Age-specific resource investment strategies: evidence from female Richardson’s ground squirrels
(Spermophilus richardsonii)

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Abstract
To avoid a possible cost to their future survival and/or reproduction, individuals must balance their somatic and reproductive investments. The van Noordwijk and De Jong model of resource investment predicts that investments into reproduction and soma can vary among individuals of a population based on the variation in the total amount of energy that individuals acquire. With principal components analysis (PCA), we created two axes of life history for female Richardson’s ground squirrels Spermophilus richardsonii: an index of total energy investment (PC1) and an index of investment tactic (PC2). Using these indices, we examined patterns of resource allocation to reproductive and somatic investments. Because yearling female Richardson’s ground squirrels complete growth to adult size during pregnancy and early lactation, their somatic needs exceed those of older, fully grown females. Therefore, we predicted that yearlings would show more evidence of a tradeoff between reproductive and somatic investments compared with older females. Both yearling and older females invested four to five times more mass into their litters than into their own body mass. With increasing total investment, yearling females increased investment in both reproduction and themselves, whereas older females invested relatively more in reproduction than themselves. Regardless of age, females that emerged heavier from hibernation invested fewer resources into themselves and more into their litters. Variation in total energy investment and investment tactic indices was similar for yearling and older females. Contrary to our prediction, however, yearling females showed positive associations between reproductive and somatic investments, whereas older females exhibited showed no significant association between reproductive and somatic investments.

Introduction
Life histories reflect patterns of resource allocation to fitness-related traits (Roff, 1992, 2001; Stearns, 1992). If life histories evolved under natural selection, allocation of resources should reflect two important events: survival and metabolic maintenance of an individual to reproductive age and subsequent survival and reproduction as an adult. The latter event may encompass a conflict forming the idea that there should be a ‘cost’ to increasing current reproduction in terms of future reproduction or survival (Williams, 1966). This tradeoff arises because, given a constant total energy budget, increased current reproductive investment can only occur if there is a reduced level of somatic investment, and increased current somatic investment likewise leaves fewer resources available to invest in reproduction (Hirshfield & Tinkle, 1975).

The evolutionary tradeoff between reproduction and survival may or may not be evident because some individuals may have more resources to invest than others (Reznick, 1985). Thus, two axes of life history might be envisioned: an axis of total energy investment and an axis of investment tactic of reproductive versus somatic investments at a given level of total energy investment (van Noordwijk & De Jong, 1986; Glazier, 2000). van Noordwijk & De Jong (1986) pointed out that partitioning of total energy investment can be revealed by comparing somatic and reproductive effort graphically in order to estimate the relative proportions of an individual’s resources (also called total resource investment) that are spent on soma and on reproduction. van Noordwijk & De Jong’s (1986) suggested approach has not been broadly used, in part because of the difficulty of measuring somatic and reproductive efforts and of measuring total investment.

Our goal was to create total energy investment and investment tactic axes and, in doing so, provide an approximation of the van Noordwijk & De Jong (1986) model for female Richardson’s ground squirrels Spermophilus
Richardson's ground squirrels, a hibernating species that produces a single litter per year. Yearling females complete growth to adult size during pregnancy and early lactation (Michener, 1989; Dobson & Michener, 1995), so they have somatic growth requirements that older females do not have. Consequently, we assessed whether yearling and older adult females differed in their resource investment tactics. Furthermore, the magnitude of the somatic growth requirement varies among yearlings depending on their mass at emergence from hibernation (Michener, 1984), so we expected a wider range of variation in investment patterns among yearlings than among older females, specifically in the investment tactic axis. If so, the balance of investment should shift towards soma for some lightweight yearlings, thus producing an expected negative association of reproductive and somatic investments compared with heavy yearlings.

Our measures of reproductive and somatic investments were, respectively, the mass of the litter at initiation of weaning (when maternal investments of gestation and lactation are essentially complete) and the mass gained by mothers during the period of reproduction (from minimum body mass at emergence from hibernation in the spring to maternal body mass 8 weeks later at the end of lactation). By combining these types of female investment, we developed an index of total energy investment and an uncorrelated index of investment tactic. Using these indices, we examined how Richardson's ground squirrels allocate resources during their reproductive period.

Materials and methods

Adult (≥1 year old) Richardson's ground squirrels were studied for 15 reproductive seasons from 1987 to 2001 at a site near Picture Butte, Alberta, Canada (49°52′N, 112°43′W, elevation 870 m). All resident adults on the site were of known age because they had been uniquely identified with a numbered metal tag in each ear on first capture as juveniles. All adults were uniquely marked on the fur with human hair dye for identification from a distance.

Starting in early February, the study site was surveyed daily to detect the emergence of adults from hibernation. Female Richardson's ground squirrels follow a predictable sequence of reproductive events following emergence from hibernation (Michener, 1989); they typically mate 3–4 days post-emergence, give birth in an underground burrow 23 days after mating, and start weaning the litter, typically of 6–8 young, as soon as offspring first appear above ground at 29 days old. Longitudinal data on reproductive condition and body mass were obtained by targeted live trapping of individuals around the time of each major biological event. Each adult female was captured shortly after emergence from hibernation, normally within 24 h of emergence, and then captured again near the anticipated time of estrus. Mating was confirmed from a combination of appearance of the external genitalia, assessment of vaginal cytology from cells obtained in vaginal lavages and behavioral observation (Michener & McLean, 1996; Michener, 1998). Females were recaptured ≤48 h before and again ≤48 h after the expected parturition date. Parturition was confirmed from a decrease in maternal body mass and associated changes in the appearance of the external genitalia and nipples. The first emergence of litters from the natal nest was detected by daily inspection of the burrow system occupied by each female from 26 days post-partum onward. Once a litter was observed, the emergence location was marked and trapping of juveniles began within 24 h. Litter size at emergence from the natal nest was determined by live trapping until the entire litter was captured, normally ≤3 days after first appearance of the litter. Mothers were recaptured during late lactation around the time of first emergence of the litter, and maternal mass obtained 28–33 days post-partum represented the female's somatic condition at the onset of weaning.

On each capture, adult females and juveniles were weighed on a spring scale to the nearest 5 g and the nearest 2.5 g, respectively. Litter mass at natal emergence was calculated as the sum of the individual masses of juveniles, provided that the majority (usually 100%) of juveniles had been captured and weighed when ≤33 days old. For 10% of litters in which a few juveniles were not captured until >33 days old, the average mass of their siblings was used as an estimated mass.

Mass of the litter at first emergence from the natal burrow represented the reproductive investment made by each female (Broussard et al., 2005). The amount of mass gained by each female over the 8-week period between her emergence from hibernation in late February–March and the time her litter emerged from the natal burrow in late April–May estimated her somatic investment during the reproductive period (Michener, 1989; Humphries & Boutin, 1996; Broussard et al., 2005).

Data analyses

All statistical analyses were performed using SAS (1990) statistical software. Broussard et al. (2005) found that reproductive and somatic investments differed between yearling and older (2–5 years of age) female Richardson's ground squirrels, but not among older females. Therefore, data for females ≥2 years of age were pooled for comparisons between yearlings and all older females. The smallest litter size recorded at birth for captive Richardson's ground squirrels was 4 (Michener, 1989), and attrition in litter size between birth and first emergence averaged <1 young (Michener, 1989). We eliminated from analysis all lactating females that weaned 0–2 offspring because observations indicated that such small litters were usually the result of total or partial predation by North American badgers Taxidea taxus (Michener, 2004) and long-tailed weasels Mustela frenata.

Data were analyzed using major axes regression (PRINCOMP procedure), general linear model procedure (GLM procedure) and linear regression procedure (REG procedure) (SAS, 1990). Unless stated otherwise, P values of ≤0.05 were considered significant in all analyses. Averages are presented throughout as mean ± 2 SE. Because
reproductive output in 1 year did not significantly affect a female’s reproductive output in the next year (Michener & Locklear, 1990; Dobson & Michener, 1995; Broussard et al., 2005) and because no significant interaction between age and individual was found for any of the maternal and reproductive variables (all P’s > 0.05), we assumed that maternal and reproductive characteristics of females measured in different years were statistically independent samples and that data on individuals from different years were biologically independent.

Because some maternal and reproductive characteristics varied among years, all data were standardized for year effects using residuals of ANOVA (GLM procedure). Year-standardized data were used for statistical analyses. However, we present unstandardized data for descriptive statistics and figures.

Female Richardson’s ground squirrels for whom we knew both reproductive investment and somatic investment during reproduction were used to generate indices of total energy investment and investment tactic (Fig. 1). To create an index of total energy investment, major axis regression with the intercept forced through the origin was used with year-standardized somatic investment and year-standardized reproductive investment as variables (Sokal & Rohlif, 1995). Because the energy expended by mothers to achieve the outcomes of a weaned litter and a personal gain in mass was not known, scores, which are the calculated values on the PC1 and PC2 axes, were calculated using correlation matrices. The score on PC1 of reproductive investment and somatic investment on the major axis regression line was the index of total energy investment, and the magnitude of the score on PC2 (deviations of points perpendicular from the major axis regression line) was taken as a female’s life-history tactic at a given total energy investment; positive residual values represented a reproductive investment tactic, whereas negative values indicated a somatic investment tactic. The intercept was forced through the origin for two reasons: (1) to ensure that total energy investment increased as the regression line extended through the data and (2) to divide the females roughly in half into those above the total energy investment line and those below (Fig. 1).

### Results

Yearling female Richardson’s ground squirrels were, on average, 11% lighter in mass at emergence from hibernation compared with older females (Table 1). Gain in personal mass between a female’s emergence from hibernation and first emergence of her litter from the natal burrow, her somatic investment during reproduction, was variable (40–265 g for yearlings; 35–225 g for older females), but yearling females made a greater somatic investment in themselves during reproduction than did older females.

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**Table 1** Maternal and reproductive characteristics for yearling and older (≥ 2 years old) female Richardson’s ground squirrels *Spermophilus richardsonii* pooled for 15 years from 1987 to 2001

<table>
<thead>
<tr>
<th></th>
<th>Yearling</th>
<th>Older</th>
<th>t</th>
<th>P</th>
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</thead>
<tbody>
<tr>
<td>Emergence mass (g)</td>
<td>230 ± 2</td>
<td>259 ± 2</td>
<td>15.5</td>
<td>&lt; 0.0001</td>
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<tr>
<td>(414)</td>
<td>(240)</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Post-partum mass (g)</td>
<td>332 ± 4</td>
<td>355 ± 4</td>
<td>7.43</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>(393)</td>
<td>(229)</td>
<td></td>
<td></td>
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<tr>
<td>Mass at litter emergence (g)</td>
<td>358 ± 4</td>
<td>369 ± 4</td>
<td>3.84</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>(414)</td>
<td>(240)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Somatic investment during reproduction (g)</td>
<td>127 ± 4</td>
<td>111 ± 4</td>
<td>5.52</td>
<td>&lt; 0.0001</td>
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<tr>
<td>(414)</td>
<td>(240)</td>
<td></td>
<td></td>
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<tr>
<td>Reproductive investment (g)</td>
<td>502 ± 10</td>
<td>508 ± 14</td>
<td>0.70</td>
<td>0.50</td>
</tr>
<tr>
<td>(414)</td>
<td>(240)</td>
<td></td>
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<td></td>
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<tr>
<td>Litter size</td>
<td>6.7 ± 0.2</td>
<td>6.5 ± 0.2</td>
<td>1.27</td>
<td>0.20</td>
</tr>
<tr>
<td>(414)</td>
<td>(240)</td>
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Data are presented as unadjusted mean ± 2 SE, with sample size in parentheses; year-adjusted means were compared using a Student’s t-test. Emergence mass is maternal mass obtained ≤ 48 h after first emergence from hibernation. Somatic investment during reproduction is the mass gained by females from hibernation emergence to the first emergence of their litter from the natal burrow. Reproductive investment is litter mass at first emergence from the natal burrow.
both absolutely (Table 1) and relative to their emergence mass (57 ± 0.02 vs. 43 ± 0.02%; \( t = 10.0, P < 0.0001 \)). Consequently, the discrepancy in mass between yearling and older females declined to 7% just after pups were born and 3% at litter weaning (Table 1), indicating that yearling females completed growth during their first reproductive season. Litter masses and litter sizes at weaning did not differ significantly between yearling and older females, but litter mass at weaning was significantly greater for yearlings than older Richardson’s ground squirrels when expressed relative to maternal mass at emergence from hibernation (221 ± 5.0% for 414 yearlings, 198 ± 5.4% for 240 older females; \( t = 5.74, P < 0.0001 \)).

Using principal components analysis (PCA), we found differences in the total energy investment and investment tactic indices between yearling and older female Richardson’s ground squirrels. The scores on the PC1 axis reflected the total resources invested into both reproduction and somatic needs, whereas the scores on the PC2 axis reflected the amount of resources a female invested in either reproduction or herself for a given total resource investment (Fig. 1). The scores on the PC1 axis and PC2 axis accounted for 62 and 38% of the variation in traits, respectively, for yearlings and 52 and 48%, respectively, for older females. The index of total energy investment differed significantly between yearling and older females (means in PC1 scores: yearling, 0.10 ± 0.10; older, −0.17 ± 0.13; \( t = 3.17, \) d.f. = 652, \( P = 0.02 \)) as did the female’s investment tactic (means in PC2 scores: yearling, −0.14 ± 0.8; older, 0.25 ± 0.12; \( t = 5.37, \) d.f. = 652, \( P < 0.0001 \)) (Fig. 2). For both yearling and older females, the total energy investment axis was strongly positively correlated with both reproductive and somatic investments (Table 2). Additionally, for both yearling and older females, the index of female investment tactic was strongly positively associated with reproductive investment but strongly negatively correlated with somatic investment (Table 2).

Variance of total energy investment (PC1 scores) and investment tactic (PC2 scores) were calculated for yearling and older females. Variance in total energy investment was slightly higher for yearlings (1.15) than older females (1.12), whereas variance in investment tactic was lower for yearling females (0.70) than older females (0.99).

**Discussion**

Both yearling and older female Richardson’s ground squirrels increased in mass substantially during the 8-week reproductive period coincident with producing a litter that, at weaning, was about twice as heavy as the mother’s mass when she began her reproductive investment. Because yearlings were still growing during gestation and early lactation, we expected that they would have different tactics of resource investment based on total energy investment compared with older females. Specifically, we predicted that yearling females would show more evidence of a tradeoff between reproductive and somatic investments compared with older females. For both yearling and older females, we found little evidence of tradeoffs between their reproductive and somatic investments. Furthermore, contrary to our prediction, with increasing total resource investment, yearling Richardson’s ground squirrels invested highly in both their litters and themselves, whereas older females invested highly in their litters and less in themselves.

The second axis of life history, the index of investment tactic, was strongly positively correlated with reproductive investment but negatively correlated with somatic investment, in both yearling and older female Richardson’s ground squirrels (Table 2). However, the second axis may have been partially obfuscated by an interaction with the initial body mass of females on emergence from hibernation. On average, females of all ages that emerged heavier from hibernation had lower mass gains and greater reproductive investments (Broussard et al., 2005). Thus, some heavier females increased their reproductive investment while investing little in their soma, probably because they could afford to because of their greater personal resources coming out of hibernation.

The first axis of life history, which represents an estimate of total energy investment, was strongly positively correlated to our measures of reproductive investment and somatic investment (Table 2). Because correlation matrices were used to calculate principal component scores (as opposed to using covariance matrices), somatic investment contributed to the variation in the first axis of life history, even though reproductive investment was four to five times as great in absolute mass as somatic investment by mothers during the reproductive period. Our measure of somatic investment only included mass gain by mothers during the reproductive period and, thus, did not include metabolic expenditures such as milk production, which can be high (Kenagy, Sharbaugh & Nagy, 1989). Nonetheless, female Richardson’s ground squirrels clearly invest substantially in themselves during reproduction.
Yearling Richardson’s ground squirrels had greater increases in personal body mass during reproduction (and, thereby, completed growth) than older females that had already reached adult structural body size (Michener, 1989; Dobson & Michener, 1995). Yearlings exhibited slightly higher variation in the total energy investment axis than older females and lower variation in the investment axis compared with older females (Fig. 1). The van Noordwijk & De Jong (1986) model predicts that the age group with greater variation in total energy should exhibit a positive association of reproductive and somatic investments. Those individuals with higher total energy investments will be able to invest more resources into both reproduction and themselves compared with individuals with lesser energy investments. As predicted by the van Noordwijk & De Jong (1986) model, yearling female Richardson’s ground squirrels showed positive associations between our measures of reproductive and somatic investment, whereas older females exhibited no association between these two forms of investment. Yearling females completed growth and weaned litters of similar size and mass as those of older females even though they were significantly lighter at emergence from hibernation. Yearlings presumably compensated for this high energetic demand by increasing their total energy budget, such as through increased time spent feeding, or by minimizing their maintenance costs, such as avoiding inclement above-ground conditions, thereby showing positive associations between reproductive and somatic investment (Broussard et al., 2005). The energetic mechanism by which yearling females are able to invest heavily in reproduction while completing growth warrants further study.

Levels of resource investment can be estimated from the accumulation of mass. We examined personal mass gained by mother Richardson’s ground squirrels in the reproductive period, when they were also investing mass in reproduction. The total mass gained, however, does not represent total resource investment because the costs of producing personal tissues and offspring tissues undoubtedly differ. An important difference is the cost of adding fat or protein directly into the mother’s body versus nurturing the growth of offspring via manufacture of milk that is then exported to infants. Even though we did not measure the comparative costs of such metabolic activities by the mother, we could make a reasonable estimate of resource investment by calculating a regression line via PCA through the origin of the van Noordwijk & De Jong (1986) graph and the centroid of a data scatter of mothers’ mass gains versus reproductive masses near the time of weaning (Fig. 1). As reproductive and somatic investments increase, total investment must also increase. Thus, points on the regression line can be used to compare mothers that have greater and lesser levels of resource investment, via ‘scores’ on the first principle component (namely the regression line). A second problem is also solved by this procedure. The regression line now divides the mothers into two groups: those that have personal investment (namely soma) emphasized in their resource division and those that emphasize reproduction. Scores on the second principal component axis can thus be used to compare individuals with respect to this emphasis, with individuals with scores on the upper left of the second axis emphasizing personal investment and those on the lower right emphasizing reproduction (Fig. 1).

The value of this exercise becomes apparent when we compare Richardson’s ground squirrel mothers of different ages. Because yearling females are still growing, we expect that they will invest more in themselves and proportionately less in reproduction. Indeed, their scores on the second principal component show that they do this (Fig. 2). Surprisingly, however, yearlings also had significantly higher scores than older mothers on the first principal component, indicating greater total resource investment and thus greater resource acquisition. Thus, PCA provided a clear demonstration that mothers that are still growing (i.e. yearlings) can actually accumulate resources for investment at a greater rate than more experienced older mothers.

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