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1 **PHENOTYPIC PLASTICITY IN REPRODUCTIVE AND**
2 **SOMATIC EFFORTS OF FEMALE COLUMBIAN GROUND**
3 **SQUIRRELS**

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18

19 **Abstract.**

20 Phenotypic plasticity of life-history traits is well known among vertebrate species. We
21 estimated reproductive and somatic efforts of female Columbian ground squirrels (*Urocitellus*
22 *columbianus* (Ord, 1815)) to test for plasticity of these important resource allocations. We
23 examined a 27-year dataset of life-history traits on these long-living (8-10 years), hibernating,
24 montane-living mammals. Environmental variation was estimated from two important traits of
25 mothers, their relative timing of breeding and spring maternal body mass (initial “capital” for use
26 in subsequent reproduction). Results from 183 known-aged mothers and 508 litters revealed
27 considerable variation in the relative timing of breeding, initial maternal mass, and reproductive
28 and somatic efforts, as well as significant variation among age and years. Results from 125
29 mothers that reproduced more than once (and 450 litters) revealed significant plasticity of
30 reproductive and somatic efforts with respect to relative timing of breeding and spring maternal
31 mass. A within-subject centering statistical approach showed that phenotypically plastic
32 reproductive and somatic efforts were due to variation within individuals, but were not always
33 reflected by the pattern of responses among individuals in the population. The plastic responses
34 of different mothers appeared to be similar in strength.

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37 **Key words:** Columbian ground squirrel, phenotypic plasticity, repeatability, reproductive effort,
38 somatic effort, *Urocitellus columbianus*

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INTRODUCTION

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How maternal resources are allocated to reproduction in iteroparous species (where individuals reproduce more than once in their lifetime) is a fundamental question in evolutionary biology. At the simplest, the options are allocation to current reproduction versus allocation in oneself, viz. somatic allocation, the latter supporting reproduction at a later time. This basic division for iteroparous organisms led Hirshfield and Tinkle (1975) to point out that for a given energy budget, resources should be allocated in a way that maximizes reproductive value (Fisher 1930). Reproductive value, in turn, has two components (Williams 1966): current and future reproduction (termed “residual reproductive value”). Thus, for organisms that reproduce more than once, we should expect natural selection to favor a “trade-off” between resource allocations to current and future reproductive efforts (Stearns 1976). Future reproduction, of course, is supported by additional underlying factors, including somatic growth, stored resources, and enough personal maintenance to provide the best chance of survival to reproduce again. For the trade-off to evolve via natural selection, it must have a genetic basis, something that has proved difficult to demonstrate in nature (Reznick 1985; Houle 1991; Reznick et al. 2000). Even documenting a phenotypic basis for the trade-off of current reproductive effort and residual reproductive value faces substantial challenges, such as bias from variation in resource availability among individuals (e.g., van Noordwijk and de Jong 1986).

Over an iteroparous lifespan, individuals with traits that respond to changing environmental conditions, that is, traits that are phenotypically plastic, should be favored by natural selection (reviewed by de Villemereuil et al. 2020). For instance, traits such as reproductive effort should be greater when more environmental resources are available, and less

62 when environmental resources are scarce (van Noordwijk and de Jong 1986). Plastic responses
63 of traits, such as individual reproductive effort, to alternative environmental conditions are
64 termed “reaction norms” (Stearns 1989). The occurrence of several reaction norms for a given
65 trait in a population indicates the presence of several trait forms and genetic variation in
66 plasticity, and thus a genotype by environment interaction (Via and Lande 1980; Scheiner 1993;
67 Via et al. 1995).

68 In the presence of genetic variation in phenotypic plasticity, we might expect to see
69 considerable variation in fitness, and a genotype by environment interaction in fitness traits such
70 as reproductive effort. Alternatively, a “general-purpose genotype” that produces the best
71 phenotype for each environment circumstance might be shared among individuals, *i.e.*, a
72 genotype for which trait responses are variable, but in an optimal manner given alternative
73 environments. In this case, considerable phenotypic variation might be produced by organismal
74 or environmental variation, rather than by genetic variation. A review of plastic responses to
75 temperature found no significant evidence of selection on phenotypic plasticity (Arnold et al.
76 2019), suggesting at least the possibility that variation within populations due to climatic change
77 might be underlain by one or a very few reaction norms.

78 Columbian ground squirrels (*Urocitellus columbianus* (Ord, 1815)) are ideal for a study
79 of phenotypic plasticity in reproductive and somatic efforts. These hibernating rodents show
80 considerable variation in reproduction, growth, and investments in survival, both within and
81 among individuals (Murie and Dobson 1987; Risch et al. 1995; Dobson et al. 1999; Broussard et
82 al. 2003, 2006; Rubach et al. 2016). They inhabit montane environments where there is
83 considerable yearly variation in reproductive traits with variation in environmental conditions,
84 such as daily resource abundance and growing season length (Murie and Harris 1982; Dobson

85 and Kjelgaard 1985a, 1985b; Zammuto and Millar 1985a, 1985b; Dobson et al. 1986; Dobson
86 and Murie 1987; Dobson 1988, 1995). The montane environment appears to constrain female
87 reproductive effort, since mothers have relatively lower litter size for their body size when faced
88 with shorter growing seasons (Murie and Harris 1982; Zammuto and Millar 1985a, 1985b;
89 Dobson and Murie 1987; Dobson 1988; Dobson et al. 1992).

90 Reproductive effort might be influenced by the initial condition of a mother when
91 breeding starts (Broussard et al. 2005; Rubach et al. 2016). Ground squirrel females that begin
92 the breeding season in top body condition have greater reproductive success, a condition termed
93 capital breeding (Jönsson 1997; Broussard et al. 2005). However, most of their annual
94 reproductive effort is supported by daily foraging, and the great majority of mothers gain
95 personal body mass during the reproductive period, while they both gestate and lactate
96 (Broussard et al. 2003). As such, reproductive effort may trade off with personal allocations that
97 mothers make in themselves as they are breeding, part of their somatic effort (Dobson et al.
98 1999; Broussard et al. 2003, 2005, 2008; Skibieli et al. 2009; Rubach et al. 2016; Viblanc et al.
99 2016a). Indeed, mothers that begin the breeding season in poor condition gain considerable
100 personal mass while reproducing, compared to mothers that are initially better endowed with
101 capital in the form of body mass (Rubach et al. 2016). The allocations that mothers make to
102 reproductive and somatic efforts might exhibit a negative association between reproductive and
103 personal mass allocations, as expected under the trade-off model of van Noordwijk and de Jong
104 (1986). Alternatively, the same model could produce a positive association of reproductive and
105 somatic efforts if individuals differed greatly in their total resource acquisition. Thus, we tested
106 whether a negative or positive association of reproductive and somatic allocations occurred.

107 Next, we examined the repeatability of reproductive and somatic efforts for individual
108 breeding females in different years. High repeatability would indicate low scope for plasticity
109 within individuals, and low repeatability would indicate greater scope for plasticity with respect
110 to reproductive effort. Given sufficient variation in reproductive and somatic efforts of maternal
111 ground squirrels, we made an initial evaluation of the plasticity of these efforts. For this, we
112 used traits of the females themselves as integrative reflections of the environmental conditions
113 that they faced. The first trait was the timing of breeding within years, relative to other mothers
114 that were breeding in the same year, statistically controlled for the age of the mother. This trait
115 is closely associated with emergence from hibernation, the latter trait under significant selection
116 favoring earlier timing (Viblanco et al. 2022). The second trait was the initial body mass of
117 mothers at the beginning of the breeding season, statistically controlled for both age of the
118 mother and the specific year in which she bred. Maternal body mass at the initiation of breeding
119 has strong and significant influences on the number and size of subsequent production of
120 offspring (Dobson et al. 1999; Skibielski et al. 2009). We used these initial conditions for breeding
121 as reflections of previous environmental conditions that might influence preparations for
122 breeding, and examined whether subsequent reproductive and somatic efforts were sensitive to
123 these initial conditions.

124 If individuals exhibited similar reaction norms, it might indicate a general-purpose
125 genotype for reproductive effort or for somatic effort. We tested whether the mean associations
126 of reproductive and somatic efforts with initial breeding conditions of mothers within the
127 population could be accounted for by the plasticity of individual females. For this, we tested
128 whether the patterns for individual females were significant, and whether they differed from the
129 patterns among the females in the population at large (after van de Pol and Wright 2009).

130 Additionally, large deviations of slopes among mothers might indicate individual differences in
131 reproductive or somatic tactics favored by either natural selection or perhaps genetic migration
132 of alternative tactics into the population. Thus, we tested for significant differences among
133 mothers in the slopes of their plastic responses of reproductive and somatic efforts to their initial
134 breeding conditions (relative timing of the breeding season and initial body mass), using only
135 those mothers that successfully bred more than once.

136

137 METHODS

138 *Study population and monitoring*

139 From 1992 to 2020, we studied Columbian ground squirrels in a 1.8 ha subalpine
140 meadow along the Sheep River drainage in southwestern Alberta, Canada, within Sheep River
141 Provincial Park (1550m elevation; 50°38010"N, 114°39056"W). Over the years, the spring
142 population at emergence from hibernation varied in size between 32 and 120, and averaged about
143 62.7 female ground squirrels (does not include young-of-the-year). A total of 195 females
144 produced 559 litters (a mean of 19.2 litters/year) of an average of 2.82 weaned young per single
145 annual litter during this time.

146 Breeding ground squirrels emerged from hibernation in the spring in mid- to late-April,
147 through mid-May. At spring emergence, we trapped all ground squirrels on the study site,
148 usually within a couple of days of their first sighting. We captured ground squirrels in live traps
149 (13x13x40 cm, Tomahawk Live Trap Co., Hazelhurst, WI, USA) baited with a small amount of
150 peanut butter, placed near a burrow opening that was used by the active ground squirrel. Each
151 captured individual was weighed to the nearest 5g in a cloth handling bag using a spring-slide
152 balance (Pesola AG, Schindellegi, Switzerland) and examined for reproductive condition,

153 wounds, and ectoparasites. If not already permanently ear-tagged, a pair of uniquely numbered
154 fingerling tags (Monel #1; National Band & Tag Co., Newport, KY, USA) were attached, one to
155 each ear. Finally, each ground squirrel received an individually unique dye-mark symbol on the
156 dorsal pelage via application of hair dye (Clairol ® Hydrience, 052 Black Pearl, Proctor and
157 Gamble, Stamford, CT, USA). These dye-marks were used for later identification from a
158 distance, using binoculars, from ground locations on the meadow and five elevated wooden
159 benches (2-4m high) that were spread about the study site.

160 Most females began to breed at 2 years of age, producing a single litter each year
161 (Rubach et al. 2020). The annual mating period for a female was 5-7 hours long, usually 3-5
162 days after emerging from hibernation (Murie and Harris 1982; Murie 1995). We monitored the
163 mating day of females with observations of unique behaviors associated with the estrous period
164 (such as female behavioral solicitation of matings), examination of vaginal swelling, and from
165 copulatory plug material deposited in the fur or vulva of the female (for details, see Murie 1995;
166 Manno and Dobson 2008; Manno et al. 2008; Raveh et al. 2010, 2011). After mating, males
167 make little or no subsequent investment in raising offspring (Festa-Bianchet and Boag 1982;
168 Murie and Harris 1988; Nesterova et al. 2011). For females, mating is followed by about 24
169 days of gestation, birth, and about 27 days of lactation (Murie and Harris 1982, 1988). During
170 lactation, mothers nurse their young in a specially constructed, single-entrance nest burrow.
171 Observations of mothers entering and leaving their nest burrow allowed us to anticipate the
172 emergence of litters at about the time of weaning.

173 As young ground squirrels emerged above ground for the first time from nest burrows
174 (near the time of weaning), we trapped complete litters and their mothers, usually within a day of
175 their first sighting and rarely up to 2 days later; at these times young were still dependent on the

176 mother's milk. Newly emerged young were weighed to the nearest 1 g with a spring-slide
177 balance. The young were fitted with a pair of numbered fingerling ear tags and given a unique
178 black dye marking on the dorsal pelage. Since the young had begun their lives in utero at a body
179 mass close to zero, we used the summed mass of the young in a litter at initial capture as an
180 index of the mass that the mother had allocated to reproduction, and termed this her reproductive
181 effort (Broussard et al. 2006). The difference between the mass of the mother when the young
182 first emerged from nest burrows and her mass when she emerged from hibernation (near the time
183 of mating) was used to estimate her personal mass allocation during the breeding period. This
184 latter estimate was used as an index of the somatic effort of the mother, during the period when
185 she was also investing in reproduction (Michener 1989; Broussard et al. 2003; Broussard et al.
186 2005). These two indices represent the total allocation of energy to mass by the mother while
187 breeding (gestating and lactating for young that were subsequently weaned) (Viblanco et al.
188 2016a). Subsequent to weaning the young, all ground squirrels fattened for the 8-9-month
189 hibernation period that began in mid-to-late summer (Dobson et al. 1992).

190 All field procedures, including trapping, handling and marking, and field observations
191 were approved by animal care and use committees of Auburn University, the University of
192 Calgary, and Alberta Fish & Wildlife.

193

194 *Initial conditions, reproductive effort and somatic effort*

195 We selected cases of mothers and their litters from those with complete annual data
196 during the 28-year study period (n = 508 records and 183 females, a mean of 2.8 litters/mother).
197 We also examined initial conditions that appear important to successful breeding and fitness:
198 relative date of mating and body mass at the start of the season (Dobson et al. 1999; Broussard et

199 al. 2005; Rubach et al. 2016). To estimate the initial “capital” (“IM”) that mothers could allocate
200 while breeding, we used their mass at emergence from hibernation, 3-5 days before mating
201 (Murie and Harris 1982). On average, mothers began their breeding season by mating around 1
202 May (± 6.3 days standard deviation) at an initial spring mass of 421.2 grams (± 53.3 g). Our
203 measure of reproductive timing was the estimated relative mating date (“RMD”). For this, we
204 subtracted the mean date of mating from the individual mating dates of mothers within each year
205 (after Viblanc et al. 2022). For individual mothers, RMD ranged from -12.8 days to 16.1 days
206 (mean = 0.0 ± 4.3 days). Initial mass of mothers was not adjusted to be relative within years,
207 since in an especially good or poor year all females might be in relatively good or poor condition
208 with respect to their initial body mass and thus have more or less resources, on average, to
209 allocate to reproductive and somatic efforts.

210 The mass of litter (viz., reproductive effort) that these mothers produced, measured near
211 the time of weaning, was 300.2g (± 90.1 g). Over the same period these mothers gained
212 (concurrent somatic effort) an average of 101.8g (± 48.5 g). The association of reproductive and
213 somatic efforts was trivial and not significantly different from zero ($r = 0.043$, $t_{[506]} = 0.98$, $p =$
214 0.33).

215

216 *Basic patterns of age and year*

217 Female ground squirrels begin breeding at different ages, usually as 2- or 3-year-olds and
218 very rarely during their 1st year of post-hibernation activity (Rubach et al. 2020). Reproductive
219 and somatic efforts vary with age of the mothers and from year to year, with the oldest females
220 showing signs of reproductive senescence (Broussard et al. 2003, 2008). Yearling mothers are
221 also significantly lighter than older females (Dobson 1992; Broussard et al. 2003). Reproductive

222 effort varies considerably from year to year, and the timing of the reproductive season also
223 changes from year to year (Murie and Harris 1982; Dobson et al. 1999; Skibieli et al. 2009). A
224 measure related to reproductive effort, annual fitness (based in part on litter size) varied strongly
225 over a 20 to 30-year period (Lane et al. 2012; Dobson 2016; Viblanc et al. 2022). Therefore, we
226 examined the effects of age and year and their interaction, using regression models. Mothers
227 aged 9 to 13 years were pooled to obtain a suitable sample of the oldest age classes. Statistically
228 controlling for age, year, and maternal identity confirmed the lack of relationship between
229 reproductive and somatic efforts (mixed model of RE ~ SE; marginal $R^2 = 0.004$, conditional R^2
230 $= 0.354$; $F_{[1,372.0]} = 2.17$, $p = 0.14$). Thus, we examined these two allocations separately in
231 further analyses of phenotypic plasticity.

232 We examined possible influences on initial maternal body mass, using an intercept mixed
233 regression model in which maternal age, year, and identity were random variables. Maternal
234 identity could potentially explain 25.5% (± 0.8 standard deviations) of the variation in IM, year
235 explained 6.2% (± 0.4), and age explained 51.3% (± 1.1) (total variance = 4376.7, $n = 508$
236 mother-years, combined 82.9% of the variance in IM explained) In a similar analysis of relative
237 mating date (but without year because data were year-mean standardized), maternal identity
238 explained 21.7% (± 10.6) of the variance in RMD, and age explained 8.1% (± 6.5) (total
239 variance = 19.1, $n = 508$ mother-years, combined 29.8% of the variance in RMD explained). In
240 further analyses, maternal identity, year, and age were entered, where possible, as fixed factors in
241 repeatability analyses and random variables in mixed models.

242

243 *Population patterns*

244 We examined whether the initial breeding traits of relative reproductive timing and
245 maternal body mass (independent variables) were associated with energy allocations, measured
246 in grams of mass, to the mother's reproductive effort and concurrent somatic effort. For this,
247 relative date of mating and initial maternal body mass were standardized, since they were
248 measured on different scales (days and grams). Maternal age and identity, as well as year, were
249 included as random variables. Analyses were run on the complete dataset of 183 mothers and
250 508 successful reproductive events and on smaller dataset of 125 mothers that reproduced more
251 than once during their lifetimes (450 weaned litters, mean 3.60 litters/mother, range 2-9
252 litters/mother). Results were very similar, and we present results only for the 125 mothers that
253 reproduced more than once. The sample of 125 mothers should have produced suitable power to
254 detect patterns of plasticity (Martin et al. 2011; van de Pol 2012). We examined the interaction
255 between relative mating date and initial maternal body mass in both models, but excluded them
256 because they were low and not significant (reproductive effort, $t_{[441.2]} = 1.0$, $p = 0.32$; somatic
257 effort, $t_{[420.2]} = 1.7$, $p = 0.08$).

258

259 *Repeatability*

260 For the 125 females that produced more than a single litter in their lifetime, we examined
261 repeatability (the intraclass correlation coefficient, or ICC), where maternal identity was used as
262 the class variable. ICC was calculated as $s^2 / (s^2 + s^{2^{\wedge}})$. $s^{2^{\wedge}}$ is the among-individual variance
263 component and s^2 is the within-individual variance component (Lessels and Boag 1987;
264 Nakagawa and Schielzeth 2010, 2013; Nakagawa et al. 2017). Repeatability varies between 0.0
265 and 1.0, and is usually calculated using a single partitioning of the variance in a trait into that
266 accounted for by individual identity and an error term. Low repeatability indicates considerable

267 flexibility in a trait, due perhaps to phenotypic plasticity but also reflecting sampling variation.
268 High repeatability reflects trait inflexibility, as would occur if a trait were highly heritable,
269 though repeatability is not a direct measure of heritability. We examined the repeatability of
270 relative timing of breeding, initial spring body mass of mothers, reproductive effort, and somatic
271 effort. To adjust for influences of age and year, we included these as fixed factors. We used a
272 Monte Carlo method of estimation of repeatability (Nakagawa et al. 2017), using 1000 bootstrap
273 values.

274

275 *Within versus among mothers*

276 Phenotypic plasticity was examined using the mixed-model procedures described by van
277 de Pol and Wright (2009), that evaluate variations in characteristics within versus among
278 mothers. For these analyses, we used the 125 females that produced more than one litter. We
279 partitioned variation in reproductive and somatic efforts into within-subject and among subject
280 effects, regressed onto the initial conditions of relative breeding date and maternal body mass.
281 When within-individual effects were significant (Table 1b), we moved on to examine whether
282 the two types of effects differed in their slopes, by running a further model that compared
283 individual and population-wide patterns (Table 1c).

284 These models assumed that the slopes for individual females were similar. Finally, we
285 tested whether females differed in their slopes of responses, by asking whether a “random slope”
286 model was a significant improvement over the model that assumed similar slopes. For this last
287 test, the models were compared statistically and the preferred model was the one with the lowest
288 Akaike Information Criterion (AIC). For the influence of initial maternal mass on somatic effort,
289 the model fit was singular and did not converge when we examined mothers that produced at

290 least 2 litters. So, we used a smaller dataset of mothers that produced at least 3 litters (370 litters
291 for 85 mothers) and dropped the variables age and year from the model.

292

293

294

RESULTS

295 *Population patterns*

296 Reproductive effort was significantly and positively influenced by both relative timing of
297 breeding and initial maternal body mass, with the former influence about half that of the latter
298 (Table 1a, column RE~RMD and RE~IM; relative mating date, $t_{[418.4]} = 2.7, p = 0.007$; initial
299 maternal mass, $t_{[277.0]} = 4.7, p < 0.001$). The influence of the two initial variables, however, was
300 moderate at best (marginal $R^2 = 0.069$, conditional $R^2 = 0.348$). Somatic effort was also
301 significantly influenced by both relative timing of breeding (a positive association) and initial
302 maternal body mass (a negative association), with the former influence about a third that of the
303 latter (Table 1a, column SE~RMD and SE~IM; relative mating date, $t_{[415.4]} = 5.6, p < 0.001$;
304 initial maternal mass, $t_{[318.6]} = -12.5, p < 0.001$), and the influence of these variables was fairly
305 strong (marginal $R^2 = 0.308$, conditional $R^2 = 0.729$). In summary, later breeding led to higher
306 reproductive and somatic efforts, while a higher initial mass resulted in higher reproductive, but
307 lower somatic, effort. Because we had identified these significant influences, we further
308 examined variation within individual mothers, reflecting phenotypic plasticity, and variation
309 among the mothers in our population.

310

311 *Repeatability*

312 ICC (and standard error) of relative mating date (RMD) was 0.252 (\pm 0.055, $P < 0.001$),
313 initial spring body mass (IM) was 0.581 (\pm 0.044, $P < 0.001$), litter mass near weaning (RE) was
314 0.218 (\pm 0.053, $P < 0.001$), and change in maternal mass during the breeding season (SE) was
315 0.137 (\pm 0.054, $P < 0.001$). Despite significant repeatabilities for all four traits, unexplained
316 variation (about 42% to 86%) still showed quite a bit of “scope” for change over time in the
317 “initial” breeding variables (RMD and IM) and subsequent allocation variables (RE and SE). Of
318 course, the unexplained variation also contained an unknown amount of sampling variation.

319

320 *Within versus among mothers*

321 Reproductive effort varied significantly and positively with the relative timing of
322 breeding (Table 1b, column RE~RMD; within individual effect, $F_{[1,317.1]} = 6.7$, $p < 0.01$; among
323 individual effect, $F_{[1,137.6]} = 0.1$, $p = 0.78$). Individual mothers exhibited a change in the mass of
324 their litters of about 2.99 grams per day; thus, compared to other females and over a 3-week
325 mating period, this could result in about a 63g increase in RE). However, the pattern among
326 females (at about 0.52 grams/day) was not significant. The individual and population-wide
327 patterns did not differ significantly in slope (Table 1c; $F_{[1,243.1]} = 1.3$, $p = 0.26$). Nor did the
328 inclusion of random slopes, which we used to test for differences in plasticity among individuals,
329 improve the model (Figure 1a; AIC without random slopes = 5296, with random slopes = 5299,
330 $\chi^2_2 = 1.0$, $p = 0.60$). In summary, within-individual pattern indicated significant phenotypic
331 plasticity in reproductive effort in response to relative breeding date, and the plasticity appeared
332 fairly similar among mothers.

333 Reproductive effort was much more responsive to maternal body mass at about the time
334 that females mated. Reproductive effort increased significantly with spring body mass (at 0.37

335 grams of weaned litter/gram of initial maternal body mass) and a similar significant pattern
336 occurred among mothers (at 0.46 grams of weaned litter/gram of maternal mass) (Table 1b,
337 column RE~IM; within individual effect, $F_{[1,266.7]} = 7.6, p < 0.01$; among individual effect,
338 $F_{[1,136.4]} = 13.4, p < 0.001$). Comparison of the slopes of the within versus among mother
339 patterns was not significant (Table 1c; $F_{[1,346.4]} = 0.3, p = 0.58$). We included random slopes in
340 our comparison of litter mass at weaning to initial spring maternal mass, and allowing slopes to
341 vary did not significantly improve the model (Figure 1b; AIC without random slopes = 5284,
342 with random slopes = 5287, $\chi^2_2 = 0.7, df = 2, p = 0.70$). The significant within-individual effects
343 indicated that reproductive effort was phenotypically plastic in response to the initial spring
344 maternal body mass, and again, individual mothers did not appear to greatly differ in the
345 strengths of their plastic responses.

346 Somatic effort during breeding varied significantly with the timing of breeding (Table 1b,
347 column SE~RMD). Individual mothers gaining about 2.67 grams during breeding for every
348 additional 1-day delay in the relative timing of breeding, compared to other females (over a 3-
349 week mating period, this could result in about a 56g increase in SE), and among mothers this
350 average was very similar at 2.66 grams gained for each day of delay (respectively; $F_{[1,316.2]} =$
351 $24.3, p < 0.001, F_{[1,137.0]} = 12.7, p < 0.001$). The slopes of the within individual and among
352 individual effects of timing on maternal change in body mass were not significantly different
353 (Table 1c; $F_{[1,273.3]} = 0.0, p = 1.00$). Random-slope models for both datasets of females with 2 or
354 more and 3 or more litters were singular, likely due to the similarity of the individual and
355 population responses (Table 1b, 1c). While the singularity precluded statistical testing, visual
356 examination suggested a roughly similar pattern of slopes among mothers (Figure 1c).
357 Phenotypic plasticity was indicated by the significant within-individual change in somatic effort

358 with relative mating date. This pattern was also reflected by the significant among-individual
359 result and the virtual lack of difference between the within- and among-individual patterns.

360 Somatic effort during the breeding season was significantly influenced by the mother's
361 initial body mass when breeding was initiated (Table 1b, column SE~IM). Individual mothers
362 gained 0.76 grams less in personal body mass during breeding for each additional gram of mass
363 when they initiated breeding ($F_{[1,329.4]} = 184.4, p < 0.001$), and a weaker negative pattern was
364 evident among individuals that lost on average 0.32 grams of initial gram of mass for every
365 additional gram of initial capital ($F_{[1,140.7]} = 33.2, p < 0.001$). In this case, the slopes of the
366 within-individual and among-individual declines in mass gain during breeding with increases in
367 maternal body mass at the beginning of the breeding season were significantly different, with
368 individuals showing a significantly stronger pattern (Table 1c; $F_{1,326.6} = 33.7, p < 0.001$). We
369 included random slopes in our comparison of litter mass at weaning to initial spring maternal
370 mass, and allowing slopes to vary did not significantly improve the model (Figure 1d; analysis of
371 the 125 mother dataset was singular, likely due to similarity of slopes; statistical comparison of
372 models with the reduced dataset of 85 mothers with ≥ 2 litters, AIC without random slopes =
373 3828, with random slopes = 3830, $\chi^2_2 = 2.3, df = 2, P = 0.33$). Somatic effort was phenotypically
374 plastic with respect to spring maternal mass (initial capital), such that females with greater initial
375 body mass put on much less personal body mass during breeding. The within-individual
376 plasticity was much stronger than the among-individual population wide effect, and slopes of
377 individual mothers did not greatly differ.

378

379

DISCUSSION

380 Phenotypic plasticity is commonly examined over variable environmental conditions
381 (e.g., review by Forsman 2015). We examined how allocations of energy (as expressed by
382 accumulated mass) to concurrent reproductive and somatic efforts were influenced by two
383 important initial traits of the mothers themselves. One was the timing of breeding with respect to
384 other females, a trait with a strong genetic association with the timing of emergence from
385 hibernation (Lane et al. 2011), itself under significant selection for earlier activity and thus
386 perhaps earlier breeding (Viblanco et al. 2022). The other initial trait was female body mass at
387 emergence from hibernation, closely associated with body condition and with strong influences
388 on subsequent reproductive and somatic allocations (Dobson et al. 1999; Broussard et al. 2003,
389 2005; Skibieli et al. 2009; Rubach et al. 2016). Body mass may be considered “capital” that
390 mothers can later use to augment their reproductive and active season somatic efforts (Jönsson
391 1997; Broussard et al. 2005). These two traits not only influence subsequent reproductive and
392 somatic allocations, but likely reflect to at least some degree the environmental conditions that
393 influenced past energy acquisition and expenditure by individual mothers (Neuhaus et al. 1999;
394 Lane et al. 2012; Dobson et al. 2016).

395 We examined the allocation of mass by mother Columbian ground squirrels to their
396 offspring while breeding, an estimate of reproductive effort (after Hirshfield and Tinkle 1975).
397 At the same time, most mothers also allocated resources to themselves by putting on body mass,
398 an aspect of somatic effort. We specifically wanted to know if and to what extent reproductive
399 and somatic efforts during breeding were phenotypically plastic traits, given that ground
400 squirrels are highly iteroparous, maturing at 1-3 years of age (Rubach et al. 2020) and some
401 living to ages of 8-10 years (rarely to 14 years of age, Viblanco et al. 2016b; Sosa et al. 2020).
402 Thus, mothers allocate resources to both their current reproduction and to their own maintenance

403 and survival, and the latter involves gaining personal mass. Because they have a long
404 hibernation season of about 70% of their year (Young 1990; Dobson et al. 1992; Lane et al.
405 2019), mothers must accumulate sufficient energy reserves in the form of body mass (primarily
406 fats, Buck and Barnes 1999; Humphries et al. 2003) to survive winter conditions and reproduce
407 again. This is likely an issue for many hibernating mammals that are also annual breeders
408 (Constant et al. 2020).

409 An initial problem was the possible influences of age and year on reproductive and
410 somatic efforts. For Columbian ground squirrels, a few one-year-old mothers were not fully
411 grown in body size (though only 12 of 183 mothers first bred as yearlings), as reflected by
412 structural skeletal measures (Dobson 1992) and by body mass (Dobson and Murie 1987; Dobson
413 et al 1999; Broussard et al. 2003). Furthermore, considerable among-year variation has been
414 found in several life-history variables, including maternal body mass (Dobson 1988; Neuhaus et
415 al. 1999; Dobson et al. 2016). Maternal age and year of breeding accounted for between about
416 7% and 22% of the variation in relative mating date and initial maternal mass. Thus, we
417 accounted for the influences of age and year statistically.

418 Our best index of reproductive and somatic allocations was the mass of the litters that
419 mothers were producing and the concurrent personal changes in body mass that females
420 exhibited. For the latter variable, it was noteworthy that in 98% of cases (496 of 508 breeding
421 events), mothers increased in body mass while breeding, augmenting their body mass by an
422 average of about a quarter of their initial spring body mass (Broussard et al. 2005). Examination
423 of individual females showed that these allocations of energy to mass were highly variable, even
424 when known variation associated with age and year-to-year variations were accounted for
425 statistically. Reproductive and somatic efforts of mothers, however, were not closely linked with

426 respect to their magnitudes; despite our large samples, they exhibited an insignificant and trivial
427 correlation. As pointed out by van Noordwijk and de Jong (1986), variation among mothers in
428 resource availability or acquisition can cause reproductive and somatic efforts to exhibit a variety
429 of associations, even positive. Thus, we conservatively conducted separate analyses of plastic
430 responses of reproductive and somatic efforts to initial conditions of the timing of breeding
431 (relative mating date) and personal resources (initial maternal body mass after emergence from
432 hibernation).

433 Previous evidence suggested that many life-history traits of these ground squirrels are
434 plastic and highly variable under geographic and temporal variations, as well as with both natural
435 and experimental changes in food resources (e.g., Dobson and Murie 1987; Dobson 1988, 1995;
436 Neuhaus et al. 1999; Risch et al. 1995; Dobson et al. 1999; Dobson and Oli 2001). Reproductive
437 and somatic efforts, however, were not previously tested for phenotypic plasticity. A few
438 species have been examined for plasticity in reproductive traits, and these traits were associated
439 with changes in body mass (e.g., lava lizards (*Microlophus delanonis* Baur, 1890), Jordan and
440 Snell 2002; house sparrows (*Passer domesticus* Linnaeus, 1758), Westneat et al. 2014;
441 rockhopper penguins (*Eudyptes chrysocome* J.R. Forster, 1781), Dehnhard et al. 2015).
442 Plasticity has also been found in reproductive traits (number or size of offspring) with respect to
443 differences in breeding date (e.g., common tern (*Sterna hurundo* Linnaeus, 1758), Dobson et al.
444 2017; red deer (*Cervus elaphus* Linnaeus, 1758), Froy et al. 2017; Canada geese (*Branta*
445 *canadensis* (Linnaeus, 1858)), Clermont et al. 2018; red squirrels (*Tamiasciurus hudsonicus*
446 (Erxleben, 1777)), Lane et al. 2018; blue tit (*Parus caeruleus* Linnaeus, 1758), Chik et al. 2022).
447 Such studies suggest that life histories are highly phenotypically plastic in response to changes in
448 environmental conditions. Among mammalian species, plasticity of allocations of resources to

449 both reproduction and soma have been little studied. In Columbian ground squirrels, we found
450 an ideal situation for testing plasticity in energy allocations. In this species, at least some sources
451 of environmental variation, specifically age and year, could be included in the analyses to
452 statistically control their significant influences.

453 Repeatability of reproductive and somatic efforts provided an initial test of phenotypic
454 plasticity. When repeatability is high, mothers are similar among years in their allocations of
455 mass to their litters and themselves. If reproductive and somatic allocations were highly
456 phenotypically plastic and changeable from year-to-year, however, we would expect their
457 repeatability to be low. We found that repeatability of reproductive effort was about 22%, and
458 somatic effort was about 14% for individual mothers that successfully bred more than once.
459 While these values were highly significant, statistical tests are for deviations from 0%, given the
460 expected variation due to sampling. However, our interest was in “scope” for plasticity; that is,
461 variation that was not explained by age of the mother or year of sampling. For both reproductive
462 and somatic efforts, there was substantive unexplained variation, 78% and 86% respectively.
463 This indicates the presence of variation that may have been due to plastic responses.

464 We began a more direct analysis of plasticity with a comparative examination of the
465 influences of relative timing of breeding and initial personal resources on subsequent
466 reproductive and somatic efforts (Table 1a). A mother’s initial personal body mass appeared to
467 be at least twice as important as the timing of breeding to reproductive effort, though both had
468 significant influences. Despite these variables accounting for only about 7% of the variation in
469 reproductive effort, allocations to reproduction were greater for later breeding females and those
470 that were heavier when emerging from hibernation and mating. This was surprising, since
471 annual fitness is greatest for early emerging females (Viblanco et al. 2022). Perhaps mothers

472 compensated for later emergence with greater allocations of energy to reproduction, perhaps
473 facilitated by the ongoing “green-up” of the growing season. During the breeding season (from
474 conception through weaning), mothers that emerged later compared to their peers put on a bit
475 more personal body mass (viz., had greater concurrent somatic effort). However, much more
476 evident and significant was a pattern of females emerging from hibernation at low body mass
477 putting on more personal mass (Rubach et al. 2016). Together, timing of breeding and initial
478 maternal mass accounted for a substantial ~30% of the variation in somatic effort during
479 breeding.

480 One caveat with this first analysis (i.e., Table 1a) was that it did not examine the
481 plasticity of individual mothers (van de Pol and Wright 2009). Within-subject effects of timing
482 of breeding and initial maternal capital on reproductive and somatic efforts were significant and
483 fairly substantial, indicating plastic responses of individual mothers (Table 1b). In addition,
484 slopes that likely reflected the strength of the plastic responses were not significantly different
485 among mothers. Thus, mothers were not only plastic in their allocations to reproduction and
486 themselves, but their plasticity exhibited similar characteristic changes. Some mothers
487 undoubtedly had higher quality home ranges to extract resources from, and this is consistent with
488 differences in intercepts of females in their plastic responses (Figure 1). Similar plastic
489 responses of reproductive effort (number or mass of offspring) but lack of significant differences
490 in the degree of plasticity among mothers have been found in other species (e.g., red deer, Froy
491 et al. 2017; blue tits, Chik et al. 2022; review by Arnold et al. 2019).

492 Population responses mainly mirrored these patterns, but for two cases: the influence of
493 relative timing of the breeding season on reproductive effort and the influence of initial maternal
494 capital on somatic effort (Table 1c). In the first case, the population pattern was much weaker

495 than the within-mother pattern (Table 1b); mean responses of individuals (reflected by the dots in
496 Figure 1a) were scattered widely among the relative mating dates and showed little pattern.
497 Thus, mothers were plastic in reproductive effort with respect to mating date, but widely variable
498 in their mean responses, perhaps reflecting variation in resource availability on their foraging
499 ranges (a mismatch between processes that produce individual and population levels; Westneat et
500 al. 2020). In the latter case, mothers were highly plastic in somatic effort with respect to their
501 initial body mass, but again the population pattern was more mild than the plastic response of
502 individual mothers (Figure 1d), perhaps reflecting differences in the quality or quantity of
503 resources on different foraging ranges. It appeared that in both cases, the population patterns
504 were diluted, and further examination of this phenomenon seems warranted, since one might
505 conclude a lack of plasticity (or less so) from population-level analyses, where stronger
506 individual-based plasticity actually exists.

507 The plasticity of reproductive and somatic efforts to the initial spring maternal body mass
508 indicated a partial tradeoff. Mothers that began breeding with greater mass-capital allocated
509 more energy to reproductive effort and less to somatic effort. For example, compared to a
510 mother that mated weighing 380g, a mother weighing 480 grams allocated, on average, about 36
511 grams more to reproductive effort and 76 grams less to herself over the course of the breeding
512 season. On average, the heavier female at the start of breeding would also allocate 40 grams less
513 overall. Again, our evidence on plasticity suggests that these differences could be present in an
514 individual mother in different years. Clearly, energy dynamics are complicated in Columbian
515 ground squirrels, and the low marginal coefficients of determination in our analyses suggest that
516 other influences on reproductive and somatic efforts are likely. These might include such things

517 as the number of offspring produced (Dobson et al. 1999), and the resource quality and quantity
518 of the territories that females maintain during breeding (e.g., Murie and Harris 1988).

519 Female Columbian ground squirrels live in mountain environments at a variety of
520 elevations (Murie and Harris 1982; Dobson and Kjelgaard 1985a; Zammuto and Millar 1985a,
521 1985b; Dobson and Murie 1987; Dobson 1995; Dobson and Oli 2001; Oli and Dobson 2003).
522 Likely due to these environments, individuals exhibit high degrees of phenotypic plasticity in
523 many life-history traits, including date of emergence from hibernation, age at maturity, body
524 mass, litter size, and both juvenile and adult differences in rates of survival (Dobson and
525 Kjelgaard 1985b; Dobson and Murie 1987; Murie and Dobson 1987; Dobson 1988). In this
526 study, we showed that reproductive and somatic efforts were also phenotypically plastic. Given
527 the fairly high rates of gene flow among Columbian ground squirrel populations at different
528 elevations and habitats (Dobson 1994), the hypothesis that mothers in different populations have
529 similar genetic propensities for phenotypic plasticity of life-history traits seems to be supported.
530 The long lives of the ground squirrels and year-to-year variations in ecological conditions might
531 also favor plastic responses (e.g., Lane et al. 2012). Here we tested and found support for similar
532 phenotypic plasticity among mothers in their concurrent reproductive and somatic efforts,
533 providing preliminary support for the hypothesis of similar genotypes underlying the plasticity in
534 these traits. However, phenotypic variation in individual plasticity was always present (Figure
535 1), and thus underlying genetic variation may have been present, though perhaps unlikely
536 (Nussey et al. 2007).

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538

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566 COMPETING INTERESTS

567 The authors declare no competing interests.

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570 DATA ACCESSABILITY STATEMENT

571 Data available upon request.

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782 Figure 1. Changes in traits of reproductive female Columbian ground squirrels (*Urocitellus*
783 *columbianus* (Ord, 1815)) with relative mating date and initial body mass at the beginning of
784 breeding, both latter variables standardized. Dependent variables are reproductive effort (total
785 weaning mass of offspring) and somatic effort (mass gained by females during the breeding
786 season). Dashed lines are the mean within-individual slopes and solid lines are the mean among
787 individual slopes. Solid colored lines show the slopes of the individual females, with dots
788 showing their mean responses during their reproductive life-times. Sample sizes are 125 mothers
789 and 450 litters.
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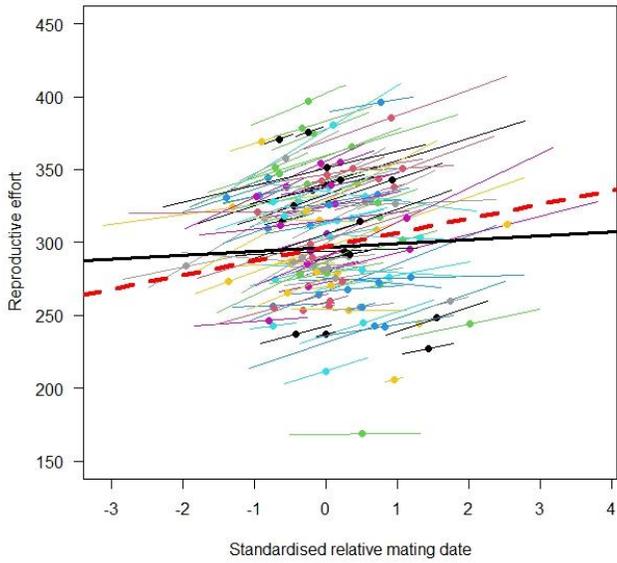
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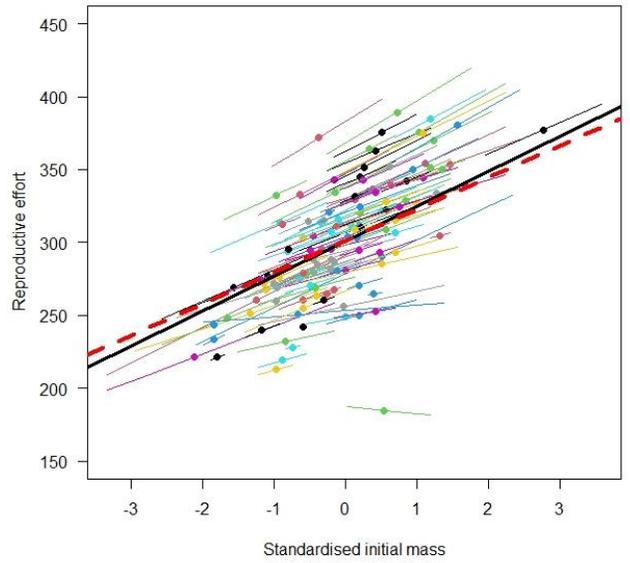
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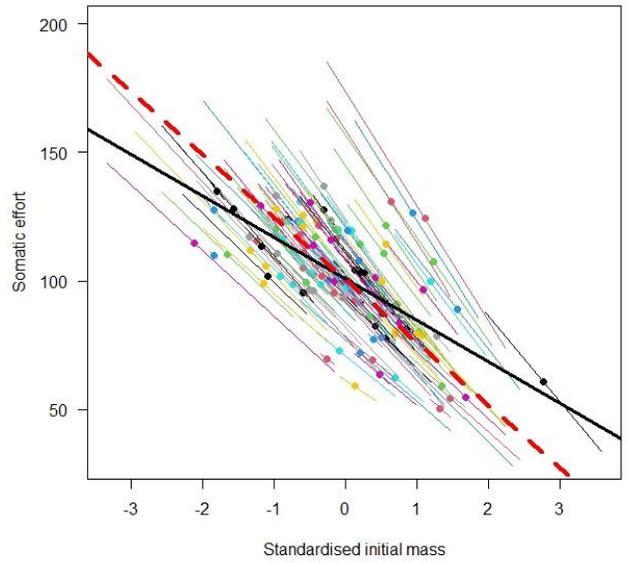
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811 Table 1. Mixed regression models that test variation in reproductive (RE) and somatic efforts (SE) with relative to within-year
812 reproductive timing (relative mating date, RMD) and spring capital (initial body mass near the time of mating, IM). *a*) regressions
813 that test for variation of RE and SE separately on both RMD and IM. *b*) regressions that test for variation of, separately, RE and SE
814 within individual mothers and among those mothers, evaluated for RMD and IM separately (4 tests). *c*) tests for significant
815 differences in the slopes of the regressions of, separately, RE on RMD and on IM, and then the same comparisons for SE. In all
816 models, age, year, and maternal identity are included as random effects. Both marginal and conditional R^2 values are given for models
817 *a*) and *b*). Sample sizes are 125 mothers and 450 litters.

	RE ~ RMD	RE ~ IM	SE ~ RMD	SE ~ IM
Model parameters	Estimate \pm SE (SD for variances)	Estimate \pm SE (SD for variances)	Estimate \pm SE (SD for variances)	Estimate \pm SE (SD for variances)
<i>a</i>) $y_{ij} = \beta_0 + \beta_1(\text{mating date}) + \beta_2(\text{initial mass}) + u_{0j} + v_{0j} + w_{0j} + e_{0ij}$				
β_0 (intercept)		301.1 \pm 9.6**		103.3 \pm 8.1**
β_1 (relative mating date)		11.1 \pm 4.1*		9.1 \pm 1.6**
β_2 (initial mass)		22.9 \pm 4.9**		-27.3 \pm 2.2**
σ_{age}^2		399.3 \pm 20.0		360.4 \pm 19.0

σ_{year}^2	292.7 ± 17.1		495.8 ± 22.3	
σ_{ID}^2	1662.5 ± 40.8		373.2 ± 19.3	
σ_e^2	5480.2 ± 74.0		792.3 ± 28.2	
$R_{marginal}^2$	0.0686		0.3081	
$R_{conditional}^2$	0.3485		0.7289	
b) $y_{ij} = \beta_0 + \beta_w(x_{ij} - \bar{x}_j) + \beta_A \bar{x}_j + u_{0j} + v_{0j} + w_{0j} + e_{0ij}$				
β_0 (intercept)	297.2 ± 13.6 **	105.3 ± 53.7 **	105.5 ± 6.8 **	239.0 ± 24.9 **
β_w (within-subject effect)	2.990 ± 1.148 *	0.365 ± 0.129 *	2.667 ± 0.539 **	-0.757 ± 0.055 **
β_A (among-subject effect)	0.523 ± 1.897	0.462 ± 0.125 **	2.663 ± 0.743 **	-0.324 ± 0.056 **
σ_{age}^2	1143.2 ± 33.8	349.7 ± 18.7	83.3 ± 9.1	338.6 ± 18.4
σ_{year}^2	397.5 ± 19.9	261.3 ± 16.2	812 ± 28.5	539.9 ± 23.2
σ_{ID}^2	1860.9 ± 43.1	1603.1 ± 40.0	198.3 ± 14.1	356.2 ± 18.9
σ_e^2	5494.5 ± 74.1	5642.5 ± 75.1	1212.9 ± 34.8	792.5 ± 28.2

R^2_{marginal}	0.0100	0.0604	0.0520	0.2650
$R^2_{\text{conditional}}$	0.3886	0.3252	0.5016	0.7127
c) $y_{ij} = \beta_0 + \beta_W x_{ij} + (\beta_A - \beta_W) \bar{x}_j +$ $u_{0j} + v_{0j} + w_{0j} + e_{0ij}$				
β_w (within-subject effect)	$2.990 \pm 1.148 *$	$0.365 \pm 0.129 *$	$2.667 \pm 0.539 **$	$-0.757 \pm 0.055 **$
$\beta_A - \beta_W$ (difference)	-2.467 ± 2.161	0.097 ± 0.174	-0.004 ± 0.921	$0.432 \pm 0.074 **$

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$*p \leq 0.01, **p < 0.001$

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