

INDIRECT FITNESS BENEFITS DO NOT COMPENSATE FOR THE LOSS OF DIRECT FITNESS IN YELLOW-BELLIED MARMOTS

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The contribution of indirect fitness to inclusive fitness is expected to increase as the reproductive skew increases, with indirect fitness being the only component of inclusive fitness of sterile individuals in eusocial species. However, the relative contribution of indirect fitness to inclusive fitness has rarely been evaluated empirically. Using data from a long-term study (1962–2003), we show that female yellow-bellied marmots that have a later age of 1st successful reproduction incur a substantial loss of direct fitness with no corresponding gain in indirect fitness. Additionally, although females that survive to reproductive age but do not successfully reproduce have a greater indirect fitness than those that reproduce at least once, indirect fitness benefits of foregoing reproduction are insufficient to compensate for the loss of direct fitness resulting from later reproduction. Although indirect fitness composed 22.2% of the inclusive fitness of females that reproduced at least once, females that reproduced at least once had 2.3 times higher inclusive fitness than those that survived to reproductive age but never reproduced. These results suggest that, in yellow-bellied marmots and other species with similar life histories, the contribution of indirect fitness to inclusive fitness does not compensate for loss of direct fitness.

Key words: age of 1st reproduction, costs of reproduction, direct fitness, inclusive fitness, indirect fitness, life-history theory, *Marmota flaviventris*, reproductive strategy, reproductive suppression, yellow-bellied marmot

Many animal societies are characterized by unequal apportionment of reproduction such that only a fraction of individuals surviving to reproductive age produce offspring. Among individuals that achieve reproduction, age of 1st reproduction can vary widely (Allainé 2000; Clutton-Brock 1998; Faulkes et al. 1991; Haydock and Koenig 2002; McGraw and Caswell 1996; Oli and Armitage 2003; Oli et al. 2002; Waterman et al. 2002). Given that reproduction is a critical component of fitness, why do animals of reproductive age delay age of 1st reproduction or fail to reproduce altogether? Life-history theory (“cost of reproduction”) postulates that delayed breeding can evolve if fitness benefits of delayed reproduction balance or exceed benefits of early reproduction (Stearns 1989, 1992). Specifically, delayed age of primiparity is likely to evolve if early reproduction reduces survival or future reproductive potential, or if delayed breeding enhances

indirect fitness. Although the cost of reproduction idea can explain the evolution of delayed breeding, it cannot explain why animals of reproductive age fail to reproduce altogether.

Hamilton’s theory of inclusive fitness (Hamilton 1963, 1964, 1972) offers an evolutionary explanation of many perplexing biological phenomena, including reproductive skew, cooperative breeding, and eusociality (Griffin and West 2002; Oli 2003). The inclusive fitness theory suggests that the contribution of indirect fitness to inclusive fitness increases as the reproductive skew increases, with indirect fitness being the only component of inclusive fitness of sterile individuals in eusocial species. However, the presumed importance of indirect fitness to inclusive fitness has rarely been tested in natural populations.

Here, we examine the costs and benefits of reproductive strategies and the relative contribution of direct and indirect fitness to inclusive fitness in a ground-dwelling social rodent, the yellow-bellied marmot (*Marmota flaviventris*). Specifically, we tested the hypothesis that females that delay age of 1st successful reproduction gain sufficient indirect fitness to account for the loss of direct fitness that may result from delaying age of primiparity, and that females that survive to reproductive age but do not successfully reproduce gain

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sufficient indirect fitness to balance the loss of direct fitness that arises from not reproducing. Our long-term (1962–2003) study of individually marked marmots provided data that allowed us to estimate direct and indirect components of inclusive fitness, and investigate the relative contribution of indirect fitness to inclusive fitness of individual marmots.

MATERIALS AND METHODS

Study species.—The yellow-bellied marmot in our study area occupies montane habitats that are patchily distributed (Svendsen 1974). Marmots live in social groups (matrilines) that consist of closely related females (mothers, daughters, and sisters), and matrilines occupying a habitat patch form a colony (Armitage 1998). Detailed description of the biology of yellow-bellied marmots is given elsewhere (Armitage 1991, 2003a).

Study area and field methods.—The study was conducted in the East River valley, at elevations ranging from 2,867 to 3,008 m above sea level, near Rocky Mountain Biological Laboratory, Gunnison County, Colorado. Each year, from 1962 to 2003, marmots were livetrapped, and sex, age, and mass were recorded. Each marmot received a pair of numbered ear tags on 1st capture. We defined successful reproduction as the weaning of a litter, and estimated age of 1st reproduction as the age (years) at which the 1st litter of a female emerged from her burrow. Litter size was the number of weaned pups that emerged from a natal burrow. Reproductive history of each female was monitored until she disappeared from the study area. All field procedures were approved by the University of Kansas’s Institutional Animal Care and Use Committee and meet the guidelines recommended by the American Society of Mammalogists (Gannon et al. 2007).

Coefficient of relatedness (r).—Based on long-term observational data, we constructed a genealogy for each female. The coefficient of relatedness was then estimated following Hamilton (1972): a female was related to her full sibs by one-half; to her aunts, half sibs, and double 1st cousins by one-fourth; 1st cousins by one-eighth; and so on. Estimates of relatedness were limited to the colony level. Estimates of relatedness based on genealogy required 2 assumptions. First, we assumed that a female that produced a litter in a given year mated with only 1 male, and second, the dominant resident male fathered all the

young within his territory. Both of these assumptions are supported by genetic studies (Schwartz and Armitage 1980). Although examination of genetic data utilizing DNA analyses could have provided more rigorous estimates of relatedness, such data are unavailable and difficult to obtain for long-term studies such as ours, and the methods for such analyses were not available during early years of our study.

Estimation of inclusive fitness and its components.—Two important components of inclusive fitness of an individual are direct fitness (fitness gained by an individual through its own reproduction) and indirect fitness (fitness gained by an individual through the reproduction of relatives who share some of their genes with the focal individual—Hamilton 1963, 1964, 1972; Oli 2003). We estimated direct individual fitness using the matrix method (McGraw and Caswell 1996; Oli 2003). A population projection matrix was constructed for each individual k with survival probability of 1 along the lower subdiagonal during the lifetime of the individual, and age-specific direct fertility rates along the 1st row of the matrix:

$$\mathbf{A}_{direct}^{(k)} = \begin{bmatrix} 0 & 0 & \dots & F_{\alpha}^{(k)} & F_{\alpha+1}^{(k)} & \dots & F_{\omega-1}^{(k)} & F_{\omega}^{(k)} \\ 1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 1 & \dots & 0 & 0 & \dots & 0 & 0 \\ \vdots & & \ddots & & & \ddots & & \vdots \\ 0 & 0 & \dots & 1 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 1 & \dots & 0 & 0 \\ \vdots & & \ddots & & & \ddots & & \vdots \\ 0 & 0 & \dots & 0 & 0 & \dots & 1 & 0 \end{bmatrix},$$

where $F_i^{(k)}$ was estimated as one-half times the number of pups weaned by individual k at age class i (to account for genetic contribution of each parent to each offspring). Note that direct fertility rates may be nonzero only between ages of 1st (α) and last (ω) reproduction (Oli 2003). The direct individual fitness was estimated as the dominant eigenvalue of the matrix $\mathbf{A}_{direct}^{(k)}$.

An individual may gain indirect fitness if 1 or more relatives (who share some of their genes with that individual) reproduce. We estimated indirect individual fitness using a matrix approach described in detail by Oli (2003). Briefly, we constructed a population projection matrix for each individual k using estimates of age-specific rates of indirect reproduction, $\theta_i^{(k)}$, and age-specific survival rate of 1 until its death at age β :

$$\mathbf{A}_{indirect}^{(k)} = \begin{bmatrix} \theta_1^{(k)} & \theta_2^{(k)} & \dots & \theta_{\alpha}^{(k)} & \theta_{\alpha+1}^{(k)} & \dots & \theta_{\omega}^{(k)} & \theta_{\omega+1}^{(k)} & \dots & \theta_{\beta-1}^{(k)} & \theta_{\beta}^{(k)} \\ 1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 1 & \dots & 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ \vdots & & \ddots & & & \ddots & & & \ddots & & \vdots \\ 0 & 0 & \dots & 1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 1 & \dots & 0 & 0 & \dots & 0 & 0 \\ \vdots & & \ddots & & & \ddots & & & \ddots & & \vdots \\ 0 & 0 & \dots & 0 & 0 & \dots & 1 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 & \dots & 0 & 1 & \dots & 0 & 0 \\ \vdots & & \ddots & & & \ddots & & & \ddots & & \vdots \\ 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 & \dots & 1 & 0 \end{bmatrix},$$

where $\theta_i^{(k)}$ is the indirect reproductive rate of individual k in age class i . The indirect reproductive rate was estimated as the sum of relatedness-weighted direct reproductive rates of all non-descendent relatives when individual k was in age class i (Oli 2003):

$$\theta_i^{(k)} = \sum_{l=1}^n r_{kl} F_i^{(l)},$$

where r_{kl} is the coefficient of relatedness between individual k and individual l and was estimated as described previously, n is the total number of relatives who share some of their genes with individual k , and $F_i^{(l)}$ is the direct reproductive rate of individual l when individual k is in age class i . $F_i^{(l)}$ was estimated as one-half times the size of the litter produced by individual l when individual k was in age class i . We note that individual l will not contribute to $\theta_i^{(k)}$ if it is unrelated to individual k (because $r_{kl} = 0$) or if it fails to reproduce when individual k is in age class i (because $F_i^{(l)} = 0$). Indirect fitness was then estimated as the dominant eigenvalue of the matrix $\mathbf{A}_{indirect}^{(k)}$ (Oli 2003). Using this method, an individual would accrue indirect fitness during its lifetime, but not before birth or after death.

Hamilton (1964, 1972) defined inclusive fitness as the fitness "... stripped of all components which can be considered as due to the individual's social environment, leaving the fitness he would express if not exposed to any of the harms or benefits of that environment ... augmented by certain fractions of the quantities of harm and benefit which the individual himself causes to the fitness of his neighbours" (italics added). Based on this definition, inclusive fitness can be estimated as (Oli 2003):

$$\lambda_{inclusive}^{(k)} = \lambda_{total}^{(k)} - (\lambda_{direct}^{(k)} - \lambda_{no\ behavior}^{(k)}) + \sum_{l=1}^n r_{kl} (\lambda_{direct}^{(l)} - \lambda_{no\ behavior}^{(l)}),$$

where $\lambda_{total}^{(k)} = \lambda_{direct}^{(k)} + \lambda_{indirect}^{(k)}$ is the sum of direct and indirect fitness of individual k ; $\lambda_{direct}^{(k)}$ is direct fitness of individual k ; $\lambda_{indirect}^{(k)}$ is indirect fitness of individual k ; $\lambda_{no\ behavior}^{(k)}$ is expected direct fitness of individual k in the absence of behaviors directed toward it by other conspecific individuals; r_{kl} is coefficient of relatedness between individual k and individual l ; $\lambda_{direct}^{(l)}$ is direct fitness of individual l ; $\lambda_{no\ behavior}^{(l)}$ is expected direct fitness of individual l in the absence of behaviors directed toward it by individual k ; and n is total number of conspecific individuals ("neighbors") that are a part of the social environment of individual k .

The term $(\lambda_{direct}^{(k)} - \lambda_{no\ behavior}^{(k)})$ quantifies the effect of the social environment of individual k on its direct fitness that Hamilton (1964) suggested should be removed from the estimation of inclusive fitness. The term $(r_{kl}(\lambda_{direct}^{(l)} - \lambda_{no\ behavior}^{(l)}))$ quantifies the effect of individual k on the direct fitness of each of its neighbors, weighted by the coefficients of relatedness between individual k and each of its neighbors; this is the quantity Hamilton (1964) suggested should be augmented while estimating inclusive fitness (Oli 2003).

Behavioral interactions that can influence fitness of female marmots likely occur during mating and gestation periods. For example, 84% of all interactions between dominant and subordinate female alpine marmots (*Marmota marmota*) occurred during gestation period (Hacklander et al. 2003), and similar observations were reported for yellow-bellied marmots from a low-elevation study site (Armitage 1965). Agonistic interactions between dominant and subordinate female marmots can result in complete reproductive failure in subordinate females; the mechanism by which this can occur may include suppressing ovulation, preventing copulation, and inducing abortion or reabsorption of fetuses (Armitage 1965; Hacklander et al. 2003). Regardless of the mechanism involved, the ultimate outcome is failure to wean a litter, and, thus, loss of direct fitness. Quantification of fitness consequences of such interactions, however, was not possible, because weather in our study area is frequently stormy and most of the study area is typically under snow cover during mating and gestation periods (mean date of 50% snow cover can be as late as 30 May—Van Vuren and Armitage 1991). Access to field sites and observation of marmots under such conditions, therefore, was frequently not possible. Consequently, we could not objectively quantify fitness effects of behavioral interactions among female marmots, and, thus, $(\lambda_{no\ behavior}^{(k)})$ and the components $(\lambda_{direct}^{(k)} - \lambda_{no\ behavior}^{(k)})$ and $\sum [r_{kl}(\lambda_{direct}^{(l)} - \lambda_{no\ behavior}^{(l)})]$. Therefore, we considered the outcome of behavioral interactions (i.e., failure to reproduce), and estimated the inclusive fitness as:

$$\lambda_{inclusive}^{(k)} = \lambda_{total}^{(k)} = \lambda_{direct}^{(k)} + \lambda_{indirect}^{(k)}.$$

Statistical analysis.—We used Pearson's correlation analysis to examine the relationship between age of 1st reproduction and postmaturity survival, litter size, lifetime number of reproductive events, indirect fitness, and direct fitness. Two-sample *t*-tests were used to test for the difference in mean indirect and inclusive fitness between females that reproduced (i.e., weaned a litter) at least once and those surviving to reproductive age but that never reproduced. All statistical analyses were performed using SAS (SAS Institute Inc. 1999).

RESULTS

Of 233 females that survived to reproductive age (2 years), 123 (52.8%) weaned at least 1 litter. Age of 1st reproduction varied from 2 to 6 years, but some females lived up to 7 years of age and never weaned a litter. If early reproduction is costly, 1 would expect females that delay onset of reproduction to survive better, produce larger litters, experience a greater number of reproductive events, or a combination of these, compared to females that begin reproduction at an earlier age (Stearns 1992). However, females that delayed age of 1st successful reproduction did not survive better ($r = -0.109$, $P = 0.32$), did not produce larger litters ($r = -0.09$, $P = 0.23$), nor did they experience a greater number of successful reproductive events compared to females that began reproduction at an earlier age ($r = -0.13$, $P = 0.16$). Consequently,

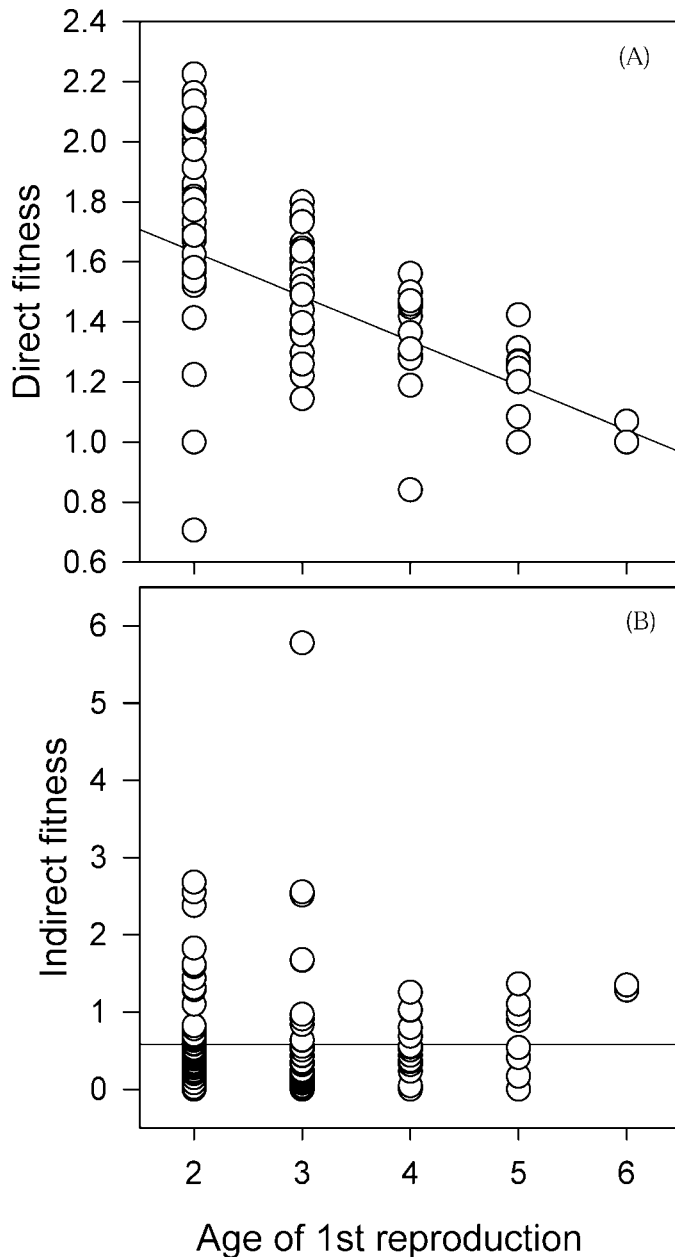


FIG. 1.—The relationship between age of 1st reproduction and A) direct fitness, and B) indirect fitness in yellow-bellied marmots (*Marmota flaviventris*; $n = 123$ for both panels) over the individual's lifetime. A circle may represent ≥ 1 data points. The straight line in each panel is the fitted linear regression line.

direct fitness declined significantly as age of 1st reproduction was delayed (Fig. 1A; $r = -0.51$, $P < 0.0001$). Clearly, direct fitness benefits of early reproduction exceeded the associated costs. Why, then, do female yellow-bellied marmots delay age of 1st reproduction? One possibility is that delayed breeders gain sufficient indirect fitness to balance the loss of direct fitness; however, that was not the case (Fig. 1B; $r = -0.00093$, $P = 0.99$). Another possibility is that females tried but failed to successfully reproduce; however, we could not test this possibility because of data limitations.

Females that survived to reproductive age but did not wean a litter had a greater indirect fitness than those that did (Fig. 2; $t = 2.80$, $d.f. = 231$, $P = 0.006$). However, females that weaned at least 1 litter had a significantly higher inclusive fitness compared to those that survived to reproductive age but never weaned a litter (Fig. 2; $t = 9.48$, $d.f. = 231$, $P < 0.0001$). Overall, indirect fitness comprised 22.23% ($SE = 0.018\%$) of inclusive fitness of females that weaned at least 1 litter.

DISCUSSION

Delayed age of 1st reproduction can reduce direct fitness in many species of birds and mammals (McGraw and Caswell 1996; Oli and Armitage 2003; Oli et al. 2002), but the influence of delayed age of 1st reproduction on indirect fitness remains unknown. Female marmots are capable of reproducing at 2 years of age, but many do not successfully reproduce for several more years. We found that direct fitness declined significantly as the age of 1st successful reproduction was delayed. However, females who failed to wean at least 1 litter or delayed age of 1st successful reproduction did not gain sufficient indirect fitness to balance the loss of direct fitness. These results suggest that delayed age of 1st successful reproduction reduces direct fitness with no corresponding gain in indirect fitness; consequently, inclusive fitness declines significantly as the age of 1st reproduction is delayed.

Perhaps a more perplexing question is: why do nearly half of the female yellow-bellied marmots surviving to reproductive age never wean a litter? Clearly, females that do not wean a litter during their lives will have no direct fitness, and indirect fitness is the only component of inclusive fitness of these individuals. Inclusive fitness theory suggests that females that survive to reproductive age but do not reproduce should have a greater indirect fitness than those that reproduce such that inclusive fitness of the 2 groups would be similar. Indeed, females that survived to reproductive age but never weaned a litter had significantly higher indirect fitness than those who weaned at least 1 litter ($P = 0.006$; Fig. 2). However, indirect fitness benefits of foregoing reproduction were much less than loss of direct fitness. Consequently, females who successfully weaned at least 1 litter, on average, had 2.3 times greater inclusive fitness than those who survived to reproductive age but never weaned a litter. Females that survived to reproductive age but do not successfully reproduce try to “make the best of a bad job” (Koprowski 1993; Lee and Hays 2004), possibly in an attempt to compensate for the loss of direct fitness.

Given these results, it seems unlikely that traits such as delayed age of 1st reproduction could evolve by means of natural selection. Why, then, do female marmots surviving to reproductive age forego or delay reproduction? It has been suggested that female marmots do not delay or forego reproduction by choice but are forced to do so via reproductive

suppression by dominant females (Armitage 2003b; Armitage and Schwartz 2000; Oli and Armitage 2003). For example, 25.6% of 2- and 3-year-old females reproduced when 1 or more older females were present, whereas 54.1% weaned a litter when no older female was present (Armitage 2003b).

Possibly some 2-year-old females may fail to reproduce because they are immature. This possibility was tested by comparing the body mass of 36 individuals that weighed 1.85 kg or more in May, the month in which hibernation terminated. No female weighing <1.85 kg reproduced. These females could have been immature, but all lived with their mothers; thus, reproductive suppression could not be ruled out as a possible cause of failure to reproduce. The mean body mass (2.17 kg) of the 13 females that reproduced did not differ significantly from that (2.11 kg) of the nonreproductive females (Armitage 2003b). These 2-year-old females were significantly more likely to reproduce when older females were absent (Armitage 2003b).

Ecological constraints could affect the age of 1st reproduction (e.g., Dickinson 2004; Dickinson et al. 1996). The key resources for yellow-bellied marmots are burrows (for protection from predators and weather and for hibernation) and food. Resource-sharing, measured as overlap of home ranges, was highest among members of a matriline whose mean relatedness (r) was 0.5 and declined when $r \leq 0.25$ at a rate greater than that expected if resource-sharing was proportional to r (Armitage 1996b). Members of a matriline often live in the same burrow system; members of different matriline never share burrows (Armitage 1991). Likewise, members of a matriline share foraging areas and exclude females from other matriline (Frase and Armitage 1984). It is unlikely that food availability played a major role in the reproductive failure of young adult yellow-bellied marmots. In our study sites, marmots utilize only about 2–6.4% of the available net primary production (Kilgore and Armitage 1978). The possibility that food limitation precluded young adult females from reproducing was tested by providing 2 colonies with supplemental food for several years. Older adult females were present at these colonies. Food supplementation did not affect the age of 1st successful reproduction (Woods and Armitage 2003). Only 2 of nine 2-year-olds from the supplemented groups reproduced; the percentage (22%) of those reproducing was similar to that of nonsupplemented 2-year-old females (19.6%—Armitage 2003b). Only 1 of six 3-year-olds (16.6%) reproduced, a proportion lower than that (32.6%—Armitage 2003b) of females who did not receive supplemental food. Two older females (ages 9 and 4 years at the start of the experiment) each reproduced during the first 3 years of the study; the older female did not return in the 4th year, but the surviving female reproduced in the 4th and 5th years. The 3-year-old female reproduced after the older female failed to return. The two 2-year-old females reproduced when living at the edge of the matrilineal home range where they presumably could escape agonistic behavior from the older females (Woods and Armitage 2003). The body masses of the 2- and 3-year-old females were among the largest ever recorded in our study area (Armitage 2003b). Furthermore, only 20.0% (2 older females)

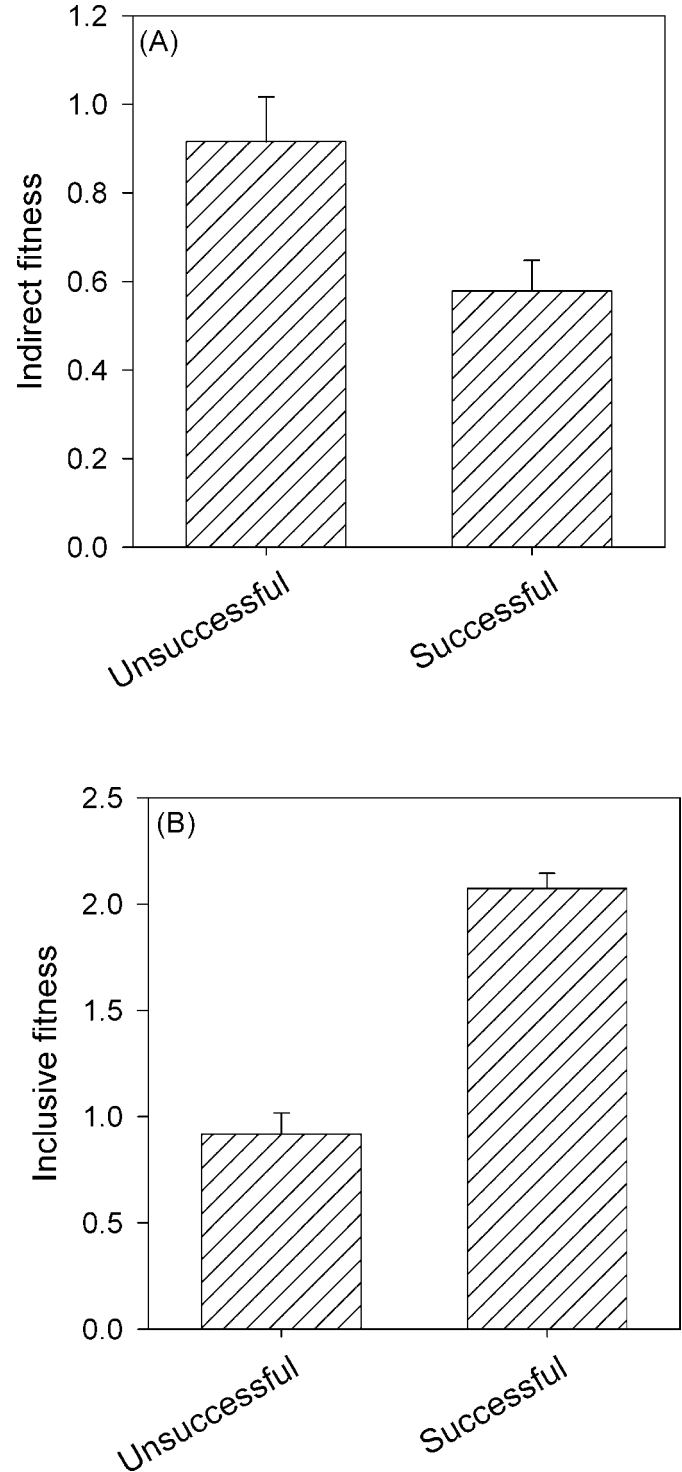


FIG. 2.—A) The mean (with SE) indirect fitness of female yellow-bellied marmots (*Marmota flaviventris*) that survived to reproductive age. B) The mean (with SE) inclusive fitness of females that survived to reproductive age. The indirect and inclusive fitness are given for females that successfully reproduced at least once (Successful; $n = 123$), and those that did not (Unsuccessful; $n = 110$). Vertical lines represent SEs.

to 25.2% (1 older female) of young females wean litters when older females are present (Armitage 2003b). Thus, the preponderance of evidence indicates that reproductive suppression, and not ecological constraint, is the major factor affecting the age of 1st reproduction.

Reproductive suppression is widespread among the social marmots (Armitage 1992, 1996b, 2000; Blumstein and Armitage 1998, 1999; Hacklander et al. 2003), but is rare or absent in the solitary woodchuck (*Marmota monax*). About 72% of adult female woodchucks reproduce each year, whereas only 22–53% of the adult females of social marmots reproduce (Armitage 1996a). Although some of the low frequency of female reproduction can be attributed to physiological stress, the pattern of reproduction of younger and older females described above, and the persistence of nonbreeding subordinate adults in some species implicate reproductive suppression (Armitage 1996a; Oli and Armitage 2003). Furthermore, in many social species the age of 1st reproduction is delayed beyond the age at which reproduction is physiologically possible, and reproductive suppression has been suggested as the cause of delayed age of 1st reproduction (Abbott 1987; Allaine 2000; Armitage 1999; Bennett 1994; Solomon and French 1997; Wasser and Barash 1983; Waterman 2002). The formation of matriline and the reproductive suppression of younger, subordinate females are the major components of the reproductive strategies of female yellow-bellied marmots with fitness consequences (Armitage 1999, 2003b, 2007). Survival and net reproductive rate increase as matriline size increases, then decrease in matriline with >3 adult females (Armitage and Schwartz 2000). About 63% of the matriline had 2 or more adult females. In the absence of older females, the presence of younger kin increased the percentage of females reproducing and females living with younger kin produced more litters than females in matriline of 1 (Armitage 2003b). Matriline of 2 or more adult females can prevent incursions of nonmatrilineal females, either other colonial residents or potential immigrants, into the matrilineal home range (Armitage 2003b, 2003c). Recruitment of daughters into the matriline increases the likelihood that a female will produce reproductive descendents (Armitage 2002). By suppressing reproduction of younger females, likely their daughters, older females increase the probability of recruiting additional daughters (coefficient of relatedness, $r = 0.5$) rather than granddaughters ($r = 0.25$) into the matriline. Obviously, fitness increases when daughters eventually reproduce and highly successful females produce daughters that produce their granddaughters (Armitage 1991, 1992).

Is an alternative strategy available to young females other than remaining in the matriline and encountering reproductive suppression? The alternative is to disperse and attempt to secure residency in another habitat patch. Dispersal occurs primarily when females are yearlings, the summer before reaching the reproductive age of 2 years (Armitage 1991). However, mortality is higher in dispersers than in residents (Van Vuren and Armitage 1994). The probability of successful immigration into a colony is low; only 6 of 32 yearling female dispersers trapped at a colony site were successful immigrants.

None were successful if philopatric yearlings were present (Armitage 2003c).

The philopatric female becomes a recruit at age 2 years, but the mean age of known-age immigrants was 2.8 years. Effectively, an immigrant is unlikely to reproduce before age 3 years (Armitage 2003c) and only 20 (26%) of 77 immigrant adults reproduced in their year of immigration (Armitage and Schwartz 2000). By contrast, 39.6% of philopatric recruits are likely to reproduce by age 3 (Armitage 2003b). Thus, dispersal and subsequent immigration into a colonial site does not represent a gain in fitness and probably, given the higher mortality of dispersers and lower percentage of immigrants reproducing, results in lower fitness. Furthermore, the philopatric female may avoid reproductive suppression; for example, highly successful matriline of 4 were characterized by nearly all older and young females weaning litters (Armitage 2007). Finally, the young female may have the opportunity to move to a vacant space in the habitat patch, bud off a new matriline, and reproduce or the older female may die, thus providing the young female with a reproductive opportunity (Armitage 2003b; Armitage and Schwartz 2000). We conclude that remaining in the matriline, even with the possibility of reproductive suppression, is a more viable strategy than dispersing and attempting immigration elsewhere.

Inclusive fitness theory is frequently invoked to explain behaviors such as cooperative breeding and reproductive skew (Griffin and West 2002). The inclusive fitness-based explanation of such behaviors assumes that indirect fitness benefits of delaying or foregoing reproduction balance or exceed loss of direct fitness from not reproducing. Our results show that neither the future component of direct fitness nor the indirect fitness gained from delaying or foregoing reproduction are sufficient to balance the loss of direct fitness that results from delaying or foregoing reproduction. Very few studies have empirically examined the relative contribution of direct and indirect fitness to inclusive fitness (Creel and Waser 1994; Dickinson 2004; MacColl and Hatchwell 2004). In the cooperatively breeding western bluebird (*Sialia mexicana*), helpers had a higher indirect fitness, but they adjusted helping behavior in response to the potential for direct, rather than indirect, fitness benefits (Dickinson 2004; Dickinson et al. 1996). Our study suggests that indirect fitness is an important component of inclusive fitness of individuals who reproduce at least once, because indirect fitness composes 22% of the inclusive fitness. However, indirect fitness benefits are insufficient to compensate for the loss of direct fitness resulting from foregoing reproduction. We suggest that delayed age of 1st successful reproduction in yellow-bellied marmots is primarily a response to social, rather than ecological, constraints (Armitage and Schwartz 2000). However, we note that despite our best efforts, our study suffered from 2 potential shortcomings. First, an important component of inclusive fitness is the component of fitness attributable to behavioral interactions among individuals (Grafen 1984; Griffin and West 2002; Hamilton 1964). Behavioral interactions that influence fitness likely occur in yellow-bellied marmots (Armitage 2003b; Armitage and Schwartz 2000). Unfortunately, however,

quantifying fitness consequences of behavioral interactions is notoriously difficult, and we were not able to quantify the component of inclusive fitness attributable to interactions among individuals; consequently, the generality of our conclusions may be somewhat constrained. Second, some of the females who mated, produced a litter, or both, could have aborted or lost the litter before weaning (e.g., Waterman 2002). However, both of these events occur in the reproductive suppression of subordinate alpine marmots by dominant females (Hacklander et al. 2003). We could not determine reproductive status of females before weaning because of inaccessibility of our study site during estrus or the mating season. Consequently, we could not differentiate between reproductive delay (failure to achieve physiological maturity) from reproductive failure (failure to wean a litter—Wasser and Barash 1983). However, progesterone concentrations from a sample of 81 adult females indicate that reproductive suppression and not reproductive delay is the critical factor responsible for the lack of reproductive success. Progesterone concentrations are high in early gestation, decrease in late gestation, and increase during lactation (Armitage and Wynne-Edwards 2002). Of seventeen 2-year-old nonreproductive females with gestational progesterone concentrations significantly lower than those of reproductive females, 16 lived with at least 1 older female. Two 2-year-olds that initiated reproduction, as evidenced by significantly higher progesterone levels than those of nonreproductive females, lived with older females and failed to wean a litter. Only 2 of six 2-year-olds that weaned litters lived with older females; this proportion of 2-year-olds weaning litters in the presence of older females does not differ greatly from the long-term population mean. The pattern of progesterone concentrations in yellow-bellied marmots is similar to that in reproductive and reproductively suppressed alpine marmots (Hacklander et al. 2003). Thus, it seems unlikely that reproductive delay accounts for the reproductive failure of young females. Nonetheless, we recognize that our data are limited, and advise caution in the interpretation of our results.

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