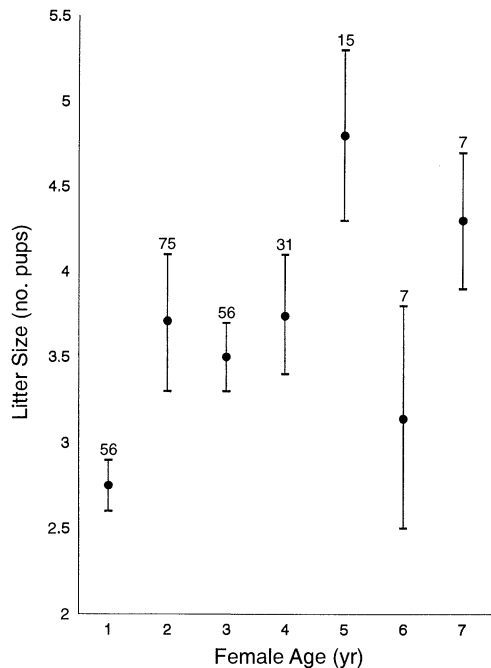
FIG. 1. Litter size for female Columbian ground squirrels by age at Turnbull (means ± 1 SE) . Sample sizes (no. litters) are given above error bars. Age given includes individuals of known age ($n$ = 147 females) and individuals assigned a minimum known age ($n$ = 100 females). Exclusion of individuals with a minimum known age does not alter any conclusions.
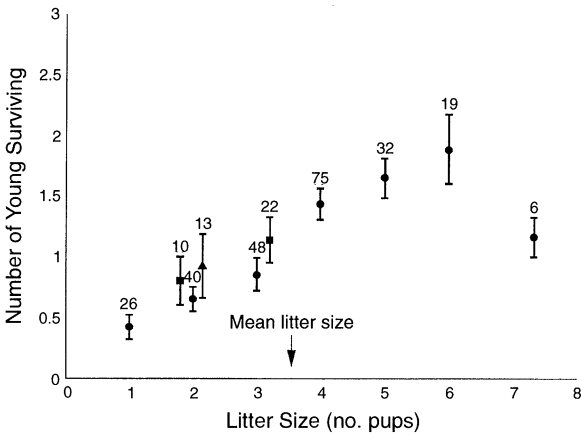


FIG. 2. Number of offspring surviving to 1 yr of age from different litter sizes of Columbian ground squirrels (means ± 1 SE). ● Turnbull; ■ Alberta low elevation reference population; ▲ Alberta high elevation reference population. Pooled litter size classes are: litters of 7 and 8 pups at Turnbull; litters of 1 with 2 pups and 3 with 4 pups at Alberta low elevation; litters of 1–3 pups at Alberta high elevation. Values for pooled litter sizes appear at the mean point for each grouping. "Mean litter size" refers to the Turnbull population. Sample sizes (no. litters) are given above error bars.

litter sizes 1–3 young at high elevation, and at low elevation pooled litter sizes 1 and 2 and litter sizes 3 and 4 young, for comparison with the data on recruitment from Turnbull. Comparing the pooled recruitment at high elevation to the litter size of 2 young at Turnbull revealed no significant difference ($t$ = 0.967, df = 16, $P$ > 0.35), nor did the distribution of recruitment by litter size differ between the low elevation reference population and the Turnbull population (litter sizes of 1 and 2 pups pooled from Alberta, vs. litter size 2 at Turnbull, $t$ = 0.678, df = 48, $P$ > 0.50; 3 and 4 pooled to litter size 3 at Turnbull: $t$ = 1.202, df = 68, $P$ > 0.23).

### Lack's hypothesis

A regression of the number of juveniles surviving on litter size at Turnbull revealed a significant association (Fig. 2; $r^2$ = 0.16, $n$ = 246, $P$ < 0.0001). The most productive litter size was 6 young. To address whether juvenile survival from the largest litters (litter sizes 7 and 8 pups, $n$ = 6 litters) was unusually low we generated a null expectation. The number of offspring surviving was regressed on litter size for litter sizes 1–6 pups ($r^2$ = 0.19, $n$ = 240 litters, $P$ < 0.0001), to predict the mean number of juveniles expected to survive to 1 yr of age from litters of 7–8 young. We used the variance about the regression to calculate the standard error of this predicted value, yielding $\bar{X}$ ± 1 SE = 2.5 ± 0.31 young using $n$ = 6 litters). The value predicted from the regression was significantly larger than the observed survival of young from litters larger than six ($\bar{X}$ = 1.2 juveniles; $t$ test, $t$ = 3.2, df = 5, $P$

TABLE 3. Date of juvenile emergence for litters of Columbian ground squirrels at Turnbull. Day of year is given as mean ± 1 SE; mean calendar date is given in parentheses. All analyses on timing of reproduction exclude data from 1983 due to low sample size.

| Variable | 1983 | 1984 | 1985 | 1986 |
|---|---|---|---|---|
| Date of emergence | 120 ± 0.70 (30 April) | 134 ± 0.68 (14 May) | 140 ± 0.63 (20 May) | 123 ± 0.42 (3 May) |
| Sample size (no. litters) | 6 | 30 | 20 | 33 |
| Variable | 1987 | 1988 | 1989 | 1990 |
| Date of emergence | 125 ± 0.62 (5 May) | 129 ± 0.54 (9 May) | 140 ± 0.90 (20 May) | 129 ± 0.73 (9 May) |
| Sample size (no. litters) | 26 | 36 | 32 | 32 |

* Date of juvenile emergence varies among years (ANOVA: $F$ = 97.56, df = 6, 208, $P$ < 0.0001).

< 0.02), suggesting a significant decline in productivity for the largest litters.

Litter size at weaning in this population averaged $3.51 \pm 0.10$ young ($n = 248$ litters [$\bar{X} \pm 1$ SE]; Fig. 1). We adjusted mean litter size by excluding yearlings, since yearlings gave birth to smaller litters than older females at Turnbull (Fig. 1; $\bar{X} = 2.75$ vs. 3.73 pups, respectively; $t$ test, $t = 5.24$, $P < 0.0001$). We compared the adjusted (viz., older female) mean litter size of 3.73 pups to the most productive litter size of 6 pups, and found a highly significant difference (comparison with a known standard, Bailey 1974; $t = 20.4$, $P < 0.0001$).

### Individual optimization

The regression of number of offspring surviving on litter size suggested that production increased with litter size with the exception of litter sizes of 7 and 8 young, which had reduced survival. To examine whether this reduced survival was due to a high incidence of total litter failure we regressed the proportion of litters that failed to produce at least one recruit (arcsine transformed) on litter size. This regression revealed a significant negative association between litter size and the percentage of total litter failure (Table 1; $r^2 = 0.95$, df = 7, $P < 0.0001$).

To examine whether survival of individual juveniles was independent of litter size, we regressed the proportion of young surviving (arcsine transformed) on litter size. This regression was weighted by litter size, and was not significant at Turnbull (Table 1; $r^2 = 0.0001$, $n = 246$ litters, $P > 0.87$). A pattern similar to the one shown in Table 1 was found for all the Alberta populations, and the regression of proportional offspring survival to litter size was not significant at either reference population in Alberta (low elevation $r^2 = 0.001$, $n = 32$ litters, $P > 0.87$; high elevation $r^2 = 0.06$, $n = 13$, $P > 0.41$), or at either experimental population in Alberta, both during food supplementation (low elevation $r^2 = 0.01$, $n = 42$ litters, $P > 0.49$; high elevation $r^2 = 0.03$, $n = 16$, $P > 0.52$), and subsequent to food supplementation (low elevation $r^2 = 0.02$, $n = 112$ litters, $P > 0.10$; high elevation $r^2 = 0.10$, $n = 29$, $P > 0.06$). The above results suggest that survival of individual offspring was independent of litter sizes.

Structural growth in Columbian ground squirrels is determinate, leveling off at age 2 yr (Dobson 1992). Therefore, changes in mass in mothers $\geq 2$ yr old should reflect changes in physiological condition. We investigated the relationship between annual change in mass (from emergence from hibernation in one spring to the next spring's emergence) and concurrent annual change in litter size (from summer to summer). We predicted a significant association, despite the confounding influence of mothers gaining significant mass from the time of first emergence from hibernation to the early summer when litters emerge (J. O. Murie and F. S. Dobson, *unpublished data*). The result was a significant

correlation at Turnbull (Fig. 3a; $r = 0.21$, $n = 96$ litters, $P < 0.05$). In Alberta annual change in mass was positively correlated with annual change in litter size in all 4 populations, but only significantly in 3 populations: low elevation experimental (Fig. 3b; $r = 0.30$, $n = 98$ litters, $P < 0.003$), high elevation experimental (Fig. 3c; $r = 0.39$, $n = 28$, $P < 0.04$), high elevation reference (Fig. 3d; $r = 0.93$, $n = 10$, $P < 0.001$), low elevation reference (Fig. 3e; $r = 0.49$, $n = 12$, $P > 0.109$).

### Cliff-edge hypothesis

At first glance, the distribution of litter size at Turnbull showed a tail to the right, suggesting a positively skewed distribution (Table 1; $g_1 = 0.215$), but this skew was not significant (Sokal and Rohlf 1981: 174; $t = 0.349$, $n = 248$ litters, $P > 0.50$). Proportional survival of offspring at Turnbull exhibits no significant association with litter size.

### Bad-year effect

Litter size was significantly larger in experimental populations during food supplementation ("good years"), than after cessation of food supplementation ("bad years"; Dobson 1988, 1995). At high elevation, litters were 43% larger during good years, while at low elevations this difference was 42%. At Turnbull there was a 67% difference in litter size between the two most extreme years (Table 2). Comparison of this percentage difference at Turnbull to the percentage increase in the Alberta populations demonstrated the presence of good and bad years for reproduction during the course of the eight years of data collection at Turnbull. At Turnbull, mean litter size by year showed a significant association with the number of offspring surviving per litter by year (Table 2).

For experimental populations in Alberta, the number of offspring surviving from litters at each size was higher during good years at both elevations (Figs. 4 and 5). For example, individuals in litters of 3 pups were significantly more likely to survive in good than bad years (low elevation $t = 7.47$, df = 54, $P < 0.0001$; high elevation $t = 3.44$, df = 19, $P < 0.003$). Means of offspring survival by litter size at Turnbull fell within the range of variance delineated by experiments in Alberta (compare Fig. 2 to Figs. 4 and 5). Litter size and mean number of offspring surviving to 1 yr of age varied significantly among years at Turnbull (Table 2).

Variance in offspring survival increased with litter size at Turnbull (Table 1; litter sizes 1–6 pups; $r^2 = 0.80$, df = 1,5, $P < 0.01$). Among-year variance in surviving offspring from litters of 3 pups at Turnbull was compared to litters of 3 pups in experimental populations in Alberta where experiments caused the environment to fluctuate by extremes. This comparison showed a dramatic increase in the variance in the Alberta populations (167% higher at low elevation, $F =$
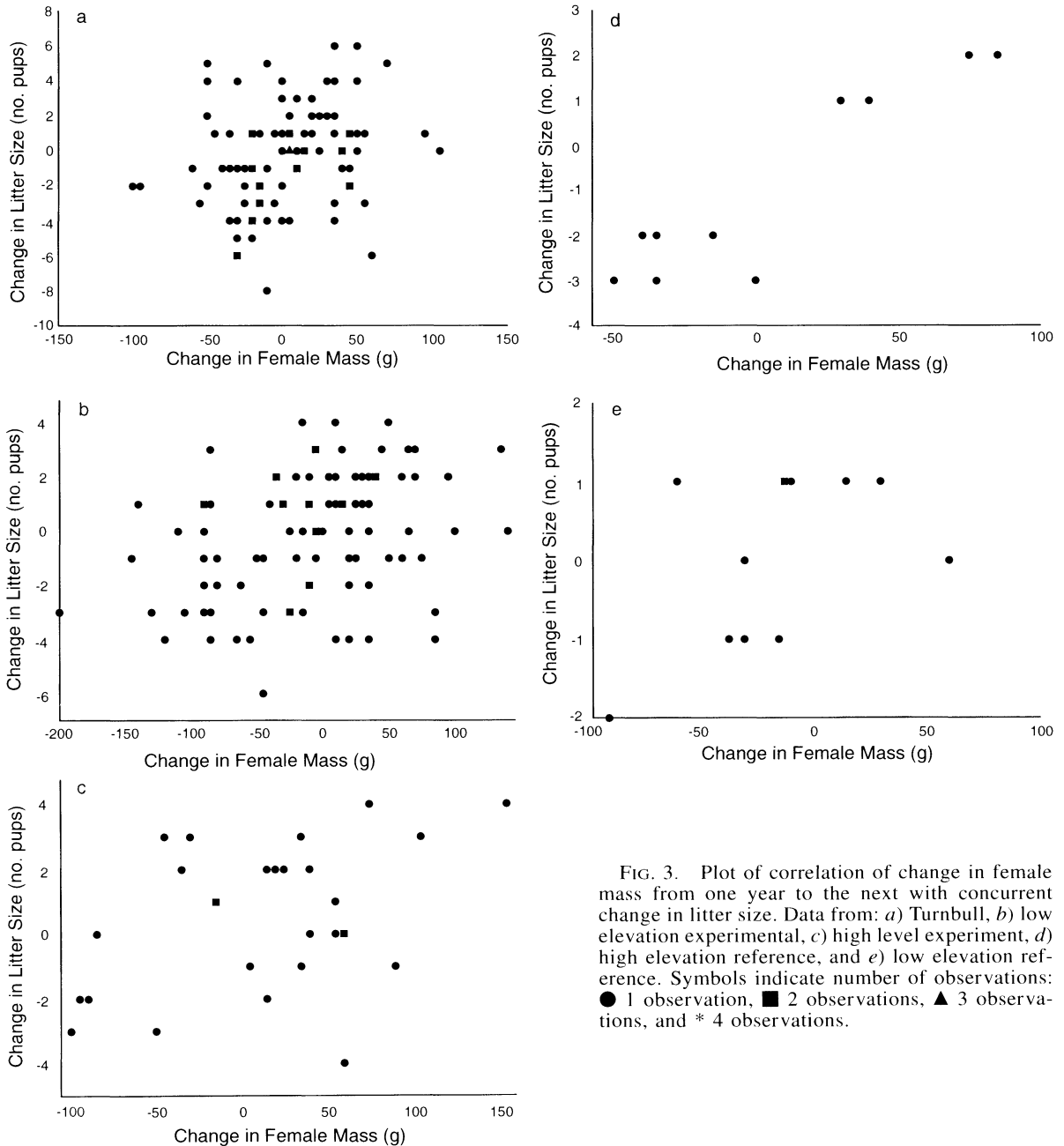
FIG. 3. Plot of correlation of change in female mass from one year to the next with concurrent change in litter size. Data from: *a*) Turnbull, *b*) low elevation experimental, *c*) high level experiment, *d*) high elevation reference, and *e*) low elevation reference. Symbols indicate number of observations: ● 1 observation, ■ 2 observations, ▲ 3 observations, and * 4 observations.

16.77, df = 4, 7, $P < 0.003$; 107% higher at high elevation, $F = 10.72$, df = 4, 7, $P < 0.009$).

### Costs of reproduction

We investigated whether large litters affected either parental survival or subsequent litter size for female ground squirrels at Turnbull. Since yearlings had a significantly smaller litter size than adults, they were excluded from these analyses. There was no significant heterogeneity in the distributions of mothers that did and did not survive until the next breeding season among different litter sizes (Table 4; $\chi^2 = 3.18$, df = 5, $P > 0.50$). Next, we compared mean litter size of mothers that survived to the next year ($\bar{X} = 3.59$ pups) to mothers that failed to survive ($\bar{X} = 3.36$ pups), and this difference was not significant ($t = 1.03$, df = 112, $P > 0.33$). Finally, a female's litter size in one year was found to have no significant association with her litter size in the following year (Fig. 6; Kendall correlation; $r = 0.03$, $n = 110$, $P > 0.726$).
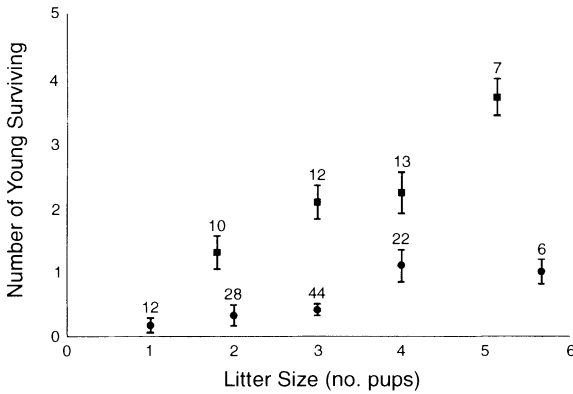
FIG. 4. Number of offspring surviving to 1 yr of age from different litter sizes of Columbian ground squirrels at the low elevation site in Alberta (mean ± 1 SE). ● bad years; ■ good years. Pooled litter size classes are: litters of 1 with 2 pups and 5 with 6 pups during good years; and 5 with 6 pups during bad years. Values for pooled litter sizes appear at the mean point for each grouping. See text for description of good and bad years. Sample sizes (no. litters) are given above error bars.

TABLE 4. Number of females by litter size that died before next breeding season or survived until next breeding season, at Turnbull.

| Fate | Litter size | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7+ |
| Survived | 10 | 17 | 26 | 45 | 20 | 13 | 4 |
| Died | 8 | 7 | 8 | 15 | 8 | 6 | 2 |

## DISCUSSION

Our results indicated that the most productive litter size in Columbian ground squirrels was larger than the mean (Fig. 2). We therefore reject Lack's hypothesis as an explanation for the distribution of litter sizes in Columbian ground squirrels. The deviation of the most productive litter from mean litter size could not be explained by the influence of yearlings having small litters on mean litter size, as has been suggested as an explanation for this pattern in birds (e.g., Klomp 1970). It is well documented that first time breeders produce smaller groups of young than older individuals, both for birds (e.g., Krapu and Doty 1979, Raveling 1981, Birkhead et al. 1983, Afton 1984, Steen and Unander
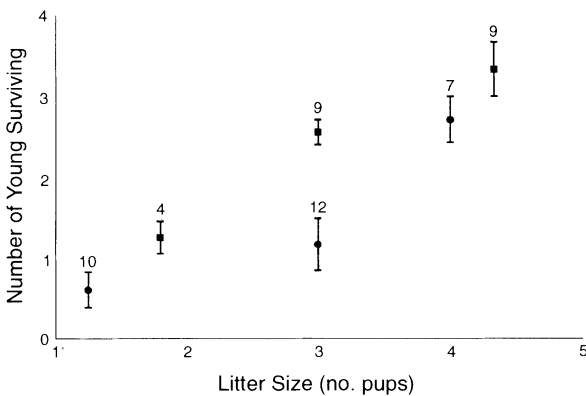
1985) and mammals (Biggers et al. 1962, Hasler and Banks 1975, Anderson and Boonstra 1979, Krohne 1981, Myers and Master 1983, Dobson and Myers 1989), and for squirrels in particular (Armitage and Downhower 1974, Costain and Verts 1982, Sherman and Morton 1984; Fig. 1). Other studies have also reported mean litter size to be below the most productive in small mammals (Rieger 1991, Morris 1992), but these studies did not address the influence of first-time breeders on mean litter size.

At Turnbull, there was evidence for a "drop-off" in production of surviving offspring for the largest litters. This decrease in production may be because parents are not able to provide sufficient resources to all offspring in a large litter, as Lack (1948b) suggested. However, in the Alberta populations, samples did not include litter sizes larger than 6 pups and this drop-off in production for large litters was absent (Figs. 4 and 5). Decrease in juvenile survival from largest litters has been found in muskrats (*Ondatra zibethicus*; Boutin et al. 1988) and white-footed mice (*Peromyscus leucopus*; Morris 1992). Absence of litters larger than six in our sample from Alberta, and low frequencies of these large litters in the Turnbull population, suggests two conclusions. First, Lack's suggestion (1948b) of low production from large litters may have been an important influence in the evolution of intermediate litter sizes in Columbian ground squirrels. Second, long term studies of mammalian populations that exhibit a

FIG. 5. Number of offspring surviving to 1 yr of age from different litter sizes of Columbian ground squirrels at high elevation in Alberta (mean ± 1 SE). Pooled litter size classes are: litters of 1 with 2 pups and 4 with 5 pups during good years; and 1 with 2 pups during bad years. Presentation otherwise as in Fig. 4.
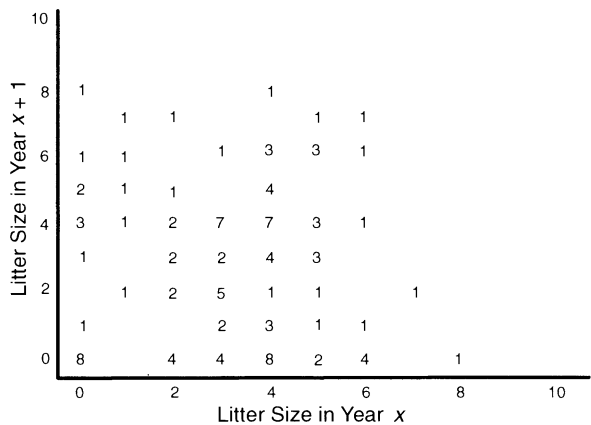
FIG. 6. Litter size of individual females at Turnbull in one year by their litter size the following year. Numbers in data field indicate number of observations.

large range of naturally occurring litter sizes are required to collect adequate information on declines in juvenile survival from extreme litter sizes.

Evidence for individual optimization can be found in studies of unmanipulated clutch size where larger clutches produced more recruits than smaller ones (e.g., Perrins and Moss 1975, Smith 1981, Lessells 1986, Gustafsson and Sutherland 1988, Nur 1988), and in manipulative studies where females originally laying a clutch of $x$ eggs produced more recruits than clutches enlarged to that size (Högstedt 1980, Gustafsson and Sutherland 1988, Pettifor et al. 1988, Pettifor 1993). In mammals, evidence for individual optimization comes from studies reporting no relationship between litter size and individual survival of offspring (Boutin et al. 1988, Rieger 1991), and studies that report larger litter sizes as more productive than mean litter size (Rieger 1991, Hoogland 1995).

Most of our results support the individual-optimization hypothesis. As predicted by individual optimization, number of offspring surviving to 1 yr of age increased with litter size in all populations (Figs. 2, 4, and 5), except the largest sizes of litters at Turnbull (Fig. 2), which were observed infrequently (2.4% of 248 litters; Table 1). However, total litter failure declined with increasing litter size and was absent in litters of 7 and 8 young (Table 1). Also, in all populations, individual offspring survival was independent of litter size (Table 1), which strongly suggests individual optimization.

The individual-optimization hypothesis argues that females optimize number of offspring based on their ability to raise offspring, which is dependent on territorial quality (Perrins and Moss 1975, Högstedt 1980) or on parental quality, as measured by body condition, age, or experience (Perrins and Moss 1975, Coulson and Porter 1985). Some mammals, such as white-footed mice begin gestation of a litter while still providing milk resources to a previous litter (Morris 1986). Morris (1986, 1987) developed a model of individual optimization for species with postpartum estrus called "optimal investment" to predict the optimal allocation of resources for females faced with the simultaneous costs of lactation and gestation for successive litters. We used change in mass of female ground squirrels $\geq 2$ yr old as a measure of changes in body condition (Dobson 1992), and predicted a significant association with concurrent changes in litter size. The correlations between change in pre-gestation mass from one year to the next and concurrent change in litter size (Fig. 3) provides evidence for individual optimization. Despite small samples in some populations, this correlation was significant in four of five populations, and approached significance in the fifth population.

Litter size in Columbian ground squirrels at Turnbull shows a continuous range of variation from 1 to 8 young (Table 1) and a very broad range of year-to-year change within individuals (Fig. 6). Possible explanations for such a broad range of phenotypic expression include the additive effects of many genes, reaction norms, and an interaction between these two influences. A reaction norm is a continuous distribution of phenotypes produced by a single genotype across a range of environments (sensu Stearns 1992). Life history traits in Columbian ground squirrels are phenotypically plastic (Dobson and Murie 1987, Dobson 1988). Individual females produce small litters in bad years and larger litters in good years (Dobson 1988). This increase in litter size during periods of food abundance, or in years of high individual condition, suggests that individual optimization of litter size in Columbian ground squirrels should be viewed as a norm of reaction. Selection may operate on a range of litter sizes, represented by one (or more) reaction norm(s). When this is the case, the mean litter size in a single season should be dependent on the shape of the reaction norm, the distribution of environments, and distribution of the condition of females.

Reaction norms of litter size in Columbian ground squirrels have not been precisely "mapped." Results of a study on optimal forging (Ritchie 1990), however, suggested that these reaction norms can be determined by an examination of energy intake and concurrent reproductive effort. Modeling the individual optimization or optimal investment hypotheses as reaction norms based on energy intake represents an approach advocated as "state-dependent" life history modeling (McNamara and Houston 1992).

It is unlikely that Mountford's (1968) cliff-edge hypothesis explains deviation of mean litter size from the most productive in Columbian ground squirrels. Although we were unable to address underlying genetic assumptions of the hypothesis, our results did not meet the mathematical requirements of the model. The cliff-edge hypothesis requires proportional offspring survival to fall off dramatically for large litter sizes (Mountford 1968: 364). Although litter size at Turnbull was distributed in a manner consistent with the cliff-edge hypothesis (Table 1), proportional offspring survival of Columbian ground squirrels was independent of litter size at Turnbull (Table 1) and in all four Alberta populations, contrary to requirements of the model.

The bad-years hypothesis suggested that when environmental conditions relating to reproduction and offspring survival vary among reproductive seasons, the most productive clutch as measured by geometric mean fitness will approximate the mean clutch size (Boyce and Perrins 1987). Our feeding experiments simulated extremes in food, the resource that regulates population size in Columbian ground squirrels (Dobson and Kjelgaard 1985b, Dobson 1995). Using the results of these experiments as a means of comparison suggests the occurrence of good and bad years for the production of litters and subsequent offspring survival in the unmanipulated population at Turnbull (Table 2).

The bad-years hypothesis requires that variance in

offspring survival increase with clutch size. Sample sizes of litters with 1–6 offspring from Turnbull were adequate to investigate this necessary condition of the bad-years hypothesis. The increase in variance of offspring survival with litter size at Turnbull (Table 1) suggests that fitness calculated as the geometric mean will be lower than fitness calculated as the arithmetic mean of offspring survival for the largest litters. Simulation of a widely fluctuating environment with food supplementation in Alberta caused the among-year variance in offspring survival to increase dramatically compared with the Turnbull population. The experimental results from Alberta revealed that offspring survival can respond to environmental conditions in a manner consistent with the bad-years hypothesis (Dobson and Kjelgaard 1985a, Dobson 1988).

However, directly testing the bad-years hypothesis with field measurements of geometric mean fitness is made difficult by infrequent occurrence of extreme litter sizes. Liou et al. (1993) demonstrated that clutch sizes represented by few samples will have low estimated mean geometric fitness, because the variance in number of surviving offspring increases with smaller sample sizes. This situation will result in the distribution of geometric fitness reflecting the sample size distribution of clutch sizes. When this is the case, the most productive clutch calculated by the geometric mean will be near the modal clutch, even in the absence of the effects of good and bad years. Furthermore, applicability of the bad-years hypothesis has not been modeled to consider the optimization of offspring survival in a fluctuating environment via a reaction norm for litter size (Stearns 1992). Because of the difficulties in computation and interpretation, the applicability of the bad-years hypothesis to the evolution of litter size in Columbian ground squirrels remains unclear.

The cost-of-reproduction hypothesis was originally formulated as a modification to Lack's hypothesis (Williams 1966). We attempted to test whether the cost-of-reproduction hypothesis can explain the deviation of the most productive clutch from mean clutch size. Our analyses, like previous studies (Murie and Dobson 1987, Hare and Murie 1992), failed to show a short-term phenotypic cost of reproduction for Columbian ground squirrels. There were no significant relationships between litter size and subsequent reproduction or survival (Fig. 6, Table 4). We, therefore, reject the cost-of-reproduction hypothesis as a direct explanation for deviation of the most productive litter size from the mean. Our tests did not address evolutionary costs of reproduction in Columbian ground squirrels (see Reznick 1985, Bell and Koufopanou 1986, Lessells 1991). Rather, our results indicated that reproductive costs alone were unlikely to account for differences between the mean and the most productive litter size. Failure to demonstrate a short-term cost of reproduction using phenotypic correlations, however, was consistent with individual optimization (Morris 1992).

In summary, our results indicate that mean litter size is smaller than the most productive litter size in Columbian ground squirrels. We are able to reject Lack's hypothesis that mean litter size is optimal for number of surviving offspring, and also the cost-of-reproduction hypothesis, as direct explanations for the deviation of the most productive litter size from the mean. A necessary condition of the cliff-edge hypothesis was not present in our data; therefore it is unlikely that this hypothesis is relevant for Columbian ground squirrels. We were unable to directly test the bad-years hypothesis, and were unable to reject this hypothesis via indirect tests. Currently, it is unclear how the bad-years effect would operate in a species that shows phenotypic plasticity in litter size. Our results include several lines of evidence suggesting that female Columbian ground squirrels may be individual optimizers. Although these hypotheses are not mutually exclusive, and may contribute in different degrees at different times to the evolution of litter size (Morris 1992), our results suggest that litter size in Columbian ground squirrels is most strongly affected by individual optimization.

### LITERATURE CITED

Afton, A. D. 1984. Influence of age and time on reproductive performance of female Lesser Scaup. Auk 101:255–265.

Anderson, J. L., and R. Boonstra. 1979. Some aspects of reproduction in the vole Microtus townsendii. Canadian Journal of Zoology 57:18–24.

Armitage, K. B., and J. F. Downhower. 1974. Demography of yellow-bellied marmot populations. Ecology 55:1233–1245.

Bailey, N. T. J. 1974. Statistical methods in biology. The English Universities Press, London, England.

Balfour, D. 1983. Infanticide in the Columbian ground squirrel, Spermophilus columbianus. Animal Behaviour 31:949–950.

Bell, G. 1980. The costs of reproduction and their conse-
quences. American Naturalist 116:45–76.

Bell, G., and V. Koufopanou. 1986. The cost of reproduction.
Pages 83–131 in R. Dawkins, editor. Oxford surveys in
evolutionary biology. Volume 3. Oxford University Press,
Oxford, England.

Biggers, J. D., C. A. Finn, and A. McLaren. 1962. Long-
term reproductive performance of female mice II. Variation
of litter size with parity. Journal of Reproduction and Fer-
tility 3:313–330.

Birkhead, M., P. J. Bacon, and P. Walter. 1983. Factors af-
fecting the breeding success of the Mute Swan Cygnus olor.
Journal of Animal Ecology 52:727–741.

Boag, D. A., and J. O. Murie. 1981. Population ecology of
Columbian ground squirrels in southwestern Alberta. Ca-
nadian Journal of Zoology 59:2230–2240.

Boutin, S., R. A. Moses, and M. J. Caley. 1988. The rela-
tionship between juvenile survival and litter size in wild
muskrats (Ondatra zibethicus). Journal of Animal Ecology
57:455–462.

Boyce, M. S., and C. M. Perrins. 1987. Optimizing Great
Tit clutch size in a fluctuating environment. Ecology 68:
142–153.

Bulmer, M. G. 1985. Selection for iteroparity in a variable
environment. American Naturalist 126:63–71.

Charnov, E. L., and J. R. Krebs. 1974. On clutch size and
fitness. Ibis 116:217–219.

Costain, D. B., and B. J. Verts. 1982. Age determination and
age-specific reproduction in Belding's ground squirrels.
Northwest Science 56:230–235.

Coulson, J. C., and J. M. Porter. 1985. Reproductive success
of the Kittiwake Rissa tridactyla: the roles of clutch-size,
chick growth rates and parental quality. Ibis 127:450–466.

Dobson, F. S. 1988. The limits of phenotypic plasticity in
life histories of Columbian ground squirrels. Pages 193–
210 in M. S. Boyce, editor. Evolution of life histories of
mammals. Yale University Press, New Haven, Connecticut,
USA.

———. 1990. Environmental influences on infanticide in
Columbian ground squirrels. Ethology 84:3–14.

———. 1992. Body mass, structural size, and life-history
patterns of the Columbian ground squirrel. American Nat-
uralist 140:109–125.

———. 1995. Regulation of population size: evidence from
Columbian ground squirrels. Oecologia, in press.

Dobson, F. S., M. J. Badry, and C. Geddes. 1992. Seasonal
activity and body mass of Columbian ground squirrels. Ca-
nadian Journal of Zoology 70:1364–1368.

Dobson, F. S., and J. D. Kjelgaard. 1985a. The influence of
food resources on life history in Columbian ground squir-
rels. Canadian Journal of Zoology 63:2105–2109.

Dobson, F. S., and J. D. Kjelgaard. 1985b. The influence of
food resources on population dynamics in Columbian
ground squirrels. Canadian Journal of Zoology 63:2095–
2104.

Dobson, F. S., and J. O. Murie. 1987. Interpretation of in-
traspecific life history patterns: evidence from Columbian
ground squirrels. American Naturalist 129:382–397.

Dobson, F. S., and P. Myers. 1989. The seasonal decline in
the litter size of meadow voles. Journal of Mammalogy 70:
142–152.

Festa-Bianchet, M., and W. J. King. 1991. Effects of litter
size and population dynamics on juvenile survival and ma-
ternal survival in Columbian ground squirrels. Journal of
Animal Ecology 60:1077–1090.

Gillespie, J. H. 1977. Natural selection for variances in off-
spring numbers: a new evolutionary principle. American
Naturalist 111:1010–1014.

Godfray, H. C. J., L. Partridge, and P. H. Harvey. 1991.

Clutch size. Annual Review of Ecology and Systematics
22:409–429.

Gustafsson, L., and W. J. Sutherland. 1988. The costs of
reproduction in the collared flycatcher Ficedula albicollis.
Nature (London) 335:813–815.

Hare, J. F., and J. O. Murie. 1992. Manipulation of litter size
reveals no cost of reproduction in Columbian ground squir-
rels. Journal of Mammalogy 73:449–454.

Hasler, J. F., and E. M. Banks. 1975. Reproductive perfor-
mance and growth in captive collared lemmings (Dicros-
tonyx groenlandicus). Canadian Journal of Zoology 53:
777–787.

Högstedt, G. 1980. Evolution of clutch size in birds: adaptive
variation in relation to territory quality. Science 210:1148–
1150.

———. 1981. Should there be a positive or negative cor-
relation between survival of adults in a bird population and
their clutch size? American Naturalist 118:568–571.

Hoogland, J. L. 1995. The black-tailed prairie dog: social
life of a burrowing mammal. University of Chicago Press,
Chicago, Illinois, USA.

King, W. J., M. Festa-Bianchet, and S. E. Hatfield. 1991.
Determinants of reproductive success in female Columbian
ground squirrels. Oecologia 86:528–534.

Klomp, H. 1970. The determination of clutch-size in birds:
a review. Ardea 58:1–124.

Krapu, G. L., and H. A. Doty. 1979. Age-related aspects of
Mallard reproduction. Wildfowl 30:35–39.

Krohne, D. T. 1981. Intraspecific litter size variation in Mi-
crotus californicus: variation within populations. Journal
of Mammalogy 62:29–40.

Lack, D. 1947. The significance of clutch size, parts I and
II. Ibis 89:302–352.

———. 1948a. The significance of clutch size, part III.—
some interspecific comparisons. Ibis 90:25–45.

———. 1948b. The significance of litter size. Journal of
Animal Ecology 17:45–50.

———. 1954. The natural regulation of animal numbers.
Clarendon Press, Oxford, England.

———. 1966. Population studies of birds. Clarendon Press,
Oxford, England.

Lessells, C. M. 1986. Brood size in Canada Geese: a ma-
nipulation experiment. Journal of Animal Ecology 55:669–
689.

———. 1991. The evolution of life histories. Pages 32–65
in J. R. Krebs and N. B. Davis, editors. Behavioural ecol-
ogy: an evolutionary approach. Third edition. Blackwell
Scientific, London, England.

Liou, L. W., T. Price, M. S. Boyce, and C. M. Perrins. 1993.
Fluctuating environments and clutch size evolution in Great
Tits. American Naturalist 141:507–516.

McNamara, J. M., and A. I. Houston. 1992. State-dependent
life-history theory and its implications for optimal clutch
size. Evolutionary Ecology 6:170–185.

Morris, D. W. 1986. Proximate and ultimate controls on life-
history variation: the evolution of litter size in white-footed
mice (Peromyscus leucopus). Evolution 40:169–181.

———. 1987. Optimal allocation of parental investment. Oi-
kos 49:332–339.

———. 1992. Optimum brood size: tests of alternative hy-
potheses. Evolution 46:1848–1861.

Mountford, M. D. 1968. The significance of litter size. Jour-
nal of Animal Ecology 37:363–367.

Murie, J. O. 1992. Predation by badgers on Columbian
ground squirrels. Journal of Mammalogy 73:385–394.

Murie, J. O., D. A. Boag, and V. K. Kivett. 1980. Litter size
in Columbian ground squirrels (Spermophilus columbi-
anus). Journal of Mammalogy 61:237–244.

Murie, J. O., and F. S. Dobson. 1987. The costs of repro-

duction in female Columbian ground squirrels (*Spermoph-ilus columbianus*). Oecologia **73**:1–6.

Murie, J. O., and M. A. Harris. 1982. Annual variation of spring emergence and breeding in Columbian ground squir-rels (*Spermophilus columbianus*). Journal of Mammalogy **63**:431–439.

Murie, J. O., and M. A. Harris. 1984. The history of indi-viduals in a population of Columbian ground squirrels: source, settlement, and site attachment. Pages 353-373 *in* J. O. Murie and G. R. Michener, editors. The biology of ground-dwelling squirrels. University of Nebraska Press, Lincoln, Nebraska, USA.

Murphy, E. C., and E. Haukioja. 1986. Clutch size in nidi-colous birds. Pages 141–180 *in* R. F. Johnston, editor. Cur-rent ornithology. Volume 4. Plenum, New York, New York, USA.

Myers, P., and L. L. Master. 1983. Reproduction by *Pero-myscus maniculatus*: size and compromise. Journal of Mammalogy **64**:1–18.

Nur, N. 1988. The consequences of brood size for breeding Blue Tits. III. Measuring the cost of reproduction: survival, future fecundity, and differential dispersal. Evolution **42**: 351–362.

Partridge, L., and P. H. Harvey. 1985. Costs of reproduction. Nature (London) **316**:20.

Perrins, C. M., and D. Moss. 1975. Reproductive rates in the Great Tit. Journal of Animal Ecology **44**:695–706.

Pettifor, R. A. 1993. Brood-manipulation experiments. I. The number of offspring surviving per nest in Blue Tits (*Parus caeruleus*). Journal of Animal Ecology **62**:131–144.

Pettifor, R. A., C. M. Perrins, and R. H. McCleery. 1988. Individual optimization of clutch size in Great Tits. Nature (London) **336**:160–162.

Price, T., and L. Liou. 1989. Selection on clutch size in birds. American Naturalist **134**:950–959.

Raveling, D. G. 1981. Survival, experience, and age in re-lation to breeding success of Canada Geese. Journal of Wildlife Management **45**:817–829.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos **44**:257–267.

Rieger, J. F. 1991. Female investment strategies and repro-ductive success in the Uinta ground squirrel, *Spermophilus armatus*. Dissertation. University of Michigan, Ann Arbor, Michigan, USA.

Ritchie, M. E. 1990. Optimal foraging and fitness in Colum-bian ground squirrels. Oecologia **82**:56–67.

Ritland, K., and S. Jain. 1984. The comparative life histories of two annual *Limnanthes* species in a temporally variable environment. American Naturalist **124**:656–679.

Shaw, W. T. 1925. Breeding and development of the Colum-bian ground squirrel. Journal of Mammalogy **6**:106–113.

Sherman, P. W., and M. L. Morton. 1984. Demography of Belding's ground squirrels. Ecology **65**:1617–1628.

Slade, N. A., and D. F. Balph. 1974. Population ecology of Uinta ground squirrels. Ecology **55**:989–1003.

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

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition. Freeman, New York, New York, USA.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. Quarterly Review of Biology **51**:3–47.

———. 1992. The evolution of life histories. Oxford Uni-versity Press, Oxford, England.

Steen, J. B., and S. Unander. 1985. Breeding biology of the Svalbard Rock Ptarmigan *Lagopus mutus hyperboreus*. Or-nis Scandinavica **16**:191–197.

VanderWerf, E. 1992. Lack's clutch size hypothesis: an ex-amination of the evidence using meta-analysis. Ecology **73**: 1699–1705.

Waterman, J. M. 1984. Infanticide in the Columbian ground squirrel (*Spermophilus columbianus*). Journal of Mammal-ogy **65**:137–138.

Williams, G. C. 1966. Natural selection, the costs of repro-duction, and a refinement of Lack's principle. American Naturalist **100**:687–690.

Winkler, D. W., and J. R. Walters. 1983. The determination of clutch size in precocial birds. Pages 33–68 *in* R. F. John-ston, editor. Current ornithology. Volume 1. Plenum, New York, New York, USA.

Ydenberg, R. C., and D. F. Bertram. 1989. Lack's clutch size hypothesis and brood enlargement studies on colonial sea-birds. Colonial Waterbirds **12**:134–137.

Zammuto, R. M., and J. S. Millar. 1985a. Environmental predictability, variability, and *Spermophilus columbianus* life history over an elevation gradient. Ecology **66**:1784–1794.

———. 1985b. A consideration of bet-hedging in *Sper-mophilus columbianus*. Journal of Mammalogy **66**:652–660.