



**HAL**  
open science

# PHENOTYPIC PLASTICITY IN REPRODUCTIVE AND SOMATIC EFFORTS OF FEMALE COLUMBIAN GROUND SQUIRRELS

F. Stephen Dobson, Claire Saraux, Vincent A Viblanc

► **To cite this version:**

F. Stephen Dobson, Claire Saraux, Vincent A Viblanc. PHENOTYPIC PLASTICITY IN REPRODUCTIVE AND SOMATIC EFFORTS OF FEMALE COLUMBIAN GROUND SQUIRRELS. Canadian Journal of Zoology, 2023, 102 (3), pp.228-238. 10.1139/cjz-2023-0108 . hal-04266890

**HAL Id: hal-04266890**

**<https://hal.science/hal-04266890>**

Submitted on 31 Oct 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

4  
5  
6  
7  
8                           F. Stephen Dobson<sup>1,2</sup>, Claire Saraux<sup>1</sup>, and Vincent A. Viblanc<sup>1</sup>

9  
10  
11  
12  
13           <sup>1</sup>University of Strasbourg, CNRS, Institut Pluridisciplinaire Hubert Curien, UMR 7178, 67000

14                           Strasbourg, France

15  
16           <sup>2</sup>Department of Biological Sciences, Auburn University, Auburn, AL 36830, USA

17

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.

35

36

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

39

40

## INTRODUCTION

41

42

43

44

45

46

47

48

49

50

51

52

53

54

55

56

57

58

59

60

61

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 ( $\pm 6.3$  days standard deviation) at an initial spring mass of 421.2 grams ( $\pm 53.3$ 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 =  $0.0 \pm 4.3$  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 ( $\pm 90.1$ g). Over the same period these mothers gained  
212 (concurrent somatic effort) an average of 101.8g ( $\pm 48.5$ 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 1<sup>st</sup> 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% ( $\pm 0.8$  standard deviations) of the variation in IM, year  
235 explained 6.2% ( $\pm 0.4$ ), and age explained 51.3% ( $\pm 1.1$ ) (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% ( $\pm 10.6$ ) of the variance in RMD, and age explained 8.1% ( $\pm 6.5$ ) (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  $\geq 2$  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).

537

538

#### ACKNOWLEDGMENTS

539 Our greatest thanks are to J.O. Murie, who initiated the long-term study (in 1992) and  
540 recorded many years of data (through 2000). Any long-term study has many assistants, students,  
541 and volunteer helpers, and ours is no exception. Literally scores of field workers contributed to  
542 our dataset and we offer the warmest thanks to them all. Alberta Parks, and Alberta  
543 Environment, Fish & Wildlife, granted access to the study sites and assigned our permits for the  
544 research. Field methods were approved by Auburn University Institutional Animal Care and Use  
545 Committee (IACUC), by the University of Calgary, and by Alberta Fish & Wildlife.  
546 Authorization for conducting research and collecting samples in the Sheep River Provincial  
547 Park was obtained from Alberta Environment and Parks and Alberta Fish & Wildlife. Housing  
548 was provided by the Biogeoscience Institute, University of Calgary, at the R.B. Miller Field  
549 Station in Alberta's Sheep River Provincial Park, under the auspices of E.A. Johnson and S.  
550 Vamosi (Directors), J. Mappan-Buchanan and A. Cunnings (Station Managers), and K.  
551 Ruckstuhl (Faculty Responsible). P. Neuhaus and K. Ruckstuhl have shared their home and  
552 conducted their research alongside us, consistently giving the best help and advice. For this and  
553 their warm camaraderie, we are very grateful. We are also grateful for the continuing support  
554 and encouragement of our long-term research provided by E.A. Johnson, over the course of  
555 many years. We thank J.F. Hare, J.O. Murie, and an anonymous reviewer substantive  
556 constructive comments on versions of the manuscript.

557 Funding came from Natural Sciences and Engineering Research Council of Canada grant  
558 to J.O. Murie, a USA National Science Foundation grant (DEB-0089473) to F.S. Dobson, funds  
559 associated with a Gutenberg Excellence Chair (region Grand Est and the Eurometropole de  
560 Strasbourg) for F.S. Dobson, a CNRS Projet International de Cooperation Scientifique grant  
561 (PICS-07143) and a research grant from the Fondation Fyssen to V.A. Viblanc, and a grant from

562 the Institute of Advanced Studies of the University of Strasbourg to F.S. Dobson and V.A.  
563 Viblanc.

564

565

#### 566 COMPETING INTERESTS

567 The authors declare no competing interests.

568

569

#### 570 DATA ACCESSABILITY STATEMENT

571 Data available upon request.

572

573

#### 574 REFERENCES

575 Arnold, P.A., Nicotra, A.B., and Kruuk, L.E.B. 2019. Sparse evidence for selection on  
576 phenotypic plasticity in response to temperature. *Philosophical Transactions of the Royal*  
577 *Society B* **374**: 20180185.

578 Broussard, D. R., Risch, T.S., Dobson, F.S., and Murie, J.O. 2003. Senescence and age-related  
579 reproduction of female Columbian ground squirrels. *Journal of Animal Ecology* **72**:  
580 212–219.

581 Broussard, D.R., Dobson, F.S., and Murie, J.O. 2005. The effects of capital on an income  
582 breeder: evidence from female Columbian ground squirrels. *Canadian Journal of*  
583 *Zoology* **83**: 546–552.

584 Broussard, D.R., Michener, G.R., and Dobson, F.S. 2006. Age-specific resource investment  
585 strategies: evidence from female Richardson's ground squirrels. *Journal of Zoology* **268**:  
586 389-294.

587 Broussard, D.R., Dobson, F.S., and Murie, J.O. 2008. Previous experience and reproductive  
588 investment of female Columbian ground squirrels. *Journal of Mammalogy* **89**: 145–152.

589 Buck, C.L., and Barnes, B.M. 1999. Annual cycle of body composition and hibernation in free-  
590 living arctic ground squirrels. *Journal of Mammalogy* **80**: 430–442.

591 Chik, H.Y.J., Estrada, C., Wang, Y., Tank, P., Lord, A., and Schroeder, J. 2022. Individual  
592 variation in reaction norms but no directional selection in reproductive plasticity of a wild  
593 passerine population. *Ecology and Evolution* **12**: e8582.

594 Clermont, J., Réale, D., and Giroux, J.-F. 2018. Plasticity in laying dates of Canada geese in  
595 response to spring phenology. *Ibis* **160**: 597-607.

596 Constant, T., Giroud, S., Viblanc, V.A., Tissier, M.L., Bergeron, P., Dobson, F.S., and Habold,  
597 C. 2020. Integrating mortality risks and the adaptiveness of hibernation. *Frontiers in*  
598 *Physiology* **11**: 706.

599 Dehnhard, N., Eens, M., Demongin, L., Quillfeldt, P., and Poisbleau, M. 2015. Individual  
600 consistency and phenotypic plasticity in rockhopper penguins: female but not male body  
601 mass links environmental conditions to reproductive investment. *PLoS ONE* **10**:  
602 e0128776.

603 de Villemereuil, P., Charmantier, A., Arlt, D., Bize, P., Brekke, P., Brouwer, L., Cockburn, A.,  
604 Côté, S.D., Dobson, F. S., Evans, S.R., Festa-Bianchet, M., Gamelon, M., Hamel, S.,  
605 Hegelbach, J., Jerstad, K., Kempnaers, B., Kruuk, L.E.B., Kumpula, J., Kvalnes, T.,  
606 McAdam, A.G., McFarlane, S.E., Morrissey, M.B., Pärt, T., Pemberton, J.M.,

607 Qvarnström, A., Røstad, O.-W., Schroeder, J., Senar, J.C., Sheldon, B.C., van de Pol, M.,  
608 Visser, M.E., Wheelwright, N.T., Tufto, J., and Chevin, L.-M. 2020. Fluctuating  
609 optimum and temporally variable selection on breeding date in birds and mammals.  
610 Proceedings of the National Academy of Sciences USA **117**: 31969-31978.

611 Dobson, F.S. 1988. The limits of phenotypic plasticity in life histories of Columbian ground  
612 squirrels. Pages 193–210 in: Evolution of life histories of mammals (M. S. Boyce,  
613 editor). Yale University Press, New Haven, Connecticut.

614 Dobson, F.S. 1992. Body mass, structural size, and life history patterns of the Columbian  
615 ground squirrel. American Naturalist **140**: 109–125.

616 Dobson, F.S. 1994. Measures of gene flow in the Columbian ground squirrel. Oecologia **100**:  
617 190-195.

618 Dobson, F.S. 1995. Regulation of population size: evidence from Columbian ground squirrels.  
619 Oecologia **102**: 44–51.

620 Dobson, F.S., and Kjelgaard, J.D. 1985a. The influence of food resources on population  
621 dynamics in Columbian ground squirrels. Canadian Journal of Zoology **63**: 2095-2104.

622 Dobson, F.S., and Kjelgaard, J.D. 1985b. The influence of food resources on life history in  
623 Columbian ground squirrels. Canadian Journal of Zoology **63**: 2105–2109.

624 Dobson, F.S., and Murie, J.O. 1987. Interpretation of intraspecific life history patterns:  
625 evidence from Columbian ground squirrels. American Naturalist **129**: 382-397.

626 Dobson, F.S., Zammuto, R.M., and Murie, J.O. 1986. A comparison of methods for studying  
627 life history in Columbian ground squirrels. Journal of Mammalogy **67**: 154-158.

628 Dobson, F.S., Badry, M.J., and Geddes, C. 1992. Seasonal activity and body mass of  
629 Columbian ground squirrels. Canadian Journal of Zoology **70**: 1364–1368.

630 Dobson, F.S., Risch, T.S., and Murie, J.O. 1999. Increasing returns in the life history of  
631 Columbian ground squirrels. *Journal of Animal Ecology* 68: 73-86.

632 Dobson, F.S., and M.K. Oli. 2001. The demographic basis of population regulation in  
633 Columbian ground squirrels. *American Naturalist* 158:236-247.

634 Dobson, F.S., Lane, J.E., Low, M., and Murie, J.O. 2016. Fitness implications of seasonal  
635 climate variation in Columbian ground squirrels. *Ecology and Evolution* 6: 5614–5622.

636 Dobson, F.S., Becker, P.H., Arnaud, C., Bouwhuis, S., and Charmantier, A. 2017. Plasticity  
637 results in delayed breeding in a long-distant migrant seabird. *Ecology and Evolution* 7:  
638 3100-3109.

639 Festa-Bianchet, M., and Boag, D.A. 1982. Territoriality in adult female Columbian ground  
640 squirrels. *Canadian Journal of Zoology* 60: 1060–1066.

641 Fisher, R.A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford.

642 Forsman, A. 2015. Rethinking phenotypic plasticity and its consequences for individuals,  
643 populations and species. *Heredity* 115: 276-284.

644 Froy, H., Martin, J., Stopher, K.V., Morris, A., Morris, S., Clutton-Brock, T.H., Pemberton, J.M.,  
645 and Kruuk, L.E.B. 2019. Consistent within-individual plasticity is sufficient to explain  
646 temperature responses in red deer reproductive traits. *Evolutionary Biology* 32: 1194-  
647 1206.

648 Hirshfield, M.F., and Tinkle, D.W. 1975. Natural selection and the evolution of reproductive  
649 effort. *Proceedings of the National Academy of Sciences USA* 72: 2227–2231.

650 Houle, D. 1991. Genetic covariance of fitness correlates: what genetic correlations are made of  
651 and why it matters. *Evolution* 45: 630–645.

652 Humphries, M.M., Thomas, D.W., and Kramer, D.L. 2003. The role of energy availability in  
653 mammalian hibernation: a cost-benefit approach. *Physiological and Biochemical*  
654 *Zoology* **76**: 165–179.

655 Jönsson, K.I. 1997. Capital and income breeding as alternative tactics of resource use in  
656 reproduction. *Oikos* **78**: 57–66.

657 Jordan, M.A., and Snell, H.L. 2002. Life history trade-offs and phenotypic plasticity in the  
658 reproduction of Galápagos lava lizards (*Microlophus delanonis*). *Oecologia* **130**: 44-52.

659 Lane, J.E., Kruuk, L.E.B., Charmantier, A., Murie, J.O., Coltman, D.W., Buoro, M., Raven, S.,  
660 and Dobson, F.S. 2011. A quantitative genetic analysis of hibernation emergence date in  
661 a wild population of Columbian ground squirrels. *Journal of Evolutionary Biology* **24**:  
662 1949-1959.

663 Lane, J.E., Kruuk, L.E.B., Charmantier, A., Murie, J.O., and Dobson, F.S. 2012. Delayed  
664 phenology and reduced fitness associated with climate change in a wild hibernator.  
665 *Nature* **489**: 554–557.

666 Lane, J.E., McAdam, A.G., McFarlane, S.E., Williams, C.T., Humphries, M.M., Coltman, D.W.,  
667 Gorrell, J.C., and Boutin, S. 2018. Phenological shifts in North American red squirrels:  
668 disentangling the roles of phenotypic plasticity and microevolution. *Journal of*  
669 *Evolutionary Biology* **31**: 810-821.

670 Lane, J.E., Czenze, Z.J., Findlay-Robinson, R., and Bayne, E. 2019. Phenotypic plasticity and  
671 local adaptation in a wild hibernator evaluated through reciprocal translocation.  
672 *American Naturalist* **194**: 516–528.

673 Lessells, C.M., and Boag, P.T. 1987. Unrepeatable repeatabilities: a common mistake. *The Auk*  
674 **104**: 116–121.

675 Manno, T.G., DeBarbieri, L.M., and Davidson, J. 2008. Why do Columbian ground squirrels  
676 copulate underground? *Journal of Mammalogy* **89**: 882–888.

677 Manno, T.G., and Dobson, F.S. 2008. Why are male Columbian ground squirrels territorial?  
678 *Ethology* **114**: 1049–1060.

679 Martin, G.G.A., Nussey, D.H., Wilson, A.J., and Réale, D. 2011. Measuring individual  
680 differences in reaction norms in field and experimental studies: a power analysis of  
681 random regression models. *Methods in Ecology and Evolution* **2**: 362-374.

682 Michener, G.R. 1989. Reproductive effort during gestation and lactation by Richardson's  
683 ground squirrels. *Oecologia* **78**: 77-86.

684 Murie, J.O. 1995. Mating behavior of Columbian ground squirrels. I. Multiple mating by  
685 females and multiple paternity. *Canadian Journal of Zoology* **73**: 1819–1826.

686 Murie, J.O., and Dobson, F.S. 1987. The costs of reproduction in columbian ground squirrels.  
687 *Oecologia* **73**: 1-6.

688 Murie, J.O., and Harris, M.A. 1982. Annual variation of spring emergence and breeding in  
689 Columbian ground squirrels (*Spermophilus columbianus*). *Journal of Mammalogy* **63**:  
690 431–439.

691 Murie, J.O., and Harris, M.A. 1988. Social interactions and dominance relationships between  
692 female and male Columbian ground squirrels. *Canadian Journal of Zoology* **66**:  
693 1414-1420.

694 Nakagawa, S., and Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a  
695 practical guide for biologists. *Biological Reviews of the Cambridge Philosophical*  
696 *Society* **85**: 935–956.



697 Nakagawa, S., and Schielzeth, H. 2013. A general and simple method for obtaining  $R^2$  from  
698 generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4**: 133-142.

699 Nakagawa, S., Johnson, P.C.D., and Schielzeth, H. 2017. The coefficient of determination  $R^2$   
700 and intra-class correlation coefficient from generalized linear mixed-effects models  
701 revisited and expanded. *Journal of the Royal Society Interface* **4**: 20170213.

702 Nesterova, A.P., Raveh, S., Manno, T.G., Coltman, D.W., and Dobson, F.S. 2011. Premating  
703 behavioral tactics of Columbian ground squirrels. *Journal of Mammalogy* **92**: 861-870.

704 Neuhaus, P., Bennett, R., and Hubbs, A. 1999. Effects of a late snowstorm and rain on survival  
705 and reproductive success in Columbian ground squirrels (*Spermophilus columbianus*).  
706 *Canadian Journal of Zoology* **77**: 879-884.

707 Nussey, D.H., Wilson, A.J., and Brommer, J.E. 2007. The evolutionary ecology of individual  
708 phenotypic plasticity in wild populations. *Journal of Evolutionary Biology* **20**: 831-844.

709 Oli, M.K., and Dobson, F.S. 2003. The relative importance of life-history variables to  
710 population growth rate in mammals: Cole's prediction revisited. *American Naturalist*  
711 **161**: 422-440.

712 Raveh, S., Heg, D., Dobson, F.S., Coltman, D.W., Gorrell, J.C., Balmer, A., and Neuhaus, P.  
713 2010. Mating order and reproductive success in male Columbian ground squirrels  
714 (*Urocitellus columbianus*). *Behavioral Ecology* **21**: 537-547.

715 Raveh, S., Heg, D., Viblanc, V.A., Coltman, D.W., Gorell, J.C., Dobson, F.S., Balmer, A., and  
716 Neuhaus, P. 2011. Male reproductive tactics to increase paternity in the polygynandrous  
717 Columbian ground squirrel (*Urocitellus columbianus*). *Behavioral Ecology and*  
718 *Sociobiology* **65**: 695-706.

719 Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos* **44**:

720 257-267.

721 Reznick, D., Nunnev, L., and Tessier, A. 2000. Big houses, big cars, superfleas, and the costs of  
722 reproduction. *Trends in Ecology and Evolution* **15**: 421–425.

723 Risch, T.S., Dobson, F.S., and Murie, J.O. 1995. Is mean litter size the most productive? A test  
724 in Columbian ground squirrels. *Ecology* **76**: 1643–1654.

725 Rubach, K.K., Wu, M., Abebe, A., Dobson, F.S., Murie, J.O., and Viblanc, V.A. 2016. Testing  
726 the reproductive and somatic trade-off in female Columbian ground squirrels. *Ecology*  
727 *and Evolution* **6**: 7586–7595.

728 Rubach, K.K., Dobson, F.S., Zinner, B., Murie, J.O., and Viblanc, V.A. 2020. Comparing  
729 fitness measures and the influence of age of first reproduction in Columbian ground  
730 squirrels. *Journal of Mammalogy* **101**: 1302–1312.

731 Scheiner, S. 1993. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology*  
732 *and Systematics* **24**:35-68.

733 Skibiell, A., Dobson, F.S., and Murie, J.O. 2009. Maternal influences on reproduction in two  
734 populations of Columbian ground squirrels. *Ecological Monographs* **79**: 325-341.

735 Sosa, S., Dobson, F.S., Bordier, C., Neuhaus, P., Saraux, C., Bosson, C., Palme, R., Boonstra, R.,  
736 and Viblanc, V.A. 2020. Social stress in female Columbian ground squirrels: density-  
737 independent effects of kin contribute to variation in fecal glucocorticoid metabolites.  
738 *Behavioral Ecology and Sociobiology* **74**: 50.

739 Stearns, S.C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* **51**:  
740 3–34.

741 Stearns, S.C. 1989. The evolutionary significance of phenotypic plasticity. *Bioscience* **39**: 436-  
742 445.

743 van Noordwijk, A.J., and de Jong, G. 1986. Acquisition and allocation of resources: their  
744 influence on variation in life history tactics. *American Naturalist* **128**: 137–142.

745 van de Pol, M. 2012. Quantifying individual variation in reaction norms: how study design  
746 affects the accuracy, precision and power of random regression models. *Methods in*  
747 *Ecology and Evolution* **3**: 268-280.

748 van de Pol, M., and Wright, J. 2009. A simple method for distinguishing within- versus  
749 between-subject effects using mixed models. *Animal Behaviour* **77**: 753-758.

750 Via, S., and Lande, R. 1985. Genotype-environment interaction and the evolution of phenotypic  
751 plasticity. *Evolution* **39**: 505-522.

752 Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S.M., Van Schlichting, C.D., and Tienderen,  
753 P.H. 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends in*  
754 *Ecology and Evolution* **10**: 212-217.

755 Viblanc, V.A., Saraux, C., Murie, J.O., and Dobson, F.S. 2016a. Kin effects on energy allocation  
756 in group-living ground squirrels. *Journal of Animal Ecology* **85**: 1361-1369.

757 Viblanc, V.A., Pasquaretta, C., Sueur, C., Boonstra, R., and Dobson, F.S. 2016b. Aggression in  
758 Columbian ground squirrels: relationships with age, kinship, energy allocation, and  
759 fitness. *Behavioral Ecology* **27**: 1716-1725.

760 Viblanc, V.A., Saraux, C., Tamian, A., Criscuolo, F., Coltman, D.W., Raveh, S., Murie, J.O., and  
761 Dobson, F.S. 2022. Measuring fitness and inferring natural selection from long-term  
762 field studies: different measures lead to nuanced conclusions. *Behavioral Ecology and*  
763 *Sociobiology* **76**: 79.

764 Westneat, D.F., Araya-Ajoy, Y.G., Allegue, H., Cass, B., Dingemanse, N., Dochtermann, N.A.,  
765 Garamszegi, L.Z., Martin, J.G.A. Nakagawa, S., Réale, D., and Schielzeth, H. 2020.

766 Collision between biological process and statistical analysis revealed by mean centring.  
767 Journal of Animal Ecology **89**: 2813-2824.

768 Westneat, F.D., Bókonyi, V., Burke, T., Chastel, O., Jensen, H., Kvalnes, T., Lendvai, A.Z.,  
769 Liker, A., Mock, D., Schroeder, J., Schwagmeyer, P.L., Sorci, G., and Stewart, I.K.R.  
770 2014. Multiple aspects of plasticity in clutch size vary among populations of a globally  
771 distributed songbird. Journal of Animal Ecology **83**: 876-887.

772 Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's  
773 principle. American Naturalist **100**: 687-690.

774 Young, P. 1990. Hibernating patterns of free-ranging Columbian ground squirrels. Oecologia  
775 **83**: 504-511.

776 Zammuto, R.M., and Millar, J.S. 1985a. A consideration of bet-hedging in *Spermophilus*  
777 *columbianus*. Journal of Mammalogy **66**: 652-660.

778 Zammuto, R.M., and Millar, J.S. 1985b. Environmental predictability, variability, and  
779 *Spermophilus columbianus* life history over an elevational gradient. Ecology **66**: 1784-  
780 1794.

781

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.  
790

791

a

792

793

794

795

796

797

798

799

800

801 c

802

803

804

805

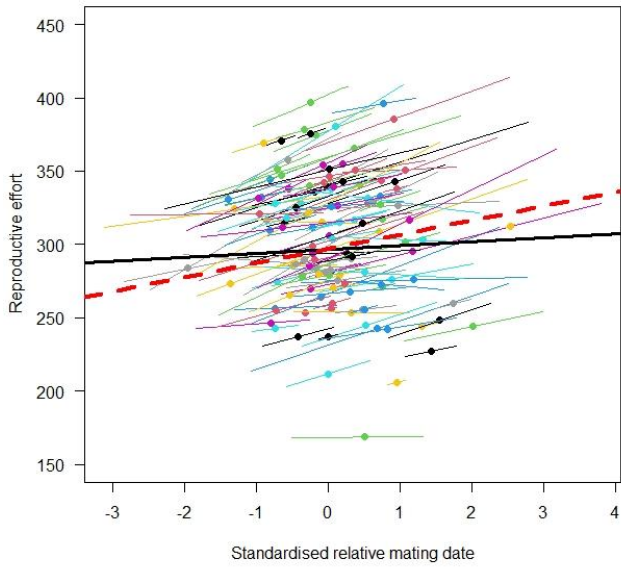
806

807

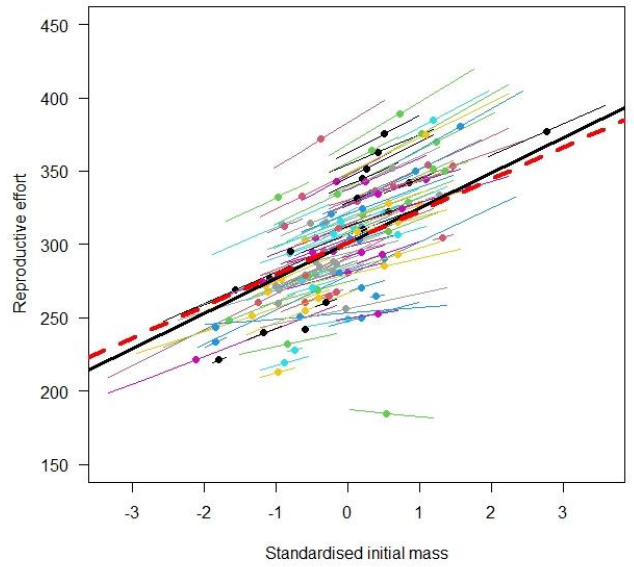
808

809

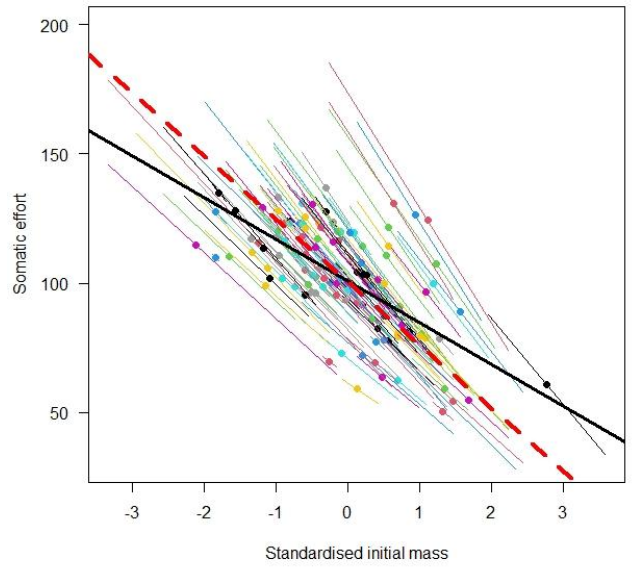
810



b



d



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

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



|  |                     |                     |                      |                       |
|--|---------------------|---------------------|----------------------|-----------------------|
| $R^2_{\text{marginal}}$  | 0.0100              | 0.0604              | 0.0520               | 0.2650                |
| $R^2_{\text{conditional}}$   | 0.3886              | 0.3252              | 0.5016               | 0.7127                |
|  |                     |                     |                      |                       |
| c) $y_{ij} = \beta_0 + \beta_W x_{ij} + (\beta_A - \beta_W) \bar{x}_j +$<br>$u_{0j} + v_{0j} + w_{0j} + e_{0ij}$ |                     |                     |                      |                       |
| $\beta_w$ (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)   | $-2.467 \pm 2.161$  | $0.097 \pm 0.174$   | $-0.004 \pm 0.921$   | $0.432 \pm 0.074 **$  |

818

819

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

820

821