Maternal influences on reproduction in two populations of Columbian ground squirrels

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Abstract. In this study, we examined influences of maternal traits on offspring birth mass, growth rate, and weaning mass for two populations of Columbian ground squirrels (Spermophilus columbianus). We tested relationships between maternal body condition, structural size, change in mass (during gestation, during lactation, and during the entire reproductive period), timing of reproduction, and litter size on offspring traits using path analyses. To assess whether maternal investment in offspring traits extended beyond the period of direct maternal care, we examined associations between offspring traits and overwinter survival of pups. In general, females in better condition raised pups that were heavier at weaning and that had faster growth rates during lactation. Litter size had a negative effect on mass and growth rate, and only litter size had a significant effect on birth mass. For both populations, the average weaning mass of pups within a litter had a positive effect on the number of pups that survived to yearling age. In a population for which birth masses and growth rates were available, pups with faster growth rates survived better to yearling age, whereas birth mass had no effect on the number of surviving offspring in litters. We found substantial maternal influences on offspring growth and size, and evidence that these influences may extend beyond the juvenile period and constitute influences on fitness. The key to arriving at these conclusions was to take the number of offspring into account before testing for maternal effects.

Key words: birth mass; body condition; Columbian ground squirrel; growth rate; litter size; mass change; maternal effects; path analysis; Spermophilus columbianus; survival; timing of reproduction; weaning mass.

INTRODUCTION

Maternal effects occur when a mother’s phenotype impacts the phenotype of her offspring, independent of their own genotype (Bernardo 1996). Maternal effects can be behaviorally and environmentally induced, whereby variation in maternal behavior (viz. parental care, nest-site selection) or maternal environment (viz. food resources, temperature) results in variation in offspring phenotype (Mousseau and Fox 1998). Offspring growth and mass are two offspring traits that can be heavily influenced by maternal effects. Mass and growth rate during postnatal development are important life history traits because they are often related to survival (Clutton-Brock et al. 1982, Murie and Boag 1984, Côté and Festa-Bianchet 2001, Dahl et al. 2006). Growth rate and mass can also have persistent effects, as indicated by their correlation with adult body size (Myers and Master 1983, Schultz and Johnson 1995, Festa-Bianchet et al. 2000).

Several factors, such as maternal size, condition, mass, and timing of the reproductive season, are known to influence offspring mass and growth rate in mammals. Offspring mass (Skogland 1984, Hoogland 1995, Biggerstaff and Ekvall 1997, Côté and Festa-Bianchet 2001) and growth rate (Mattingly and McClure 1982, Myers and Master 1983, Bowen et al. 2001) are often positively correlated with maternal body mass, which could be attributed to the enhanced ability of larger females to acquire resources and provide food for their young (Mattingly and McClure 1982). In ground-dwelling sciurids, females that reproduce earlier often give birth to offspring that are lighter than later born individuals (Dobson and Michener 1995, Rieger 1996). Mating earlier may be advantageous because it allows females and juveniles more time to grow and acquire fat reserves before hibernation (Murie and Boag 1984, Millesi et al. 1999).

There are two potential problems associated with field studies of maternal effects on mammalian species, such as Columbian ground squirrels (Spermophilus columbianus; see Plate 1), that produce multiple young at a time. First, patterns of maternal influences on offspring growth and mass may differ depending on the stage of reproduction (viz. gestation vs. lactation), and these patterns may not be evident when the entire reproductive period is examined. During gestation, energy is
required for changes in mammary tissue, production of the placenta, and fetal development, whereas during lactation, energy is required for milk production (Gittleman and Thompson 1988). In mammalian reproduction, lactation is typically more energetically expensive than gestation (Oftedal 1984, Racey and Speakman 1987, Gittleman and Thompson 1988). In Richardson’s ground squirrels (S. richardsonii), females deposit more mass in the litter during lactation than during gestation and pup mass comprises a larger proportion of the mother’s mass at weaning than at birth (Michener 1989). Therefore, maternal investment during lactation may have more of an influence on offspring traits than investment during gestation.

Second, neglecting to account for litter size when analyzing offspring traits strongly correlated with litter size could mask influences of maternal traits on reproduction. There is a great deal of literature pertaining to maternal effects on growth and mass in mammalian species that produce a single young at a time (e.g., Clutton-Brock et al. 1982, Festa-Bianchet et al. 2000, Boltnev and York 2001, Bowen et al. 2001). Examining maternal effects on offspring growth and mass in rodents, however, requires a different statistical approach because many species produce multiple offspring in a single reproductive episode. This is a problem when investigating maternal influences on reproduction because of the size-mass conflict. Due to limited resources or physiological constraints, females must compromise by investing in either more offspring or heavier individual young (Myers and Master 1983). Although there have been many empirical studies on the life history of Columbian ground squirrels (Murie et al. 1980, Murie and Harris 1982, Dobson and Kjelgaard 1985, Murie 1985, Dobson and Murie 1987, Dobson 1988, 1992, Risch et al. 1995, Dobson et al. 1999), those examining maternal influences on pup traits did not account for litter size in the analyses.

We analyzed long-term data sets on two different populations (Turnbull and Meadow B) of Columbian ground squirrels in order to get an extended range of variation in maternal investment patterns for the species. The objectives of this study were to test causal hypotheses of the influences of maternal aspects of size and timing of reproduction on offspring growth and mass using path analyses, and to test the hypothesis that maternal influences on offspring traits will have an effect on juvenile survival to yearling age. For Meadow B, data are available to examine differences in patterns of maternal investment during gestation, lactation, and the entire reproductive period. Because a female’s mass can reflect her physiological condition or her structural size (Dobson 1992, Dobson and Michener 1995, Dobson et al. 1999), body mass was partitioned into these two constituents for all analyses. Body condition is a measure of the energetic composition of an organism in the form of muscle mass (Perrins and McCleery 2001), fat reserves, protein, and water (Dobson 1992, Schulte-Hostedde et al. 2005), whereas structural size represents appendage length or skeletal size (Dobson 1992). Because females of the same structural size can vary greatly in the amount of energy stores in the body (King et al. 1991, Dobson and Michener 1995), we analyzed influences of both maternal structural size and body condition on offspring traits separately.

Mothers in better condition, with higher mass gain during reproduction, or structurally larger females are likely to have more or better quality resources available to them and they should invest more of that available energy into reproduction (Hirschfield and Tinkle 1975, Price 1998). Thus, we predicted that these females would raise offspring with greater birth and weaning masses and higher growth rates during lactation. We also expected that, as the breeding season progressed, females would produce heavier pups with faster growth rates to compensate for the nearing time of entry into their first hibernation. We predicted that survival would be positively associated with offspring birth mass, weaning mass, and growth rate.

MATERIALS AND METHODS

Study location

Field studies of Columbian ground squirrels were conducted from 1983 to 1990 in the Turnbull National Wildlife Refuge (hereafter referred to as “Turnbull”) in Washington State, USA (47°26′ N, 117°36′ W; elevation, 695 m) and from 1992 to 2006 in the Sheep River Provincial Park (hereafter referred to as “Meadow B”), Alberta, Canada (50° N, 110° W; elevation, 1550 m).

Field methods

For both populations, ground squirrels were captured at spring emergence (Turnbull, early to mid-March; Meadow B, mid-April to early May) by placing live-traps (Tomahawk #201 collapsible chipmunk trap, 48 × 15 × 15 cm; Tomahawk Live Trap, Tomahawk, Wisconsin, USA) baited with peanut butter near burrow openings. All individuals were marked with numbered fingerling ear tags, weighed using a Pesola scale (Pesola Ag, Baar, Switzerland), given unique body markings using hair dye (Lady Clairol, black), and zygomatic arch breadth measured using dial calipers (Swiss Precision Instrument, Garden Grove, California, USA). For Meadow B, zygomatic arch breadth was only measured in 1993, 1994, and 2001–2006. For missing values, zygomatic arch breadth was averaged over years for which data was available, excluding arch breadth in yearlings (females plateau in structural growth by their second spring; Dobson 1992). Averages were used where necessary for subsequent analyses, except in testing for differences in zygomatic arch breadth among females of different ages.

Juveniles were captured at emergence from natal burrows (Turnbull: early-to-late May; Meadow B: mid-June to early July), using the same techniques as previously described. Emergence of pups from natal burrows is an indication of litter weaning and cessation.
of lactation (Anderson et al. 1976, Murie and Dobson 1987, Michener 1989, Rieger 1996). Time of litter emergence was estimated by adding 51 days to the mating date: 24 days from mating to parturition (Shaw 1925, Murie and Harris 1982) and 27 days from parturition to litter emergence (Murie 1992). Mating date was determined by examination of external reproductive morphology, observation of a copulatory plug, presence of sperm in vaginal smears (Murie and Harris 1982), direct observation of copulations above ground (at Turnbull), or by observations of precopulatory behavior, such as male interest in the female prior to, but not following, copulation, or males entering burrows with estrous females. Survival of young to yearling age can be ascertained because juveniles do not disperse prior to their first hibernation (Boag and Murie 1981, Murie and Harris 1984, Dobson and Murie 1987, Risch et al. 1995). Thus, juveniles that emerge from their hibernaculum in the following spring are the ones that have survived their first hibernation.

In 1993–1996 and 1999–2006, Meadow B females that copulated were captured prior to parturition (May–June), weighed, and housed in the laboratory until they gave birth (1–9 days). Females were kept in polycarbonate microvent rat cages (267 × 483 × 203 mm³; Allentown Caging Equipment Company, Allentown, New Jersey, USA) on pine chip bedding and were given newspaper nesting material. To obscure vision from neighboring females and to simulate the burrow environment, cages were covered in vented black plastic bags and kept in a heated building. Squirrels were fed a high-protein horse feed (oats, barley, wheat, and compressed vegetable material in a molasses mix; 13% crude protein) ad libitum, and lettuce and apple twice daily. Cages were checked for pups 3–4 times per day from 05:30 to 22:30 hrs. Females and neonates were weighed at least 4 hours after birth (to ensure that parturition was complete). Neonates were marked by removing a small amount of tissue from the outer right or left toe bud on a hind limb or from the tail. The nail does not grow on the toe where tissue was removed and a small knot appears at the end of a tail that had tissue removed, allowing for identification of pups at emergence from the natal burrows. Mothers were released on the meadow by opening the cage containing mother and pups. Pups were placed in the natal burrow following immerge of the mother into that burrow. Occasionally mothers retrieved pups from the cage before pups could be placed in the burrow.

Variables

Maternal characteristics examined included body condition, structural size, mass change during reproduction, and timing of reproduction (viz. mating date). Because zygomatic arch breadth is associated with other skeletal measurements, it was used as an estimate of structural size (Dobson et al. 1999). Turnbull females mated approximately 5–6 days (Dobson et al. 1999) and Meadow B females mated, on average, 3.7 days (n = 395 females) following first capture after spring emergence. Zygomatic arch breadth was measured at this time and it was used as an estimate of structural size at the beginning of the gestation period. Body condition was estimated from the residuals of the regression of spring emergence mass on zygomatic arch breadth.

Change in mass during reproduction was calculated in several different ways. For Turnbull and Meadow B, change in mass during the entire reproductive period was estimated as the difference between a female’s body mass at spring emergence and her mass at the time of litter emergence from the natal burrow. For Meadow B only, change in mass was further divided into the two stages of the reproductive period: gestation and lactation. Change in mass during gestation was calculated as the difference between a female’s body mass at spring emergence and her mass immediately after parturition. Change in mass during lactation was calculated as the difference between a female’s body mass immediately following parturition and her mass at the time of litter emergence from the natal burrow. Timing of reproduction was the Julian date that mating occurred (day 1 = 1 January).

Offspring traits included birth mass, weaning mass, and growth rate during the nursing period. Growth rate was calculated by subtracting mass at birth from mass at weaning and dividing by the length of the lactation period. Because only Meadow B pups were born in the lab, birth mass, growth rate, and litter size at birth are known only for this population. For Meadow B, litter size at birth was used in analyses of maternal influences during gestation, whereas litter size at weaning was used for analyses of maternal influences during lactation and during the entire reproductive season. For Turnbull, litter size was counted at weaning only. For litters with more than one pup, offspring traits were averaged within litters. Litters suffering partial predation by badgers were excluded from all analyses.

Statistical analyses

All analyses were conducted using SAS statistical software for Windows (SAS Institute 2002). Tests employed included general linear models (PROC GLM, used for analysis of variance [ANOVA]), correlations (PROC CORR), mixed models (PROC MIXED) and path analysis (STB option of PROC REG). VIF and COLLINOINT options of PROC REG were utilized to detect biases due to colinearity of independent variables used in path analysis. The significance level for all tests was α = 0.05 with two-tailed distributions. Data were assessed for normality graphically or by performing Shapiro-Wilk tests.

General linear models and Tukey tests for multiple comparisons of means were used to explore differences in maternal characteristics and offspring traits among females of different ages. For Meadow B, yearlings were not included in analyses because only nine yearlings during the 15-year study raised a litter to weaning, and
complete data to run path analyses existed for only two of those yearlings. Yearlings were not pooled with other age groups because there are differences in life history traits between yearlings and older females in Columbian ground squirrels (Dobson et al. 1999, Broussard et al. 2005a). For Meadow B, females aged 7–10 years were pooled and for Turnbull, females aged 5–9 years were pooled, due to small sample sizes. General linear models were also used to examine variation in maternal and offspring traits due to the year of the study.

Standardized partial regressions (path analysis) were used to determine the interrelationships among maternal and offspring traits. Because trade-offs between litter size and offspring traits were evident, litter size was controlled for statistically by including it as an independent variable in the path analyses. Path analysis (Li 1981) involves a priori diagramming a hypothetical model that incorporates causal relationships among the variables. The null hypothesis of no causal relationship is tested by the significance of path coefficients. Path coefficients (β) are standardized partial regression coefficients that indicate the magnitude of the effect of the independent variable on the dependent variable, while all other variables are held statistically invariant (Li 1981, Pedhazur 1982, Sokal and Rohlf 1995). Standardized coefficients allow for the inclusion of variables measured on different scales, such as mass (in grams) and timing of reproduction (in days).

As in all multiple regression techniques, colinearity of independent variables in path analysis can result in erroneous conclusions. Colinearity of independent variables can inflate standard errors of path coefficients, increasing the probability of a Type II error, and can also inflate values of the path coefficients. Inflation of standard errors due to colinearity can be determined by examining variance inflation factors (VIFs; Petraitis et al. 1996). VIFs greater than 10 indicate biases of standard errors due to colinearity of independent variables (Myers 1990). Biases in values of path coefficients can be detected through condition indices. Condition indices are derived from the eigenvalues of the correlation matrices of independent variables (Petraitis et al. 1996). Condition indices between 5 and 10 suggest weak biases due to colinearity, whereas condition indices between 30 and 100 indicate strong biases (Belsley et al. 1980, SAS Institute 2002).

Mixed models were used to assess influences of offspring traits on the number of pups surviving to weaning age. Year was included in the model as a random variable and litter size was included as a fixed effect. This statistically controlled for the effects of year and litter size on the number of offspring surviving.

**RESULTS**

**Multiple records for females**

There were multiple records for females that reproduced in more than one year during the study. Multiple records for females were considered independent because (1) other studies show that reproduction in one year does not influence reproduction in the following year (Murie and Dobson 1987, Risch et al. 1995, Dobson et al. 1999, Broussard et al. 2005a), and (2) offspring traits in one year were not associated with the same trait in the following year (Spearmen rank correlation, Meadow B: for birth mass, r = 0.12, n = 91, P = 0.25; for weaning mass, r = 0.17, n = 92, P = 0.10; for growth rate, r = -0.07, n = 22, P = 0.77; Turnbull: for weaning mass, r = -0.22, n = 78, P = 0.06).

**Age differences**

In order to justify pooling of data for females of different ages, we first tested for age differences in maternal and offspring characteristics using ANOVAs and Tukey tests for multiple comparisons. For Meadow B, on average, two-year-olds were lighter at spring emergence, had later mating dates, were lighter at litter emergence from natal burrows, had narrower zygomatic arch breadths, and weighed less at parturition than did females in other age classes (Fig. 1A, C, Fig. 2A, E, and Fig. 3A). Tukey’s test also revealed significant differences in zygomatic arch breadth, female’s mass at litter emergence, female’s postpartum mass, and mass change during gestation between the 3-year-old and 6-year-old age classes. Significant differences also occurred between the 5-year-old and 3-year-old age classes and between the 5-year-old and 4-year-old age classes for female’s mass at litter emergence. Because 2-year-olds were 99% of adult body size, females of all age classes were pooled for further analyses.

For Turnbull, on average, yearlings were lighter at spring emergence from hibernation, mated later, had smaller litter sizes at weaning, were lighter when litters emerged from natal burrows, had smaller zygomatic arch breadths, and gained more mass during the breeding period than did older females (Fig. 1B, D, F and Fig. 2B, D, F). Significant differences also occurred between 2- and 4-year-olds in litter size at weaning and between 2- and 4-year-olds, the 3- and 5-year-old age groups, and the 2- and 5-year-old age groups in structural size. Because Turnbull yearlings were 94% of adult body size, we analyzed yearlings and older females separately.

**Year differences**

Before analyzing investment patterns using path analyses, we tested for year-to-year variation in maternal and offspring traits with ANOVAs. For Meadow B, significant variation among years was detected for mating date (F_{14,268} = 7.97, P < 0.0001), mother’s mass at the time of pup weaning (F_{12,204} = 3.45, P = 0.001), postpartum mass (F_{7,82} = 2.23, P = 0.04), zygomatic arch breadth (F_{14,236} = 2.46, P = 0.003), maternal spring mass (F_{14,282} = 2.66, P = 0.001), mass change during gestation (F_{7,77} = 2.92, P = 0.003), mass change during lactation (F_{6,79} = 8.83, P < 0.0001), and pup birth mass (F_{7,82} = 3.67, P = 0.002). Mother’s body condition at spring
emergence ($F_{7,110} = 1.23, P = 0.29$), litter size at birth ($F_{10,92} = 1.11, P = 0.36$), litter size at weaning ($F_{13,180} = 1.33, P = 0.20$), pup weaning mass ($F_{13,170} = 1.62, P = 0.08$), and offspring growth rate ($F_{6,70} = 0.48, P = 0.82$) did not differ significantly among years.

For Turnbull, spring body mass ($F_{6,298} = 5.08, P < 0.0001$), mating date ($F_{7,180} = 71.13, P < 0.0001$), litter size at weaning ($F_{7,311} = 9.59, P < 0.0001$), mass change during breeding ($F_{5,245} = 2.5, P = 0.03$), and spring body condition ($F_{5,232} = 6.80, P < 0.0001$) varied significantly among years. Years did not vary significantly for average pup weaning mass ($F_{6,183} = 2.16, P = 0.05$), female’s mass at litter emergence ($F_{5,318} = 2.05, P = 0.05$), and zygomatic arch breadth ($F_{5,266} = 1.39, P = 0.23$).

To account for year-to-year differences in maternal and offspring traits, we first adjusted variables that differed among age classes by using residuals extracted from

![Graphs showing data for different age classes and years.](image-url)
an ANOVA in which year was the grouping factor. Mass change during gestation was calculated by subtracting maternal spring mass from maternal mass after birth, both of which were adjusted for year effects. Mass change during lactation was calculated as the difference in year-adjusted postpartum mass and year-adjusted mass at litter emergence. Mass change during the entire reproductive period was estimated by subtracting spring mass from mass at litter emergence, both of which were adjusted for year effects. To detect variation in patterns among different years of the study, we then examined unadjusted data for years of early vs. years of late breeding and years where litter size was high vs. years of low litter size, as in Dobson et al. (1999).

**Body condition**

Of females at Meadow B, 99% gained mass during gestation ($n = 170$), 56% gained mass during lactation ($n = 146$), and 97% gained mass from spring emergence to litter weaning ($n = 293$). At Turnbull, 94% of females gained mass during the entire breeding period ($n = 89$). Physiological condition of females was estimated by extracting residuals from the regression of spring emergence mass on zygomatic arch breadth (Schulte-Hostedde et al. 2005). In both populations, spring mass increased with zygomatic arch breadth (for Meadow B, $R^2 = 0.41$, $n = 170$; for Turnbull, $R^2 = 0.42$, $n = 89$).
Maternal influences on offspring traits

Meadow B.—A standardized partial regression analysis was used to investigate patterns of maternal investment on pup mass and growth at different periods within the reproductive season (viz. gestation, lactation, and the entire reproductive period). Maternal characteristics during gestation explained a significant amount of the variation in pup birth mass \( (R^2 = 0.19, F = 2.60, n = 63, P = 0.03) \). Only litter size at birth had a significant effect on birth mass \( (t = -2.63, P = 0.01; \text{Fig. 4A}) \).

Maternal traits during lactation explained 70% of the variation in offspring weaning mass \( (F = 22.47, n = 55, P < 0.0001) \). A female’s structural size and spring condition had significant positive effects on offspring weaning mass (for structural size, \( t = 2.22, P = 0.03 \); for condition, \( t = 2.62, P = 0.01 \); \text{Fig. 4B})]. Litter size at weaning had a significant negative effect on weaning mass \( (t = -10.48, P < 0.0001) \). Maternal traits explained a high and significant amount of variation in average pup growth rate during lactation \( (R^2 = 0.73, F = 25.83, n = 55, P < 0.0001) \). Maternal body condition, structural size, and litter size at weaning contributed significantly to variation in offspring growth rate (respectively: \( t = 3.07, P = 0.004; t = 2.30, P = 0.03; t = -11.20, P < 0.0001) \). A path diagram for growth rate is not presented because weaning mass and growth rate are highly correlated and had the same patterns of significant path coefficients. When the entire breeding period was examined, maternal traits still had a significant effect on weaning mass \( (R^2 = 0.70, F = 27.85, n = 66, P < 0.0001) \). However, only body condition and litter size at weaning significantly influenced weaning mass (respectively: \( t = 3.89, P = 0.0003; t = -11.46, P < 0.0001; \text{Fig. 4C}) \).

FIG. 3. Maternal and offspring traits (mean ± SE) for each age class for Meadow B. Females age 7–10 were pooled due to low sample sizes. Mass change during gestation is the difference between spring emergence mass and postpartum mass. Mass change during lactation is the difference between postpartum mass and mass at litter weaning. Birth mass and growth rate are offspring traits, whereas all others are maternal traits. Growth rate of pups was calculated by subtracting birth mass from weaning mass and dividing by the duration of the lactation period. \( F \) and \( P \) values correspond to results of ANOVAs testing differences among age classes. Sample sizes (number of ground squirrels) are given above error bars. \( P \) values were significant at \( \alpha = 0.05 \).
Of the independent variables included in the path analysis, significant negative correlations occurred between a female’s body condition and her change in mass during gestation and between a female’s body condition and her change in mass during the entire breeding period (Table 1, Fig. 4). Mothers in better condition at spring emergence gave birth to larger litters. Mothers that were structurally larger or gained more mass during the breeding season on weaning mass both had an effect on weaning mass (condition: $R^2 = 0.17, F = 3.21, n = 28, P = 0.03$; $R^2 = 0.29, F = 7.00, n = 93, P < 0.0001$). For yearlings, only litter size at weaning had a significant influence on weaning mass for both yearlings and older females (respectively: $R^2 = 0.42, F = 3.21, n = 28, P = 0.03$; $R^2 = 0.29, F = 7.00, n = 93, P < 0.0001$). In addition, the highest condition indices for path models were 1.36 (for maternal influences during lactation on weaning mass and growth rate), 1.87 (for gestational influences on birth mass), and 2.34 (for maternal influences during reproduction on weaning mass).

**Turnbull.**—We reanalyzed the data used in Dobson et al. (1999), incorporating litter size as an independent variable in our path model to statistically control for its potentially confounding effect on weaning mass. Although no association between maternal traits and weaning mass was previously reported for this species by Dobson et al. (1999), the current path models that included litter size showed that maternal traits have a significant influence on weaning mass for both yearlings and older females (respectively: $R^2 = 0.42, F = 3.21, n = 28, P = 0.03$; $R^2 = 0.29, F = 7.00, n = 93, P < 0.0001$). For yearlings, only litter size at weaning had a significant influence on weaning mass ($t = -3.41, P = 0.003$), although the magnitude of the nonsignificant influence of spring body condition was substantial (Fig. 5A). For older females, spring body condition and litter size both had an effect on weaning mass (condition: $t = 2.88, P = 0.005$; litter size: $t = -5.22, P < 0.0001$; Fig. 5B).

Intercorrelations among independent variables occurred between mass change during the breeding period and body condition in both yearling and older females (Table 2, Fig. 5). Also, in older females, litter size at weaning and spring condition were positively correlated. Individual pups were lighter in litters that were large at weaning for both yearling and older females. Older females that mated earlier or that gained more mass during breeding had lighter individual young at weaning. The maximum variance inflation factor was 2.62 for gained more mass during lactation. Change in mass during the whole breeding period was positively associated with both mass change during gestation and mass change during lactation. Litters that were larger at birth consisted of pups that were lighter at birth and at weaning. Pups born into larger litters also had lower growth rates during lactation. Pups that were heavier at birth grew faster during lactation. Growth rate, weaning mass, and birth mass were negatively associated with litter size at weaning and litter size at weaning was positively correlated with litter size at birth. Weaning mass was positively correlated with birth mass and growth rate.

Despite intercorrelations among independent variables, collinearity was not likely a cause of strong bias in estimation of path coefficients or their standard errors. The maximum VIF for the path analyses of maternal effects during lactation on weaning mass and growth rate was 1.08; for maternal effects during gestation on birth mass maximum VIF was 1.37. The maximum VIF for path analysis of maternal influences during the entire breeding season on weaning mass was 1.90. These values are well under the value of 10 recommended by Petraitis et al. (1996). In addition, the highest condition indices for path models were 1.36 (for maternal influences during lactation on weaning mass and growth rate), 1.87 (for gestational influences on birth mass), and 2.34 (for maternal influences during reproduction on weaning mass).
yearlings and 2.01 for older females. Maximum condition indices were 2.98 for yearlings and 2.46 for older females.

**Yearly variation in maternal investment**

Data for each year of the study were insufficient for conducting path analyses to investigate year-to-year differences in patterns of maternal investment. Therefore, we examined year variation in maternal influences by partitioning data into years of early and late breeding and years of low and high litter size. Years when the average mating date was below the mean mating date for the entire study were considered early and those above the average were considered late. Years when the mean litter size was less than the mean for the entire study were considered low and those above the mean were considered years of high litter size. Variables were year-standardized within subdivisions of the data set where necessary.

### Table 1. Correlation coefficients of variables used in path analyses for Meadow B Columbian ground squirrels (Spermophilus columbianus).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mating date</th>
<th>Mass change, gestation</th>
<th>Mass change, lactation</th>
<th>Structural size (mm)</th>
<th>Birth mass (g)</th>
<th>Wean mass (g)</th>
<th>Growth rate (g/d)</th>
<th>Litter size at birth</th>
<th>Litter size at weaning</th>
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<td></td>
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<td>(192)</td>
</tr>
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<td>(183)</td>
<td>(183)</td>
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**Notes:** *P* values are given under the correlation coefficients, with sample size in parentheses. Boldface *P* values are significant (<0.05). Mass change during gestation is the difference between spring emergence mass and mass after parturition. Mass change during lactation is the difference between mass after parturition and mass at litter weaning. Body condition was estimated from residuals of the regression of mass at spring emergence on zygomatic arch breadth. Pup growth rate is the gain in mass during lactation divided by lactation duration. Structural size is the zygomatic arch breadth measured at the time of spring emergence from hibernation. Structural size, mating date, birth mass, and all mass changes were adjusted for year effects.

Meadow B.—The years 1992, 1994–2000, and 2004 were years of early breeding (mean early Julian date = 117 [Julian day 1 = 1 January] and range = 114–119); years 1993, 2001–2003, and 2005–2006 were years of late breeding (mean late Julian date = 122 and range = 120 to 126). Maternal traits during gestation in years of early breeding did not have a significant influence on birth mass (R^2 = 0.20, F = 0.61, n = 16, P = 0.69). Maternal traits during lactation in years of early breeding explained 87% of the variation in both weaning mass and growth rate (respectively: F = 12.88, n = 16, P = 0.0004; F = 13.76, n = 16, P = 0.0003). Litter size had a significant negative effect on weaning mass (F = 6.21, P = 0.0001; Fig. 6A) and growth rate (F = 6.19, P = 0.0001). A path diagram for maternal influences during lactation on growth rate in early years is not shown because patterns are the same as influences on weaning mass. In early-breeding years, during the entire breeding period, maternal characteristics explained 72% of the
variation in offspring weaning mass ($F = 10.25, n = 26, P < 0.0001$). As in all years combined, both maternal body condition and litter size at weaning had significant influences on weaning mass (respectively: $t = 3.20, P = 0.005, t = -6.70, P < 0.0001$; Fig. 6B). For path analyses of early years, the highest variance inflation factor was 1.93 and the highest condition index was 2.39. A strong negative correlation occurred between mass change during reproduction and spring body condition.

In late-breeding years, maternal traits had a significant influence on weaning mass and growth rate (for maternal influences during lactation on weaning mass, $R^2 = 0.66, F = 12.78, n = 39, P < 0.0001$; for maternal influences during lactation on growth rate, $R^2 = 0.70, F = 15.34, n = 39, P < 0.0001$; for maternal influences during entire breeding season on weaning mass, $R^2 = 0.69, F = 15.31, n = 40, P < 0.0001$). During lactation only, condition and litter size had significant effects on weaning mass and growth rate (for condition on weaning mass, $t = 2.00, P = 0.05$; for litter size on weaning mass, $t = -7.86, P < 0.0001$; for condition on growth rate, $t = 2.48, P = 0.02$; for litter size on growth rate, $t = -8.51, P < 0.0001$; Fig. 6C). Maternal body condition and litter size at weaning also had significant effects on weaning mass when the entire breeding season was analyzed (for condition on weaning mass, $t = 2.52, P = 0.02$; for litter size on weaning mass, $t = -8.50, P < 0.0001$; Fig. 6D). A path diagram for influences on growth rate during late years is not shown because patterns are the same as influences on weaning mass. Maternal traits did not have a significant influence on birth mass in late years ($R^2 = 0.19, F = 1.87, n = 45, P =$

![Fig. 5. Turnbull path models for the influence of maternal characteristics on weaning mass for yearlings and older females. Mass change is the difference between spring emergence mass and mass at litter weaning, both of which were first adjusted for year variation. Body condition was estimated from residuals of the regression of mass at spring emergence on zygomatic arch breadth. Mating date, litter size, and body condition were adjusted for year effects. Path coefficients are given to the right of maternal characteristics. Correlation coefficients for significant correlations among independent variables are located to the left of maternal characteristics. $U$ is the path coefficient for unexplained variation in offspring traits and was calculated by the equation $\sqrt{1 - R^2}$ (Li 1981). Solid lines are positive paths, and dashed lines are negative paths. Bold arrows indicate significant path coefficients. Double-headed arrows are possible correlations among independent variables.]

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<th>Weaning mass (g)</th>
<th>Litter size at weaning</th>
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<td>(128)</td>
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Notes: $P$ values are given under the correlation coefficients, with sample size in parentheses. Boldface $P$ values are significant ($<0.05$). Mass change during the breeding period is the difference between mass at spring emergence from hibernation and mass at litter emergence. Body condition was estimated from residuals of the regression of spring mass on zygomatic arch breadth. Structural size is the zygomatic arch breadth measured at the time of spring emergence. Mating date, body condition, litter size at weaning, and mass change were year-adjusted.
In late years, a strong negative correlation occurred between mass change during reproduction and body condition. However, the highest variance inflation factor was 2.62 and the highest condition index was 2.91.

In years of low litter sizes at weaning (1992, 1994, 1996, 1999–2000, 2002, and 2004; mean low litter size = 2.61 pups; range = 2.17 to 2.81 pups), path analysis of maternal traits on birth mass was not significant ($R^2 = 0.22$, $F = 2.03$, $n = 42$, $P = 0.10$). Maternal traits had a significant influence on growth rate and weaning mass (for maternal influences during lactation on growth rate, $R^2 = 0.77$, $F = 21.18$, $n = 37$, $P < 0.0001$; for maternal influences during lactation on weaning mass, $R^2 = 0.76$, $F = 19.61$, $n = 37$, $P < 0.0001$; for maternal influences during the entire breeding season on weaning mass, $R^2 = 0.71$, $F = 20.46$, $n = 48$, $P < 0.0001$). For analyses of maternal influences during lactation, only structural size and litter size at weaning had significant influences on weaning mass and growth rate (for structural size on weaning mass, $t = -3.03$, $P = 0.005$; for litter size on weaning mass, $t = -9.38$, $P < 0.0001$; for structural size on growth rate, $t = 2.82$, $P = 0.008$; for litter size on growth rate, $t = -9.88$, $P < 0.0001$; Fig. 7A). Because growth rate and weaning mass had similar patterns of significant path coefficients, only the path diagram for weaning mass is presented. During the entire breeding season, structural size, condition, and litter size at weaning had significant influences on weaning mass (respectively: $t = 2.30$, $P = 0.03$; $t = 2.62$, $P = 0.01$; $t = -9.60$, $P < 0.0001$; Fig. 7B). Mass change during the breeding season and body condition were strongly negatively correlated. The highest variance inflation factor was 1.97 and the highest condition index was 2.40.

In years of high litter sizes at weaning (1993, 1995, 1997–1998, 2001, and 2003; mean high litter size = 3.00 pups; range = 2.84–3.20 pups), maternal traits did not explain a significant amount of the variation in birth mass ($R^2 = 0.10$, $F = 32$, $n = 21$, $P = 0.89$). During lactation, maternal traits had significant effects on weaning mass and growth rate (respectively: $R^2 = 0.71$, $F = 5.84$, $n = 18$, $P = 0.006$; $R^2 = 0.74$, $F = 6.87$, $n = 18$, $P$
Only litter size had a significant negative effect on weaning mass \( (t = -4.76, P = 0.0005) \), although spring body condition had a substantial nonsignificant positive coefficient (Fig. 7C). Litter size and body condition had significant influences on growth rate (respectively: \( t = -5.15, P = 0.0002; \ t = 2.45, P = 0.03 \); Fig. 7D). Maternal traits during the entire breeding season explained 67\% of the variation in weaning mass \( (F = 4.85, n = 18, P = 0.01) \) and litter size was the only trait to affect weaning mass \( (t = -4.03, P = 0.002) \), although body condition again had a substantial, but nonsignificant, influence (Fig. 7E). The highest variance inflation factor was 2.08 and the highest condition index was 2.64. A mother’s change in mass during the entire breeding season was strongly negatively correlated with spring body condition.

**Turnbull.—** Years when breeding was earlier than the average for the entire study occurred in 1983, 1986–1988, and 1990 (mean early Julian date \( = 75; \ range = 70–78 \)) and years of late breeding were 1984–1985 and 1989 (mean late Julian date \( = 87; \ range = 83–89 \)). Years of low litter size were 1983, 1985, 1987, and 1989–1990 (mean low litter size \( = 1.79 \) pups; \ range = 1.38–2.38 pups) and years of high litter size were 1984, 1986, and 1988 (mean high litter size \( = 3.35 \) pups; \ range = 2.74–4.12 pups).
Path analyses for yearling females and older females in early-breeding years were significant (respectively: $R^2 = 0.84, F = 12.98, n = 18, P = 0.0002$; $R^2 = 0.33, F = 6.89, n = 75, P < 0.0001$). For yearling females, mass change during the breeding period, spring body condition, and litter size had significant influences on weaning mass (respectively: $t = 2.20, P = 0.05$; $t = 4.37, P = 0.001$; $t = 5.12, P = 0.0003$; Fig. 6E). For older females, significant path coefficients occurred for condition and litter size (respectively: $t = 2.74, P = 0.008$; $t = 4.87, P < 0.0001$; Fig. 6F). In late-breeding years, maternal traits did not have a significant effect on weaning mass for yearling and older females (respectively: $R^2 = 0.67, F = 1.66, n = 10, P = 0.32$; $R^2 = 0.53, F = 2.68, n = 18, P = 0.08$).

Path analyses of older females in years of low and high litter size were significant (for low litter size, $R^2 = 0.41, F = 7.21, n = 58, P < 0.0001$; for high litter size, $R^2 = 0.32, F = 3.60, n = 45, P = 0.009$). In years of low litter size, both condition and litter size at weaning had significant effects on weaning mass (respectively: $t = 2.99, P = 0.004$; $t = -5.11, P < 0.0001$; Fig. 7F), whereas in years of high litter size, only litter size had a significant impact on weaning mass ($t = -3.59, P = 0.0009$; Fig. 7G). For yearlings, maternal traits did not explain a significant amount of the variation in weaning mass in years of low vs. high litter size (for low litter size, $R^2 = 0.36, F = 1.34, n = 18, P = 0.31$; for high litter size, $R^2 = 0.81, F = 3.34, n = 10, P = 0.13$). There were several intercorrelations among the independent variables used in these path analyses. Significant correlations occurred between litter size and condition, litter size and mating date, and mass change and condition. Variance inflation factors and condition indices were low (respective maximums 4.88, 4.42).

**Survival**

To determine if pup mass and growth affected survival to yearling age, we used mixed models including year as a random variable and litter size as a fixed effect. For Meadow B, pup weaning mass and growth rate had significant positive effects on the number of pups surviving to yearling age (respectively: $F_{1,160} = 9.53, P = 0.002$; $F_{1,51} = 8.54, P = 0.005$). Birth mass did not influence pup survival ($F_{1,51} = 0.09, P = 0.76$). For Turnbull, weaning mass had a significant effect on number of offspring surviving for both yearling and older females (respectively: $F_{1,34} = 6.90, P = 0.01$; $F_{1,124} = 3.97, P = 0.04$).

**Discussion**

Before testing causal relationships of maternal traits on offspring traits, we evaluated age-specific differences in maternal variables. Corroborating other studies of Columbian ground squirrels (Dobson et al. 1999, Broussard et al. 2003), at Turnbull (low elevation and...
latitudes), we found differences between yearlings and older females in spring mass, mating date, litter size at weaning, mass at litter emergence, and structural size. At Meadow B (high elevation and latitude), 2-year-olds and older females differed in several maternal characteristics. Populations of Columbian ground squirrels inhabiting higher latitudes and higher elevations consist of few breeding yearlings (Dobson and Murie 1987). Thus, most 2-year-olds are primiparous females that tend to be lighter at spring emergence and emerge later from hibernation than older females (Table 1).

**Maternal influences on offspring traits**

Standardized partial regressions resulted in different conclusions regarding influences of maternal traits on offspring mass and growth rate than did simple correlations. For example, in correlation analysis for Meadow B, maternal body condition at spring emergence and zygomatic arch breadth were not associated with offspring weaning mass or growth rate, but these relationships were significant in path analyses. Significant effects appearing in path analyses result from testing individual pathways while holding the influence of other variables, particularly litter size, statistically invariant. This controls for correlations among independent variables, which otherwise might mask significant paths (Dobson et al. 1999).

Maternal characteristics explained a significant amount of variation in pup mass and growth rate. As expected, when we examined the period of lactation for Meadow B, path analysis revealed a significant positive effect of a mother’s body condition on both weaning mass and growth rate (Fig. 4B). Positive associations between body condition and weaning mass were also found when examining the entire breeding period at Meadow B (Fig. 4C) and for older females at Turnbull (Fig. 5B). This agrees with a study of Richardson’s ground squirrels in which a positive correlation was found between average offspring mass and maternal body condition (Dobson and Michener 1995). At Meadow B, larger females also produced heavier pups at weaning and pups with higher growth rates during lactation (Fig. 4B). Larger females may have a competitive advantage over smaller females in obtaining higher quality territories or in extracting resources to provision young (Murie and Harris 1988, Boag and Wiggett 1994).

Timing of reproduction has been shown to influence offspring mass in several species of ground-dwelling sciurids. In both Richardson’s ground squirrels (Dobson and Michener 1995) and Uinta ground squirrels (Rieger 1996), earlier reproduction resulted in lighter offspring but larger litters. However, as the active season progressed, litter size became smaller while individual offspring size increased so that offspring from both early and late litters entered hibernation at similar body masses. This does not appear to be the case for Columbian ground squirrels, as indicated by the lack of a significant relationship between mating date and offspring mass and growth rate. Any influence of seasonal timing on offspring growth and mass may be accounted for primarily by differences among females in litter size (Dobson et al. 1999).

Of the maternal characteristics included in the path analyses, only litter size had an effect on weaning mass for yearling mothers at Turnbull (Fig. 5A). Because yearlings are still growing in structural size (Dobson 1992), investment in their own growth rather than in reproduction is not surprising. In addition, only litter size had an effect on neonatal mass for Meadow B (Fig. 4A). This differs from a study on Richardson’s ground squirrels that found that timing of the season and body condition both had positive effects on neonatal mass (Dobson and Michener 1995). That females have a greater influence on the mass of their pups later in the active season (viz. at weaning) rather than at birth illustrates the importance of maternal investment during lactation relative to gestation. For most mammals, the critical period throughout reproduction, in terms of energy investment, occurs during lactation (Oftedal 1984, Racey and Speakman 1987, Gittleman and Thompson 1988).

**Yearly variation in maternal investment**

Because data were insufficient to examine patterns of reproduction among all years of the study, years were grouped according to timing of reproduction and litter size (after Dobson et al. 1999). Patterns of significant path coefficients were not drastically different when subdividing the data according to seasonal timing of reproduction. Examination of the entire breeding season in early- and late-breeding years for Meadow B produced similar results to those for all years combined (Fig. 6B, D compared to Fig. 4C). In addition, results of path analysis of older females from Turnbull in years of early reproduction were not greatly different from the combined data set (Fig. 6F compared to Fig. 5B).

Results for late and early years were similar to those for all years combined except for the lactation period in late years (Fig. 6C compared to Fig. 4B). In the combined data set, structural size had a significant impact on weaning mass and growth rate. However, in years when reproduction occurred later in the season, structural size was no longer significant. In late years, when litters are weaned at a later date, pups have less time to acquire fat reserves before hibernation. In these instances, females in better condition (reflecting energy stores) may have an advantage over structurally larger (reflecting skeletal size) females because they could potentially transfer that stored energy into pup mass gain, preparing it for hibernation.

Patterns of maternal influences on reproduction were different when years were subdivided according to litter size. For older Turnbull females, body condition no longer had a significant effect on pup weaning mass in years of high litter production (Fig. 7G compared to
hibernation. As predicted, pups that grew faster during the active season for pups to gain mass before entering into hibernation period (Murie and Boag 1984, Young 1992, 1999). In our study, Meadow B occurs at a higher elevation and latitude than the Turnbull population. In years of high litter production at Meadow B, structural size had a significant effect on weaning mass at Meadow B, but not for Turnbull. This similarity in significant maternal effects is interesting, given the substantial documented differences in life history traits among ground squirrel populations at different elevations and latitudes. Specifically, populations at higher elevations have greater adult survival, individuals begin reproducing at a later age (Murie and Harris 1982, Zammuto and Millar 1985, Dobson and Murie 1987, Dobson et al. 1992, 1999), litter size is lower, the proportion of adult females is lower, and juvenile survival is greater (Murie and Harris 1982, Dobson and Murie 1987, Dobson et al. 1992, 1999). In our study, Meadow B occurs at a higher elevation and latitude than the Turnbull population.

Dividing the data into different periods of maternal investment may shed more light on patterns of reproductive investment than when examining the reproductive season as a whole. We found different patterns of investment occurring during gestation vs. during lactation and these patterns were not always evident when viewing the reproductive period as a whole, with the overall pattern being more similar to the pattern of investment during lactation. At Meadow B during the nursing period, larger females weaned heavier pups with faster growth rates. Structural size was a significant influence on weaning mass during the lactation period, but not when the entire breeding period was considered, perhaps because its influence was masked by the lack of significance during gestation. It is important to statistically control for variables that may have potentially confounding effects on the trait in question. A principle concept in life history evolution is that when resources are limited, organisms must choose how to partition available energy. This results in trade-offs because individuals cannot invest in all traits equally.
resources maximally in many different functions. In reproduction, there is often a trade-off between litter size and individual growth rate or mass, whereby females must either invest energy in producing a larger litter or heavier individual young. In addition, during critical developmental periods such as lactation, the number of offspring can often be decremented but not increased. Thus, before examining influences of maternal traits on offspring growth or mass, it is important to hold the influence of litter size statistically invariant. Throughout our analyses, the number of offspring had highly significant influences on the size and growth rate of young, but this influence did not obviate substantial maternal effects that also occurred. Including litter size in the Turnbull path models allowed us to reach different conclusions regarding patterns of maternal investment than those in Dobson et al. (1999). Maternal characteristics appear to play an important role in offspring mass and growth rate for this species.

Acknowledgments
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