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Increasing returns in the life history of Columbian ground squirrels

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Summary

1. We examined positive associations and trade-offs of maternal and reproductive traits in a population of Columbian ground squirrels, *Spermophilus columbianus*.

2. Structural size, body condition, mother's personal allocation to body mass during reproduction, and timing of littering were estimated for live-trapped reproductive females that were observed during an 8-year period, and were compared to litter mass, litter size, and average pup mass using path analyses.

3. Mothers exhibited age-structured traits that influenced reproductive patterns. Yearling mothers were significantly smaller, bred later, and had smaller litters than older females. Mothers that gained more body mass during reproduction and older mothers in good body condition that were structurally large had larger litters.

4. Early seasonal timing of littering was an important positive influence on successful reproduction by older mothers only in early breeding seasons and in years when conditions for reproduction were good for all females.

5. The number of offspring that survived to 1 year of age was most strongly associated with litter mass and litter size; date of breeding was of secondary influence, with earlier litters exhibiting greater success.

6. In general, mothers that gained the most in body mass during reproduction were concurrently more successful in weaning large litters (perhaps due to better quality of foraging habitat).

7. In addition to expected reproductive trade-offs, reproduction by Columbian ground squirrels exhibited positive associations of life-history traits that may reflect evolutionary increasing returns.

Key-words: increasing returns, life history, path analysis, reproductive effort, *Spermophilus*.

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Introduction

Life-history theory has focused on trade-offs among traits that reflect reproduction, growth and survival (e.g. reviews by Roff 1992; Stearns 1992). Trade-offs are thought to occur because energy for life's processes is limited (Hirshfield & Tinkle 1975). For example, breeding females divide acquired energy between their own maintenance and survival, and concurrent allo-

Correspondence: Dr F.S. Dobson, Dept of Zoology, Auburn University, Auburn, Alabama 36849-5414, USA. Tel: +334-844-92521. Fax: +334-844-9234. E-mail: fdobson@acesag.auburn.edu cations to their offspring. Trade-offs occur because individual females may not have the resources to make maximal energy allocations in both themselves and in their production of offspring. An important goal of evolutionary ecology is to examine partitioning of energy between somatic and reproductive efforts (e.g. Dunham, Grant & Overall 1989; McNamara & Houston 1992).

Less attention has been paid to evaluating the positive associations among life-history traits. In some cases, however, positive associations of adult survival and reproduction have been found within populations, perhaps caused by variations in resource conditions within habitats (e.g. H'gstedt 1980, 1981; 74 Increasing returns in life history Smith 1981: Clutton-Brock, Guinness & Albon 1982. 1983; Clinton & Le Boeuf 1993). Individuals that live in the richest microhabitats probably benefit from greater total energy acquisition (Ritchie 1988). These individuals may devote more energy to both survival and reproduction, perhaps resulting in greater fitness (Ritchie 1990; Trombulak 1991). Over time, individuals that exhibit positive genetic associations of somatic and reproductive traits could thus come to predominate in populations, especially if variation in resource acquisition is high (Houle 1991). Positive associations among the fitness traits of life histories may be analogous to 'increasing returns' in human economic systems, where initial advantages in market share of particular technological products increase rapidly (reviewed by Arthur 1990). Because technological products need to be compatible, positive associations among components are created that accentuate increases in market share. Interwoven patterns of increasing returns and trade-offs (negative feedbacks) should characterize complex systems, whether life histories or economies. Increasing returns in life-history traits may result in greater fitness for individuals that exhibit sufficient phenotypic plasticity to exploit variable environmental conditions. Thus, increasing returns might explain, at least in part, the evolution of plasticity of phenotypic traits related to somatic and reproductive efforts (e.g. Via & Lande 1985; van Noordwijk & de Jong 1986; Houle 1991).

Many studies have compared influences of maternal traits such as body mass to reproduction (e.g. reviews by Klomp 1970; Murphy & Haukioja 1986; Sauer & Slade 1987). In mammalian species, influences of maternal mass on either litter size, the average mass of offspring, or both have been documented (e.g. Keller & Krebs 1970; Tamarin 1977; McClure 1981; Myers & Master 1983; Murie & Dobson 1987; Dobson & Myers 1989; Michener 1989; Bowen et al. 1994; Genoud & Perrin 1994; Hoogland 1995; Clutton-Brock et al. 1996). These studies indicate that heavy mothers devote more resources to reproduction, through larger litters or heavier young. Heavy mothers also exhibit increased somatic effort that might result in improved chances of maternal survival, and thus subsequent breeding. In such cases, evolution of life-history traits via increasing returns seems likely.

Interpretation of influences of maternal body mass on reproduction may be confounded by different aspects of maternal size (Campbell & Dobson 1992; Dobson 1992; Dobson & Michener 1995). Body mass could reflect the physiological condition of a mother through storage of fats or other energy-rich molecules, but maternal mass should also at least partly reflect a mother's overall structural size. This latter aspect of mass might be reflected by the length of the head and body (Iskjaer *et al.* 1989) or by the size of a female's skeleton (e.g. Dobson 1992). Bird and mammalian species commonly exhibit determinate growth in structural size (e.g. Ricklefs 1967; Boag 1984, 1987; Campbell & Dobson 1992; Dobson & Michener 1995), but may vary considerably in fat reserves (e.g. Barzen & Serie 1990; Michener & Locklear 1990a, 1990b; Afton & Ankney 1991; Mann & Sedinger 1993; Dobson & Michener 1995). Although physiological condition and structural size may often be positively correlated, considering their influences separately might produce a clearer understanding of the interplay of maternal traits and reproduction (Campbell & Dobson 1992; Schluter & Gustafsson 1993; Dobson & Michener 1995; Humphries & Boutin 1996).

Another possible maternal influence on reproduction is the time at which young are produced. For example, the influence of seasonal timing on reproduction has been studied extensively among bird species in the field (e.g. Klomp 1970; Perrins 1970; Drent & Daan 1980; Daan et al. 1988; Hochachka 1990; Rohwer 1992; Hepp & Kennamer 1993; Nilsson 1994) and also with modelling (Price, Kirkpatrick & Arnold 1988; Rowe, Ludwig & Schluter 1994). Studies of life histories of large mammals also indicate the influence of timing on reproduction, usually on offspring mass or survival (e.g. Clutton-Brock et al. 1982, 1983; Festa-Bianchet 1988; Berger 1992; Fairbanks 1993; Gaillard, Delorme & Jullien 1993; Green & Rothstein 1993; Lund & Boyd 1993; Bowen et al. 1994; Schultz & Johnson 1995). Finally, a few studies of small mammals have shown that seasonal timing of litter production can markedly influence the size and number of offspring (e.g. Dobson & Myers 1989; Rieger 1991; Dobson & Michener 1995).

The purpose of our study was to examine influences of maternal body size and seasonal timing of reproduction on the reproductive efforts of Columbian ground squirrels (Spermophilus columbianus, Ord). We considered estimates of structural size, body condition, and date of littering as maternal characteristics. Characteristics of resource allocation to reproduction were litter mass, number of offspring (litter size), and the average mass of juveniles, all measured near the time of weaning. We hypothesized that the maternal traits of reproductive timing and aspects of body size should have significant influences on the allocation of energy to offspring, and tested for these effects with an explicit path-analytical model of reproduction (after Dobson & Michener 1995). Maternal and reproductive traits were examined for positive relationships that might reflect increasing returns and negative associations that might reflect life history trade-offs.

Methods

Field studies were conducted from 1983 to 1990 at the Turnbull National Wildlife Refuge, about 35 km south-west of Spokane, Washington. The 9-ha study site (at 47°E26′N, 117°36′W; 695 m elevation) contained a large meadow surrounded by an open wood-

land of Ponderosa pine (Pinus ponderosa, Douglas & Lawson) and rocky outcrops. A large wetland bounded the study site on the south side with inhospitable habitat for ground squirrels. Ground squirrels were live-trapped shortly after emergence from hibernation in early to mid March, and previously uncaptured ground squirrels were captured and marked whenever they appeared. Captured individuals were weighed with a spring-slide balance, examined for reproductive condition, and marked with numbered metal ear tags for permanent identification. In addition, each ground squirrel was given a unique mark on both sides of the body with black hair dye for identification during subsequent behavioural observations. From 1985 to 1990, zygomatic arch breadth was measured near emergence for yearling and older ground squirrels by one of us (J.O. Murie), after considerable practice to standardize the measurement procedure. Two to five repeated measurements made on the same individuals in different years were very similar, as reflected by a repeatability of 0.894 (the intraclass correlation coefficient; F = 13.83, d.f. = 50,82, P < 0.0001).

Juvenile ground squirrels were captured shortly after their first emergence above ground from natal burrows (in early to late May). The time of litter emergence could usually be anticipated because the date of breeding was known or could be estimated within a few days. Copulations above ground were observed frequently. If mating was not observed, mating date was estimated from the external appearance of the vulva, behavioural evidence of underground copulation (including oral cleaning of the groin area by both sexes), detection of a copulatory plug, or the presence of sperm in vaginal smears. Dates of litter emergence were estimated by adding 51 days to the estimated or observed mating date: 24 days from mating to parturition (Shaw 1925; Murie & Harris 1982) and 27 days from parturition to first emergence of the litter (Murie 1992). The site of emergence was anticipated for many litters because natal burrows could be identified from observations of females stocking them with dry grass before young were born, or by observing females emerge from or enter them during the lactation period.

During the period of litter emergence, the study site and especially the locations of natal burrows were checked one to three times daily for newly emerged juveniles. To capture juveniles, multiple-capture wiremesh traps were placed over natal burrows or burrows were surrounded with live-traps. Most juveniles were captured, weighed, examined and marked within 3 days of first appearing above ground. Litter size was determined by observation of marked juveniles. The lactating female that associated with a natal burrow was assumed to be the mother of the litter that emerged from that burrow. Only about three-quarters of yearling females attempted breeding, but virtually all older females mated and became pregnant. Because dispersal of offspring is delayed until they are more

© 1999 British Ecological Society Journal of Animal Ecology, **68**, 73–86 than a year old, survival of young to yearling age was monitored (Boag & Murie 1981; Murie & Harris 1984; Dobson & Murie 1987; Risch, Dobson & Murie 1995).

Total litter mass was calculated from the product of litter size and average juvenile mass. Our measures of offspring size and number were taken near the time of weaning, after the substantial maternal energetic investment that occurs during lactation (Kaczmarski 1966; Mattingly & McClure 1982; Kenagy, Sharbaugh & Nagy 1989; Michener 1989). Litter size at this time is not greatly different from litter size at conception or at birth (Murie, Boag & Kivett 1980). Some litters were killed by badgers (Taxidea taxus, Schreber), and other litters may have suffered partial predation by badgers during lactation (Murie 1992), and we eliminated these litters from analyses. Maternal and reproductive data were pooled among years, resulting in multiple records from different years for some females that were older than yearlings. Pooling of multiple records for individuals was appropriate because reproduction in one year does not appear to influence either subsequent survival or future reproduction (Murie & Dobson 1987; Risch et al. 1995). In the present study, litter size in one year could explain only 4.9% and 11.4% of the variation in litter size or mass the next year, respectively (F = 1.02, d.f. = 1.20, d.f. = 1.20)P = 0.32; F = 2.58, d.f. = 1,20, P = 0.12). When influences of different years were statistically removed, very similar non-significant patterns were still evident.

We used a path model (Wright 1921; Li 1981; Pedhazur 1982) as an explicit model of reproduction. The significance of path coefficients (at $P \leq 0.05$) was used to determine whether there was support for the influence of maternal traits on reproductive effort. Path analyses allow associations among independent variables, and require a priori designation of plausible hypotheses of causal relationships between independent and dependent variables in a path diagram. Path analyses use standardized data and thus are especially appropriate when variables are measured on different scales, such as days for seasonal timing, counts for litter size, and grams for maternal and litter mass. Path analyses partition the correlation between an independent and dependent variable into a direct effect of the independent variable and indirect influences of the independent variable due to the intercorrelation with other independent variables that themselves exhibit direct effects (e.g. Wright 1921; Li 1981; Schemske & Horvitz 1988; Mitchell 1992). The specific path model that we used did not permit interpretation of indirect influences (Schemske & Horvitz 1988), and post hoc examination of path analyses indicated that this was not an onerous condition.

The standardized partial regression coefficients (viz. path coefficients) of path analyses may be biased if independent variables are collinear (Myers 1990; Petraitis, Dunham & Niewiarowski 1996). Standard errors of path coefficients may be inflated when independent variables are collinear, as revealed by variance inflation factors (VIFs). Also, the magnitude of path coefficients may be inflated if collinearity of independent variables is extreme. This bias can be revealed from examination of 'condition numbers' that are calculated from ratios of eigenvalues of the correlation matrix of the independent variables (see *Petraitis et al.* 1996 for an example).

Analyses were performed with SAS (1990) statistical software; and included *t*-tests, tests of normality, the general linear model (GLM, used for analysis of variance [ANOVA]), logistic regression (CATMOD), regression (REG), path-analytical techniques (STB option of the REG procedure), and evaluation of collinearity of independent variables in multiple regressions (COLLIN and VIF options of the REG procedure).

'Structural size' was estimated as zygomatic arch breadth, a measurement that is highly correlated with the size of the skull and skeleton in ground squirrels (r = 0.814, n = 166, P < 0.0001, correlation of zygomatic arch breadth and a skeletal index of structural size employed by Dobson 1992). Maternal physiological condition (or 'body condition') at about the time of emergence from hibernation in the spring was estimated from the residuals of the regression of body mass on zygomatic arch breadth. 'Change in mass' of mothers between first capture in spring and the emergence of young from natal burrows about 51 days later was used to estimate the energy allocation that mothers made in personal growth and physiological condition during reproduction. Females generally mate within about 5 or 6 days of spring emergence from hibernation, so mass at first capture approximates mass at the start of pregnancy. Both body condition and change in mass should accurately reflect energy stores of fats and protein (e.g. Michener & Locklear 1990a; Dobson & Michener 1995; Humphries & Boutin 1996).

Results

VARIATIONS AMONG AGES AND YEARS

Yearling and older females (2–8 years old) exhibited strikingly different patterns in several maternal and reproductive characteristics (Fig. 1). On average, older females had significantly higher body mass than yearlings at spring emergence from hibernation, greater zygomatic arch breadth, poorer physiological condition, lower gain in mass during the breeding period, earlier dates of litter emergence, greater total litter mass, and higher litter size (*t*-tests, all $P \leq 0.0001$). Amongst older females, maternal and reproductive characteristics did not exhibit substantial age-related variations, although structural size and spring body mass of older mothers exhibited slight and gradual increases of about 1% and 4% (Fig. 1).

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Maternal and reproductive variables were exam-

ined for variation among the 8 years of study. Years varied significantly for the date litters emerged (and thus mating dates 51 days before; GLM, F = 84.92, d.f. = 7,219, P < 0.0001), mother's mass at emergence from hibernation (F = 3.43, d.f. = 6,268, P < 0.01), total litter mass at first emergence from the natal burrow (F = 3.36, d.f. = 6,211, P < 0.01), litter size (F = 4.89, d.f. 7,240, P < 0.0001), and mean offspring mass (F = 3.44, d.f. = 6,225, P < 0.01). Maternal mass near the end of lactation also varied among years (F = 2.72, d.f. = 7,269, P < 0.01). Zygomatic arch breadth of mothers, however, exhibited remarkably little variation among years (F = 0.14, d.f. = 5,235, P = 0.98).

We wished to examine general patterns in reproduction over the entire study, but did not want to ignore the possibility that different patterns might be evident for different age groups or in different years. Because yearling and older females exhibited the greatest contrast in characteristics (Fig. 1), we examined these two age classes separately. Year to year variation in maternal and reproductive characteristics presented a greater problem, because we wanted to examine both general reproductive patterns and among-year variation. Thus, we first extracted residuals from ANOVAS, where each maternal and reproductive characteristic was subjected to an ANOVA in which 'year' was the grouping variable. This procedure standardized data for among-year variations (Straney 1978). Second, we examined unadjusted data for influences of early vs. late years of the reproductive season and years of small vs. large litters.

BODY CONDITION

Physiological condition of mothers was estimated as the residuals in a regression of body mass in the spring on structural size (zygomatic arch breadth). The regressions for both yearling and older females were highly significant (respectively; $R^2 = 0.21$, d.f. = 1,54, P < 0.001; $R^2 = 0.34$, d.f. = 1,156, P < 0.0001) and did not differ in slope (F = 0.41, d.f. = 1,212, P = 0.53) or intercept (t = 1.15, d.f. = 55,157, P = 0.26). Residuals were normally distributed (yearlings, W = 0.97, n = 56, P = 0.37; older females, W = 0.98, n = 158, P = 0.20), so this index of physiological condition (Fig. 1c) was used in further multivariate analyses.

We examined changes in body mass for mothers between the time of mating and the date of litter emergence (Fig. 1d). This variable indicates a mother's allocation of resources in personal body mass during gestation and lactation; virtually all mothers gained body mass during this period (98%, n = 126). Mother's mass was adjusted for year effects at the beginning and at the end of reproduction, and the change in body mass was measured by subtracting adjusted mass in spring from adjusted mass at the end



Fig. 1. Mean (\pm 1 SE) maternal and reproductive characteristics for female Columbian ground squirrels of different ages. Females aged 5–8 years were pooled due to limited samples. In (c), body condition is the residual score in a linear regression of spring body mass on zygomatic arch breadth. In (d), the change in mass is between spring emergence from hibernation and subsequent emergence of juveniles from the natal burrow near the end of lactation. Litter mass, litter size, and juvenile body mass were measured when offspring first emerged from natal burrows.

of lactation. For yearlings, change in body mass may reflect either growth in structural size, improved body condition, or both. Because older females plateaued in structural growth (Fig. 1b), change in body mass primarily reflects improved body condition. Change in body mass during reproduction varied among years in yearling and older females (respectively; F = 2.28, d.f. = 6,50, P < 0.05; F = 4.02, d.f. = 6,166, P < 0.001).

MULTIPLE REGRESSIONS AND PATH ANALYSES

Multiple regressions were used to examine the possible influence of maternal variables (date of litter emergence from natal burrows, and mother's body condition, structural size, and change in body mass during reproduction) on reproductive variables (litter mass, litter size, and average body mass of juveniles). Maternal characteristics were treated as independent variables, and reproductive traits as dependent variables. Our models for multiple regressions are of the same form as for subsequent path analyses (Figs 2 and 3). Multiple regression analyses did not examine possible influences of specific independent variables on the dependent variables; that is the purpose of path analyses.

Yearling females





Fig. 2. Path models of the influence of maternal traits of yearling and older females on litter size. Significant correlations (P < 0.05) among independent variables appear to the left of the maternal traits, standardized partial regression (path) coefficients are on the right. Significant paths (P < 0.05) appear as bold lines. Solid lines indicate positive paths, dashed lines indicate negative paths, whether significant or not. U shows the path coefficient for the unexplained variation. *n* is the sample size.

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For yearling and older mothers, maternal traits could explain significant amounts of variation in total litter mass (respectively; $R^2 = 0.34$, F = 3.02, d.f. = 4,23, P = 0.04; and $R^2 = 0.25$, F = 7.45, d.f. = 4,88, $P \leq (0.0001)$ and litter size (respectively; F = 6.90, d.f. = 4,25, $R^2 = 0.52$, P < 0.001; $R^2 = 0.21, F = 5.95, d.f. = 4,90, P < 0.001$, but not average mass of emerging juveniles (respectively; $R^2 = 0.26, F = 1.97, d.f. = 4,23, P = 0.13; R^2 = 0.07,$ F = 1.75, d.f. = 4,88, P = 0.15). Due to the lack of significance of the multiple regressions, we do not present path analyses for mean pup mass. Despite a reasonable range of litter sizes (viz. 1-8), caution has been recommended when applying discrete variables to path analyses (Petraitis et al. 1996). We only present path analyses of litter size, because litter mass and litter size were strongly correlated (Table 1) and had identical patterns of significant path coefficients.

Independent variables in the path analyses were not highly intercorrelated (Table 1), although body condition in spring and change in mass during reproduction were significantly negatively associated for both yearling and older females (Figs 2 and 3, correlation coefficients on the left). Females that emerged from hibernation in relatively poor condition gained the most body mass during reproduction. For yearling females, significant positive paths were evident from the change in mother's body mass during reproduction to both litter mass and litter size (Fig. 2). For older females, significant positive paths occurred from maternal body condition, structural size, and change in mass during reproduction to both litter mass and litter size.

Collinearity of independent variables was probably not a major bias in our path analyses of reproduction (Fig. 2). The greatest magnitude of the variance inflation factors (VIFs, that test for inflated standard errors of path coefficients) should be less than 10 (Myers 1990). For the ground squirrels, the maximum VIF for yearling mothers was 1.94 and for older mothers it was 1.77. Maximum condition numbers (not to be confused with maternal body condition in spring, described above), that test for inflated magnitudes of path coefficients, indicate significant bias from collinearity if they are over 30 (SAS 1990) or more conservatively for ecological data over about 3 (Petraitis et al. 1996). The maximum condition number for yearling ground squirrel mothers was 2.65 and for older mothers 2.18. Some collinearity of independent variables obviously occurred, however, as indicated by the significant negative correlations between body condition in spring and change in body mass during the reproductive season (Fig. 2).

SEASONAL PATTERNS

Data were insufficient to examine among-year variation in maternal influences on reproduction of year-

Offspring production



Fig. 3. Path models of the influence of maternal traits of older females on litter size; during early breeding seasons, and in years of high and low offspring production (viz. mean litter size). Significant correlations (P < 0.05) among independent variables appear to the left of the maternal traits, standardized partial regression (path) coefficients are on the right. Significant path coefficients (P < 0.05) appear as bold lines. Solid lines indicate positive paths, dashed lines indicate negative paths, whether significant or not. U shows the path coefficient for the unexplained variation. *n* is the sample size.

Table 1. Correlations among characteristics of yearling (above the diagonal) and older (below the diagonal) female Columbian
ground squirrels and their litters. Spring body mass and condition were measured near the time of mating. Change in mass is
the weight gained by mothers between dates of mating and litter emergence (near the end of lactation). All variables have been
standardized for year-to-year variation except zygomatic arch breadth (see text). Sample size for each comparison in parentheses

	Emergence date	Spring body mass	Spring condition	Change in mass	Zygomatic breadth	Litter mass	Litter size	Juvenile mass
Emergence date	_	0·06 (42)	-0·17 (32)	-0.21 (41)	-0·19 (35)	-0·27 (39)	-0·37 (42)	-0·06 (39)
Spring body mass	-0.16 (125)	_	0·86*** (50)	-0·72*** (51)	0·50** (50)	0·00 (41)	-0·26 (44)	0·39* (41)
Spring condition	-0.04 (102)	0·83*** (128)	_	-0.74*** (41)	0·00 (50)	-0.15 (31)	-0·41 (34)	0·43 (31)
Change in mass	-0.02 (111)	-0·52*** (141)	-0·66*** (114)	—	-0.28 (43)	0·31 (40)	0·56*** (40)	-0·45* (40)
Zygomatic breadth	-0.16 (112)	0·56*** (128)	0·00 (128)	0·02 (114)	_	0·19 (33)	0·12 (37)	0·09 (33)
Litter mass	0·02 (126)	0·37*** (124)	0·31* (99)	0·09 (122)	0·20 (107)	—	0·77*** (43)	0·12 (43)
Litter size	-0·10 (134)	0·29** (129)	0·22 (102)	0·12 (127)	0·19 (111)	0·80*** (134)		-0·50** (43)
Juvenile mass	0·23* (127)	0·10 (124)	0·09 (99)	-0·17 (122)	0·02 (108)	-0.02 (134)	-0·53*** (134)	·

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 $\label{eq:prod} ^{\ast}P\leqslant0{\cdot}01;\, ^{\ast\ast\ast}P\leqslant0{\cdot}001;\, ^{\ast\ast\ast\ast}P\leqslant0{\cdot}0001.$

80 Increasing returns in life history ling females. For older females, we divided our data into years of early (1986-88 and 1990) and late (1985 and 1989) reproductive seasons, defined as before or after the mean date of litter emergence for the entire study (mean early and late Julian dates = 126 and 139, respectively, t = 11.57, d.f. = 93, P < 0.0001). Also, we defined years of high (1986 and 1988) and low (1985, 1987 and 1989-90) offspring production from whether litter size was above or below the average for the entire study (mean high and low litter size = 4.67 and 4.08, respectively, t = 2.06, d.f. = 93, P < 0.05). Within each subdivision of the data set, adjustment was made for variations among years (Straney 1978) and data were then pooled. Multiple regressions and path analyses were performed on the partitioned data sets.

Multiple regressions of litter size on the maternal traits of older females were significant for years of early reproduction ($R^2 = 0.25$, F = 6.11, d.f. = 4,72, P < 0.001), and both high ($R^2 = 0.30$, F = 4.40, d.f. = 4,41, P < 0.01) and low offspring productivity $(R^2 = 0.20, F = 2.70, d.f. = 4,44, P = 0.04)$, but perhaps due to low sample size were not significant for years of late reproduction ($R^2 = 0.35$, F = 1.73, d.f. = 4,13, P = 0.20). Multiple regressions of litter mass on maternal traits were significant for years of early reproduction ($R^2 = 0.21$, F = 4.56, d.f. = 4,70, P < 0.003), and low offspring productivity ($R^2 = 0.35$, F = 6.01, d.f. = 4,44, P < 0.001). Patterns of significant path coefficients were identical for litter size and litter mass, so we only present path analyses for litter size. In addition, path analyses of subdivisions of the data are only presented for significant multiple regression models.

Years of early reproduction by older mothers had a similar pattern to the combined year-adjusted data (compare Fig. 3 with Fig. 2), but seasonal timing (emergence date) had a significant negative path to litter size. In years of high offspring production by older mothers, the significant path coefficients were again similar to those in the overall data set, except that emergence date had a significant negative path to litter size (Fig. 3). Years of above average litter size were also years of earlier spring emergence of mothers (mean early and late Julian dates = 125 and 132, respectively, t = 5.24, d.f. = 93, P < 0.0001). In years of low offspring productivity, body condition had a significant path (positive) to litter size, but the path from emergence date to litter size was virtually nonexistent.

Collinearity of independent variables was probably not a major bias in our path analyses of reproduction for subsamples of the total data set (Fig. 3). The maximum VIF (tests of bias in standard errors of path coefficients) for the significant multiple regressions was 1.88. Maximum condition number (tests of inflated magnitudes of path coefficients) was 2.31. Some collinearity of independent variables was again indicated by the significant negative correlations

© 1999 British Ecological Society Journal of Animal Ecology, **68**, 73–86 between body condition in spring and change in body mass during the reproductive season (Fig. 3).

SURVIVING OFFSPRING

On average, yearling mothers had only 0.80 young survive to become yearlings, while 1.84 of offspring of older mothers survived to yearling age (significantly different, t = 2.58, d.f. = 263, P = 0.01), and the number of surviving young did not differ significantly among years for either younger or older females (respectively; GLM, F = 0.88, d.f. = 6,43, P = 0.52; F = 1.48, d.f. = 7,164, P = 0.18). Thus, we examined unadjusted number of surviving offspring for associations with maternal and reproductive characteristics. For yearling mothers, only total litter mass was significantly positively associated with the number of surviving offspring (r = 0.393, n = 43, P < 0.01), but a positive association of litter size and number of surviving offspring approached significance (r = 0.255, n = 46, P = 0.09). For older females, total litter mass and litter size were significantly positively associated with number of surviving offspring (respectively; r = 0.384, n = 134, $P \le 0.0001$; r = 0.343, $n = 157, P \le 0.0001$).

Mean mass of offspring at weaning was not positively associated with the number of surviving offspring, whether litters that had no surviving offspring were included (r = -0.045, d.f. = 175, P = 0.55) or not (r = -0.066, d.f. = 128, P = 0.45). In addition, there was little difference between average body mass of weanlings in litters that did not produce surviving yearlings and litters that did (respectively, mean = 95.9 g and 98.1 g, t = 0.58, d.f. = 175, P = 0.56). Examination of the litters of yearling and older mothers separately produced very similar results, suggesting the absence of influence of the average mass of weaned offspring on their survival to yearling age.

The mass that yearling and older females gained during reproduction was not significantly correlated with the number of their offspring that survived to yearling age (respectively; r = 0.163, n = 44, P = 0.29; r = 0.157, n = 136, P = 0.07). For older females, however, maternal body condition when juveniles were emerging for the first time from natal burrows was significantly positively correlated with both adjusted litter size and number of surviving yearlings (respectively; r = 0.376, n = 110, $P \le 0.0001$; r = 0.215, n = 120, P = 0.02). At juvenile emergence from natal burrows, older mothers that survived to the next year (mean survival rate = 74.4%, n = 129) were in better body condition than those that did not survive to the next year (respectively, mean condition = 3.37 g and -9.81 g; logistic regression, $\chi^2 = 4.21$, d.f. = 1,119, P = 0.04). For older females, unadjusted date of litter emergence was negatively associated with number of surviving yearlings both among the means for years (r = -0.816, n = 8 years, P < 0.05) and in the overall data set (r = -0.165, n = 142, P < 0.05).

Discussion

MATERNAL INFLUENCES ON REPRODUCTION

Before we examined the maternal influences on reproductive effort in Columbian ground squirrels, we separated mother's body mass into two underlying components, structural size and body condition (cf. Dobson & Michener 1995). Our estimate of structural size, field-measured zygomatic arch breadth, was highly repeatable and therefore provided an acceptable estimate of the size of the skull and skeleton. Because body condition was estimated as the residual of body mass regressed on structural size, body condition and structural size were uncorrelated, and thus their relative influences on reproductive effort could be easily contrasted. Change in maternal mass might also be considered an aspect of maternal size, but we prefer to interpret this variable as an index of energy acquisition during reproduction.

Much of the energy allocated to reproduction must come from daily feeding, because fat reserves at emergence from hibernation are only a fraction of the total mass of weaned offspring (e.g. Michener 1989; Michener & Locklear 1990b). Mothers that increased most in personal mass were expected to devote some of their additional energy to reproduction. Maternal aspects of size had significant influences on reproductive success, primarily through influences on litter size. For yearling females that were probably still growing in structural size (Fig. 1b; Dobson 1992), change in maternal mass between mating and weaning had a strong positive influence on reproduction (Fig. 2). Also, yearling females that gained the most in body mass during reproduction might have been most likely to complete structural growth.

All of the aspects of maternal size that we measured had significant influences on reproduction by older females. Spring body condition exhibited a strong positive influence on reproduction, with additional positive influences from structural size and change in maternal mass during reproduction. Older mothers on good foraging areas might have retained some energy reserves from the previous year, and such reserves should positively influence reproduction. Mothers with larger structural size exhibited increased reproduction, perhaps reflecting behavioural dominance in competition for foraging areas (Festa-Bianchet & Boag 1982; Murie & Harris 1988; Boag & Wiggett 1994).

It was somewhat surprising that both yearling and older mothers that gained more mass during the reproductive season also exhibited increased reproduction through larger litter sizes. Subsequent to mating and implantation of zygotes, litter size can only decrease, so adjustments to reproductive effort via litter size are constrained. There are two mechanisms that might produce a strong association of increase in mother's body mass during reproduction and reproductive effort. First, mothers that acquire less energy (i.e. exhibit low change in body mass) during the reproductive period might suffer greater mortality of zygotes or young during pregnancy and lactation, respectively, than mothers with abundant energy. This first mechanism seems unlikely, because mothers that gained less body mass during reproduction started out the active season with relatively high spring emergence mass and body condition; as indicated by the significant negative correlations between both spring mass and body condition with change in mother's body mass during gestation and lactation (Table 1). Secondly, if some mothers anticipate excellent resource conditions, perhaps due to occupation of a superior foraging area, they may produce and nurture larger litters and make increased somatic efforts during the reproductive period. This latter hypothesis is supported by the finding that the path from change in maternal mass during reproduction to litter size was significantly positive in years of above average litter size, but the same path was weaker and not significant in years of below average litter size (Fig. 3).

Maternal traits influenced reproduction primarily through variation in litter size, and the lack of influence of maternal traits such as change in body mass during reproduction on the average mass of offspring was also somewhat surprising. In Richardson's ground squirrels (S. richardsonii, Sabine), Dobson & Michener (1995) found significant influences of mother's spring body condition on the body mass of neonatal offspring, but not on litter size. In addition, maternal traits explained more of the variation in average mass of neonates than in litter size. In Uinta ground squirrels (S. armatus, Kennicott), philopatric females survived better to yearling age if they were heavier as weanlings (Rieger 1991). In Columbian ground squirrels, however, maternal traits had little influence on body mass of weaned offspring, and there was no positive influence of weaning mass on subsequent survival to yearling age. We currently have no explanation for these interspecific patterns, and further research into causal influences seems warranted.

SEASONAL PATTERNS

We found that patterns of reproductive effort by older mother Columbian ground squirrels depended somewhat on the timing of the breeding season among years. In years that exhibited early breeding, aspects of older mother's body size and energy acquisition (viz. change in mass) had similar influences on litter size as in the combined data, with the additional influence of a significant seasonal decline in litter size (compare Figs 2 and 3). Thus, there may have been two important aspects of reproductive timing: early

vs. late years, and a seasonal decline in litter size during years of early breeding. Apparently, a lack of influence of timing of breeding on litter size during years of late breeding obscured the predicted importance of seasonal timing of reproduction in the combined data set.

For mothers older than yearlings, years of high production of offspring (viz. high mean litter size) exhibited a similar pattern as that apparent in years of early breeding: significant influences of maternal traits on litter size and a seasonal decline in litter size (Fig. 3). In years of low offspring production there was no seasonal decline in litter size. Patterns of reproduction associated with seasonal timing and offspring production, however, were not independent because the same data set has been partitioned in two different ways, causing some similarity in the partitioning of years. In fact, years of high offspring production were also years of early emergence from hibernation. We prefer to interpret years of high and low offspring production, however, as years of favourable and unfavourable environmental conditions for reproduction. Not surprisingly, superior body condition in spring appeared to influence litter size positively during unfavourable years (Fig. 3).

The absence of influence of seasonal timing on litter size in the combined data set was surprising. Seasonal declines in litter size occur in the clutches of temperate birds (e.g. Klomp 1970; Perrins 1970; Drent & Daan 1980; Newton & Marquiss 1984; Daan et al. 1988; Hochachka 1990; Aparicio 1994; Wiggins, Part & Gustafsson 1994). In Uinta ground squirrels, Rieger (1991) found that as the breeding season progressed, litter size decreased and average juvenile mass at weaning increased. This pattern subsequently resulted in similar body mass at entry into hibernation of juveniles produced at different times during the breeding season. Dobson & Michener (1995) found a similar pattern of seasonal decline in litter size coincident with increased individual mass of neonatal Richardson's ground squirrels. The lack of concordance of the ground squirrel studies might result from examination of only 1 year of data by Dobson & Michener (1995) and 2 years of data by Rieger (1991). Patterns of seasonality of reproduction were only evident in Columbian ground squirrels in some years (Figs 2 and 3).

EVALUATION OF PATH ANALYSES

Path analyses revealed influences of maternal traits on reproduction that would not have been evident from simply examining correlations among the variables. For example, change in mass and litter size of yearling females had a much stronger path coefficient than correlation coefficient (compare Fig. 2 & Table 1). For older females, structural size and change in mass during reproduction were not significantly correlated with litter mass or litter size, and body condition in spring was not significantly correlated with litter size

© 1999 British Ecological Society Journal of Animal Ecology, **68**, 73–86 (Table 1). Paths from these independent variables, however, were significant and much higher than the correlations (Fig. 2). As in Dobson & Michener's (1995) study of reproduction in Richardson's ground squirrels, path analyses probably eliminated confounding effects of non-significant associations among independent variables.

If independent variables are highly intercorrelated (i.e. collinear), assignment of causal effects in path analyses may be obscured (Pedhazur 1982; Myers 1990; Petraitis et al. 1996). In all of our path analyses, the only significant association of independent variables was a negative correlation between spring body condition and change in maternal mass during reproduction (Figs 2 and 3). Analyses of collinearity, however, did not reveal strong sources of bias. Multiple regression techniques, including path analyses, rest on a variety of assumptions concerning sampling, normality of data, and linearity of associations of variables (reviewed by Petraitis et al. 1996). Thus, even though path analyses may reveal patterns of results that are obscured in examination of correlations among variables, they still must be viewed with caution.

Another limitation of the analyses was the pooling of data from different years for females older than yearlings. This procedure could have influenced the path analysis of reproduction among older females via pseudoreplication of individuals. The dependent variable of litter size, however, was statistically independent from year to year for individual females (see Methods). This result probably reflects the extreme phenotypic plasticity of litter size in Columbian ground squirrels (see below). Nonetheless, evolutionary interpretations of the patterns revealed by our path analyses must also be viewed with caution.

One final caveat concerns the pooling of data from different years. Although there appeared to be no statistical impediment to pooling, different reproductive patterns were evident in different years (Fig. 3; see also Boutin & Larsen 1993). Elucidation of these patterns required subdivision of the data set. An alternative analysis based on entry of mean date of breeding as an independent variable in the path analysis for mothers that were older than yearlings (as in Fig. 2, but with five independent variables and unadjusted data; unpublished results) indicated possible effects of different years, but did not reveal the nature of results for different years (viz., those shown in Fig. 3). Thus, when data are pooled for path analyses, some patterns may be masked by interaction effects among pooled samples, and examination of subdivisions of the data set for underlying patterns may be necessary.

SURVIVAL OF OFFSPRING

We examined whether maternal and reproductive characteristics at the time of weaning influence the numbers of offspring that survive to yearling age.

Some yearlings bred, so survival to yearling age may approximate age at maturity. Of the maternal traits, only date of litter emergence (and thus breeding date) was significantly negatively associated with the number of surviving yearlings from litters. For older mothers, as unadjusted date of breeding increased, survival to yearling age declined; but no similar association was evident for adjusted date of breeding (r = 0.018, n = 142, P = 0.83). Thus, success in producing offspring that survive to become yearlings may have resulted from larger litters being produced early in the reproductive season during early years for reproduction (Fig. 3). The strongest influence on success at producing offspring that survive to the yearling stage was litter size (see also Festa-Bianchet & King 1991; King, Festa-Bianchet & Hatfield 1991). This pattern most likely reflects individual optimization of litter size, rather than alternative hypotheses such as Lack's (1947, 1948) litter and clutch size model (Högstedt 1980; Morris 1992; Risch et al. 1995; see Boutin, Moses & Caley 1988 for a counter example).

INCREASING RETURNS

The positive relationship between increasing maternal body condition (change in mass, Fig. 2) and reproduction indicates that some mothers concurrently made greater allocations of energy to both somatic and reproductive efforts during the breeding period. In addition, reproductive effort was associated with numbers of offspring surviving to 1 year of age and somatic effort was associated with maternal survival to the next year (greater body condition of mothers at the weaning period may have resulted from superior condition in the spring or from above average gain in body mass during reproduction). Such patterns have been called 'state-dependent' life histories (McNamara & Houston 1992), and may result from underlying genetic correlations among traits that are positive. In a quantitative genetic model, Houle (1991) showed that when variation among individuals in resource acquisition is high, genetic variation in positive associations of fitness traits (viz. life-history traits) can be maintained by mutation.

We believe that positive associations of statedependent fitness traits may reflect the more general phenomenon of 'increasing returns' in complex systems, that has not been explored in life-history theory. In economic theory, Arthur (1990) found that the concept of trade-offs resulted in a lack of appreciation for strong influence of positive associations leading to increasing returns, where slight initial advantages in market share are rapidly compounded. Economic increasing returns may provide a good analogy for the evolution of some life-history traits of Columbian ground squirrels. Mothers with superior reproduction and survival should leave more offspring for future generations, and thus come to predominate in populations (given the absence of phenotypic costs

© 1999 British Ecological Society Journal of Animal Ecology, **68**, 73–86 to reproduction; Murie & Dobson 1987; Risch *et al.* 1995; see Festa-Bianchet & King 1991 for a counter example). Such mothers should exhibit plastic lifehistory traits that facilitate positive associations of growth, survival, and reproduction (Via & Lande 1985), such as the positive associations found in our study. The life-history traits of the ground squirrels are extremely plastic (Dobson & Kjelgaard 1985; Dobson, Zammuto & Murie 1986; Dobson & Murie 1987; Dobson 1988), and such plasticity might be evolutionarily favoured by selection for increasing returns in life-history traits.

Increasing returns do not replace or obviate important trade-offs in life histories. For example, an important life-history trade-off occurred in our population of Columbian ground squirrels between the number and size of offspring (Table 1). In addition, evidence of positive phenotypic associations of life-history traits cannot be used as evidence to reject costs of reproduction (Reznick 1985; Murie & Dobson 1987). Increasing returns and evolutionary trade-offs probably occur together, and both kinds of interactions may be important determinants of life histories. Complete understanding of both the occurrence and the evolution of life histories requires consideration of both positive and negative feedbacks within the life history, and between organisms and their environment. Current explanation in life-history theory relies primarily on trade-offs, however, so future research might also attempt to identify and evaluate increasing returns.

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