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Who pays? Intra- versus inter-generational costs of reproduction

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Abstract. Reproduction is thought to be costly for female mammals due to high energetic costs associated with pregnancy and lactation. Such costs of reproduction can be particularly high for younger females, who are less experienced and smaller than fully grown adults, and can manifest themselves within (intra-individual or intra-generational trade-offs) or between (inter-generational trade-offs) generations. Using lifetime survival and reproductive histories of 416 female golden-mantled ground squirrels (*Callospermophilus lateralis*) in Colorado, USA, we tested for the evidence of intra- and inter-generational trade-offs between age of first reproduction and fitness and its components. Females who waited to begin reproduction lived longer but they did not experience a greater number of lifetime reproductive events, did not produce larger litters, nor did they have higher lifetime reproductive success than those females who attained reproductive maturity earlier. However, delaying age of first reproduction substantially reduced individual fitness, quantified as the dominant eigenvalue of the population projection matrix, suggesting that fitness benefits of earlier maturity exceeded associated costs. Females born to mothers who delayed age of first reproduction had a higher probability of surviving to reproduce at least once during their lifetimes. Thus, in our study system, daughters pay for their mothers' reproductive decisions, suggesting that some costs of reproduction can transcend a generation. Studies testing for costs of reproduction on survival or reproductive output within a short timeframe or those focusing within a generation may fail to detect inter-generational trade-offs.

Key words: age of first reproduction; *Callospermophilus lateralis*; Colorado; cost of reproduction; individual fitness; intra- vs. inter-generational trade-offs; life history trade-offs; lifetime reproductive success.

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INTRODUCTION

Life history theory posits that a simultaneous optimization of multiple fitness traits is constrained by life history trade-offs, such that an increase in fitness due to a beneficial change in one trait is counteracted by a decrease in fitness due to a detrimental change in another trait (Williams 1966, Partridge and Harvey 1985, Reznick 1985, Stearns 1989, Roff and Fairbairn 2007). One type of trade-off that features prominently in life history theory is the cost of reproduction, a negative trade-off between current reproduction and survival and/or current reproduction and future reproduction (Williams 1966, Reznick 1985, Stearns 1989, 1992, Roff 2002). Virtually all optimality models of life history evolution assume costs of reproduction (Stearns 1992, Roff 2002), and empirical studies have shown that such costs do exist in many taxa, including plants (Law 1979, Primack and Hall 1990, Obeso 2002), insects (Fowler and Partridge 1989, Ellers 1996, Prowse and Partridge 1997, Flatt 2011), fish (Reznick 1983, Roff 1984, Lester et al. 2004), reptiles (Miles et al. 2000, Rivalan et al. 2005), birds (Dijkstra et al. 1990, Nilsson and Svensson 1996, Tettamanti et al. 2012), and mammals (Clutton-Brock et al. 1983, Bercovitch and Berard 1993, Festa-Bianchet et al. 1998, Fisher and Blomberg 2011, Desprez et al. 2014).

Most empirical studies of the cost of reproduction in vertebrates have been short-term studies focusing on the trade-off between reproduction in one breeding season and survival/reproduction in the next or next few seasons (Nilsson and Svensson 1996, Miles et al. 2000, Koivula et al. 2003, Hanssen et al. 2005, Cox et al. 2010, Hamel et al. 2010). Fewer studies have examined costs of reproduction using lifetime, composite measures of fitness (but see McGraw and Caswell 1996, Oli et al. 2002, Oli and Armitage 2003, Kruger 2005, Hadley et al. 2007, Descamps et al. 2009). Rarity of studies examining the costs of reproduction using lifetime fitness measures is due primarily to the fact that such studies require survival and reproductive histories of individuals during their lifetimes; these studies are generally time-consuming and expensive (Clutton-Brock and Sheldon 2010).

The cost of reproduction can occur within a generation (intra-generational costs or trade-offs), but they can also transcend generations (inter-geneational costs or trade-offs; Stearns 1989, 1992). However, studies of inter-generational costs of reproduction have been rare, with most work focusing on experimental manipulation of litter/clutch size or environment of the mother to examine effects on offspring survival or reproduction (Nur 1984, Dijkstra et al. 1990, Hare and Murie 1992, Koivula et al. 2003, Hanssen et al. 2005, Plaistow et al. 2006; also see Morris 1986), or field studies comparing parental survival or reproduction in one season to offspring survival the next (or next few) seasons (Hamel et al. 2010). Rarer still are empirical studies of inter-generational costs using lifetime fitness measures.

Here, we examine intra- and inter-generational costs of reproduction in golden-mantled ground squirrels (*Callospermophilus lateralis*; hereafter, GMGS) using lifetime fitness measures and components thereof. Costs of reproduction are thought to be particularly high in female mammals because of the energy and nutrient requirements and physical changes that an individual must undergo due to pregnancy and lactation (Speakman 2008). In particular, age of first reproduction is thought to be an important life history trait, with substantial intra- and inter-generational fitness costs (Cole 1954, Stearns 1992, Lindstrom 1999). Thus, we examined whether or to what extent age of first reproduction influences fitness (and its components) both within and between generations. Specifically, we expected that early age of first reproduction would: (1) reduce longevity, reproductive lifespan, average litter size, lifetime number of reproductive events, and lifetime measures of fitness within a generation, and (2) reduce daughters' probability of survival to maturity, and lifetime fitness measures and components thereof. Our study system was ideal for testing the intra- vs. inter-generational costs of reproduction because age of first reproduction varies widely in GMGS, and also because we had complete survival and reproductive information on 416 females over a 24-year study period.

METHODS

Study area and species

We studied GMGS at the Rocky Mountain Biological Laboratory (RMBL) in the East River Valley, Gunnison County, Colorado, USA (38° 58′N, 106° 59′W, elevation 2890 m). The study area is a 13-ha subalpine meadow, interspersed with spruce (*Picea* spp.) groves and aspen (*Populus tremuloides*) woodlands. The meadow is bordered on two sides by water, the East River to the west and Copper Creek to the south, which form barriers for dispersal. The other two sides of the meadow (north and east) are aspen woodlands, which are not inhabited by GMGS. The nearest population of GMGS outside of the study area is about 250 m to the east, but dispersal events typically involve moves of less than 250 m, though they can range more than 1000 m (Jesmer et al. 2011).

Golden-mantled ground squirrels prefer open habitats such as meadows and rocky slopes close to grasslands, and they occur along a broad elevational gradient (~1000–4000 m;Bartels and Thompson 1993, Shick et al. 2006). The GMGS is an omnivore (Bartels and Thompson 1993), and at RMBL they mostly forage on herbaceous vegetation such as forbs and grasses. GMGS are an asocial diurnal species, which hibernate during the winter because of cold temperatures and food shortages, with entrance and emergence times from hibernation dependent on snowfall and altitude (Ferron 1985, Bartels and Thompson 1993).

At RMBL, they usually emerge from hibernation in May, and reenter hibernation in late August or early September. Females breed after emergence from hibernation, with their litters emerging from their natal burrow typically in late June to mid-July. After emerging from hibernation, the squirrels quickly gain weight, and store fat before the next winter (Phillips 1984). Population size fluctuates substantially over time, as do the demographic parameters (Kneip et al. 2011, Hostetler et al. 2012). Their main predators at RMBL were red fox (*Vulpes vulpes*), long-tailed weasel (*Mustela frenata*), and short-tailed weasel (*Mustela erminea*).

Field methods

We censused the GMGS population annually for 24 consecutive years (1990–2014) by trapping with Tomahawk live traps (Model 201) during late May and early June until all squirrels were captured and identified. Each squirrel received numbered ear tags for permanent identification and a unique dye mark to the dorsal pelage for visual identification at a distance. Survival was based on presence or absence in the annual census. Reproduction by adult females was suggested by swollen nipples early in the active season, and then confirmed by emergence of a litter from the mother's burrow. Pups in each litter were trapped, sexed, and ear-tagged upon emergence.

A total of 1301 GMGS were trapped during this study period, of which 416 were females with known lifetime reproductive performance and survival. The rest of the trapped GMGS were either males, or transient individuals that passed through the study area but did not become resident.

Life history traits and measures of fitness

We measured the following life history traits: (1) age of first reproduction (α), the earliest age a female successfully weaned a litter, (2) age of last reproduction (ω), the latest age a female successfully weaned a litter, (3) longevity or lifespan (β), the number of years a female was alive, (4) reproductive lifespan (β_R), the number of years between the age of first and last reproduction, (5) lifetime number of reproductive events (RE), the number of times a female successfully weaned a litter during her lifetime, (6) average litter size (LS), the average size of successfully weaned litters throughout a female's lifetime, (7) litter size at weaning, the size of litter an individual was born into when it first emerged from the natal burrow, and (8) litter order, the number corresponding to the position of the litter an individual was born into in regards to all litters of the mother. We used the age at which a female successfully weans a litter as a measure of age of first reproduction. Age of first mating or first oestrous cycle are other candidates for the age of first reproduction; however, these events would not contribute to individual fitness unless they lead to weaned offspring.

For each female, we quantified fitness using two methods. The first, lifetime reproductive success (LRS; Clutton-Brock 1988, Newton 1989), is simply the total number of offspring that a female weaned over her lifetime. The second fitness measure we used was the individual fitness (λ), calculated using the matrix method (McGraw and Caswell 1996, Oli and Armitage 2003). We constructed a population projection matrix $\mathbf{A}_i$ for each female GMGS with one-half times the litter size as an estimate of age-specific fertility rate (the first row of the matrix) until reproduction stopped at age ω, and survival probability of 1.0 along the lower diagonal until the female died. The individual fitness, λ, was then calculated as the dominant eigenvalue of the matrix. This fitness measure takes into account both the timing and the amount of reproduction, whereas LRS only considers the number of offspring (McGraw and Caswell 1996, Oli and Armitage 2003). The appropriateness of each fitness measure has been debated (Brommer et al. 2002), so both measures were included in the present study.

Statistical analysis

Intra-generational costs of reproduction

We tested for intra-generational costs of reproduction by examining the relationship between a female's age of first reproduction (α) and lifetime measures of fitness (LRS and λ) and their components (β, β_R, RE, LS). All female squirrels that reproduced at least once with known age of first reproduction were included in the analysis (n = 57; Fig. 1). Because β and RE represent discrete count data, we modeled the relationship between α and these traits using

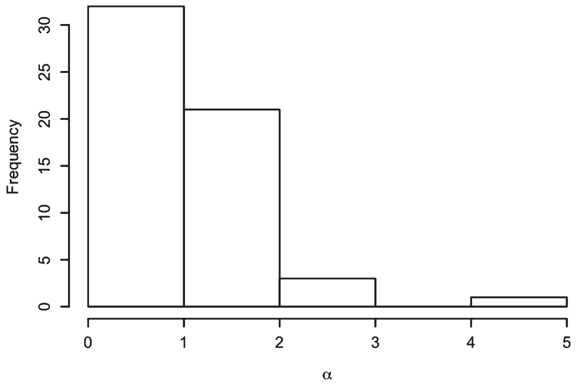

Fig. 1. Frequency distribution of the age of first reproduction (α) in female golden-mantled ground squirrels in Rocky Mountain Biological Laboratory, Colorado, USA.

Poisson regression (i.e., generalized linear model with Poisson distribution; Crawley 2007). The relationships between α and LRS and α and β_R were modeled using negative binomial regression (i.e., generalized linear model with negative binomial distribution) due to poor fit of the Poisson model attributable to overdispersion. We modeled the relationship between α and LS and log-transformed λ using ordinary least square regression (i.e., generalized linear model with Gaussian distribution). We tested for non-linearity in the aforementioned relationship by including a quadratic term; a model including quadratic term was favored over a linear model only for the relationship between α and log-transformed λ.

Inter-generational costs of reproduction

We examined inter-generational costs of reproduction by examining the relationship between mother's age of first reproduction and their daughter's lifetime measures of fitness and their components. The probability that a daughter survives to wean at least one litter was modeled using logistic regression (i.e., generalized linear model with binomial distribution). The relationship between mother's α and daughter's fitness and its components were modeled using the same distributions as specified above for intra-generational trade-offs. These analyses were run using all mother and daughter pairs, when the daughter weaned at least one litter during her lifetime and had known α (n = 29). Lastly, we modeled the relationship between daughters' fitness (LRS and λ), and litter order and litter size they were born into using negative binomial regression and log normal regression, respectively.

All statistical analyses were performed using R version 3.1.1 (R Development Core Team 2008).

RESULTS

Of the 416 female GMGS for which we had complete lifetime survival and reproductive data, 57 (14%) successfully weaned at least one litter during their lifetime. The majority (56%) of the squirrels successfully weaned a litter during their first year, with the latest age of first reproduction at 5 years of age (Fig. 1). The number of reproductive events ranged from 1 to 7, but most squirrels (58%) weaned only one litter during their lifetime. Lifetime mean litter size ranged from 1 to 7 individuals, lifespan ranged from 1 to 9 yrs, and reproductive lifespan ranged from 0 to 6 yrs. Measures of fitness also varied substantially, with LRS ranging from 1 to 37, and λ from 0.707 to 4.781 (Table 1).

Intra-generational costs of reproduction

Female GMGS who delayed age of first reproduction lived longer (slope parameter, $\beta \pm SE = 0.243 \pm 0.081$, $P = 0.003$) but did not have longer reproductive lifespans ($\beta \pm SE = 0.100 \pm 0.267$, $P = 0.709$). They did not have a higher number of reproductive events during their lifetimes ($\beta \pm SE = 0.399 \pm 0.131$, $P = 0.761$),

Table 1. Summary statistics for fitness and its components.

Life history trait/fitness measure	Mean ± SE	Minimum	Maximum
α	1.544 ± 0.100	1	5
β	3.211 ± 0.195	1	9
β_R	0.754 ± 0.159	0	6
RE	1.702 ± 0.150	1	7
LS	4.792 ± 0.166	1	7
LRS	8.579 ± 0.905	1	37
λ	2.213 ± 0.113	0.71	4.8

Note: α = age of first reproduction; β = longevity or lifespan; β_R = reproductive lifespan; RE = lifetime number of reproductive events; LS = mean litter size; LRS = lifetime reproductive success; and λ = individual fitness.

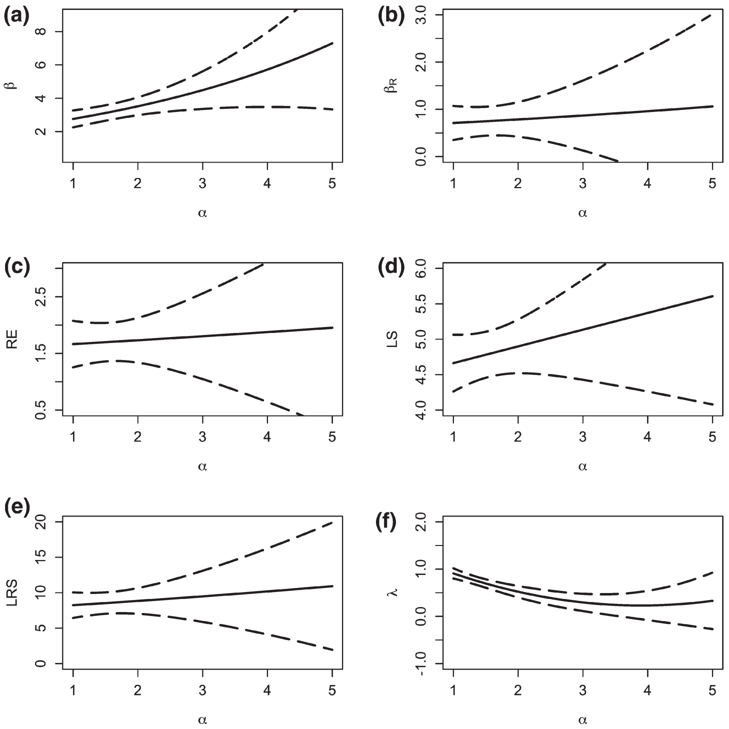

Fig. 2. The relationship between age of first reproduction (α) and (a) longevity (β), (b) reproductive lifespan (β_R), (c) number of reproductive events (RE), (d) mean litter size (LS), (e) lifetime reproductive success (LRS), or (f) individual fitness (λ).

nor did they have larger litters overall ($\beta \pm SE = 0.236 \pm 0.220$, $P = 0.289$; Fig. 2). Delaying the age of first reproduction did not affect LRS ($\beta \pm SE = 0.070 \pm 0.119$, $P = 0.553$); however, it significantly reduced λ ($\beta_1 \pm SE = -0.631 \pm 0.178$, $P = 0.0008$, $\beta_2 \pm SE = 0.081 \pm 0.037$, $P = 0.033$; Fig. 2).

Inter-generational costs of reproduction

GMGS females whose mothers began reproduction at a later age had a marginally higher probability of surviving to reproduce at least once ($\beta \pm SE = 0.3288 \pm 0.1869$, $P = 0.079$; Fig. 3). Mother's age of first reproduction did not affect daughter's age of last reproduction ($\beta \pm SE = -0.048 \pm 0.108$, $P = 0.657$), longevity ($\beta \pm SE = -0.012 \pm 0.087$, $P = 0.891$), or lifetime number of reproductive events ($\beta \pm SE = -0.005 \pm 0.119$, $P = 0.964$). Daughters born to females who delayed age of first reproduction generally produced smaller litters ($\beta \pm SE = -0.304 \pm 0.171$, $P = 0.087$; Fig. 4). Mothers' age of first reproduction generally negatively influenced their daughters' LRS and λ (LRS: $\beta \pm SE = -0.069 \pm 0.089$, $P = 0.440$; λ: $\beta \pm SE = -0.053 \pm 0.062$, $P = 0.407$; Fig. 4).

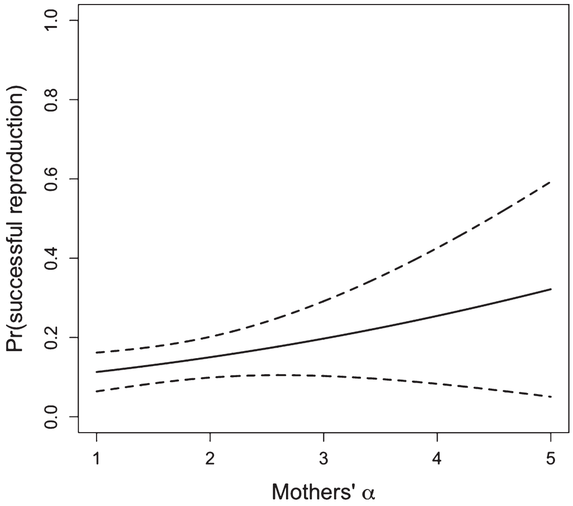

Fig. 3. The relationship between mothers' age of first reproduction (α) and the proportion of their daughters that successfully weaned at least one litter.

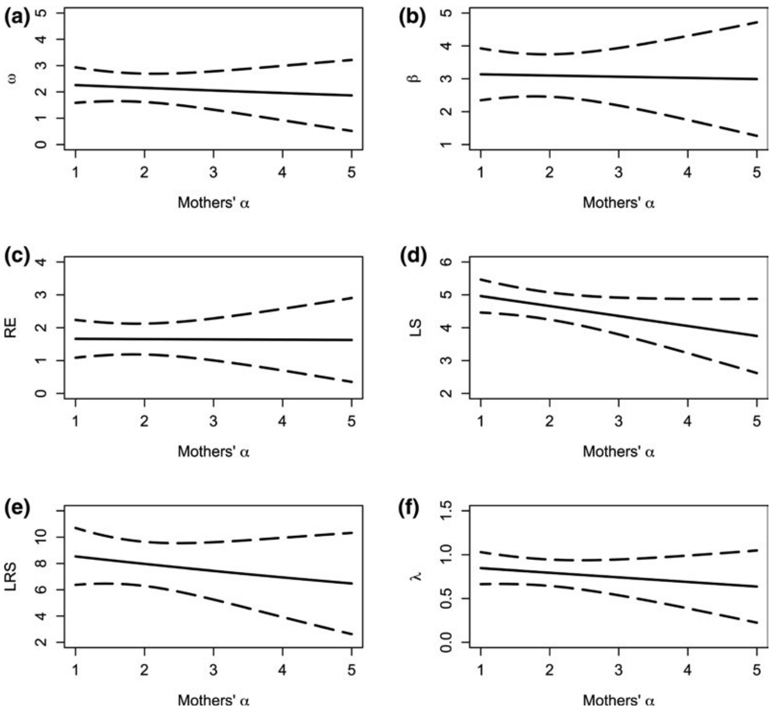

Fig. 4. The relationship between mother's age of first reproduction (α) and daughter's (a) age of last reproduction (ω), (b) longevity (β), (c) number of reproductive events (RE), (d) mean litter size (LS), (e) lifetime reproductive success (LRS), or (f) individual fitness (λ).

Daughters' LRS and λ were negatively affected by litter order in which they were born; fitness of female GMGS born into mothers' earlier litters was higher than those for the later litters (LRS: $\beta \pm$ SE = −0.216 ± 0.101, $P = 0.032$; λ: $\beta \pm$ SE = −0.137 ± 0.058, $P = 0.025$). Finally, daughters born into smaller litters had higher fitness than those born into larger litters (LRS: $\beta \pm$ SE = −0.183 ± 0.081, $P = 0.025$; λ: $\beta \pm$ SE = −0.168 ± 0.055, $P = 0.005$; Fig. 5).

DISCUSSION

Virtually all optimality models of life history evolution assume that reproduction is costly (Stearns 1989, 1992, Roff 2002). Among various reproductive investments, age of first reproduction is particularly important because it can affect survival, future reproduction, and ultimately, individual fitness (Cole 1954, Stearns 1992, Lindstrom 1999). Age of first reproduction of mothers can potentially influence life history traits and fitness of the offspring as well. For example, offspring born to young, inexperienced females who may not have fully grown to adult size are less likely to survive to reproductive age and may thus have lower fitness compared to those born to older, more experienced mothers (Stearns 1989, 1992). Thus, costs of earlier age of first reproduction can be expressed both within as well as between generations. But, who pays these costs? Is it the individuals, their offspring, or perhaps both?

Female GMGS who delayed age of first reproduction lived longer, but they did not necessarily experience a longer reproductive lifespan. However, contrary to our expectations, females that delayed age of first reproduction did not reproduce more frequently or produce larger litters. Although these results are correlative in nature and do not necessarily imply causation, it appears that benefits of earlier age of first reproduction far exceed any potential costs in GMGS. Similar results have been reported for North American red squirrels (*Tamiasciurus hudsonicus*; Descamps et al. 2009), Soay sheep (*Ovis aries;*

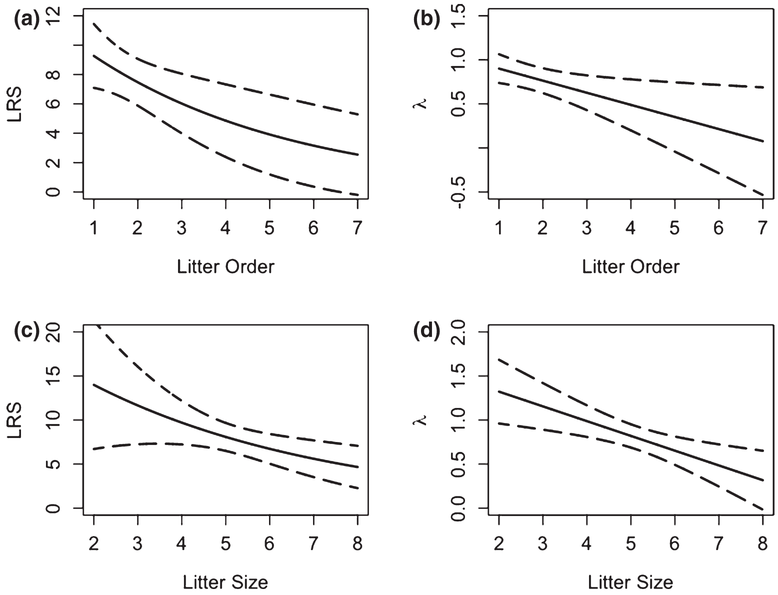

Fig. 5. The relationship between daughter's fitness (LRS and λ) and litter order (a–b), or litter size (c–d).

Clutton-Brock and Pemberton 2004), Weddell seals (*Leptonychotes weddellii;* Hadley et al. 2007), brown antechinuses (*Antechinus stuartii*; Fisher and Blomberg 2011), and brown anoles (*Anolis sagrei*; Cox et al. 2010).

Phenotypic correlational studies have been the primary focus of life history trade-offs in vertebrates (Stearns 1992, Roff 2002). However, what ultimately matters is how reproductive investments affect integrative, lifetime measures of individual fitness (McGraw and Caswell 1996, Oli and Armitage 2003). This is because natural selection acts on fitness, and favors a combination of life history traits that maximize fitness, subject to appropriate constraints and trade-offs (Bell 1980, Reznick 1985, Stearns 1989). Thus, we also examined whether or to what extent age of first reproduction influenced two lifetime measures of fitness: λ and LRS (Clutton-Brock 1988, Newton 1989, McGraw and Caswell 1996). Interestingly, fitness costs of earlier age of first reproduction in GMGS depended on the fitness measures considered (see Brommer et al. 2002 for discussion of various fitness measures): earlier age of first reproduction had no effect on LRS, but it significantly increased λ. Similar results were reported by many studies that used both LRS and λ as fitness measures (e.g., European sparrowhawks (*Accipiter nisus*) and blue tits (*Cyanistes caeruleus*): McGraw and Caswell 1996, Ural owls (*Strix uralensis*): Brommer et al. 1998, wood ducks (*Aix sponsa*): Oli et al. 2002, yellow-bellied marmots (*Marmota flaviventris*): Oli and Armitage 2003). Given these somewhat different results, what can one conclude regarding the costs of early reproductive maturity?

In the context of our study, λ is probably a better measure of fitness than LRS because λ simultaneously considers timing as well as amount of reproduction, whereas LRS only considers the amount of reproduction (McGraw and Caswell 1996, Oli and Armitage 2003). Arguably, timing of reproduction is an important component of fitness, because it substantially affects the rate at which one's genes are represented in future generations; everything else being equal an individual or a genotype that begins reproduction earlier will have a higher fitness (Oli 2003). Furthermore, it is reasonable to expect that natural selection favors age of first reproduction that yields the highest fitness. Thus, if delaying age of first reproduction leads to reduction in fitness, one can predict that most individuals in the population should attempt to reproduce at the earliest possible age. Consistent with this expectation, a majority of GMGS started breeding during their first year of reproductive maturity. Similar results have been reported for wood ducks (Oli et al.

2002), yellow-bellied marmots (Oli and Armitage 2003), and Ural owls (Brommer et al. 1998). Nevertheless, several studies have concluded that delaying age of first breeding has little or no influence on fitness or its components. For example, early age of first reproduction did not affect survival of female rhesus macaques (*Macaca mulatta;* Bercovitch and Berard 1993), mountain goats (*Oreamnos americanus;* Hamel et al. 2010), female bighorn sheep (*Ovis canadensis;* Berube et al. 1999), or wandering albatross (*Diomedea exulans;* Weimerskirch 1992). Why these conflicting results?

We suggest that costs of earlier age of first reproduction in mammalian species depend on the tempo of life history (Oli 2004) – the relative position of a species along the fast-slow continuum (Gaillard et al. 1989, Read and Harvey 1989, Promislow and Harvey 1990). Species that occupy the "fast" end of the continuum begin reproduction earlier in life, produce large litters, have short generation times and die young, whereas those occupying the "slow" end of the continuum mature later, produce smaller litters, have long generation times and live longer (Gaillard et al. 1989, Read and Harvey 1989, Promislow and Harvey 1990, Oli 2004). It has been proposed that fitness is highly sensitive to changes in reproductive parameters, especially age of first reproduction, in species that occupy the fast end of the continuum (Oli and Dobson 2003, Oli 2004, Dobson and Oli 2008). In such species, delaying age of first reproduction would lead to substantial reduction in fitness; costs of early reproduction in such species, if any, should be a reduction in survival but fitness benefits of earlier maturity should balance or exceed these costs. Consequently, earlier age of first reproduction should be favored by natural selection. In contrast, fitness is relatively insensitive to changes in age of first reproduction (and reproductive parameters generally) in species that occupy the slow end of the continuum. In such species, changes in age of first reproduction would have little effect on fitness; consequently, we expect little selection pressure on earlier maturity. Hence, we predict that earlier maturity should be favored in species at the fast end of the continuum, and that optimal age of first reproduction in such species should be the earliest possible age at which reproduction is possible, which should also be the most frequent age of first reproduction. In contrast, we predict weaker selection pressure on the age of first reproduction in species with slow life histories, and consequently, little directional selection on this variable and a wide distribution of age of first reproduction. Because species at the slow end of the continuum are generally characterized by higher survival and lower reproductive rates, any cost of reproduction in such species is likely to be the survival cost.

To test this idea, we calculated the ratio of the magnitude of reproduction relative to the onset of reproduction (F/α and m/α ratios; F – fertility rate, α – age of first reproduction, m-average fecundity; Oli 2004, Oli and Dobson 2005). The m/α ratio for GMGS calculated based on data presented in Table 1 was 3.2, showing that this species occupies the fast end of the continuum, using Oli and Dobson's (2003, 2005) criteria. Thus, one would expect to see a discernible cost of reproduction in this species. Similarly, early reproduction was costly in terms of survival but there was little evidence for reproductive cost in North American red squirrels ($m/\alpha = 1.48$) and Soay sheep ($m/\alpha = 1$) (Clutton-Brock and Pemberton 2004, Descamps et al. 2006). A majority of yearlings attain reproductive maturity in both species, as expected for species occupying the fast end of the continuum. Rhesus macaques ($m/\alpha = 0.09$) fall onto the slow end of the continuum. As expected, early reproduction did not affect survival but negatively affected future reproduction, with the majority of macaques reproducing for the first time at 4 years of age (Bercovitch and Berard 1993). Likewise, there was no evidence for the survival cost of early maturity in Mountain gorillas (*Gorilla beringei;* $m/\alpha \approx 0.125$), another species occupying the slow end of the continuum (Robbins et al. 2011). Lastly, the Weddell seal ($m/\alpha = 0.36$) falls in the middle of the continuum. Early reproduction was costly in this species in terms of future reproductive potential (Hadley et al. 2007). As expected, age of first reproduction varied widely in this population from 4 to 14 years, with no evidence for directional selection on the age of first reproduction (Hadley et al. 2007).

We note that variation in individual quality (Cam et al. 2004, Wilson and Nussey 2010) can potentially explain some of our results. Some individuals are inherently of higher quality than the others; they begin reproducing earlier in life, reproduce more often and/or have a longer reproductive lifespan, and thus have higher fitness than lower quality individuals. Variation in individual quality could be based on the actual genotype of the individual, or due to the environment in which it was raised (Wilson and Nussey 2010). This can potentially lead to a positive correlation between age of first reproduction and fitness as well as other fitness traits, or between fitness of mothers and of their offspring.

GMGS females born to mothers with delayed age of reproduction had a higher probability of surviving to realize reproduction. However, among females who survived to successfully reproduce at least once, mothers' age of first reproduction had no effect on fitness. These results suggest that the inter-generational cost of earlier maturity is survival of daughters to reproductive age. The fact that only 14% of GMGS females survive to realize reproduction and that the probability of surviving to reproductive age is strongly influenced by mothers' age of first reproduction point to the possibility that daughters pay for mothers' early age of first reproduction. Also, females born into smaller litters generally had higher fitness compared to those born into larger litters. These results suggest trade-offs between number and quality of offspring (Stearns 1992), although some of these results may be influenced by shared phenotypes or environments, as discussed previously. Experimental studies manipulating clutch or litter size have found similar trade-offs between the number and quality of offspring (e.g., Tree swallow (*Tachycineta bicolor*): De Steven 1980, Columbian ground squirrels (*Urocitellus columbianus*): Neuhaus 2000, bank vole (*Myodes glareolus*): Koivula et al. 2003, common eider (*Somateria mollissima*): Hanssen et al. 2005).

Over 25 years ago, Stearns (1989) pointed out that mothers' allocation decisions could potentially influence offspring's fitness (or fitness components). He further argued that inter-generational trade-offs are just as important as intra-generational trade-offs in life history evolution, yet they do not receive as much attention. Even today, studies investigating intra- as well as inter-generational costs of reproduction using lifetime fitness measures are uncommon. Adequate quantification of intra- and inter-generational costs of reproduction requires lifetime reproductive and survival data for at least two generations, which are more difficult to collect than data needed to test if reproductive allocation in one season influences survival or reproduction in the next (or next few) seasons. Our study is one of the first to examine both intra- and inter-generational effects of age of first reproduction in mammals using lifetime fitness measures. We find that fitness benefits of earlier maturity exceeded any associated costs, leading to the preponderance of females attempting to breed as yearlings. However, inter-generational survival costs of reproduction may be substantial enough to cause variation in age of first reproduction in our study population. We note that our results are based on a correlative study; correlations can obscure important costs or create apparent benefits. Nonetheless, our results are consistent with those of Oli and Armitage's (2003, 2008) and suggest that GMGS's reproductive decisions tend to maximize fitness of the mothers at the potential detriment of fitness of their offspring.

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