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Kristin Rubach, F Stephen Dobson, Bertram Zinner, Jan Murie, Vincent Viblanc

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1 **Comparing fitness measures and the influence of age of first**
2 **reproduction in Columbian ground squirrels**

3

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5 KRISTIN K. RUBACH, F. STEPHEN DOBSON*, BERTRAM ZINNER, JAN O. MURIE, AND

6 VINCENT A. VIBLANC

7

8

9 *Department of Biological Sciences, Auburn University, Auburn, AL 36849, USA (KKR,*
10 *FSD)*

11 *Université de Strasbourg, Centre National de la Recherche Scientifique, Institut*

12 *Pluridisciplinaire Hubert Curien, Unité Mixte de Recherche 7178, 67087 Strasbourg,*

13 *France (FSD, VAV)*

14 *University of Strasbourg Institute of Advanced Sciences (USIAS), 67083 Strasbourg,*

15 *France (FSD)*

16 *Department of Mathematics and Statistics, Auburn University, Auburn, AL 36849, USA*

17 *(BZ)*

18 *Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9,*

19 *Canada (JOM)*

20

21

22

23 **Correspondant: fsdobson@msn.com*

24 The timing of life-history traits may have strong influences on the evolution of
25 lifecycles and on population demography. This is especially true of the age at
26 which females first reproduce (Cole's principle). We examined whether the age
27 at which females first reproduce influences fitness in Columbian ground squirrels,
28 for which females varied in the age at which they initially produce weaned
29 offspring, from ages 1 through 5 years. With 148 females with complete known
30 lifespans in a 28-year data set, we examined four fitness measures: individual
31 fitness (λ_{ind}), individual fitness relative to the pattern of growth of the population
32 (λ_{rel}), lifetime reproductive success (LRS), and LRS relative to the total LRS for
33 each female's cohort (LRS_{rel}). These metrics were calculated for offspring
34 produced at the time of weaning and offspring that survived to emerge after their
35 first hibernation period. Individual fitness (λ_{ind}) was significantly associated
36 with population growth during a female's lifetime (λ_{Leslie}) ($R^2 = 0.523$, $P <$
37 0.0001); indicating the need to adjust individual fitness for demonstrated changes
38 in population growth and thus producing a relative individual fitness index (λ_{rel}).
39 We regressed λ_{rel} on age at first reproduction, and found significant selection
40 favoring earlier reproductive success ($\beta \pm SE = -0.20 \pm 0.06$; $R^2 = 0.306$, $P <$
41 0.0001). When using an earlier (offspring at weaning) versus later (those that
42 survived their first hibernation) measure of fecundity, we found that the latter
43 introduced considerable variation, likely environmental, into the estimate of
44 selection. This greatly weakened the regression of relative fitness on the age at
45 first successful reproduction. LRS and LRS_{rel} exhibited non-significant changes
46 with age at first reproduction. Finally, those females that reproduced successfully

47 at younger ages had similar litter sizes but significantly shorter lifespans than
48 females that matured when older, perhaps reflecting costs to early reproduction.

49

50 Key Words: age at first reproduction, Columbian ground squirrels, individual fitness,
51 Leslie matrix, lifetime reproductive success

52

53

54 As the size of populations change, demography must change as well (Caswell 1989,
55 2001; Oli, Slade, & Dobson 2001; Dobson and Oli 2001, 2008). Demography is
56 composed of life-history traits, including age at first reproduction, survival, and the
57 magnitude of reproduction at different ages. Life-history traits may evolve, and they can
58 have a strong impact on fitness. Thus, life-history traits are often termed “fitness traits”
59 (e.g., Roff 1996; Merila and Sheldon 2000; Kosova et al. 2010). One life-history trait in
60 particular, the age at which reproduction begins, should be under strong selection to be as
61 early as possible (Cole 1954; Lewontin 1965; Meats 1971; Charnov and Schaffer 1973;
62 Bell 1976, 1980; Sibly and Calow 1986). In iteroparous mammals, however, numerous
63 factors (e.g., the quality or quantity of resources) might cause a delay in reproduction,
64 potentially resulting in fitness declines. In growing populations, individuals are thought
65 to have abundant resources and thus females may begin to reproduce earlier in their
66 lifetimes (Stearns 1992). On the contrary, in declining populations individuals are
67 assumed to have fewer resources, resulting in their devoting more energy to survival and
68 perhaps delaying their first reproduction to a later age. In either case, these expectations
69 might depend on the study species and the choice of fitness measure.

70 In selecting a fitness measure, it is important to remember that what is being
71 estimated is the fitness of traits, in our case a female's age at first reproduction. The
72 relevant comparison is then among females that display alternative forms of the trait, as
73 estimates of the fitness of the trait forms. Lifetime reproductive success (LRS) is a
74 widely used fitness measure, defined as the number of offspring produced over a lifetime
75 (after Grafen 1988; examples in Clutton-Brock 1988; Merilä and Sheldon 2000; Jensen et
76 al. 2004; Descamps et al. 2006; McLoughlin et al. 2007). LRS, however, does not
77 account for the timing of reproduction during the lifecycle, which can have a significant
78 influence on the estimation of fitness (Cole 1954; Lewontin 1965; Roff 1992; Stearns
79 1992; Brommer et al. 2002).

80 Another suggested measure of trait fitness, developed by McGraw and Caswell
81 (1996) and termed "individual fitness", was patterned on the Leslie (1945) projection
82 matrix that describes population growth. Individual fitness encompasses an individual's
83 life history parameters over its lifetime, to produce a growth rate similar to that for
84 populations (termed lambda, λ). Use of this method to estimate fitness assumes that a
85 population of individuals similar in genotype would produce the same lambda value as
86 the individual under study. For example, individual fitness can be estimated for
87 individuals that carry a specific life history trait (i.e., age at first successful reproduction).
88 A lambda value is estimated for each individual that expresses an alternative form of the
89 life history trait, and a mean and variance are calculated for individual fitness of the
90 different trait forms. Previous studies have used LRS and individual fitness to estimate
91 selection on age at maturity, and these two methods often produced very different results
92 (e.g., McGraw and Caswell 1996; Brommer et al. 2002; Oli et al. 2002). Thus, the

93 efficacy of either method has been questioned (e.g., Brommer et al. 2004; Reid et al.
94 2019), and a unified definition of fitness is lacking (Sæther and Engen 2015).

95 The individual fitness measure of McGraw and Caswell (1996), however, does
96 not give the context of the fitness values of other females in the population, and it is
97 against this larger group of females that an individual female's fitness should be
98 compared. In an increasing population, average fitness is greater than 1.0, and in a
99 decreasing population, less than 1.0. So, a female with individual fitness equal to 1.0
100 could be below or above average, respectively, depending on the mean fitness in the
101 population. During the lifespan of a particular female, mean fitness in the population can
102 be estimated from the growth rate of all co-occurring females, during the years of that
103 female's reproductive life, since the estimate is the result of reproduction and survival of
104 all of the females. By comparing individual fitness to population growth rate during a
105 female's lifetime, a relative measure of how the individual compares to the contemporary
106 population can be obtained. Such an adjusted individual fitness value (i.e., relative
107 individual fitness) can be compared among individuals that express alternative trait forms,
108 and used in a comparative evaluation of the selective advantage of age at first
109 reproduction.

110 Alternative methods of estimating fitness have been used to examine reproduction
111 in long-term studies of marmotine rodents. For instance, Neuhaus et al. (2004) concluded
112 that female Columbian ground squirrels (*Urocitellus columbianus*) match their
113 reproductive output with environmental circumstances. With fewer individuals,
114 resources were less limiting, leading to better body condition, greater survival and earlier
115 reproduction. Even so, reproductive success of females that first reproduced at ages 2

116 and 3 were not significantly different. However, this study was based on a relatively
117 small sample size and used the LRS approach that does not adjust for population changes
118 or the timing of reproduction during the life cycle when estimating fitness. Using a
119 matrix estimate of individual fitness, Oli and Armitage (2003, 2008) found that selection
120 favored early maturity in Yellow-bellied marmots (*Marmota flaviventris*). However, they
121 did not adjust their fitness estimates for fluctuations in population size. It would thus be
122 interesting to compare such results to those obtained using alternative fitness evaluation
123 methods that account for the timing of breeding schedules and changes in population size.

124 Here, we used 28 years of longitudinal monitoring of a Columbian ground
125 squirrel population to establish the entire life cycles (from birth to death) of 148 females.
126 Our purpose was four-fold. First, we examined whether earlier age at first successful
127 reproduction led to increased fitness (“Cole’s prediction”, see Oli and Dobson 2003) for
128 female Columbian ground squirrels. We investigated whether the influence of age at first
129 reproduction on individual fitness changed with population growth. We predicted that
130 individual fitness would be greater for those females that began reproducing earlier,
131 particularly in years of increasing population growth rate, when resources should have
132 been most abundant (Dobson and Kjelgaard 1985a, 1985b). Alternatively, under limited
133 resources most likely associated with years of declining population growth, mean
134 individual fitness for females should be lower, but should remain relatively high for those
135 that reproduce earlier (i.e., above average compared to females reproducing later under
136 similar conditions of population growth).

137 Second, we compared LRS and relative fitness, that is individual fitness adjusted
138 for population growth, in order to evaluate similarities and differences between them.

139 Third, we regressed relative fitness on the trait (viz., age at first reproduction) to test for
140 the presence of a selection differential (Lande and Arnold 1983; Arnold and Wade
141 1984b). We focused our analyses on two periods at which reproductive success could be
142 measured, near the time of weaning and when young survived to emerge from their first
143 hibernation season. We also conducted these analyses for relative individual fitness and
144 an index of relative LRS (LRS_{rel}) that was based on the lifetime success of the cohort into
145 which a female was born. In our fourth and final set of analyses, we compared litter size
146 and longevity for females that first reproduced at different ages, to test for possible
147 tradeoffs between reproduction and survival for females that began investing in
148 reproduction at different points in their lifecycle.

149

150

MATERIALS AND METHODS

151 *Study species.* - We studied a colony of Columbian ground squirrels in a montane
152 meadow at the Sheep River Provincial Park, Alberta, Canada (50°38'N, 114°39'W,
153 elevation 1,550 m). This population was monitored from 1992 to 2019. Population size
154 for females ≥ 1 year old fluctuated between 14 and 77, with a mean of 38 (Fig. 1).
155 Squirrels were caught with live traps (Tomahawk Live Trap Co., Tomahawk, WI, USA,
156 15x15x48 cm³ and 13x13x40 cm³) baited with a small amount of peanut butter. All
157 squirrels were trapped in the spring, within about three days of emergence from
158 hibernation, and weighed to the nearest 5 g with a Pesola spring scale (Pesola Ag, Baar,
159 Switzerland). Each ground squirrel was given a pair of uniquely numbered ear tags
160 (National Band and Tag Company, Newport, KY, US; Monel metal tag # 1) and an
161 individually distinctive black mark on their back using black hair dye (Clairol

162 Corporation, Stamford, CT, USA). Above ground activity of squirrels was easily
163 observed using binoculars from 3m tall wooden observation benches that were dispersed
164 throughout the study site.

165 Columbian ground squirrels are medium sized (adults were typically 300-600 g at
166 emergence from hibernation) diurnal rodents that hibernate for approximately eight to
167 nine months of the year (Dobson and Murie 1987; Dobson et al. 1992). At our study site,
168 squirrels became active above ground in mid- to late April and remained active until late
169 July to mid-August. Within a week of emergence from hibernation, female ground
170 squirrels copulated with males on a single day, usually in underground consortships
171 (Murie 1995; Raveh et al. 2010, 2011). After about 24 days of gestation and 27 days of
172 lactation, pups emerged above ground for the first time from the single-entrance nest
173 burrow that was maintained by the mother (Murie and Harris 1982). Newly emerged
174 pups were caught, weighed to the nearest gram, and uniquely marked. Subsequent
175 observations of the complete litter ensured that we captured all young at the time of
176 emergence, which coincided with the process of weaning. Mothers were trapped and
177 examined at the same time that weaned young were caught, to ensure that they had
178 lactated. Thus, both maternal association and weaned litter size were accurately
179 measured.

180

181 *Population census.* - We conducted a modified post-breeding census using the
182 long-term data set on female Columbian ground squirrels (after Dobson and Oli 2001).
183 In a post-breeding census, each individual is counted just after annual reproduction. We
184 estimated survival from emergence in one spring to the next, since residents from the

185 previous year remain in the spring populations. Further, the dispersal period, usually of
186 younger males, occurs later in the active season at about the time of weaning (Wiggett
187 and Boag 1989). Spring populations best reflected the individuals that were residents in
188 the population, as indicated by having hibernated in the study colony. The number of
189 weaned young that emerged from nest burrows at the end of the lactation period or that
190 survived to emerge from hibernation in the next spring were used to measure
191 reproduction.

192 For 148 females, we constructed individual age-specific matrices that varied in
193 size (1-14 years; average 4.70 years). For each matrix, we estimated individual fitness
194 (see below), using the individual fitness approach (after McGraw and Caswell 1996; Oli
195 and Armitage 2003, 2008; Viblanc et al. 2010; Dobson et al. 2012). Age at first
196 reproduction was defined as the first time a female successfully weaned a litter. Some
197 females produced weaned litters for the first time when they were yearlings (1-year-old,
198 N = 13). Most females weaned their first litter at age 2 (N = 96), and occasionally a
199 female's initial weaning success was prolonged to 3-years-old (N = 30), 4-years-old (N =
200 8), and 5-years-old (N = 1). For some analyses we combined the last three groups of
201 mothers into a category of 3 years of and older.

202

203 *Fitness analyses.* - The fitness of females that first bred at different ages was
204 estimated using four fitness measures: LRS, LRS relative to the total LRS of the
205 female's cohort, individual fitness (λ_{ind}), and relative individual fitness (adjusted for
206 population growth, λ_{rel}).

207 *Lifetime reproductive success (LRS) and relative lifetime success (LRS_{rel}):* We
 208 calculated LRS by simply adding up the number of offspring that were weaned over a
 209 female's lifetime. To estimate LRS of individual females relative to their peers, we
 210 regressed LRS on the total LRS of the cohort of females into which each individual
 211 female was born, and used the residual as the estimate of her relative lifetime success
 212 (LRS_{rel}). This method avoided the use of ratios, which have statistical shortcomings
 213 (Hinkley 1969). For this analysis, only 132 females were included, because only
 214 complete cohorts were used (number of years = 20, females born in 1991-2010).

215 *Individual fitness (λ_{ind}) and cohort fitness (λ_{Leslie}):* To obtain λ_{rel} , we estimated
 216 both individual fitness (McGraw and Caswell 1996) and population growth rate for each
 217 female's cohort during her lifetime. Both of these were modifications of the population
 218 growth projection matrix developed by Leslie (1945). Briefly, an example of the Leslie
 219 matrix approach for a post-breeding population census is:

220

$$\begin{bmatrix} F_0 & F_1 & F_2 & 0 \\ S_0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 \\ 0 & 0 & S_2 & 0 \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \\ N_{2,t} \\ N_{3,t} \end{bmatrix} = \begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \end{bmatrix}$$

221

222 Subset 0, 1, 2, and 3 are age groups, and t and t+1 are time periods. Average fertility is
 223 across the top row of the matrix, and is defined as:

224

$$F_x = S_x * m_{x+1} * 0.5$$

225 S_x is the survival rate, calculated as the proportion of females that survive from year x to
 226 year x+1. Fecundity, m_{x+1} , is defined the mean number of offspring at age x+1. Since
 227 the analysis is only for the female part of the population, m_{x+1} is multiplied by a half

228 (Dobson and Oli 2001). In the case of Columbian ground squirrels, we estimated
229 fecundity in two ways; either using half the size of litters at weaning, or using half the
230 young that survived to be 1 year old in the subsequent year (viz., half the number of
231 surviving yearlings). We used both reproductive output measures to test for similarity in
232 fitness patterns, and expected that the latter measure would reflect more closely those
233 surviving to reproductive age, perhaps a better fitness measure (Brommer et al. 2002).
234 The last column represents the year that the female died; hence it is comprised of zeros.
235 The Leslie projection matrix represents age structured information about reproduction
236 and survival for a population. The dominant right eigenvector of this matrix is the finite
237 growth rate of the population, usually called lambda ($\bar{\lambda}$).

238 Based on McGraw and Caswell (1996), we modified the above population growth
239 matrix to calculate the growth of a specific genotype based on the reproduction and
240 survival of an individual female. In this case, the formulation of the matrix becomes:

$$\begin{bmatrix} F_0 & F_1 & F_2 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{bmatrix}$$

241
242 The top row of the individual matrix is calculated as above by multiplying survival by
243 fecundity, m_{x+1} , and by one half for an individual female. Survival is binary, however, 1
244 in the years in which the female lived, zero otherwise. Litter size at each age is used for
245 fecundity, or as above the number of offspring that survive to become yearlings. In this
246 case, the dominant right eigenvalue is the population growth rate for a given genotype, as
247 estimated for a single female, and individual females are then averaged to yield the mean

248 estimate of fitness of the trait form. The dominant right eigenvalue is the individual
249 fitness measure, λ_{ind} . These matrices have different dimension (are of different size) for
250 different females, because individual lifespans vary.

251 We adjusted individual fitness (λ_{ind}) for changes in population size (i.e., periods
252 of increases and decreases in size as estimated by population “growth”) by constructing a
253 Leslie (1945) projection matrix for the specific years of each individual female’s lifetime
254 (λ_{Leslie}). These estimates were then used to typify mean fitness during the female’s
255 lifetime. Using the notation for the modified Leslie matrix above, S_x was thus the
256 survival from year x to year $x+1$ for all females in the female’s cohort, as in the typical
257 Leslie matrix, and m_x was the mean litter size for all of the adult females of age x . For
258 example, S_1 , was the mean survival of all females between the ages of 1 and 2, when the
259 individual female under examination was age 1 and then 2. Another example, m_2 was the
260 mean litter size of all females that were age 2 in the year that the individual female was
261 age 2. Individual fitness values (λ_{ind}) were regressed on the resulting modified Leslie
262 matrix estimate of lambda (λ_{Leslie}), to produce residuals that represented individual
263 fitness adjusted for population growth during her lifetime. These residuals were added to
264 one to yield adjusted lambda for the Leslie matrix (λ_{rel}), since lambda of 1.0 represents
265 non-growing populations in population ecology (e.g., Stearns 1992). This method is
266 similar to that used by Viblanc et al. (2010) and Dobson et al. (2012), but those studies
267 used changes in population size and the individual fitness matrix in place of our use of
268 the modified Leslie matrix to estimate population growth. In comparison to changes in
269 population size, the modified Leslie matrix is based on a female’s cohort and takes actual
270 survival patterns into account.

271 Population growth might influence individual fitness differently for different ages
272 at first reproduction, if the population were increasing or decreasing. To test this
273 possibility, we regressed individual lambda (λ_{ind} , the dependent variable) on our
274 modified Leslie matrix (viz., population growth during the lifetime of the reproductive
275 adult females, λ_{Leslie} , the independent variable), made age at first reproduction a
276 covariate, and included the interaction between λ_{Leslie} and age at first reproduction. For
277 this analysis, we pooled females that first reproduced at age three and above, because the
278 oldest females were limited in sample size.

279

280 *Selection analyses.* - To determine if there was directional selection for age at first
281 reproduction, we regressed relative fitness (λ_{rel}) and separately LRS_{rel} on age at first
282 successful reproduction (Lande and Arnold 1983; Arnold and Wade 1984a, 1984b). The
283 sign of the coefficient (β) indicates the direction of selection. We also used a quadratic
284 regression to estimate stabilizing selection (γ) as evidenced by significant regression
285 coefficients. Significant directional or stabilizing selection on age at first reproduction
286 occurs when β and γ are significantly different from 0 (Lande and Arnold 1983; McGraw
287 and Caswell 1996).

288

289 *Statistics.* - We used the statistical program R (version 3.5.2, 2018) to analyze
290 matrices and calculate lambda (scripts available on request). Differences among age at
291 first reproduction, lambda, population growth, and LRS were tested using linear models.
292 For significant differences among ages at first reproduction, Tukey's honest significant
293 differences (HSD) tests for multiple comparisons were used. Means were given with

294 standard errors, and Hedges g was used to estimate effect sizes.

295

296

RESULTS

297 *Relationship between individual fitness (λ_{ind}) and population growth (λ_{Leslie}). -*

298 We regressed individual fitness (λ_{ind}) on the rate of population growth (λ_{Leslie}), both
299 calculated over the lives of individual mothers. We included age at first reproduction as a
300 covariate (ages 1, 2, and 3 and above;), and found no significant interaction between age
301 at first reproduction and population growth (Fig. 2a, overall model $R^2 = 0.523$, $F = 52.6$,
302 $df = 3, 144$, $P < 0.0001$; interaction $\beta = -0.063 \pm 0.087$, $df = 1,144$, $t = -0.72$, $P = 0.47$).

303 For females that first reproduced as yearlings, 2-year olds, and 3+ year olds, the estimate
304 of individual fitness changed in a similar rate as population growth rate increased (Table
305 1).

306 We then used the number of yearlings that survived to emerge from hibernation in
307 the following spring to estimate offspring production by individual mothers and again
308 regressed individual fitness (λ_{indY}) on the rate of population growth (λ_{Leslie}), accounting
309 for age at first reproduction as a covariate (ages 1, 2, and 3 and above), and found no
310 significant interaction between age at first reproduction and population growth (Fig. 2b,
311 overall model $R^2 = 0.419$, $F = 34.6$, $df = 3,144$, $P < 0.0001$; interaction $\beta = -0.005 \pm$
312 0.185 , $df = 1,144$, $t = -0.03$, $P = 0.98$). For females that first reproduced as yearlings, 2-
313 year olds, and 3+ year olds, this estimate of individual fitness changed in a similar rate as
314 population growth rate increased (Table 1).

315

316 *Age at first reproduction and relative individual fitness (λ_{rel}).* - When using the
317 numbers of weaned offspring to measure fecundity, relative individual fitness was
318 significantly different among females that first reproduced at different ages (Fig. 3a, $R^2 =$
319 0.309, $F = 65.3$, $df = 1,146$, $P < 0.0001$). Post-hoc Tukey tests revealed that each age
320 group (for ages 1, 2, and 3 and above) were significantly different from the others (all $P <$
321 0.0001). Effect sizes of the comparisons were all large and highly significant (Hedges g
322 and 95% CI: ages 1 vs. 2 = $1.63_{[1.01 - 2.25]}$; 1 vs. 3+ = $2.34_{[1.56 - 3.11]}$; 2 vs. 3+ = $1.01_{[0.61 -$
323 $1.40]}$).

324 Using the numbers of surviving yearling offspring to measure fecundity, relative
325 individual fitness (λ_{relY}) was not quite significantly different among females that first
326 reproduced at different ages (Fig. 3b, $R^2 = 0.022$, $F = 3.27$, $df = 1,146$, $P = 0.07$). Post-
327 hoc Tukey tests revealed that each age group (ages 1, 2, and 3 and above) was not
328 significantly different from the others ($0.18 < P < 0.48$). Effect sizes of the comparisons
329 were small to medium (Hedges g and 95% CI: α at 1 vs. 2 = $0.34_{[-0.24 - 0.92]}$; 1 vs. = $0.61_{[-$
330 $0.04 - 1.25]}$; 2 vs. 3+ = $0.22_{[-0.16 - 0.59]}$).

331

332 *Age at first reproduction in relation to LRS and LRS_{rel} .* - Similar analysis of LRS
333 among mothers that first reproduced at different ages were not significant (Fig. 3c; $R^2 =$
334 0.001, $F = 0.20$, $df = 1,146$, $P = 0.65$). Post-hoc Tukey tests revealed that each age group
335 ($\alpha = 1, 2$, and 3 and above) was not significantly different from the others ($0.77 < P <$
336 0.98). Effect sizes of the comparisons were small or negligible (Hedges g and 95% CI;
337 ages 1 vs. 2 = $-0.07_{[-0.65 - 0.51]}$, 1 vs. 3+ = $0.06_{[-0.57 - 0.70]}$, 2 vs. 3+ = $0.13_{[-0.25 - 0.50]}$). LRSY
338 (lifetime reproductive success measured by surviving yearling offspring) among mothers

339 that first reproduced at different ages was not significant (Fig. 3d; $R^2 = 0.005$, $F = 0.67$,
340 $df = 1, 146$, $P = 0.41$). Post-hoc Tukey tests revealed that each age group (ages 1, 2, and 3
341 and above) was not significantly different from the others ($0.72 < P < 0.98$). Estimates of
342 the effect sizes of the comparisons were small to negligible (Hedges g and 95% CI: ages
343 1 vs. 2 = $0.05_{[-0.53 - 0.64]}$; 1 vs. 3+ = $0.24_{[-0.40 - 0.87]}$; 2 vs. 3+ = $0.15_{[-0.23 - 0.52]}$).

344 Analyses of LRS_{rel} among mothers that first reproduced at different ages were not
345 significant ($R^2 = 0.001$, $F = 0.19$, $df = 1, 130$, $P = 0.67$). Post-hoc Tukey tests revealed
346 that each age group (ages 1, 2, and 3 and above) was not significantly different from the
347 others ($0.74 < P < 1.00$). Effect sizes of the comparisons were all negligible (Hedges g
348 and 95% CI; ages 1 vs. 2 = $0.13_{[-0.51 - 0.76]}$, 1 vs. 3+ = $-0.03_{[-0.71 - 0.65]}$, 2 vs. 3+ = $0.14_{[-0.54 -$
349 $0.28]}$). Similar analyses using the number of surviving yearling offspring to calculate
350 relative LRS (LRS_{relY}) were also not significant ($R^2 = 0.000$, $F = 0.01$, $df = 1, 130$, $P =$
351 0.92). Post-hoc Tukey tests showed that the age groups (ages 1, 2, and 3 and above) were
352 not significantly different in LRS_{relY} ($0.99 < P < 1.00$). Finally, effect sizes of the
353 comparisons were all negligible (Hedges g and 95% CI; ages 1 vs. 2 = $0.03_{[-0.60 - 0.66]}$, 1
354 vs. 3+ = $0.04_{[-0.64 - 0.72]}$, 2 vs. 3+ = $0.01_{[-0.38 - 0.40]}$).

355

356 *Selection analyses on age at first reproduction.* - Linear regression of fitness
357 adjusted for population growth (λ_{rel} , based on numbers of weaned offspring) on age at
358 first reproduction (here varying between 1 and 5) suggested directional selection for early
359 age at first reproduction (Fig. 4a; $\beta \pm SE = -0.20 \pm 0.06$; $R^2 = 0.306$, $F = 64.2$, $df = 1, 146$,
360 $P < 0.0001$). Slight but significant disruptive selection was also evident by quadratic
361 regression ($\gamma \pm SE$, 0.05 ± 0.02 , $P = 0.01$; overall $R^2 = 0.335$, $F = 36.5$, $df = 2, 145$, $P <$

362 0.0001). A similar analysis using LRS_{rel} as a fitness measure regressed on age at first
363 reproduction was not significant ($\beta \pm SE = -0.59 \pm 0.75$; $R^2 = 0.005$, $F = 0.62$, $df = 1,130$,
364 $P = 0.43$), nor was evidence of stabilizing selection significant ($\gamma \pm SE, -0.29 \pm 0.65$, $P =$
365 0.66 ; overall $R^2 = 0.006$, $F = 0.40$, $df = 2,129$, $P = 0.67$). When fitness was based on
366 surviving yearling offspring (λ_{relY}), linear regression of relative fitness on age at first
367 reproduction only approached significance, but revealed a similar pattern to λ_{rel} (Fig. 4b;
368 $\beta \pm SE = -0.08 \pm 0.05$; $R^2 = 0.022$, $F = 3.25$, $df = 1,146$, $P = 0.07$), and evidence of
369 disruptive selection was trivial ($\gamma \pm SE, 0.02 \pm 0.04$, $P = 0.59$; overall $R^2 = 0.024$, $F =$
370 1.77 , $df = 2,145$, $P = 0.17$). A similar analysis using LRS_{relY} as a fitness measure was not
371 significant ($\beta \pm SE = -0.48 \pm 0.40$; $R^2 = 0.011$, $F = 1.44$, $df = 1,130$, $P = 0.23$), and
372 evidence of stabilizing selection was trivial ($\gamma \pm SE, -0.11 \pm 0.35$, $P = 0.74$; overall $R^2 =$
373 0.012 , $F = 0.77$, $df = 2,129$, $P = 0.47$).

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375 *Testing for a trade-off and the cost of reproduction.* - We examined litter sizes for
376 females that first reproduced at ages 1, 2, and 3 and above. There were no significant
377 differences in mean litter sizes among females in the year in which they first reproduced
378 (Table 2). There were also no significant differences in mean number of yearling
379 offspring produced from their first litter when females first reproduced at different ages
380 (Table 2). Finally, we examined the length of life for females that first reproduced at
381 ages 1, 2, and 3 and above. Length of life increased significantly for females that
382 matured later in life (Table 2). Post-hoc Tukey tests indicated that this was significant
383 only when comparing females that matured at 2, and 3 and above (1 vs. 2, $P = 0.86$; 1
384 vs. 3+, $P = 0.10$; 2 vs. 3+, $P = 0.02$), but the effect sizes of all comparisons were relatively

385 large (Hedges g and 95% CI: α at 1 vs.2 = 1.60_[1.32 – 1.89]; 1 vs.3+ = 1.48_[1.13 – 1.83]; 2 vs.3+
386 = 2.02_[1.73 – 2.30]).

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DISCUSSION

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Among life-history traits, reproduction and survival have received substantial research attention (e.g., Stearns 1992; Roff 1992). The timing of lifecycle events is also important in the evolution of life-history tactics (e.g., Oli and Dobson 2003). For long-lived species, events such as the age at which females begin to reproduce can have major evolutionary influences on life-history patterns. Not surprisingly, age at first reproduction can have a substantial influence on fitness, with fitness substantially diminished by a late start to breeding (Bell 1976, 1980; especially in avian studies, McGraw and Caswell 1996, Brommer et al. 2002, Oli et al. 2002). We asked whether age at first reproduction made a significant difference to the fitness of individual female Columbian ground squirrels.

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To examine the importance of first reproducing at different ages to fitness, we were faced with three problems; one was whether to adjust for population growth. It seemed plausible that fitness should be measured differently in increasing versus decreasing populations, considering that our population of Columbian ground squirrels fluctuated substantially from year to year. The second problem was to determine which of two possible techniques to apply to our question: the individual fitness approach of McGraw and Caswell (1996) or the widely used LRS. The third problem was when to measure offspring production. The end of intense period of maternal care (viz., gestation and lactation) that occurs when young are weaned seems reasonable, at least for an initial

408 examination. However, a better measure might be when those offspring become
409 surviving descendants that themselves reproduce (Boyce and Perrins 1987; Brommer et
410 al. 2004). Thus, we examined the production of yearlings, a subadult age class for most
411 individuals (but an age at which a few females successfully reproduce). We also made a
412 preliminary analysis of the strength of natural selection on the age of first reproduction
413 for a species in which it was variable. Finally, we examined litter size at first
414 reproduction and longevity for females that began reproduction at different ages, in a
415 preliminary test of the potential for tradeoffs of the age at which females began to
416 reproduce with initial reproduction or subsequent survival.

417 In years of population increase, mean fitness in a population will be relatively
418 higher, and conversely in years of population decline. Thus, it might be reasonable to
419 adjust fitness for changes in population size. We compared individual fitness (λ_{ind}) to the
420 change in population size over the lifetimes of females using a Leslie matrix (λ_{Leslie}).
421 This analysis tested whether individual fitness changes significantly with an estimate of
422 mean fitness (viz., population growth rate) during the lifetimes of individual females.
423 Both when using the number of weaned offspring and number of yearling offspring to
424 measure fecundity, we found significant differences in λ_{ind} (and λ_{indY}) that were
425 associated with changes in population growth. This was true for females that first
426 reproduced at different ages, and for those females combined, regardless of which
427 measure of fecundity was used. Therefore, we recommend adjustment for population
428 growth (λ_{rel} , see also Viblanc et al. 2010; Dobson et al. 2012).

429 Because LRS is rate insensitive (Brommer et al. 2002), there was no obvious way
430 to adjust LRS for population growth or decline. To compare reproductive success and

431 estimate fitness relative to each female's peers, we regressed LRS for each female on the
432 total reproductive success of the cohort into which she was born, and used the residuals
433 of this analyses as an estimate of relative LRS. This estimate was based on the cohort
434 into which females were born, similar to the estimate of relative individual fitness.
435 Relative LRS, however, did not appear to yield additional insight to simply using LRS as
436 an estimate of fitness. Estimates of fitness are problematical, as estimates from
437 individual fitness and LRS, and estimates from descendants over an extended pedigree
438 may not closely agree (Brommer et al. 2004; Reid et al. 2019). In addition, the most
439 appropriate measures may depend on both changes in population density and on
440 environmental fluctuations (Sæther and Engen 2015). We accounted for changes in
441 population density among years for individual females by statistically comparing their
442 individual fitness to changes in population growth rate for their cohort.

443 Next, we compared λ_{rel} and LRS for similarity of measures. Because λ_{rel} is rate-
444 sensitive (sensu Brommer et al. 2002), we expected it to show a pattern of decline with
445 age at first reproduction, as in earlier studies (McGraw and Caswell 1996). Similar to
446 those previous results, and when number of offspring at weaning was used to measure
447 fecundity, λ_{rel} declined significantly with age at first reproduction. A similar pattern was
448 found when yearling offspring were used to measure fecundity (λ_{relY}), though it only
449 approached significance. It is likely that variation in survival introduced by the vagaries
450 of living in a fluctuating environment (with both ecological and social changes) rendered
451 the association between age at first reproduction and fitness weaker. If we were able to
452 track a suitable number of female offspring through their age at first reproduction, we
453 would expect the association with fitness to be even weaker. This phenomenon is

454 particularly important because it is only offspring that survive to reproduce that can pass
455 on any genetic propensity for the trait form to future generations. Our conclusion is that
456 there is likely little or weak selective advantage to earlier onset of reproduction in
457 Columbian ground squirrels, if one measures fitness from those that are most likely to
458 contribute to future generations.

459 LRS (lifetime reproductive success) has been used as a measure of fitness in
460 many species (e.g., Clutton-Brock 1988; Newton 1989; Merilä and Sheldon 2000; Jensen
461 et al. 2004; Descamps et al. 2006; McLoughlin et al. 2007). LRS is limited by the fact
462 that it does not consider the timing of reproduction, which can have a significant
463 influence on the fitness of a trait group (Cole 1954; Lewontin 1965; Roff 1992; Stearns
464 1992). Females who mature later might have a similar LRS value to those maturing
465 earlier, if particular life-history traits exhibit tradeoffs (Brommer et al. 2002). LRS did
466 not show significant evidence of fitness advantage with respect to age at first
467 reproduction in our study, regardless of whether LRS was estimated from offspring near
468 the time of weaning or at their emergence from their first hibernation. These results
469 reflect similar findings in European sparrowhawks (*Accipiter nisus*; McGraw and
470 Caswell 1996), Ural owls (*Strix uralensis*; Brommer et al. 1998), and wood ducks (*Aix
471 sponsa*; Oli et al. 2002).

472 One might expect females that reproduce later in life to have lower LRS, because
473 each breeding season skipped is a missed chance to reproduce. However, if there were a
474 survival cost to reproduction at earlier ages (e.g., Williams 1966; Reznick 1985), that
475 pattern might be obscured in long-lived species. In any case, there were no significant
476 changes in LRS for female ground squirrels that matured at different ages, whether LRS

477 was measured as weaned offspring or the production of yearling offspring. A slight
478 decline in LRS occurred for females that successfully weaned offspring at ages 3, 4, and
479 5, but this pattern was not significant, regardless of whether LRS was measured at
480 weaning or using the number of yearling offspring. Studies of allelic contributions to
481 future generations suggest that LRS and λ_{ind} produce roughly comparable estimates of
482 long-term fitness measures, though such long-term allele measures require pedigrees that
483 include both males and females (Brommer et al. 2004; Reid et al. 2019). The apparent
484 paradox of differences in patterns of λ_{ind} and LRS with respect to life event timing may
485 be that the seeming advantage of early reproduction degrades somewhat over time, with
486 the two measures becoming more similar as offspring are counted closer to when the
487 offspring themselves become reproductive adults. The pattern of difference between
488 individual fitness and LRS seemed to show a decrease over time in our population of
489 Columbian ground squirrels.

490 Our next goal was to quantify selection on age at first reproduction, by regressing
491 λ_{rel} on age at first reproduction (the regression of relative fitness on the trait, after Lande
492 and Arnold 1983). When offspring were counted at weaning, there was significant
493 directional selection for reproducing earlier (see also McGraw and Caswell 1996).
494 Similar results were obtained for yellow-bellied marmots (Oli and Armitage 2003, 2008).
495 In our case, this was accompanied by significant, though very mild disruptive selection.
496 However, while disruptive selection favors extreme phenotypes, the main polynomial
497 influence on age at first reproduction was obtained from yearling females that had
498 somewhat greater success, on average, than expected from the linear model. A similar
499 pattern was evident when fecundity was measured from the number of surviving yearling

500 offspring (λ_{relY}), although it only approached significance and had a trivial effect size.
501 Measuring fecundity from yearling offspring caught at emergence from hibernation in the
502 next spring in the estimation of individual fitness likely introduced extrinsic variation in
503 our measure of selection. Such variation may be caused by differential offspring
504 mortality due to infanticide, predation, and overwinter mortality during hibernation (e.g.,
505 Murie and Boag 1984; Dobson 1990; Maron et al. 2010). Apparent fitness advantages
506 for trait forms that occur early in life, like age at first reproduction, may be diluted by the
507 time that the offspring themselves reproduce, and perhaps render natural selection on
508 such trait forms relatively trivial.

509 Brommer et al. (2002) suggested that individual fitness was only appropriate in
510 non-equilibrium populations, citing Stearn's (1992) book on life histories. The fitness of
511 alternative trait forms, however, is more at issue than the overall growth of the population.
512 Trait frequencies may change largely independently of changes in population growth,
513 despite the fact that both depend on reproduction, survival, and migration. Fitness
514 differences favor alternative trait forms, and the fitness of individuals is only a means of
515 estimating the fitness of trait forms. Thus, in an equilibrium population in terms of
516 population growth, a trait form may increase through a process akin to population growth
517 and eventually reach fixation. This is also true for changes in trait frequency in
518 populations, as most in nature, that exhibit nearly constant periods of increase (from
519 reproduction and immigration) and decrease (from mortality and emigration). This basic
520 concept has led to ideas about selection for traits associated with changes in the balance
521 of reproduction and survival in times of population change (Boyce and Perrins 1987).

522 Yearling females were still growing in structural size (reflected by skeletal
523 growth; after Dobson 1992), and those that were successful at reproducing had slightly
524 smaller litters than females that first produced offspring at older ages. This pattern was
525 not significant, nor were there any significant differences among these initial
526 reproductive efforts in yearling offspring production, though 1st-time breeders may have
527 slightly lower reproductive success than multiparous mothers (Neuhaus et al. 2004;
528 Broussard et al. 2008). Nonetheless, females that were reproducing for the first time had
529 comparable fecundity, on average, regardless of their age. There was a significant pattern
530 of greater length of life for females that began reproduction later in life; however, that
531 might reflect a cost of early commitment to reproductive adulthood. Trade-offs of
532 current reproduction and subsequent reproduction and survival have been termed the
533 “costs of reproduction” in life-history theory (e.g., Williams 1966; Reznick 1985).
534 Columbian ground squirrels appear to lack such a trade-off, at least phenotypically
535 (Murie and Dobson 1987; Hare and Murie 1992; Neuhaus 2000; Skibieli et al. 2013;
536 Rubach et al. 2016). Our results suggest that the age at which females first reproduce
537 might be a trait to consider when looking for potential life-history trade-offs.

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723

724 **Figures**

725 **Fig. 1.** - Spring population size of females in a colony of female Columbian ground
726 squirrels (≥ 1 year old) in Sheep River Provincial Park, Alberta Canada from 1992-2018.

727

728 **Fig. 2.** - Regression of individual lambda (λ_{ind}) on finite population growth (λ_{Leslie})
729 during the lifetimes of individual females, for three ages at which females first
730 reproduced (ages 1, 2, and 3 and above). a) Fecundity was based on the number of
731 offspring at weaning. b) Fecundity was based on the number of these offspring that
732 survived to emerge from hibernation as yearlings.

733

734 **Fig. 3.** - Fitness estimate for females that first reproduced at different ages, from mean
735 relative fitness with standard errors for: a) fecundity estimated from number of offspring
736 at weaning, and b) fecundity estimated from number of offspring that survive their first
737 hibernation to become yearlings. Fitness estimate for females that first reproduced at
738 different ages, from mean lifetime reproductive success with standard errors for: c)
739 lifetime reproductive success based on weaned offspring, and d) lifetime reproductive
740 success based on numbers of yearling offspring.

741

742 **Fig. 4.** - Selection on age at first reproduction from regression of fitness (estimated by
743 relative fitness) on age at which females first reproduced (ages 1 through 5), where
744 fecundity was estimated by either a) number of weaned offspring or b) number of
745 surviving yearling offspring. The black line shows the linear least-squares best fit, and
746 the gray line in a) shows the quadratic best fit.