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

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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.

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

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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 λ). Use of this method to estimate fitness assumes that a
85 population of individuals similar in genotype would produce the same λ 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 λ 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

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

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

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

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

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

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

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

MATERIALS AND METHODS

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

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

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

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

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

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

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

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

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:

$$224 \quad F_x = S_x * m_{x+1} * 0.5$$

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

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

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

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

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

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

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

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

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

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

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

RESULTS

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

We regressed individual fitness (λ_{ind}) on the rate of population growth (λ_{Leslie}), both calculated over the lives of individual mothers. We included age at first reproduction as a covariate (ages 1, 2, and 3 and above;), and found no significant interaction between age at first reproduction and population growth (Fig. 2a, overall model $R^2 = 0.523$, $F = 52.6$, $df = 3, 144$, $P < 0.0001$; interaction $\beta = -0.063 \pm 0.087$, $df = 1,144$, $t = -0.72$, $P = 0.47$). For females that first reproduced as yearlings, 2-year olds, and 3+ year olds, the estimate of individual fitness changed in a similar rate as population growth rate increased (Table 1).

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

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

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

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

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

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

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

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

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

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+ = 2.02_[1.73 – 2.30]).

DISCUSSION

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.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Figures

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

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

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

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