

How do animals optimize the size–number trade-off when aging? Insights from reproductive senescence patterns in marmots

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Abstract. We investigated the influence of female age on five reproductive traits and on the offspring size–number trade-off from an extensive data set spanning 20 years of study on free-ranging Alpine marmots. Offspring mass increased with female age, whereas litter size and reproductive allocation remained constant in females up to 10 years of age and declined thereafter. Although reproductive allocation declined, post-weaning juvenile survival and the size–number trade-off did not change markedly throughout a female's lifetime. Senescence of annual reproductive success (i.e., the number of offspring surviving their first hibernation within a given litter) only resulted from senescence of litter size. The data were insufficient to determine whether the decrease in litter size with age was caused by declining litter size at birth, offspring pre-weaning survival, or both. Regardless, our findings demonstrate that marmot females display a size–number trade-off invariant with age, and that their reproductive tactic involves increasing offspring size at the cost of decreasing litter size with increasing age. As a result, reproductive performance remains constant throughout a female's lifetime, despite the deleterious effects of senescence in litter size.

Key words: aging; annual reproductive success; La Grande Sassièrre Nature Reserve, French Alps; litter size; *Marmota marmota*; offspring mass; reproductive allocation.

INTRODUCTION

Understanding the life-history trade-off between the size and number of offspring is crucially important, because it shapes reproductive allocation and thereby parental fitness (Smith and Fretwell 1974, Stearns 1992). Lack (1947) proposed that parents should maximize the number of offspring that they can successfully recruit. In his formulation, the optimal number of offspring is common to all individuals in a given population. However, the number of offspring produced by females varies across individuals (Roff 1992, McNamara and Houston 1996). These observations led Pettifor et al. (1988) to propose that the optimal number of offspring is a state-dependent process that is determined at the individual scale (the optimal investment hypothesis; Morris 1985, 1998). As age is a strong determinant of an individual's state, the number of offspring could be directly influenced by parental age.

While the prediction that the size and number of offspring should co-vary negatively has been intensively investigated (e.g., Walker et al. 2008), how such a trade-off should change with age in iteroparous species remains unknown. However, McNamara and Houston (1996) stated that trade-offs are mediated by individual state, and thus age could be expected to influence the

magnitude of trade-offs. Moreover, the Y model proposed by van Noordwijk and de Jong (1986) demonstrated that the detection of trade-offs is determined by the relative importance of the variation in resource acquisition and in resource allocation. Evidence of age-specific variation in resource acquisition has rapidly accumulated in recent years (e.g., Rutz et al. 2006, MacNulty et al. 2009). Resource acquisition is thus expected to play a key role in shaping the magnitude of trade-offs between the size and number of offspring.

Although no theoretical model has yet launched explicit predictions on how females should partition their reproductive energy budget between allocation to size and number of offspring with increasing age, a few models have included age dependence (Begon and Parker 1986, Kindsvater et al. 2010). Thus, according to Begon and Parker (1986), a decrease in resource acquisition with increasing age should cause either the size or the number of eggs to decrease with female age. Using an age- and state-dependent model, Kindsvater et al. (2010) supported this prediction, but showed that complex patterns of age dependence in offspring size and number occur when the state-dependent response of individuals differs with age. Empirical studies of age-specific variation in the size and in the number of offspring have shown a diversity of patterns. For example, offspring mass at weaning decreased with age in meerkats (*Suricata suricatta*) (Sharp and Clutton-Brock 2010), remained constant in red squirrels (*Ta-*

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miasciurus hudsonicus) (Descamps et al. 2008), and increased in moose (*Alces alces*) (Ericsson et al. 2001). To our knowledge, the influence of maternal age on the size–number trade-off has been tested only on Soay sheep (*Ovis aries*) and did not reveal any alteration of the trade-off with age (Wilson et al. 2009). We do not know whether a constant trade-off is representative of other long-lived species, nor do we know whether it remains after accounting for the many contributing environmental factors that influence life history. Thus, we use detailed individual-based longitudinal data to investigate the effect of female age on offspring size, number, reproductive allocation, the size–number trade-off, post-weaning survival, and annual reproductive success in a long-lived polytocous mammal, the Alpine marmot (*Marmota marmota*).

A reliable measure of an “optimal tactic” implies that the size and the number of offspring should be measured at the end of the maternal allocation (Fisher 1930, Lack 1947), which corresponds to weaning in mammals (Clutton-Brock et al. 1989). However, high mortality before weaning makes it difficult to disentangle the respective contributions of maternal and environmentally driven factors in shaping variation in the size and the number of offspring (e.g., Hayward et al. 2013). Fortunately, in ground-dwelling mammals like marmots, the effects of environmental factors are weak until emergence from the natal burrow (Rödel et al. 2009), allowing us to measure offspring size and number at weaning, when offspring emerge from the natal burrow (see also Broussard et al. 2003, Sharp and Clutton-Brock 2010). Offspring mass and litter size at emergence thus provide reliable measures of total maternal allocation in marmots.

Senescence occurs in most age-structured populations of birds and mammals in the wild (Nussey et al. 2013), but varies in both timing and intensity among traits (e.g., Hayward et al. 2013). We can thus predict that offspring size and number should decline with increasing age, but with different onsets and rates of senescence between traits. Consequently, we expect a female’s overall reproductive allocation to decrease with age. Given that reproductive traits are expected to show highly diversified age-specific patterns (mosaic aging sensu Walker and Herndon [2010]), and considering that age-dependent resource acquisition should influence the magnitude of trade-offs (van Noordwijk and de Jong 1986), we further predict that the size–number trade-off should vary in strength and shape with age. Such changes in resource allocation to the size and/or the number of offspring are likely to impact a female’s fitness, so we also investigated age-specific variation in post-weaning survival and annual reproductive success of females.

METHODS

Population, study site, and data collection

The Alpine marmot is a monogamous cooperative and despotic breeder living in family groups composed

of a dominant pair monopolizing reproduction of sexually mature and immature (yearling) subordinates, and of pups of the year (Cohas et al. 2008). Dominant individuals mate after emergence from hibernation in early to late April. Females give birth to one litter per year after a 30-day gestation period. Litter size varies (in our study) between one and seven offspring with a mean of 3.59 ± 1.25 (all means presented with standard error). Offspring remain in the burrow while nursing, and once weaned emerge aboveground between mid-June and mid-July (see Plate 1).

We collected all data from a wild population located in the Grande Sassi re Nature Reserve (2340 m above sea level, French Alps, 45°29' N, 6°59' E). We monitored 24 different family groups of marmots from mid-April to mid-July between 1990 and 2011 with a combination of capture–mark–recapture (using two-door live traps) and observations (see Cohas et al. [2008] for further details). We tranquilized captured marmots with Zol til 100 at 0.1 mL Zol til per 1 kg marmot mass (Virbac Suisse, Galtbrugg, Switzerland). We individually marked them with a transponder (Trovan, Munich, Germany) and a numbered ear tag. We categorized dominant animals on the basis of sexual maturity (males with a developed scrotum and females with developed teats), and categorized all other animals as subordinates. Social status was further confirmed by behavioral observations. Intensive observations in spring allowed us to record the date and the number of weaned offspring emerging from the natal burrow. We confirmed mother–pup relationships by genetic analyses (Cohas et al. 2008).

Reproductive traits

We recorded five measures of reproductive performance for all dominant females producing at least one offspring in a given year (Appendix A). We measured individual offspring size as the individual mass at weaning with an electronic scale (± 1 mg), litter size as the number of offspring at weaning, reproductive allocation as the total litter mass at weaning (the sum of the standardized individual offspring masses for a given litter, see Appendix C), post-weaning survival as the probability for an offspring to survive its first hibernation, and annual reproductive success as the number of offspring surviving their first hibernation within a given litter (we could not obtain longer estimates of annual reproductive success because most marmots leave their natal family group from two years of age; Cohas et al. 2007). Both post-weaning survival and annual reproductive success were measured accurately because the combination of field observations with the capture–mark–recapture data guaranteed that all pups and yearlings were identified (Cohas et al. 2007). Few Alpine marmots disperse as yearlings. Those few yearlings that attempt to disperse die shortly after (only three cases of yearling dispersal were observed

during the 24 years of study; all led to the death of the individual within a couple of weeks).

We measured litter size, post-weaning survival, and annual reproductive success from 202 litters produced by 69 females and offspring mass for 549 offspring from 158 litters (produced by 63 females; 193 pups could not be captured shortly after weaning). We measured reproductive allocation from the 137 litters (produced by 58 females) for which all offspring were captured. Although dominant female marmots gave birth each year, they consistently failed to raise any offspring when a change of dominant male occurred before weaning (we excluded these data from analysis; Appendix B). Accordingly, the probability that a female reproduces is independent of age in Alpine marmots (Appendix B).

Age determination

We measured female age (in years) from birth and assigned the age of 0 to offspring. The age of mothers varied from 3 to 15 years with a mean of 6.3 years and a median of 6 years. Three- to nine-year-old females produced 172 litters. Females aged 10, 11, 12, 13, 14, and 15 years produced nine, eight, three, three, one, and one litters, respectively. We knew exactly the age of reproductive females born on the study site ($N = 57$ females), but not the age of immigrant reproductive females ($N = 12$). As most marmots disperse at two years of age and never reproduce before three years of age (no female among the 57 females of known age), we assigned the age of three to immigrant females when they became dominant (43 of 57 females of known age became dominant at age three).

We further recorded longevity for 34 females (the remaining 35 females were still alive at the end of the study). Our data set for these females yielded 75 litter masses at weaning, 304 offspring masses at weaning, 109 litter sizes at weaning, 384 post-weaning survival events, and 109 annual reproductive success events. Indeed, individuals in better-than-average quality are expected to live longer, not accounting for selective disappearance that could mask senescence (van de Pol and Verhulst 2006). In addition, we tested for a “last year effect” (LYE, a binary variable indicating whether or not we measured the female’s reproductive traits during its last year of life, see Nussey et al. [2011]), because senescence can involve a sudden deterioration in performance, independent of age, rather than a continuous and progressive decline of performance. Previous studies in wild vertebrates have reported such sudden deterioration of performance during the last year of life (so-called terminal decline; Nussey et al. 2011). Conversely, other studies have reported reproductive success to increase the year prior to death (so-called terminal investment when associated with fitness costs or terminal allocation when not; Weladji et al. 2010). These two opposite processes also have consequences on the detection of senescence.

Statistical analysis

We fitted models involving five traits as dependent variables: offspring mass and litter mass with a normal error distribution, litter size and annual reproductive success with a Poisson distribution, and post-weaning survival (number of offspring from a given litter that survived until the following year as the response variable and the number of offspring at weaning per litter as the binomial denominator) with a binomial distribution. We included mother identity, family, and offspring identity as random effects for all models with offspring mass and solely mother identity for all other models.

The five reproductive traits depend on environmental factors varying in time and space. To account for potentially confounding effects, we included year and the aspect of the territory as factors in all models before testing for any age effect. We further added the age of offspring as a covariate in models of offspring mass, and both the change of dominant male as a factor and the number of helpers as a covariate in models of post-weaning survival and annual reproductive success. From these full models, we selected a baseline model for each reproductive trait by retaining only the confounding variables with statistically significant effects on a given reproductive trait (see Appendix C for further details).

We then fitted age-specific models by adding age as a covariate to the baseline models using linear, quadratic, or smoothed (using penalized regression splines in generalized additive mixed models; GAMM) functions, or as a categorical factor. We further fitted threshold models by holding constant a given reproductive trait until a threshold age, beyond which it started to depend on age. We used the deviance profiles of a continuous-age model with a varying threshold and selected the age leading to the lowest deviance as the threshold age (see Ulm 1989).

We fitted all models with GAMMs to test the potential nonlinear effect of the covariates and to account for the nonindependence of the data caused by repeated measures of mass of a given pup and by multiple litters produced by a given female. We selected models based on the Akaike information criterion (AIC), considering each random effect as one parameter (Pinheiro and Bates 2000). We retained the model with the lowest AIC as the best model. When the difference in AIC between competing models was less than two, we retained the simplest model (Burnham and Anderson 2002). We calculated the Akaike weight (AIC_w) for each model to provide the relative likelihood that the model was the best among the candidate models. We estimated parameters of litter size and annual reproductive success on log scales. We performed analyses in the R software, version 2.14.1 (R Development Core Team 2011) using the function `gamm` in the `mgcv` library (Woods 2006). We report only the results for the best models. Full details of each analysis are included in Appendix C.

In order to assess the robustness of each age-specific model, we repeated all analyses using a data set

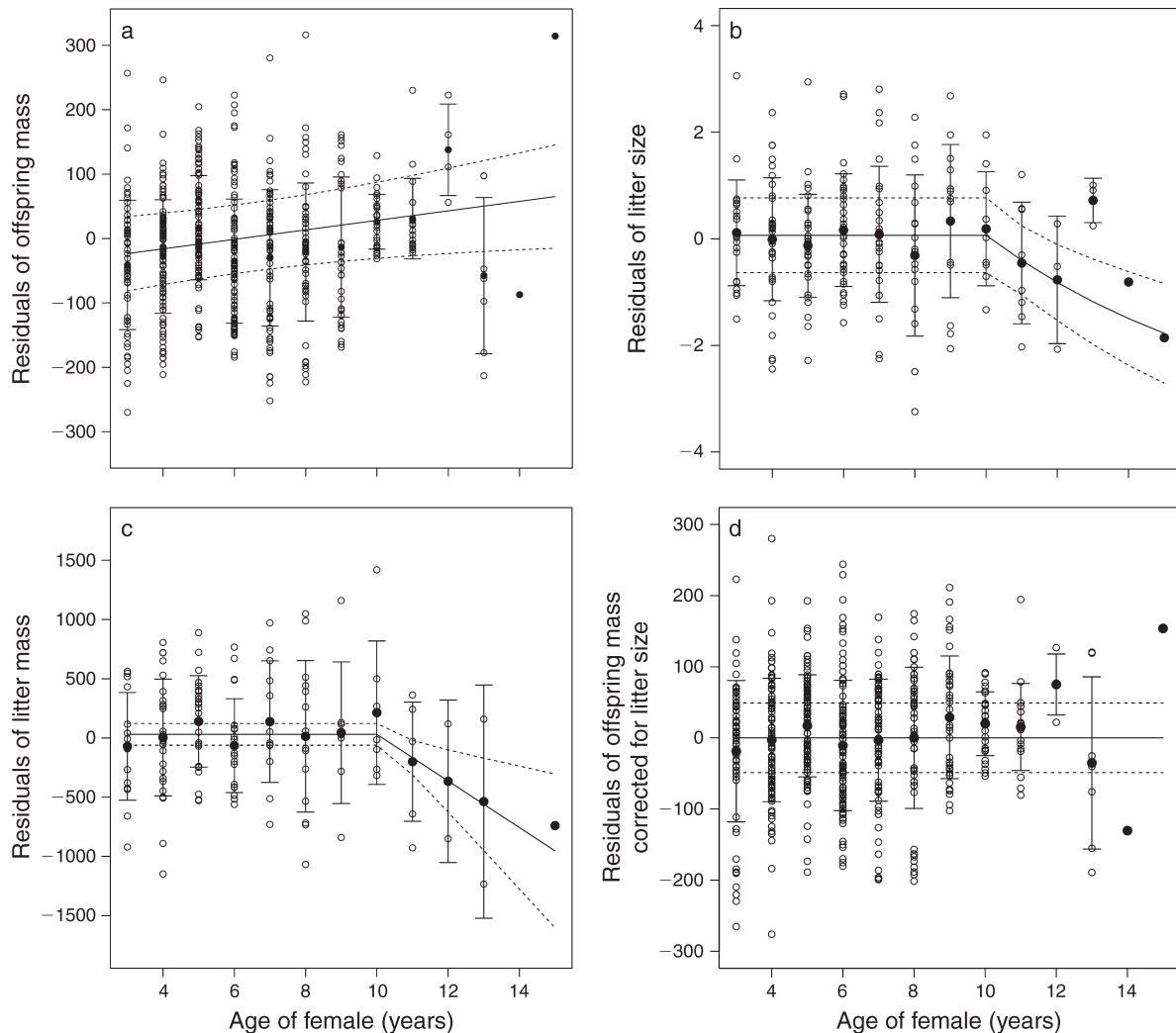


FIG. 1. Age-specific variation in (a) offspring mass, (b) litter size, (c) litter mass, and (d) offspring mass corrected for litter size in female Alpine marmots (*Marmota marmota*) at La Grande Sassi re (French Alps). Residuals are corrected for confounding factors (year and aspect of the territory for all analyses, plus the age of offspring for analyses of offspring mass). Solid circles represent mean residual reproductive traits per age with their associated standard error bars. Open circles represent the observed residual reproductive traits. Solid lines represent predictions of the best model, with 95% confidence intervals (CI) indicated as dashed lines in panels: (a) increasing offspring mass with female age, (b) a constant litter size until 10 years of age followed by a linear decline with increasing female age, (c) a constant litter mass until 10 years of age followed by a linear decline with increasing female age, and (d) a constant offspring mass corrected for litter size with female age.

restricted to females younger than 13 years old. We also repeated all analyses with a data set restricted to females of known age only. The results were unchanged, so we do not report them here.

RESULTS

Offspring mass increased with female age ($N = 549$ offspring, $\beta = 7.31 \pm 3.58$, $P = 0.04$; Appendix C: Table C2; Fig. 1a). The model with age as a categorical factor was the best model of age-specific variation in offspring mass when considering all data (Appendix C: Table C2). However, when we removed the pup produced by the oldest females, the linear model yielded a lower AIC. To assess the robustness of these results, we removed litters

produced by all females aged between 13 and 15 ($N = 4$ litters). Even so, offspring mass increased with age ($N = 540$ offspring, $\beta = 8.51 \pm 3.82$, $P = 0.02$), supporting the absence of senescence for this trait. The oldest females produced the biggest offspring.

Litter size, however, remained constant until females reached 10 years of age, then markedly decreased thereafter on average by 0.87 offspring per additional year ($N = 202$ litters, $\beta = -0.13 \pm 0.05$, $P < 0.01$; Appendix C: Table C2; Fig. 1b). The eight (16% of total female population) reproductive females that reached at least 10 years of age thus experienced reproductive senescence. This result remained qualitatively unchanged ($N = 197$ litters, $\beta = -0.25 \pm 0.10$, $P < 0.01$)

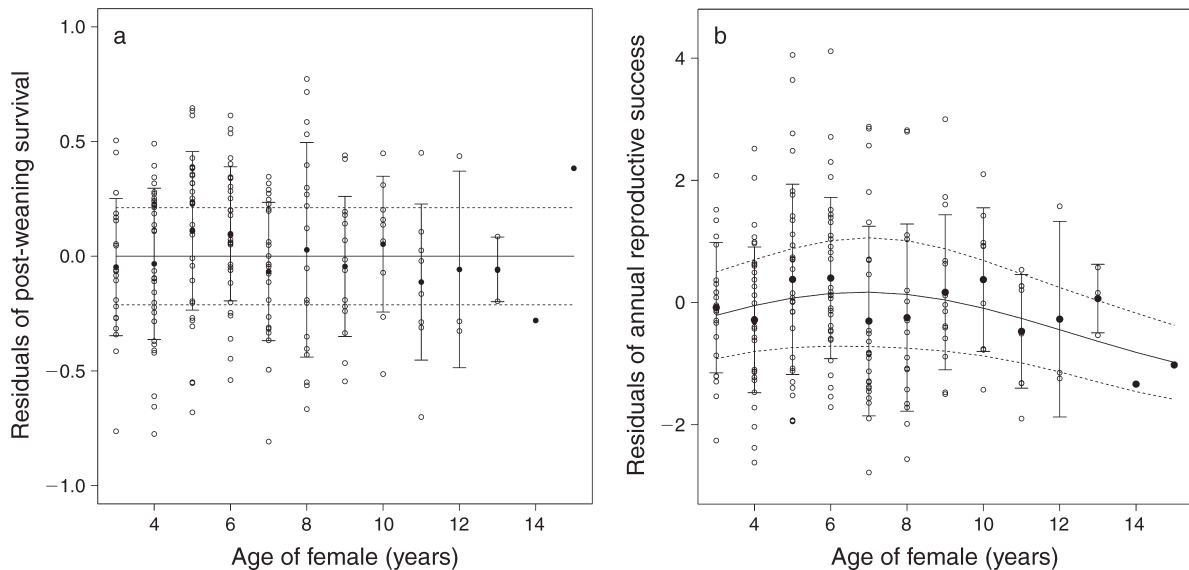


FIG. 2. Age-specific variation in (a) post-weaning survival and (b) annual reproductive success in female Alpine marmots at La Grande Sassi re, corrected for confounding factors (year, aspect of the territory, the change of dominant male, and the number of helpers). Solid circles represent mean reproductive traits per age with their associated standard error bars. Open circles represent the observed residual reproductive traits. Solid lines represent predictions of the best model, with 95% CI indicated as dashed lines in panels: (a) no age-specific effect of age on post-weaning survival and (b) a quadratic relationship between annual reproductive success and age.

when we removed litters produced by the oldest (between 13 and 15 years old, $N = 5$ litters) females.

As a consequence, litter mass also remained constant until females reached 10 years of age and markedly decreased thereafter ($N = 137$ litters, $\beta = -179.63 \pm 62.26$, $P < 0.01$, Appendix C: Table C2; Fig. 1c). This result also remained qualitatively unchanged ($N = 134$ litters, $\beta = -257.4 \pm 115.60$, $P = 0.03$) when we removed litters produced by all females aged between 13 and 15 ($N = 3$ litters).

In order to properly analyze variation in the size–number trade-off with female age, we added litter size as a factor in the offspring-mass baseline model. The baseline model with no age-specific variation and the linear model including maternal age had similar AIC values ($\Delta AIC = 0.26$; Appendix C: Table C2; Fig. 1d), so we retained the baseline model as the most parsimonious. Consequently, our data are most consistent with a size–number trade-off that does not vary with maternal age. This result remained qualitatively unchanged ($N = 540$ offspring, $\beta = 6.20 \pm 3.32$, $P = 0.07$) when we removed litters produced by the oldest females (between 13 and 15 years old, $N = 4$ litters).

Post-weaning survival was not affected by female age ($N = 725$ post-weaning survival events, $\beta_{\text{age}} = -0.004 \pm 0.05$, $P = 0.94$, Appendix C: Table C2; Fig. 2a). Once again, the pattern of age-specific variation remained unchanged ($N = 711$ post-weaning survival events, $\beta = 0.003 \pm 0.05$, $P = 0.95$) when we removed litters produced by the oldest females (≥ 13 years old, $N = 5$ litters).

The influence of maternal age on annual reproductive success was best explained by a quadratic effect. Annual reproductive success was maximal between six and 10 years of age and declined thereafter ($N = 202$ reproductive successes, $\beta_{\text{age}} = 0.25 \pm 0.12$, $P = 0.04$, $\beta_{\text{age}^2} = -0.02 \pm 0.01$, $P = 0.03$; Appendix C: Table C2; Fig. 2b). The pattern was similar even when litters produced by females 13 years of age and older ($N = 5$ litters) were removed from the analysis (annual reproductive success tended to increase until seven years of age and to decrease afterward; $N = 197$ reproductive successes, $\beta_{\text{age}} = 0.29 \pm 0.15$, $P = 0.05$, $\beta_{\text{age}^2} = -0.02 \pm 0.01$, $P = 0.05$).

Neither longevity nor LYE had any statistically significant influence on offspring mass, litter size, reproductive allocation, offspring mass corrected for litter size, post-weaning survival, or annual reproductive success ($P > 0.3$ in all instances, Appendix C: Table C3).

DISCUSSION

Our results provide clear evidence of life-history senescence in female Alpine marmots and support the view that senescence patterns vary markedly among reproductive traits (see also Hayward et al. 2013). Offspring mass increased with female age, but mean litter size remained constant until females reached a threshold of 10 years of age and declined thereafter. Reproductive allocation followed the same pattern as litter size.

Although the patterns of senescence differed between offspring size and offspring number, and despite a decrease of reproductive allocation with increasing age, the offspring size–number trade-off did not change with



PLATE 1. Alpine marmot offspring a few days after their first emergence from the burrow, in early July. Photo credits: Carole and Denis Favre-Bonvin, Lumières des Alpes.

maternal age. Post-weaning survival remained constant with female age, and maternal age had a quadratic effect on annual reproductive success, leading annual reproductive success to peak between six and 10 years of age before declining. Longevity and last year of reproduction had no detectable effect on any of the reproductive traits. Female marmots thus appear to adjust their litter size relative to their ability to care for offspring.

In Alpine marmots, reproductive allocation declined with female age but somatic maintenance remained constant with age, as indicated by a constant female body mass with age (Tafari et al. 2013). We do not know whether this pattern was caused by lower resource acquisition or lowered allocation of resources to reproduction. Longevity is the main determinant of variation in individual fitness in long-lived species (Clutton-Brock 1988). Therefore, in such species, maintaining body mass might be favored at the expense of reproduction in old females. This interpretation appears consistent with available data. The Columbian ground squirrel, another long-lived rodent (with a longevity >9 years), also shows senescence of reproductive traits but not of body mass (Broussard et al. 2003). Richardson's ground squirrel, a shorter-lived rodent (with a longevity of about 6 years) shows the opposite pattern, with a marked somatic senescence and no

decline of reproductive traits with age (Broussard et al. 2005).

The relative allocation to offspring size and number is inherent to an individual's age-specific reproductive tactic, and is thereby subject to natural selection. Strong directional selection on offspring size could lead to the absence of senescence of this trait in long-lived mammals. In a wide range of mammalian species, offspring size is indeed positively related to offspring survival because a large size allows individuals to cope better with harsh environmental conditions (Gaillard et al. 2000). For instance, in the closely related yellow-bellied marmots, heavier offspring are more likely to survive their first hibernation than lighter offspring (Lenihan and Van Vuren 1996).

The age-specific variation in allocation to offspring size and number can also result from physiological constraints. The decline of litter size could be associated with a progressive physiological deterioration of female ability to reproduce when aging. For example, a decline in the number of ovarian oocytes with increasing age is common in mammals (Finch 1990). Litter size could also be constrained by implantation failure. For example, in both the golden hamster (*Mesocricetus auratus*) and roe deer (*Capreolus capreolus*), implantation failure has been identified as the major factor driving senescence in litter size (Parkening and Soder-

wall 1975, Hewison and Gaillard 2001). Moreover, we cannot exclude the possibility that the observed decline in litter size with increasing age in marmots could partly result from a decrease in pre-weaning offspring survival before young emerge from the natal burrow. The causes of pre-weaning mortality in burrow-dwelling species remain virtually unknown because of the difficulty of access to newborns, and has consequently received much less attention than post-weaning survival. However, in the European rabbit (*Oryctolagus cuniculus*), Rödel et al. (2009) reported that 57.65% of pre-weaning mortality was due to maternal factors and 42.34 % was due to environmentally driven causes. In Alpine marmots, pre-weaning mortality is expected to be low because burrows protect young from predators and cannot be flooded. The decline in offspring number in marmots is thereby unlikely to be caused by environmentally driven pre-weaning mortality, and is thus most likely an adaptive outcome of a female's age-dependent life history.

In summary, Alpine marmots contradict our prediction that the offspring size–number trade-off should vary with female age. Strong selection for high offspring mass when entering hibernation appears to constrain the life history of all females independent of their age or condition. All females thus share the same life-history trade-off between number and size of offspring, independently of their age. Interestingly, Wilson et al. (2009) also found a constant size–number trade-off with female age in Soay sheep (*Ovis aries*), although reproductive traits display markedly different patterns of senescence in that species (Hayward et al. 2013). However, the responses of offspring size and number to aging were opposite in Soay sheep compared to marmots. In sheep, litter size remained constant from seven years of age onward, whereas offspring mass peaked at seven years of age and declined thereafter, meaning that old female sheep traded offspring size for offspring number. Such opposite ways of optimizing the size–number trade-off between marmots and sheep are likely caused by differences in the environments these species face. Spring weather at St. Kilda Island, where Soay sheep have been studied, is highly unpredictable. Early offspring survival of sheep is thereby low and highly variable among years (Jones et al. 2005). The relatively constant living conditions within marmot burrows buffer environmental conditions from birth to weaning, suggesting a quite high and constant pre-weaning survival among years.

Our study reveals the complexity of reproductive senescence patterns that are likely to characterize mammals living under different conditions and with differing life histories. We suggest that future theoretical and empirical studies of reproductive senescence should be placed in the context of the size–number trade-off and we urge others to include age-specific variation when investigating this trade-off. Such an approach should help us to better understand whether and how

selection might operate on age-specific trait values in order to maximize fitness.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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