Oecologia (Berlin) (1987) 73:1–6

Oecologia

Original papers

The costs of reproduction in female columbian ground squirrels

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Summary. The cost of reproduction for female Columbian ground squirrels was assessed using seven years of data from three populations in southwestern Alberta, Canada. Short-term costs, measured as reduced survival or lowered subsequent fecundity, were not directly associated with whether a female reproduced or not, nor with the females' litter size. In one of the populations, females that first reproduced as yearlings had slightly shorter lifespans, but almost 1.5 times the lifetime reproductive success, compared to those that first reproduced when older. Although short-term reproductive costs were not apparent from our data, we cannot conclude that reproduction was not costly. Such costs might exist but be masked by females' adjusting reproductive investment to their body condition. A weak association of spring (minimum) body weight of females and subsequent reproduction supported this possibility, as did correlated increases in body weight and litter size in a population given supplemental food.

Key words: *Spermophilus* – Cost of reproduction – Survivorship – Reproductive success – Ground squirrel

Evolutionary models of life histories often begin with the assumption that a "cost" is associated with reproduction (Lack 1966; Williams 1966a; Hirshfield and Tinkle 1975; Bell 1980). This cost may be expressed as lowered subsequent survival or as lowered future fecundity (Williams 1966b; Bell 1984a; Millar 1984). The hypothesis that reproduction entails a cost has been examined in several species and the results have been mixed (reviewed by Bell 1984a; Reznick 1985). Striking exceptions to predictions of the cost hypothesis (e.g., DeSteven 1980; Smith 1981; Bell 1984a, b; Boyce and Perrins 1987) have encouraged some researchers to assert that the cost hypothesis is unnecessary, and should be replaced by "cost-free" models (Tuomi et al. 1983).

We studied the proximate costs of reproduction in female Columbian ground squirrels, *Spermophilus columbianus*. The active season of this ground squirrel is about 90 to 100 days each year (Dobson and Murie 1987), and during this period females mate, gestate, lactate, and then fatten for a subsequent period of hibernation that lasts for about 70% of the year. Females produce no more than one litter each year. Litter size is relatively low and survival is relatively high compared to other ground squirrel species (Armitage 1980; Heaney 1984; Dobson et al. 1986). Population size and reproduction are likely limited by food resources (Dobson and Kjelgaard 1985a, b), and the squirrels are normally faced with a short forage-growing season of about 75 to 115 days (Zammuto and Millar 1985a).

We predicted that if there were short-term costs to current reproduction, then either survival of individuals or their subsequent fecundity would covary inversely with current reproduction. Our procedure was similar to that Clutton-Brock et al. (1983) applied in their study of costs of reproduction in red deer, *Cervus elaphus*, and represents a first step in evaluating the role of reproductive costs in the life history of Columbian ground squirrels.

Methods

Three populations of Columbian ground squirrels were studied in the Sheep and Highwood River drainages in southwestern Alberta. Murie and his co-workers (Murie et al. 1980; Murie and Harris 1982; Murie 1985) studied populations of ground squirrels in 8 ha of meadowland at Gorge Creek (GC) (50°39′N, 114°39′W; 1500 m) from 1976 to 1982, and in 8 ha of subalpine meadow at Highwood Pass (HP) (50°38′N, 114°58′W; 2170 m) from 1974 to 1980. King (1984), Festa-Bianchet and King (1984), and S. Hatfield (unpublished work) provided data from ground squirrels occupying 0.76 ha of meadowland near Dyson Creek (DC) (50°37′N, 114°39′W; 1570 m) from 1979 to 1985. The populations are within 30 km of each other. For brevity, we refer to these populations by the initials given above.

All populations were studied in a similar manner. Body weight and sexual condition (swelling and openness of the vulva for females) were recorded from squirrels trapped within a few days of their emergence from hibernation each spring. Numbered metal tags were affixed to both ears of every individual, and each ground squirrel was given a distinctive mark with black fur dye. Ground squirrels were recaptured later to determine those that lactated from their enlarged nipples. Lactating females were assumed to have given birth, although not all of them weaned young. Litters were trapped after they emerged for the first time from their natal burrows, and weaned litter sizes were recorded. Mothers of litters were identified by their morning emergence from and use of natal burrows during lactation and

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when juveniles were first active above ground. Only litters for which the number of juveniles and the identity of the mother were firmly established were used in analyses.

Survival of adult females (≥ two years old) was measured as the proportion of those present in the population at the time of weaning that emerged from hibernation in the following spring. This period was used because in some years the spring census was more complete than the census at the time juveniles emerged, and annual survival could confound the costs of two reproductive events. In any case, disappearance of females from their emergence in spring to the time juveniles emerged was rare. Yearling males are the primary dispersers in this species, and adult females are highly sedentary (Boag and Murie 1981a; Festa-Bianchet and King 1984; Murie and Harris 1984). Unlike adult females of some other ground squirrel species (e.g., Belding's ground squirrel, *S. beldingi*, Sherman 1981), female Columbian ground squirrels are not likely to disperse if they lose their litters prior to weaning (Murie and Harris 1984). Thus, biases in survival of females due to dispersal are likely to be small (Dobson and Kjelgaard 1985a).

Some females reproduced as yearlings in the population at DC (Festa-Bianchet 1981; King 1984). In the other populations, however, females first matured at two years of age or older (Murie and Harris 1978). As litter sizes of yearling females are smaller than those of older females (Zammuto 1983; Dobson and Kjelgaard 1985b), yearlings were deleted from analyses except where explicitly stated.

Some characteristics of life history differ significantly among populations of ground squirrels (Dobson et al. 1986). Each population, therefore, was treated separately, and data were pooled only when values for different populations were similar or were standardized by subtracting the population mean from each value and dividing by the standard deviation (Sokal and Rohlf 1981, p 105). Potential costs of reproduction were assessed for the populations at GC, HP, and DC, using data from 71, 74, and 38 adult females, respectively. On average, data were available for each female for 2.2 years (range, 1–7). Hence, some individuals appear more than once in most analyses. Creating a single subset of the data with individuals appearing only once was not done because 1) not all variables were available for each female in each year, making it difficult to choose a subsample in an unbiased manner, and 2) decreasing the sample sizes makes it less likely that any differences in comparisons would be identified. Since the usual result of including multiple observations of individuals in an analysis is to increase the probability of a Type I error (Machlis et al. 1985), our main conclusions based on a lack of difference should not be affected greatly by using the entire data set.

Results

Survival

Adult female ground squirrels that weaned litters in the population at GC survived less well to the next spring than those that did not wean litters (Table 1). At DC and HP, however, females that weaned litters and those that did not survived about equally well, and this was true of the pooled sample as well. A subsample of the females that did not wean litters also did not lactate, and thus did not suffer any energetic costs of lactation. Non-lactating females survived no better than females that weaned litters (Table 1). This was true for each population, including GC, when analyzed separately (all $P > 0.25$).

Table 1. Subsequent survival of adult female Columbian ground squirrels that did and did not wean litters, and that did not lactate, in three populations

Study site	Number of adult females	Percent surviving	P[a]
GC			
No litter	33	91%	0.04
Weaned litter	74	74%	
DC			
No litter	16	75%	0.71
Weaned litter	58	79%	
HP			
No litter	61	82%	0.33
Weaned litter	67	88%	
Total			
No litter	110	84%	
Weaned litter	199	80%	0.48
No lactation	74	80%	0.90

[a] G-tests

The relationship between litter size and subsequent survival was evaluated in two ways. First, the survival rates of females that had different-sized litters were not significantly different (Table 2). Second, the litter size of adult females that survived to the following year was not significantly different from those that did not survive in any of the three populations (Table 3). Both analyses indicated no relationship between litter size and survival within populations.

Fecundity

Litter size did not increase, on average, for adult females in different age classes (Kruskal-Wallis tests, all $P > 0.05$). Weaning a litter in one year had no discernable effect on the likelihood of weaning a litter in the following year in any of these populations (G-tests, all $P > 0.35$). Of 117 surviving adult females that weaned a litter in one year (populations pooled), 72% weaned a litter in the following year, and of 52 adult females that did not wean a litter in one year, 67% weaned a litter in the following year (G-test, $P = 0.69$).

In all three populations, females that had weaned a litter in the previous year tended to have *larger* litters than those that had not; the difference was significant at HP (Table 4). Furthermore, there was no significant influence of litter size in one year on litter size in the following year in any of the three populations, or in the standardized pooled data (pooled rank $r = 0.11$, $n = 61$, $P = 0.38$). Litter size in one year explained only 3% ($P = 0.20$) of the variation in litter size in the following year in a regression analysis of the pooled data.

Age at maturity

Some of the females in the population at DC matured as yearlings (Festa-Bianchet 1981; King 1984). For 17 yearlings, we were able to examine longevity and lifetime reproductive success. Females that weaned a litter as a yearling lived, on average, a shorter period than females that did

Table 2. Subsequent survival rates of adult female Columbian ground squirrels that had different litter sizes in three populations. Sample sizes in parentheses

Study site	Litter size						
	1	2	3	4	5	6	P^a
GC	0.63 (8)	0.76 (17)	0.81 (31)	0.62 (13)	1.00 (3)		0.75
DC	1.00 (1)	1.00 (4)	0.76 (17)	0.78 (18)	0.83 (12)	0.60 (5)	0.93
HP	0.82 (11)	0.91 (22)	0.86 (29)	1.00 (1)			0.97

[a] Kruskal-Wallis tests

Table 3. Mean litter size for adult female Columbian ground squirrels that did and did not survive to the subsequent spring in three populations

Study site	Litter size	Number of adult females	P^a
GC			
Did survive	2.8	54	0.84
Did not survive	2.7	18	
DC			
Did survive	3.8	45	0.45
Did not survive	4.2	12	
HP			
Did survive	2.3	55	0.89
Did not survive	2.3	8	

[a] Mann-Whitney U-tests

Table 4. Mean litter sizes of adult female Columbian ground squirrels that did and did not wean litters in the previous year in three populations

Study site	Litter size	Number of adult females	P^a
GC			
Weaned litter	2.6	25	0.68
No litter	2.5	13	
DC			
Weaned litter	4.0	36	0.26
No litter	3.6	10	
HP			
Weaned litter	2.7	15	0.01
No litter	2.1	10	

[a] Mann-Whitney U-tests

Table 5. Reproduction and survival of female Columbian ground squirrels that did and did not wean litters as yearlings in the population at DC. Sample sizes in parentheses

As a yearling	Mean lifespan (years)	Mean lifetime number of offspring
Weaned litter	2.6 (8)	8.0 (8)
No litter	3.0 (9)*	5.6 (9)**

* Mann-Whitney U-test, $P = 0.68$
** Mann-Whitney U-test, $P = 0.27$

Table 6. Mean weights of adult female Columbian ground squirrels that did and did not wean litters in three populations. Spring weights were taken at emergence from hibernation, and summer weights were taken when litters emerged from natal burrows. Sample sizes in parentheses

Study site	Spring body weight			Summer body weight		
	With litters	Without litters	P^a	With litters	Without litters	P^a
GC	386 (80)	371 (31)	0.09	486 (80)	519 (26)	<0.01
DC	444 (63)	414 (14)	0.18	553 (68)	562 (13)	0.65
HP	396 (32)	372 (27)	0.08	476 (67)	529 (58)	<0.01
Combined probability[b]			0.02			<0.01

[a] Mann-Whitney U-test
[b] From Sokal and Rohlf (1981) p 780

not wean a litter as a yearling (Table 5). The lifetime reproductive output of females that reproduced as yearlings, however, was about 1.5 times greater than that of females that first weaned a litter when older (Table 5). These comparisons based on small samples were not significant, but they indicate that early maturity did not have a negative effect on lifetime production of offspring.

Body weight

Body weights of female ground squirrels are at or near their minimum value of the year upon emergence from hibernation, before breeding begins (Boag and Murie 1981 b). Spring body weights tended to be greater for adult females that subsequently weaned litters than for those that did not (Table 6). This result was not significant within each population, but the patterns were similar and the relationship was significant in an *a posteriori* combined comparison (Table 6). By the time litters were being weaned, however, females that weaned litters were generally lighter in weight than those that did not (Table 6). That difference was apparently not sufficient to affect survive rates of the two groups (see above, and Murie and Boag 1984).

Regressions of litter size on spring weight were significant at GC and DC ($P < 0.01$), and spring weight accounted for 6%, 9%, and 2% of the variation in litter size at GC

($n=115$), DC ($n=69$), and HP ($n=82$), respectively. In this analysis, litter sizes of zero were included for females that did not lactate and were older than the mean age at maturity.

Discussion

We first asked if current reproduction reduced survival to the next year. Although females that weaned litters survived poorly compared to those that did not wean litters in the population at GC, this result was not evident elsewhere (Table 1). Refining the analysis by comparing mothers to females that never began lactation (Table 1), and comparing survival rates at various levels of reproduction (Table 2), did not indicate a relationship between current reproduction and subsequent survival. We also found no significant difference in average litter size between females that subsequently survived and those that did not (Table 3). The weight of evidence, therefore, suggested no short-term survival cost to current reproduction.

The second question we asked was whether current reproduction incurred a cost through lowered future reproduction. It would be best to assess lifetime reproduction to examine this question, but that was only possible for a subsample in the DC population. Weaning a litter in one year did not decrease the likelihood of an adult female weaning a litter in the next year. Also, weaning a litter in one year was associated with slightly higher (two populations) and significantly higher (one population) litter sizes in the next year (Table 4). Litter size was examined directly in females that reproduced in two consecutive years, and again no significant relationship was found between years. Thus, we could discern no short-term cost of current reproduction in terms of subsequent reproduction.

In a subsample of the population at DC, it was possible to examine the subsequent survival and lifetime fecundity for females that reproduced as yearlings and those that matured when older. Females that first reproduced as yearlings lived for a slightly shorter period than late maturing females, but had slightly more offspring during their lifetimes than those not breeding as yearlings (Table 5). Thus, early maturity did not entail an obvious cost, and perhaps was beneficial by slightly increasing the lifetime number of offspring.

Our data provide little evidence that successful reproduction was accompanied by short-term costs in terms of lower survival or reduced future reproduction. The apparent lack of such costs, however, may not indicate that reproduction is not costly. Each female may be producing as many young as she can, within the constraints of her body condition. In addition, differences in reproductive investment among litters might be minimized if small and large litters contained large and small young, respectively, as has been shown for *Peromyscus* (Leamy 1981; Millar 1983; Myers and Master 1983).

As has been pointed out by Reznick (1985), assessing costs of reproduction by using phenotypic correlations, as we have done, does not directly address the cost hypothesis as a component of life history theory. One difficulty is that individuals may be able to regulate the level of reproductive effort so as to minimize future costs (Reznick 1985, and references therein). For example, the number of young that a female produces might be constrained by environmental conditions that prevail in the local habitat. If adjustment of reproductive effort to environmental conditions, such as territory quality (Hogstedt 1981), or to parental quality (Ekman and Askenmo 1986) occurred continually, then costs of reproduction would be exceedingly difficult to measure.

In ground squirrels, adjustment of number of young may occur at several stages prior to weaning. Columbian ground squirrels apparently have fewer implantations than corpora lutea, some resorption of embryos, and some loss of young during lactation (Murie et al. 1980). Adjustment of number of young can only be a negative process, however, and there may also be times when adjustments are relatively inefficient or even physically impossible. At such times, females may "make the best of a bad job" by raising the young they have, even at a considerable cost. This may explain the difference between the results for ground squirrels, which exhibit no obvious short-term costs in survival and fecundity, and red deer on the Isle of Rhum, which do exhibit significant short-term costs (Clutton-Brock et al. 1983). Adjustments in reproductive effort may be more strongly constrained in red deer, because hinds bear only a single calf (Clutton-Brock et al. 1982).

The number of young that a female produces might be attuned to her body condition, which should, in part, be a reflection of environmental conditions. Females with low body reserves may avoid reproductive investment prior to birth or weaning, thus improving subsequent survival. Females in better condition might be able to carry on through weaning and still have adequate reserves to avoid a marked decrease in the chance of subsequent survival and future reproduction. If this scenario were true, then we would expect the weights of females at emergence from hibernation (near minimum weight) to be related to subsequent reproductive success. Also females that forego reproduction should improve their body condition (i.e., gain weight) relative to females that reproduce.

Condition may have influenced reproduction in the ground squirrels. First, there was a slight, but overall significant, positive association between spring weight and whether a female subsequently weaned a litter or not (Table 6), and between spring weight and litter size. Second, females that did not wean litters gained more weight by the summer period than successfully reproducing females, and in two populations they were then significantly heavier than successful mothers (Table 6). A final line of support for the influence of body condition on litter size comes from data on a population given supplemental food (Dobson and Kjelgaard 1985a, b). In a sample of 17 adult females, body weight at spring emergence after food was supplemented was significantly greater than before supplementation began (486 g vs 388 g, Wilcoxon matched pairs test, $P<0.001$), and litter sizes of 11 of those females that weaned litters both after and before supplementation also increased significantly (3.9 vs 2.5, Wilcoxon matched pairs test, $P=0.01$). Neither weight nor litter size of females in a nearby unsupplemented area changed significantly from year-to-year (Dobson, in press). Since growth in morphological body size increases little after two years of age (Dobson, unpublished work), we interpret the enhancement of reproduction to be a result of improved body condition.

Clearly, more rigorous data are needed to assess the effects of body condition on measures of reproductive effort in the field. Furthermore, the degree to which variation in the environment and in body condition influence the measurement of costs of reproduction needs more attention. Finally, assessment of costs of reproduction and relating the presence or absence of those costs to life history theory will require experimental manipulation of reproduction in the field (Partridge and Harvey 1985, e.g., Roskaft 1985).

Acknowledgments. Our greatest debt is to W.J. King, S. Hatfield, and M. Festa-Bianchet, for providing us with data from the Dyson Creek population. Many enthusiastic assistants helped gather the data, and we thank them, especially M.A. Harris and J.D. Kjelgaard. M.S. Boyce, H.L. Gibbs, A. Goldizen-Wilson, A.G. Kluge, G.R. Michener, J.F. Rieger, and D.L. Schultz, aided us with lively discussions of the topic, and M. Festa-Bianchet, L.R. Heaney, W.J. King, J.S. Millar, P. Myers, and R.M. Zammuto provided helpful comments on the manuscript. FSD was supported in part by a NATO Postdoctoral Fellowship at the Department of Zoology, University of Alberta, and a Canadian National Sportsman's Fund research grant. JOM was funded by grants from the Natural Sciences and Engineering Research Council of Canada.

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Received December 19, 1986