

A COMPARISON OF METHODS FOR STUDYING LIFE HISTORY IN COLUMBIAN GROUND SQUIRRELS

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ABSTRACT.—We reviewed data from three separate studies that examined the life-history characteristics of Columbian ground squirrels, *Spermophilus columbianus*, at different elevations in the Rocky Mountains of southwestern Alberta, Canada. One study used a static (vertical) life-table methodology, and the other two used a cohort (horizontal) life-table methodology. One of the latter studies also applied an experimental supplementation of food resources to two populations. Absolute values of characteristics measured by static and cohort methodologies were not directly comparable, but the pattern of change with elevation of litter size, adult survival, and body weight were similar. At high, relative to low elevations, litter size was lower, adult survival was higher, and body weight of adult females was lower. The two methodologies produced conflicting results regarding the proportion of females reproducing and juvenile survival at different elevations. The static methodology does not reveal the changes in life history that may occur in different years. An experimental method was required to demonstrate phenotypic plasticity of life-history characteristics. In two populations that received supplemental food, litter size, juvenile survival, and the body weight of adult females increased.

Extensive information on characteristics of life history is available for only a few mammalian species (Millar and Zammuto, 1983; Stearns 1977). Several methods of amassing life-history data exist (Caughley, 1977; Deevey, 1947), and because such data are difficult to gather, different methods have seldom been applied to single species. Thus, one rarely knows if disparities in results for different species studied by different methods reflected real differences, or resulted from the application of different methods. Our purpose is to indicate whether different methods can be combined by population ecologists to strengthen empirical conclusions about natural patterns of variation in life history, and hence provide some indication of comparability of different methods.

We briefly describe three independent research programs that examined variation of life-history characteristics in mountain-dwelling populations of Columbian ground squirrels, *Spermophilus columbianus*, at different elevations. One of the studies produced a static (vertical) life table, and the other two produced cohort (horizontal) life tables. One of the latter studies examined changes in life history under experimental supplementation of food resources. By comparing the data obtained by alternative means of life-table construction and alternative study approaches (comparative and experimental), we were able to identify similarities and differences among studies. The differences in particular might be of interest to those designing studies of mammalian life history who need to choose between alternative means of life-table construction or need to apply experimental techniques.

METHODS

Methods of data collection varied among the research programs. Zammuto (1983; Zammuto and Millar, 1985) collected static life-table data by kill-sampling six ground squirrel populations during pregnancy and early lactation. Three populations were collected in 1980, and three were collected in 1981. Males were designated adult if they had scrotal testes or a darkly pigmented scrotum, and females were designated adult if they contained embryos or placental scars. Litter size was estimated by counting embryos or placental scars in utero, and reproductive females were identified by the presence of embryos or recent placental scars. In each population, juvenile survival was estimated from the number of yearling ground squirrels divided by the total number of embryos and placental scars dissected from females. The ages of

ground squirrels, and thus annual survival (after Deevey, 1947), were estimated by examination of annual rings of bone deposition in the periosteum of the lower jaw (Klevezal and Kleinenberg, 1967; Millar and Zwickel, 1972). Body weight was measured on freshly killed adult females during mid-to-late pregnancy and early lactation (including weight of embryos for most females).

Murie and his co-workers (Boag and Murie, 1981a, 1981b; Murie, 1985; Murie and Harris, 1982; Murie et al., 1980) collected cohort life-table data with live-trapping studies of two populations of ground squirrels from 1974 to 1982. Dobson (1984; Dobson and Kjelgaard, 1985a, 1985b) also collected cohort life-table data with live-trapping studies of four populations from 1981 to 1984. Ground squirrels were designated adult if they were known from trapping records to be 2 years old or older. Litter size at weaning was estimated from young that were trapped shortly after they emerged from natal burrows. Females that underwent estrus were designated mature, and females that lactated were designated reproductive. Estrus was determined from swelling of the vulva, and complete splitting of the skin covering the vulva. Lactation was determined from the examination of nipples, which become swollen and elongate, and in Dobson and Kjelgaard's (1985b) study milk was expressed from a teat. Rates of juvenile and adult survival were estimated as the proportions of ground squirrels that emerged from natal burrows or hibernacula that subsequently emerged from hibernation in the following year. The weights of adult females were recorded soon after emergence from hibernation (usually within 3 days, virtually always within 7 days). Mean values of life-history characteristics were obtained by pooling several years of data. Most of the populations were monitored in an unmanipulated condition (reference populations), but two populations in one of the studies received supplemental food resources for a 2-year period (experimental populations; Dobson and Kjelgaard, 1985a, 1985b).

In the present study, we will not report on litter size and survival of yearlings. Litter sizes of yearling females were significantly lower than those of adults in some populations (Dobson and Kjelgaard, 1985b; Festa-Bianchet, 1981; Zammuto, 1983). Measurement of survival of yearlings, particularly males, was biased because of extensive dispersal (Boag and Murie, 1981a; Murie and Harris, 1984).

RESULTS AND DISCUSSION

Within the past few years, changes in life-history patterns over elevational gradients have been documented in ground squirrels. Bronson (1979), working on golden-mantled ground squirrels, *Spermophilus lateralis*, found smaller litters, later maturity, and higher survival of adult females at higher elevations. He pointed out that the differences among populations could have been either genetically-fixed or phenotypically-plastic responses to environmental conditions. Genetically-fixed responses are expressed invariantly, but phenotypically-plastic responses are variable developmental conversions or environmentally-induced modulations (Caswell, 1983; Smith-Gill, 1983).

Murie and his co-workers (Murie, 1985; Murie and Harris, 1982; Murie et al., 1980) showed that similar variation to that found by Bronson (1979) was evident in a 7-year study of Columbian ground squirrels at two different elevations (Table 1). Similar variation was documented in additional populations by Zammuto (1983; Zammuto and Millar, 1985), and in a 3-year study of two more populations by Dobson and Kjelgaard (1985b). These studies found that at high, compared to low elevations: 1) litters were smaller; 2) maturity of females was later; 3) adult survival was greater; and 4) body weight of females was lower.

Application of an experimental methodology might indicate whether life-history characteristics were phenotypically-plastic, rather than genetically-fixed, responses to the environment. Evidence on variation within populations suggested that characteristics should be phenotypically-plastic responses (Boag and Murie, 1981a, 1981b; Festa-Bianchet, 1981; Moore, 1937; Murie, 1985; Murie and Harris, 1982; Murie et al., 1980), and this conclusion was confirmed by the experimental results (Table 1). When provided with supplemental food: 1) adult females had larger litters; 2) females matured earlier; 3) juvenile survival increased; and 4) adult females were heavier. Food resources, therefore, appeared to be a key environmental factor that influenced life-history patterns (Dobson and Kjelgaard, 1985b).

The combined results from static and cohort life table approaches, and experimental and unmanipulated populations, were more illuminative than any of the studies could have been alone. The results indicated that different methods and investigators could produce similar

conclusions concerning the influence of the environment on differences among populations in litter size, age at maturity, and body weight; and that these characteristics were subject to large variation in phenotypic expression.

Some novel results were evident, however, when these studies were compared, and these results might provide insight into the limitations of different methods. First, both static (Zammuto, 1983) and cohort (Murie, 1985) methods yielded the same estimate of litter size ($\bar{X} = 2.9$) at the same site (at 1,500 m, see Table 1). Earlier estimates of litter size made by embryo counts (the static method) at this site by Murie et al. (1980) were slightly higher ($\bar{X} = 3.2$, $n = 28$) than Zammuto's (1983) estimates. Also, at 2,170 m, Murie and Harris (1982) found that litters were significantly smaller in years of late, compared to early spring snow melt-off. Thus, there may be differences among years that could bias static estimates of litter size. Litter size was greatly increased by supplementation of food (Table 1), indicating that natural variation in food resources between years might produce differences in litter size.

Second, among females that were 2 years old or older ("adults" in the cohort approach), the proportion that were reproductive showed no consistent pattern of change with elevation in the study that employed the static approach (Table 1). In both of the cohort studies, however, this proportion decreased with increasing elevation. At the 1,500 m site, the estimates from static and cohort studies were different, with 62% and 84% of females 2 years old or older estimated reproductive, respectively. The static estimate should be, if anything, higher than the cohort estimate because it was determined earlier in the season (largely by the presence of embryos versus numbers of lactating females). The anomaly might indicate significant year effects. We found that over 7 years of study, the proportion of reproductive females varied between 61% and 93% at 1,500 m, and between 40% and 85% at 2,170 m. In the experimental study, the proportion of reproductive females increased when supplemental food was present at high elevation (Table 1).

Third, in the static life-table study, no relationship was found between juvenile survival and elevation (Table 1). In the cohort life-table studies, however, survival of juveniles was greater at higher elevations. Murie and Harris (1982) and Zammuto (1983) estimated juvenile survival at the same site (again, both at 1,500 m) as 31% and 61%, respectively (Table 1). While this difference might be due to differences in methods of data collection, it might also indicate that juvenile survival is extremely variable in nature, and very sensitive to annual variations in food resources. During 7 years of study at this site, Boag and Murie (1982a) found that the proportion of juveniles surviving varied between 27% and 49%. In the experimental study, juvenile survival increased significantly when supplemental food was present (Table 1).

Fourth, adult survival increased with elevation, but it did not appear to be strongly influenced by food supplementation (Table 1). When surplus energy from supplemental food was available, adults may have put most of it into increasing reproductive effort (Dobson and Kjelgaard, 1985b; Hirshfield and Tinkle, 1975). Alternatively, food resources may not be a key factor that influences adult survivorship (other possibilities include predation and overwinter conditions).

Static and cohort life-table approaches can produce similar results, but appear to differ in estimating some variables. The similarities and differences in empirical results can be coalesced into the following conclusions. The static life-table approach allows rapid sampling, and thus facilitates simultaneous study of several populations. It requires accurate aging of individuals, and thus facilitates study of age-structured phenomena (Charlesworth, 1980). The static approach assumes that the age distribution is stable and that the rate of population change is known (Caughley, 1977). Depending on the application, the static approach may assume that year effects are insignificant.

The static approach may also require empirical assumptions. For example, Zammuto's (1983) static study estimated: 1) litter size from embryo and placental scar counts (assumes proportion of embryos lost is equal in all populations); 2) reproductive females from presence of embryos (may assume the same proportion of females terminate pregnancy prematurely or lose whole litters at birth in all populations, depending on use); 3) the proportion of juveniles and adults

TABLE 1.—A summary of life-history data from Zammuto (1983; Zammuto and Millar, 1985), Murie (1985; Murie et al., 1980; Murie and Harris, 1982), and Dobson (1984; Dobson and Kjelgaard, 1985a, 1985b). The method applied (static or cohort life table) is indicated for each research group. Sample sizes are given in parentheses.

Source	Method	Elevation (m)	Litter size of females (≥ 2 years old)	Percent females (≥ 2 years old) reproductive	Percent yearling females mature	Percent juveniles surviving annually	Percent adults surviving annually	Adult female weight (g)	Food resource treatment ¹
Zammuto	Static	1,300	4.6 ² (30)	100 (30)	86 ³ (21)	25 (186)	57 ⁴ (84)	482 ^{2,5} (48)	Ref
		1,360	3.9 (22)	88 (25)	21 (28)	45 (105)	46 (47)	528 (28)	Ref
		1,500	2.9 (18)	62 (29)	0 (19)	61 (53)	54 (42)	548 (18)	Ref
		1,675	4.2 (26)	74 (35)	11 (9)	34 (114)	55 (44)	462 (28)	Ref
		2,000	3.4 (39)	98 (40)	0 (14)	24 (134)	69 (64)	498 (39)	Ref
		2,200	3.7 (14)	93 (15)	0 (3)	23 (52)	65 (20)	463 (14)	Ref
Murie	Cohort	1,500	2.9 ⁶ (62)	84 ⁶ (111)	0 (64)	31 ⁶ (182)	65 ⁶ (240)	413 (27)	Ref
		2,170	2.3 (61)	65 (298)	0 (47)	60 (172)	71 (621)	399 (21)	Ref
Dobson	Cohort	1,580	2.9 ^{6,7} (21)	92 ⁶ (25)	0 ⁷ (20)	35 ⁷ (37)	64 (47)	402 ⁷ (33)	Ref
		2,100	2.3 ⁷ (8)	50 ⁷ (18)	0 ⁷ (8)	60 ⁷ (15)	76 (33)	378 ⁷ (28)	Ref
		1,580	3.6 (56)	95 (84)	93 (59)	65 (156)	68 (104)	452 (94)	Exp
		2,100	3.2 (19)	96 (28)	50 (20)	85 (40)	78 (45)	479 (37)	Exp

¹ Ref = unmanipulated population, provides comparison or reference; Exp = food supplemented population.

² Negatively correlated with elevation, $P < 0.05$.

³ A higher proportion of yearling females matured at 1300 m and 1360 m than at higher elevations, $P < 0.05$.

⁴ Positively correlated with elevation, $P < 0.05$.

⁵ When females were collected at 1,300 m 25 had given birth, at 2,000 m 26 females had given birth, and at 2,200 m 8 had given birth.

⁶ Reference populations at the two elevations differ, $P < 0.05$, Mann-Whitney U and Chi-square tests.

⁷ Ref and Exp differ, $P < 0.05$, Mann-Whitney U , Fisher exact, and G-tests.

surviving from, in part, the total number of embryos and recent placental scars in the population (see both of the above assumptions); and 4) the weights of adult females during gestation and early lactation (assumes all populations at the same point in the annual cycle of embryo development and weight change).

The cohort life-table approach avoids some theoretical and empirical assumptions, but it takes a long time to collect the data, and thus much effort is required to obtain results on relatively few populations (see also Sherman and Morton, 1984; Slade and Balph, 1974). Cohort samples have the advantage of allowing measurement of temporal variation in life-history characteristics, however, and estimated means of characteristics should become more accurate as cohorts are followed over longer periods of time.

Empirical assumptions may be required by the cohort approach. In Murie's and Dobson's (references in Table 1) studies, it was assumed that the effects of long-term trapping and observations did not significantly influence life-history characteristics. For example, predators might have been attracted or discouraged, and the activity schedules of the ground squirrels might have been significantly altered. Such effects, if present and influential on characteristics of life history, might have been of unequal impact in different populations, even if the same procedures were uniformly applied. Data that bear on these possible empirical problems may be difficult to obtain.

Finally, an experimental method can indicate if some life-history characteristics are phenotypically plastic, and whether some particular environmental factor strongly influences changes in life history (Dobson, 1984; Dobson and Kjelgaard, 1985b). If a life-history characteristic is invariant under experimental manipulation, however, it may not indicate that the characteristic is genetically fixed. The characteristic might be near its minimum or maximum value in a population, and thus incapable of response to manipulation (e.g., the proportion of reproductive females at 1,580 m, Table 1); or the characteristic might be capable of response, but preempted by changes in other variables.

In conclusion, data on patterns of life history must be evaluated carefully, because different methods can give different results. When alternative methods give similar results, however,

empirical conclusions are strengthened. Each method that we employed has its own detriments and merits, and which is applied will probably depend on the animal under study and the particular questions under investigation. We hope that our results, and the conclusions drawn from them, will assist the design of other studies of mammalian life-history patterns.

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