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Sociality and individual fitness in yellow-bellied marmots: insights from a long-term study (1962–2001)

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Abstract Theoretical and empirical studies suggest that the age of first reproduction (the age at which reproduction begins) can have a substantial influence on population dynamics and individual fitness. Using complete survival and reproductive histories of 428 female yellow-bellied marmots (*Marmota flaviventris*) from a 40-year study (1962–2001), we investigated causes and fitness consequences of delayed maturity. Most females (86%) died without reproducing. The age of first reproduction of females that survived to reproduce at least once (n=60) ranged from 2 to 6 years. Females maturing later did not have a larger lifetime number of successful reproductive events or offspring production, nor did they experience improved survival. Females reproducing earlier had a higher fitness than those that delayed maturity. These results suggest that the net cost of early maturity was less than fitness benefits associated with early onset of reproduction, and that age of first reproduction in our study population is under substantial directional selection favoring early maturity. We conclude that female yellow-bellied marmots delay onset of reproduction not because of fitness benefits of foregoing reproduction at an earlier age, but due to the social suppression of reproduction by older, reproductive females, which enhances their own fitness to the detriment of the fitness of young females. Our results indicate that female yellow-bellied marmots that survive to reproduce may act to increase their own direct fitness, and that social suppression of reproduction of young females is a part of that strategy.

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Introduction

The evolution of a trait by means of natural selection depends on the relationship between the trait and fitness. As such, the concept of fitness explicitly links the environment, organisms, and traits to the evolutionary process, and thus serves as a central, unifying concept in biology (de Jong 1994; McGraw and Caswell 1996; Brommer et al. 2002; Link et al. 2002). Fitness has been variously defined, but most authors consider it to be a demographic concept, and use quantities such as intrinsic rate of natural increase, r, and net reproductive rate, R_0, to quantify fitness (Partridge and Harvey 1988; de Jong 1994). These fitness measures use age-specific life-history data, and provide an estimate of fitness for a group of organisms but do not consider the fitness of individuals that compose the population. Ironically, it is the individual that is born, that survives, matures, reproduces, and dies. Consequently, most empirical studies apply the concept of individual fitness by measuring survival and fecundity of individuals (Clutton-Brock 1988; de Jong 1994). The concept of individual fitness can provide valuable insights into the pattern and strength of natural selection (McGraw and Caswell 1996; Kääar and Jokela 1998; Link et al. 2002).

Life-history theory predicts that natural selection should favor a combination of traits that maximizes fitness. Traits that maximize fitness include beginning reproduction soon after birth, producing a large number of offspring frequently, and living forever. However, trade-offs among life-history traits prevent the simultaneous evolution of these traits in a species (Law 1979; Stearns 1989, 1992; Roff 1992). An increase in current reproductive effort is thought to adversely influence survival or future reproduction because somatic and reproductive processes compete for the same limiting resources. Thus,

an increase in allocation of resources for one biological process must be accompanied by a corresponding decrease in allocation of resources for the other (Hirshfield and Tinkle 1975; Reznick 1985; Oli 1999). This type of trade-off is thought to play an important role in the evolution of life histories.

One such case of trade-offs focuses on the fitness consequences of the age at which reproduction begins (hereafter, age of first reproduction). If early maturity is not costly in fitness currency, an individual or a genotype that attains sexual maturity early would have a greater fitness (Cole 1954; Lewontin 1965; Bell 1980). However, fitness benefits of earlier maturity may be balanced by associated costs: (1) if earlier reproduction inhibits growth, survival, or future reproduction; (2) if it reduces quality or viability of offspring; or (3) if delaying maturity allows additional growth or experience, and thus substantially increases future reproductive output (Stearns 1989, 1992; Oli et al. 2002). In the face of this conflict, optimum age of first reproduction (the age of first reproduction that maximizes fitness) is attained when costs and benefits of early maturity are balanced. Because of the potential influence of age of first reproduction on fitness and substantial variation in age of first reproduction in many species, fitness consequences of delayed maturity have received substantial attention in the life-history literature. Most theoretical studies predict substantial reduction in fitness as the age of first reproduction is delayed (Cole 1954; Lewontin 1965; Stearns 1992). However, conclusions of empirical studies have been varied, depending on the study species and the choice of fitness measure. For example, when a matrix population model-based measure of individual fitness (λ^m) was used to quantify fitness, substantial fitness consequences of deferred breeding were found in the wood duck (*Aix sponsa*; Oli et al. 2002), Ural owl (*Strix uralensis*; Brommer et al. 1998), blue tit (*Parus caeruleus*; McGraw and Caswell 1996), and the European sparrowhawk (*Accipeter nisus*; McGraw and Caswell 1996). When lifetime reproductive success (LRS) was used as a measure of fitness, however, no relationship was found between fitness and age of first reproduction in any of these species. In the western gull (*Larus occidentalis*), there was no relationship between age of first reproduction and λ^m or LRS (Pyle et al. 1997).

In many social mammals, reproduction of young animals is suppressed by adults such that age of first reproduction of young animals is substantially delayed or they fail to reproduce altogether (Wasser and Barash 1983; Bennett 1994; Bennett et al. 1996; Armitage 1998; Clarke et al. 2001; Waterman 2002). Mechanisms of reproductive suppression may vary among species, but such suppression may occur through behavioral or physiological means (Batzli et al. 1977; Drickamer 1982; Faulkes et al. 1991; Bennett 1994; Vandenbergh 1994; Bennett et al. 1996). Delayed maturity can reduce fitness, especially when delaying age of first reproduction does not improve survival or future reproduction. Moreover, size and composition of social groups can influence both the prevalence of reproductive suppression and fitness (Avilés and Tufiño 1998; Armitage and Schwartz 2000; Treves 2001; McGuire et al. 2002; Waterman 2002).

We investigated causes and fitness consequences of delayed maturity in female yellow-bellied marmots (*Marmota flaviventris*) using the concept of individual fitness and data from a long-term study (1962–2001) of individually-marked marmots. Yellow-bellied marmots live in colonies that vary in size and composition over time and space. We also investigated the influence of size and composition of colonies ("social factors") on individual fitness because social factors can affect fitness (Avilés and Tufiño 1998; Armitage and Schwartz 2000; Treves 2001; McGuire et al. 2002). Specifically, we asked the following:

1. Does individual fitness differ among colonies?
2. Does early age of first reproduction reduce lifetime reproductive output or post-maturity survival?
3. Does the size and composition of social groups influence individual fitness?
4. What are the causes and fitness consequences of delayed maturity in female yellow-bellied marmots?

Materials and methods

Study species

The yellow-bellied marmot is widely distributed in the mountainous region of the western United States (Frase and Hoffmann 1980). Marmots occupy open, montane, patchy habitats dominated by perennial forbs and grasses, and excavate burrows in suitable sites (Svendsen 1974). Individual marmots live in groups that consist of closely related females (mothers, daughters, sisters) that may persist for several generations and are known as matrilines (Armitage 1998). The matrilines occupying a habitat patch form a colony. Nearly all yearling males and about half of the yearling females disperse. There has been no evidence of cooperative breeding in yellow-bellied marmots. Biology of yellow-bellied marmots is described in detail by Armitage (1991, 2002).

Study area and field methods

The study was conducted in the East River Valley, near Rocky Mountain Biological Laboratory, Gunnison County, Colo. We included three colonies (Picnic, River, and Marmot Meadow) in our analyses because we had complete survival and reproductive histories of all females for every year. The study area is described in detail in Svendsen (1974) and Armitage (1986a).

Each year, from 1962 to 2001, marmots were live-trapped, and sex, age, mass, and reproductive status were noted. Each animal received a pair of numbered ear tags at first capture. Age of first reproduction was determined as the year in which the first litter of a female emerged from the burrow. Litter size was estimated from the number of pups that emerged from a natal burrow (Schwartz et al. 1998). Fate and reproductive history of each resident or immigrant female was monitored until she disappeared from the study area. We assumed that a female that disappeared from a colony and was not captured within the study area had died. This is a reasonable assumption because:

1. All sites occupied by marmots were intensively trapped, and trapping continued until all unmarked animals were captured

and marked. Thus, absence of an animal from the study area was most likely due to death.
2. Immigration is very rare in established colonies unless residents die such that some or all of the habitat patch becomes available for occupancy (Armitage 1991).
3. Dispersing females suffer a high mortality, and probability of dispersing females' finding a suitable habitat patch and reproducing is very low (Van Vuren and Armitage 1994a).

Because individual fitness of a female that dies without reproducing at least once is zero, regardless of the number of years she might survive, equating disappearance from the study area to mortality is unlikely to substantially influence our results. However, we recognize the possibility that some females might have dispersed outside our study area and survived to reproduce, and our estimates of fitness should be considered conservative.

Data analysis

We used the matrix method of McGraw and Caswell (1996) to estimate individual fitness of females. Data for estimating individual fitness consist of ages of first and last reproduction, and age-specific reproductive output for each female. A population projection matrix is then constructed for each individual, with age-specific fertility rates estimated from the reproductive data, and age-specific survival rate of 1; age-specific survival rate is set to 1 because an animal survives with certainty until its death (Oli 2003). Age-specific annual fertility rate (F_i) was estimated as the number of young that emerged from the natal burrows per year multiplied by one-half to account for the genetic contribution of each parent to each offspring (McGraw and Caswell 1996). Using the estimated F_i and an annual survival probability of 1 until age of last reproduction, a population projection matrix (A^m) was constructed for each female m with complete reproductive history. λ^m was then estimated as the dominant eigenvalue of the projection matrix (McGraw and Caswell 1996; Oli et al. 2002). LRS was estimated for each female as the lifetime number of pups that emerged from the natal burrows (Grafen 1988). λ^m and LRS were zero if a female had no known reproduction.

An individual may gain fitness indirectly if one or more relatives, who share some of their genes with that individual, reproduce (Hamilton 1971), and empirical estimation of total or inclusive fitness requires consideration of indirect fitness (Oli 2003). However, our estimates of fitness were based on an individual's own reproduction and did not consider fitness gained through reproduction of non-descendant relatives. Thus, our estimates should be viewed as estimates of direct fitness only as they do not consider the indirect component of total fitness (Oli 2003).

We estimated λ^m and LRS separately for females that attained sexual maturity at different ages. We used one-way ANOVA, followed by the Ryan-Einot-Gabriel-Welsch (R-E-G-W) multiple range test (SAS Institute 1999), to test if λ^m and LRS of females that reproduced at least once differed among colonies or among females that attained sexual maturity at different ages, and to test if ages of first and last reproduction of females that survived to reproduce at least once differed among colonies. The Kruskal-Wallis test was used to test if λ^m and LRS of all females differed among colonies.

We used regression of λ^m or LRS on age of first reproduction to evaluate the direction and intensity of selection on age of first reproduction (Lande and Arnold 1983). Linear regression was performed to estimate the forces of directional selection, β. Using this approach, the sign of the linear regression coefficient indicates direction of selection. A quadratic regression was then performed to estimate the forces of stabilizing selection, γ (regression coefficient for the quadratic term). A significant regression coefficient for the quadratic term provides evidence for stabilizing selection. Regression coefficients (β and γ) that are not different from zero indicate no evidence of directional or stabilizing selection on age of first reproduction (Lande and Arnold 1983; McGraw and Caswell 1996).

To evaluate the influences of the size and composition of social groups ("social factors") on fitness measures, we compiled the following data: (1) number of young ($\leq$2 years of age); (2) number of adult males ($\geq$3 years of age); (3) total number of males; (4) number of young females ($\leq$2 years of age); (5) number of adult females ($\geq$3 years of age); and (6) total number of females. These data were compiled for the year when a female was born and when she began reproduction. We performed stepwise linear regression analyses to identify variables that significantly influenced λ^m or LRS (SAS Institute 1999). A linear regression was then performed to evaluate the influences of social factors on fitness measures using only those variables selected by stepwise regression analyses.

Results

Age of first reproduction, litter size and post-maturity survival

We had complete survival and reproductive history for 428 females, of which only 14% survived to reproduce (Table 1). Age of first reproduction ranged from 2 to 6

Table 1 Total number of females, number of reproductive females, ages of first and last reproduction, individual fitness (λ^m) and lifetime reproductive success (*LRS*) in three colonies of yellow-bellied marmots in Gunnison County, Colorado, 1962–2001. Mean±SE are given

	Colony			
	Picnic	River	Marmot Meadow	All colonies combined
No. females	191	118	119	428
No. reproductive females	29 (15.18%)	18 (15.25%)	13 (10.92%)	60 (14.02%)
Age of first reproduction[a]	3.28±0.19	3.28±0.34	2.69±0.26	3.15±0.15
Age of last reproduction[a]	5.52±0.46	5.11±0.713	4.15±0.59	5.08±0.34
Individual fitness (λ^m):				
All females	0.22±0.04	0.21±0.05	0.17±0.04	0.20±0.02
Reproductive females[a]	1.44±0.04	1.40±0.08	1.52±0.09	1.45±0.04
LRS:				
All females	1.55±0.31	1.47±0.45	1.21±0.41	1.43±0.22
Reproductive females[a]	10.21±1.11	9.61±2.12	11.08±2.52	10.22±0.98

[a] Includes only those females who reproduced at least once



Fig. 1 Distribution of age of first reproduction (years) of female yellow-bellied marmots that survived to realize reproduction (n=60) in Gunnison County, Colo. during 1962–2001

years (Fig. 1), and age of last reproduction ranged from 2 to 11 years. Age of first ($F_{2,57}$=1.34, P=0.271) and last reproduction ($F_{2,57}$=1.25, P=0.294) did not differ among colonies, nor did the lifetime number of successful reproductive events ($F_{2,57}$=0.21, P=0.812) or the average litter size ($F_{2,57}$=1.51, P=0.230) of females that reproduced at least once. Females that began reproduction as 2-, 3-, 4-, or ≥5-year-olds survived (mean±SE) 1.9±0.5 (n=22), 2.4±0.6 (n=18), 2.6±0.7 (n=11), and 2.4±0.9 (n=9) additional years post-maturity, respectively. Post-maturity survival (i.e., number of years survived after age of first reproduction) did not differ among females that began reproduction at different ages ($F_{3,56}$=0.31, P=0.82). Females that began reproduction later did not have a larger lifetime number of successful reproductive events or larger litters, nor did they survive better than those that began reproduction earlier (Fig. 2).

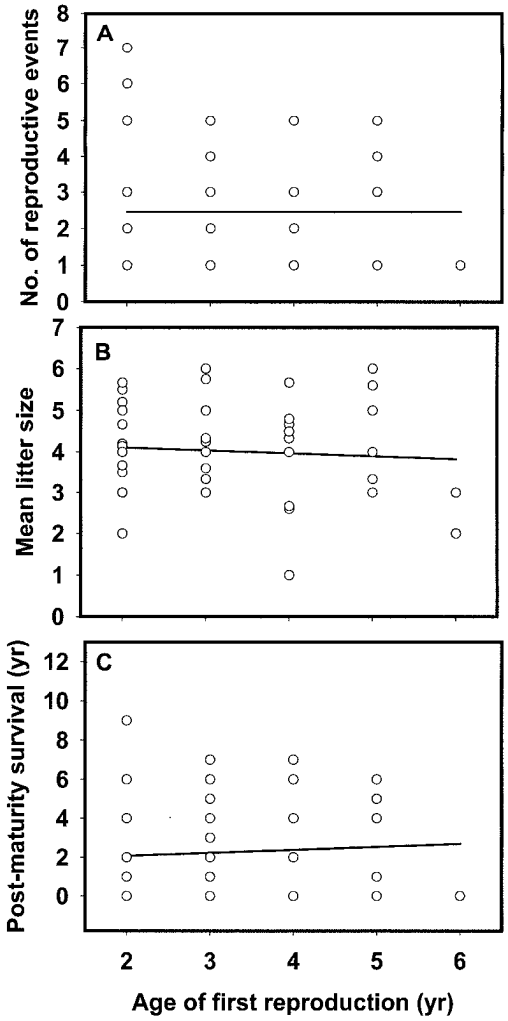

Fig. 2 The relationship between age of first reproduction (years) and **A** lifetime number of reproductive events, **B** mean litter size, and **C** number of years survived post-maturity in female yellow-bellied marmots in Gunnison County, Colo. during 1962–2001

Lifetime reproductive success

The mean LRS estimated for all females ranged from 1.2 (Marmot Meadow) to 1.6 (Picnic), and did not differ among colonies (Kruskal-Wallis test, χ^2=1.23, P=0.529). When females that did not survive to reproduce (i.e., females with LRS of zero) were excluded, mean LRS ranged from 9.6 (River) to 11.1 (Marmot Meadow; Table 1). LRS did not differ among colonies ($F_{2,57}$=0.14, P=0.872).

Because LRS did not differ among colonies, we pooled data from all three colonies for further analyses. Mean (±SE) LRS of females that began reproduction as 2-, 3-, 4-, and ≥5-year-olds was 9.5±1.8 (n=22), 11.2±1.6 (n=18), 10.9±2.0 (n=11), and 9.0±2.7 (n=9), respectively, and did not differ among females that attained sexual maturity at different ages ($F_{2,57}$=0.26, P=0.853). Linear regression of LRS on age of first reproduction indicated no evidence of directional selection for early maturity (β±SE=−0.19±0.87; P=0.884, R^2=0.0009), nor was there any evidence for stabilizing selection based on quadratic regression (γ±SE=−1.06±0.74, P=0.157; Fig. 3A).

Individual fitness (λ^m)

The mean λ^m estimated for all females ranged from 0.17±0.04 to 0.22±0.04, and did not differ among colonies (Kruskal-Wallis test, χ^2=1.17, P=0.556). When females that did not survive to reproduce (i.e., females with λ^m of zero) were excluded, mean λ^m ranged from 1.40±0.08 to 1.52±0.09 (Table 1). Again, λ^m did not differ among colonies ($F_{2,57}$=0.77, P=0.494).

Because λ^m did not differ among colonies, we pooled data from all three colonies for further analyses. Mean individual fitness of females that began reproduction as 2-, 3-, 4-, and ≥5-year-olds was 1.6±0.1 (n=22), 1.5±0.04 (n=18), 1.33±0.06 (n=11) and 1.21±0.04 (n=9), respectively. λ^m differed among females that began reproduction at different ages ($F_{3,56}$=5.54, P=0.002): females that first reproduced as 2-year-olds had the highest λ^m, whereas females that did not reproduce until 5 years of age had the lowest λ^m (P<0.05). Linear regression of λ^m on age of first

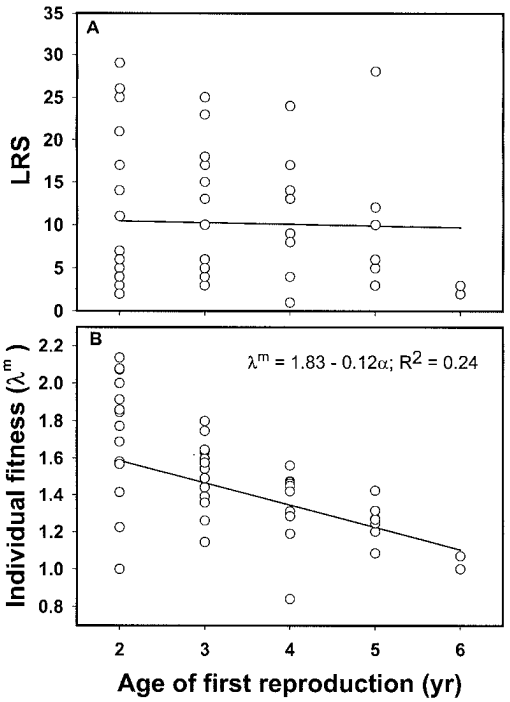

Fig. 3 The relationship between age of first reproduction (years) and **A** lifetime reproductive success (*LRS*) and **B** individual fitness (λ^m) in female yellow-bellied marmots that survived to reproduce in Gunnison County, Colo. during 1962–2001

reproduction indicated directional selection for early maturity (β±SE=–0.12±0.03; P<0.0001, R^2=0.24). Quadratic regression indicated no evidence of stabilizing selection (β±SE=0.004±0.024, P=0.859). The relationship between λ^m and age of first reproduction suggested that the optimal age of first reproduction was 2 years (Fig. 3B).

Influence of colony size and composition

Of the 12 social variables included in the stepwise linear regression model, two (number of adult females and total number of females at maturity) significantly influenced λ^m. Linear regression with these variables as predictors explained 14.1% of variation in λ^m (R^2=0.141; P=0.013). None of the social variables significantly influenced LRS.

Discussion

There are costs as well as benefits associated with early maturity (Roff 1992; Stearns 1992). Other things being equal, organisms that attain sexual maturity earlier should have a higher fitness because: (1) they spend less time as juveniles, and thus have a higher probability of surviving to maturity; and (2) their offspring are born earlier and begin reproducing sooner than those maturing later (Bell 1980; Stearns 1992). However, if early maturity causes substantial reduction in survival or future reproduction, delaying maturity can increase fitness (Reznick 1985; Stearns 1989, 1992; Pyle et al. 1997). Given these costs and benefits, optimum age of first reproduction (the age of first reproduction that maximizes fitness) is thought to evolve (Stearns and Crandall 1981; Stearns 1992).

Female yellow-bellied marmots that did not reproduce as 2-year-olds and survived to reproduce at an older age did not produce larger litters, did not survive better, and did not experience more lifetime successful reproductive events than those that first reproduced as 2-year-olds. Moreover, about 47% of females that did not reproduce at age 2 died before the next breeding season, and an additional 43% died before they could reproduce at age 4 (Schwartz et al. 1998). On the other hand, females that attained sexual maturity as 2-year-olds had a higher λ^m than those that delayed reproduction. These results indicate that the net cost of early maturity was less than fitness benefits associated with early onset of reproduction. These findings are consistent with predictions of life-history theory (Cole 1954; Lewontin 1965; Stearns 1992; McGraw and Caswell 1996), and with other studies that have investigated fitness consequences of delayed reproductive maturity (e.g., McGraw and Caswell 1996; Brommer et al. 1998; Oli et al. 2002). In the western gull, however, early maturity was reported to be costly and birds that deferred breeding until a later age had a higher fitness than those that began reproduction at a younger age (Pyle et al. 1997). Inter-specific differences in fitness consequences of deferred breeding are likely to be a result of inter-specific differences in life-history patterns. It has been suggested that early onset of reproduction may be beneficial in populations characterized by early maturity and high reproductive rates, whereas delayed age of first reproduction may be favored in populations with an opposite suite of traits (Cole 1954; Oli et al. 2002; Oli and Dobson 2003). In the western gull, which has a long lifespan, early maturity was costly and birds that deferred breeding until an older age had a higher fitness than those that began reproduction at a younger age (Pyle et al. 1997). Deferred breeding is risky in yellow-bellied marmots. Both survival and reproductive success can be markedly reduced by severe and unpredictable weather events, such as summer drought or prolonged spring snow cover (Armitage 1994, 2003a). Even normal weather patterns affect fitness: long winters and/or short growing seasons reduce litter size and decrease survival probability (Schwartz and Armitage 2002). A female may also fail to reproduce because no adult male may be present in a given year (Armitage 2003a, 2003b). Thus, it seems that marmots should begin reproduction whenever conditions permit.

When λ^m was used to quantify fitness, we found strong evidence for directional selection for early maturity. However, there was no evidence for directional selection on age of first reproduction when LRS was used as a measure of individual fitness. Similar results were reported for blue tits and European sparrowhawks (McGraw and Caswell 1996), Ural owls (Brommer et al.

1998), and wood ducks (Oli et al. 2002). This discrepancy may be due to the inadequacy of LRS to quantify fitness (McGraw and Caswell 1996; Kääar and Jokela 1998; Oli 2003). LRS is an important component of fitness, but not fitness itself because it ignores the timing of reproduction which can have substantial influence on fitness (Cole 1954; Lewontin 1965; Roff 1992; Stearns 1992). λ^m, on the other hand, incorporates timing as well as amount of reproduction, and serves as an adequate measure of individual fitness (McGraw and Caswell 1996; Kääar and Jokela 1998; Brommer et al. 2002; Oli et al. 2002; Oli 2003).

Given the substantial selection pressure for early maturity and the observation that females that attained sexual maturity as 2-year-olds had the highest fitness, one would expect age of first reproduction of 2 years to be most frequent. In our study population, only 14% of females survived to reproduce: of these, 37% began reproduction as 2-year-olds and 68% reproduced by age 3. These results are consistent with directional selection for early maturity. However, many females in our study population delayed reproduction until age 4 or later. At least three factors influence age of first reproduction in small mammals: population density, food resources, and social suppression of reproduction.

Population density influences age of first reproduction in some small mammals (Saitoh 1981; Gilbert and Krebs 1991). In our study population, population sizes differed among colonies but neither age of first reproduction, λ^m, nor LRS did. Also, population size did not significantly influence λ^m or LRS. These results suggest that population density per se did not substantially influence age of first reproduction or individual fitness in our study population.

Abundance of food resources influences reproductive rates and age of first reproduction in some ground-dwelling sciurids (Dobson and Oli 2001). In yellow-bellied marmots, however, delayed reproductive maturity seems not to be a direct response to food shortages. When a matriline consumed supplemental high-energy, high-protein food ad libitum for 5 years, all gained body mass but only two of nine (22.2%) 2-year-old females reproduced (Woods 2001). In unfed (control) matrilines, four of 17 (23.5%) 2-year-old females reproduced (Woods 2001, Armitage 2003b). These results suggest that scarce food resources did not cause delayed reproductive maturity. The temporal variation in the proportion of 2-year-old females attaining reproductive maturity (Armitage 2003b) also indicates that hibernacula quality did not influence age of first reproduction.

In our study population, only 14.5% (n=102) of 2-year-old female yellow-bellied marmots began reproduction when older females were present. In the absence of older, reproductive females, however, a substantial proportion (47.8%; n=69) of 2-year-old females reproduced (Armitage 2003b; see also Armitage 1986b, 1998; Armitage and Schwartz 2000). This observation, and the significant negative influence on λ^m of the number of adult females present in the colony when young females begin reproduction, suggest that the most likely explanation for the delayed reproduction is reproductive competition among females and, consequently, social suppression of reproduction. In yellow-bellied marmots, reproductive competition involves three major mechanisms. First, a dominant female may cause a female in another matriline to relocate. The dominant female gains access to the vacated space that is subsequently occupied by her daughters (Armitage 1992). Second, adult females are highly agonistic to non-littermate full siblings and to nieces, which causes them to disperse (Armitage 1986b), thus making space available for their own offspring. Third, where females in a matriline share space or occupy a habitat patch next to another matriline, reproductive suppression occurs (Armitage 1986b).

Social suppression of reproduction is common among female mammals (Wasser and Barash 1983), and is viewed as a major cost of sociality in marmots (Armitage 1996). In yellow-bellied marmots, social suppression of reproduction occurs predominantly within matrilines when reproduction of young females is suppressed by older, reproductive females, including their mothers (Armitage 1998, 2003b). In the absence of older, reproductive females, 62.3% of the nulliparous females began reproduction. When one or more older reproductive females are present, only 42 of 173 (24.3%) nulliparous females reproduced (Armitage 2003b). These findings suggest that delayed reproductive maturity in female yellow-bellied marmots is primarily a result of social suppression of reproduction, and that most females of age 2 years become reproductive when they are released from reproductive suppression. There is no effect on reproduction of young females by older females once the younger female has reproduced; thus reproductive suppression acts to delay the age of first reproduction (Armitage 2003b). Precise mechanisms of social suppression of reproduction in the yellow-bellied marmot remain to be ascertained.

Our results suggest that age of first reproduction of young females is delayed due primarily to social suppression of reproduction, which then causes substantial reduction in individual fitness. If so, then why do yearling female yellow-bellied marmots remain philopatric when older, reproductive females are present? The alternative is to disperse, but dispersers suffer high mortality and the probability of finding a vacant habitat patch of adequate quality is very small (Van Vuren and Armitage 1994a, 1994b). Furthermore, philopatric females may escape reproductive suppression and increase their fitness by budding-off a new matriline or by taking over a habitat patch when older females die. Additionally, dispersing females usually establish a matriline of one if they survive dispersal and gain access to an unoccupied habitat patch; females in such matrilines have low survival as well as low reproductive success (Armitage and Schwartz 2000). Thus, it seems likely that many young females remain philopatric because they may inherit the habitat patch when reproductive females die and their probability of realizing reproduction at their natal sites is generally better than those of the dispersing

young females who may not survive the dispersal or fail to find a habitat patch of adequate quality.

We conclude that age of first reproduction in female yellow-bellied marmots is under substantial directional selection favoring early maturity, that females who begin reproduction as 2-year-olds have a higher fitness than those that delayed age of first reproduction, and that females who delay reproduction do so primarily because of the social suppression of reproduction, not because of fitness benefits of delayed maturity. Female yellow-bellied marmots that survive to reproduce may act to increase their own direct fitness, and social suppression of reproduction of young females may be a part of that strategy (Armitage and Schwartz 2000). Directional selection for earlier maturity also was reflected in the distribution of age of first reproduction; about 68% of females began reproduction by 3 years of age, although some females did not begin reproduction until 5 or 6 years of age. Plasticity in age of first reproduction may allow female yellow-bellied marmots to respond rapidly to improvements in social and ecological environments.

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