



Age-specific survival in the socially monogamous alpine marmot (*Marmota marmota*): evidence of senescence

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We investigated age-specific variation in survival of dominant individuals in a long-lived and monogamous mammal, the alpine marmot (*Marmota marmota*), from a large dataset collected during a 24-year intensive monitoring of a free-ranging population. We found evidence of actuarial senescence in dominant individuals for both sexes. Survivorship was constant with age until dominant marmots were between 6 and 8 years of age and declined markedly thereafter. No between sex differences occurred in the intensity of actuarial senescence, which might be related to the weak intensity of sexual selection in this socially monogamous mammal. More investigations are needed to know whether cooperative breeding, hibernation, and monogamy, which are key features of the alpine marmot life history, could have shaped the patterns of actuarial senescence we report.

Key words: ageing, cooperative breeder, multievent models, sciurids

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Actuarial senescence is defined as the increase in annual mortality with age (Ricklefs 1998; Nussey et al. 2008). It has been argued that actuarial senescence has evolved because of the decline of natural selection forces with increasing age, as demonstrated by pioneer works (Medawar 1952; Williams 1957; Hamilton 1966). During the last century, it was believed that ageing does not occur in wild populations because individuals die before the occurrence of any sign of senescence (Medawar 1952; Comfort 1956). However, thanks to the detailed analyses of long-term individual monitoring, actuarial senescence has been widely documented in free-ranging and age-structured populations during the last 2 decades, especially in vertebrates (review in Nussey et al. 2013). In addition, there is now compelling evidence that senescence displays highly variable patterns across the tree of life (Jones et al. 2014).

As senescence is grounded into life history evolution (Jones et al. 2008; Lemaître et al. 2015), having a comprehensive view of senescence patterns allows understanding factors shaping population dynamics. To date, most senescence studies have focused on the analysis of the rate of senescence (e.g., Ricklefs 2010), which has been shown to vary greatly among individuals (Bouwhuis et al. 2010), populations (Lemaître et al. 2013), and species (Jones et al. 2008). However, variation in the age at the onset of senescence also contributes to shape senescence patterns (Péron et al. 2010; Gamelon et al. 2014). Although both Williams (1957)

and Hamilton (1966) explicitly stated that actuarial senescence should set on after the age at 1st breeding, accumulating empirical evidence indicates that it is not the case (Péron et al. 2010). For example, in alpine ibex (*Capra ibex*), the age at 1st reproduction is between 2 and 3 years old, whereas actuarial senescence only occurs from 7 years of age onward (Toïgo et al. 2007).

Studying senescence in the wild requires longitudinal data on known-aged individuals over their entire lifespan. Mammalian species that are monogamous and cooperative breeders have rarely been the target of such long-term studies, which leads our understanding of actuarial senescence in these species to be currently limited. To date, only 5 studies have investigated the age-specific variation in survival using transversal (*Alouatta palliata*—Froehlich et al. 1981, *Castor canadensis*—Bergerud and Miller 1977) or longitudinal (*Helogale parvula*—Waser et al. 1995, *Lycaon pictus*—Creel and Creel 2002, *Rhabdomys pumilio*—David and Jarvis 1985, *Alouatta seniculus*—Larson et al. 2016) data. On the contrary, mammals in which only mothers care for young have been the subject of many detailed analyses of actuarial senescence (reviewed in Nussey et al. 2013). Yet, cooperative breeder species, where nonparent individuals help in raising young of dominants (Jennions and Macdonald 1994), display typical life histories with delayed age at 1st reproduction and decreased environmentally driven mortality risks that could shape senescence.

Additionally, a growing number of studies provide evidence that in mammals, sex is an important cause of variation in actuarial senescence (e.g., Loison et al. 1999; Descamps et al. 2008; Greiner et al. 2013; Gamelon et al. 2014; Tidière et al. 2015). Williams (1957) predicted that senescence should be more rapid for the sex with the highest mortality rate and argued that males should display faster actuarial senescence. Indeed, the costs associated with fights for mating, with growing large secondary sexual characteristics, and with monopolizing resources, should all be higher in males than in females. Such sex differences led Bonduriansky et al. (2008) to launch the term for male life history strategy referred to as “live fast-die young”. However, some species do not display any sex difference in ageing patterns (see Clutton-Brock and Isvaran 2007; Tidière et al. 2015 for some interspecific analyses). Our current empirical knowledge then indicates that the influence of sex on ageing patterns is more complex and is still poorly understood.

Since 1990, a free-ranging population of alpine marmots (*Marmota marmota*) has been monitored on an individual basis. The alpine marmot is a socially monogamous species breeding cooperatively (Arnold 1990). This species displays a long lifespan in the wild, as the oldest individual observed in our population was 16 years of age. Previous studies of this population have pointed out the complexity of senescence patterns in life history traits of alpine marmots. Tafani et al. (2013) found that male body mass peaks at 8 years of age and declines thereafter, whereas female body mass does not show any sign of senescence. Likewise, Berger et al. (2015) found that litter size remains constant with age until females reach 10 years of age and declines thereafter, whereas mass of pups does not show any evidence of senescence. As new evidence suggests that senescence in traits associated with individual fitness might show heterochrony (Nussey et al. 2013; Hayward et al. 2015), it is crucial to analyze both demographic and phenotypic traits to have a comprehensive view of ageing processes within a given species. However, to date, age-specific changes in survival have not been yet investigated in this species.

Using an exceptional long-term individual monitoring of an alpine marmot population, we estimated age-specific changes of survival in dominant individuals and tested for sex differences of the rate of senescence. In our population, no subordinate individual older than 6 years of age was ever observed. All subordinates either died or become dominant before being old enough to show senescence. Based on previous analyses of age-specific variation in body mass that provided evidence of sex-specific senescence pattern (Tafani et al. 2013), we expected that actuarial senescence should be more intense in males than in females, assuming that body mass is a good indicator of condition and survivorship in this species, similarly to what has been reported for other mammals (e.g., Gaillard et al. 2000 in large herbivores, Ozgul et al. 2010 in yellow-bellied marmots, *Marmota flaviventris*).

MATERIALS AND METHODS

Study Species

Alpine marmots live in family groups of 2–16 individuals composed of a dominant couple, sexually mature (individuals from 2 years of age onward) and immature subordinates of both sexes (yearlings), and offspring of the year (Allainé 2000). Alpine marmots are territorial. The territory is shared by all family members but is mainly defended by the dominant pair.

The status of dominance is established for several years until the dominant marmot will be evicted by another individual or will die (Lardy et al. 2011). Dominant marmots mate during the 15 days following the emergence from hibernation (i.e., from early to late April). After 30 days of gestation, dominant females give birth to the sole litter of the year. The altricial offspring stay in the natal burrow during 40 days and once weaned emerge above ground between mid-June and mid-July (Psenner 1956, 1960). At sexual maturity (i.e., 2 years of age), an individual can stay as a subordinate in its natal group or attempt to become dominant by either inheriting the dominance status in its natal group or dispersing to gain dominance in another territory. A dispersing individual never joins a new family group as a subordinate (Magnolon 1999).

Dominant marmots monopolize reproduction by physiologically suppressing reproduction of almost all mature subordinates of both sexes (Arnold and Dittami 1997; Hackländer et al. 2003). However, when the group size increases, the control of subordinates through aggressive behaviors is less effective. Therefore, in large family groups, some subordinate males unrelated to the dominant female can escape the control of the dominant and mate with the dominant female. Moreover, when subordinate males disperse to try to reach the dominant position in another territory, they can mate during dispersal with dominant females unbeknownst to the dominant males. In these 2 cases, the dominant female can give birth to young fathered by both the subordinate or transient male and the dominant male (Cohas et al. 2006).

Hibernation is characterized by a cyclic process with alternate hypothermia and euthermia phases (Arnold 1990). Group members hibernate together from mid-October to early April, and produce heat during periodic arousal, a phenomenon called social thermoregulation (Arnold 1990). However, all members of a family group do not have the same length and rhythm of hibernation. In particular, at each cycle, subordinate males wake up earlier and have longer euthermic periods than other family members, leading them to warm the burrow more than other group members (Arnold 1993). Consequently, subordinate males act as helpers and their presence in a family group increases the probability of offspring to survive their 1st hibernation (Allainé and Theuriau 2004), while they pay the costs in terms of body mass loss (Arnold 1988).

Study Site and Data Collection

Marmots were captured in a free-ranging population located in the Grande Sassièr Nature Reserve (2,340 meters above

sea level, French Alps, 45°29'N, 6°59'E), from 1990 to 2013. Every year, marmots from 24 territories were monitored, from mid-April to mid-July, using both capture-mark-recapture and observations. Marmots were captured using 2-door live-capture traps baited with dandelions (*Taraxacum officinale*). Traps were placed near the entrances of the main burrows to assign easily each captured individual to its family group. Juveniles were counted and captured by hand within the 3 days following their 1st emergence from the natal burrow (i.e., approximately 40 days after their birth). Captured animals were tranquilized with Zolétil 100 (Vibrac Corporation, St. Louis, Wisconsin). At 1st capture, unmarked individuals were implanted with a PIT-tag (Trovan Ltd, www.Trovan.com, Cologne, Germany), and marked with a numbered ear tag. Tags were put on the right ear of females and on the left ear of males. In addition, a colored plastic ear tag was placed on the opposite ear of dominant marmots. At each capture, marmots were sexed and their social status was determined (assessed as dominant when testes reach the bottom of the scrotum [males] and when large mammary glands were present [females]). Daily observations were conducted and we further assessed the number of individuals of each sex and age class (pup, yearling, and adult) for each family. Scent-marking behavior was used to confirm the identity of the dominant pair (Bel et al. 1995).

We measured age (in years) from birth and assigned the age of 0 to offspring. We knew the exact age of dominant individuals born on the study site (84 females, 82 males), but not the age of immigrants (29 females, 47 males). As most marmots disperse at 2 years of age and almost never reproduce before 3 years of age (no female among the 84 females of known age, 3 males among the 82 males of known age), we assigned the age of 3 to immigrants when they first reproduce.

Genetic analyses were performed to assess the certainty of the maternity and paternity of individuals. When an individual was not captured in a given year, its survival could be accessed through genetic analyses by revealing a pup production for a given year. Details about genetic and kinship analyses are provided in Dupont et al. (2015).

Capture–Recapture Analysis

Model structure.—Between 1990 and 2013, 242 marmots were captured as dominant individuals (113 females and 129 males). We used multievent capture–recapture models (ME-CR—Pradel 2005) to investigate the influence of age on survival of dominant marmots because recapture probability of individuals was much lower than 1 (recapture probability varying from 0.380 to 0.886—Cohas et al. 2007) and not accounting for imperfect detection indeed leads to biased survival estimates (Gimenez et al. 2008). In these models, as in multistate models (Lebreton et al. 2009), each individual can only be in 1 of the 3 following states: subordinate (*s*), dominant (*D*), or dead (\dagger). Therefore, we were able to estimate different probabilities of survival for animals in the 2 live states and of transition probabilities from one state to another (Fig. 1). In addition, multievent models allow taking into account uncertainty about the state of individuals and/or any additional information. Here, we

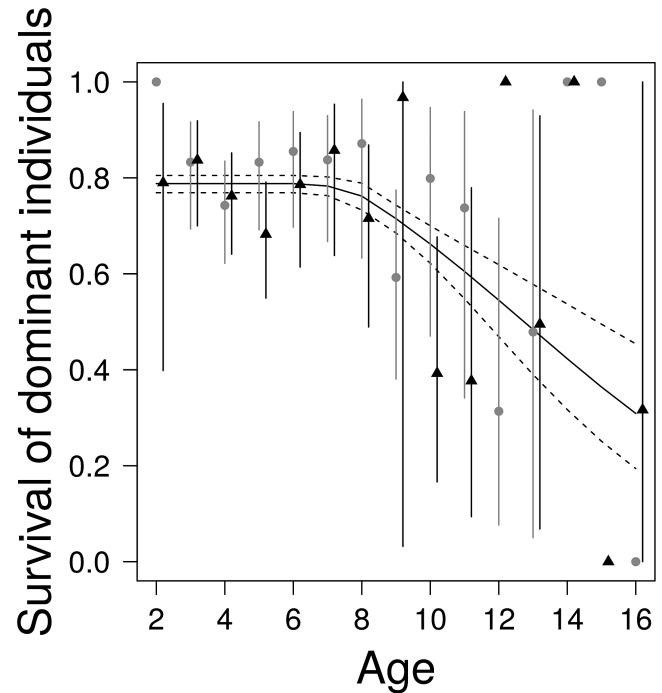


Fig. 1.—Age-specific variation in survival of dominant adult marmots (*Marmota marmota*). The solid line represents survival estimated from model averaging of the 3 competitive models (in bold in Table 2) and the dashed lines the associated SEs. The grey circles and the associated error bars represent the age-specific survival estimates and their associated confidence intervals for females, while the black triangles and the associated error bars represent the age-specific survival estimates and their associated confidence intervals for males.

incorporated additional information about the reproductive status. Indeed, based on kinship analyses, we were able to determine whether an individual successfully reproduced (i.e., young emerging from the burrows) or not in a given year, even when the individual was not captured that year, thus allowing us to refine the survival estimates (Dupont et al. 2015). The different observable events retained were no information (event 0), individual not captured but its pups were captured (event 1), individual captured as dominant but none of its pups were captured (event 2), individual captured as dominant with its pups captured (event 3), individual captured as subordinate but none of its pups were captured (event 4), and individual captured as subordinate with its pups captured (event 5). Based on these events, capture–recapture histories were constructed for each individual.

The constructed multievent model can be summarized by a transition matrix and associated vectors of survival, capture, and successful reproduction probabilities (only the 2 live states are shown since the parameters of the dead state are fixed to $p^\dagger = 0$; $\Psi^{\dagger\dagger} = 1$; $E^\dagger = 0$, see Table 1 for the glossary of abbreviations and their meanings).

$$\begin{bmatrix} 1 - \Psi^{sD} & \Psi^{sD} \\ 0 & 1 \end{bmatrix} \begin{bmatrix} \Phi^s \\ \Phi^D \end{bmatrix} \begin{bmatrix} p^s \\ p^D \end{bmatrix} \begin{bmatrix} E^s \\ E^D \end{bmatrix}$$

where probabilities of capture (p), survival (Φ), reproduction (E) and state transition conditional on survival (Ψ) are defined

as: P_t^x , the probability that an individual in state x was captured during the year t ; Φ_t^x , the probability that an individual in state x in year t survived and did not permanently emigrate from the study area between t and $t + 1$; Ψ_t^{xy} , the probability that an individual in state x in year t is in state y in year $t + 1$ given that it survived and did not permanently emigrate from the study area between t and $t + 1$ and E_t^x , the probability that an individual in state x at time t had successfully reproduced this same year. Since dominant individuals never revert to subordinate state (Grimm et al. 2003), the transition probability from the dominant state to the subordinate state was fixed to 0 ($\Psi^{SD} = 0$), thus constraining the state transition probability from dominant to 1. Additionally, we fixed to 0 the transition probability from subordinate to dominant between 1 and 2 years of age and after 6 years of age.

Model selection.—To investigate the influence of age on survival, we followed 3 steps as proposed by Lebreton et al. (1992):

1. Goodness-of-fit tests: We 1st tested whether a general model compatible with our biological knowledge fitted our data. To this purpose, we performed goodness-of-fit (GOF) tests (Pradel et al. 2005) using the program U-CARE (Choquet et al. 2009a).
2. Obtaining a baseline model: Next, we selected the most parsimonious model, starting from a general model. Following Burnham and Anderson (2002), we built the general model by considering only a priori biological hypotheses based on literature (Arnold 1993; Farand et al. 2002; Stephens et al. 2002; Grimm et al. 2003; Cohas et al. 2008; Dupont et al. 2015). We thus considered effects of age, time, sex, and their 2-way interactions on all capture, state transition, and reproduction probabilities. For survival, we also considered the effects of time, sex, and the simplest age structure in 3 classes for subordinates (yearling, 2 years old, and aged from 2 to 6) and age structure in 2 classes for dominants (2 year old and aged from 3 to 6). In addition, we considered an effect of the number of male helpers since a high number of these latter groups appeared to be beneficial in terms of juvenile survival (Allainé and Theuriau 2004). Consequently, we denoted the most general model as follows:

$$p^s(a_2; a_{3-7}) * t * sex \Phi^s(a_1 * helpm; a_2; a_3; a_{4-7}) * t * sex \\ E^s_{a_{3-7}} * t * sex p^D(a_{3-7}) * t * sex \Phi^D(a_3; a_{4-17}) * t * sex \\ E^D(a_{3-17}) * t * sex \Psi^{SD} a_1 : a_{7-17}; (a_2; a_{3-6}) * t * sex$$

Following a step-down approach, models were sequentially fitted with constrained parameterizations for recapture, survival, transitions, and reproduction probabilities, in that order. We then checked that the best model could not be improved by exploring all nested models differing by only 1 effect.

3. Testing for age-specific survival: To test for age-specific variation in survival we fitted age-specific models by

considering age as a linear or quadratic covariate, or as a categorical factor. We further fitted threshold models by holding survival constant until a threshold age, beyond which it linearly depended on age. The tested threshold age varied between 5 and 15 years. For each of these models, we also included a possible sex effect. Model selection and parameter estimation were performed using the program E-SURGE 1.8.5 (Choquet et al. 2009b). Estimates and *SEs* of regression slopes reported in the result section are on the logit scale. All other parameters are given on the absolute scale. The associated *SEs* were obtained by the delta method (Burnham and Anderson 2002). When several candidate models were competitive (i.e., differences in Akaike Information Criterion [AIC] less than 2), we performed a multimodel inference based on AIC weights (w_i) to produce mean estimates averaged across the different models of interest.

Comparing the onset of actuarial senescence estimated in marmots with the expectation based on early life history traits.—The onset of actuarial senescence in alpine marmots has not been previously investigated. Péron et al. (2010) provided a life history model that allows predicting the onset of actuarial senescence across bird and mammal species based on their early life history traits. From a dataset included species studied using capture-mark-recapture and after accounting for potentially confounding effects of phylogeny, Péron et al. (2010) found that the onset of actuarial senescence is expected to be equal to

$$\text{Onset} = \exp(0.22 \log(A) + 1.78 / (F^{0.34} S^{0.20A}))$$

where A is the age at 1st reproduction, F the annual prime age fecundity, and S the juvenile survival (between birth and 1 year of age).

We included A , F , and S values that we got from our studied population of alpine marmots to calculate the age at the onset of senescence expected for marmots. We then compared this expected value to the value obtained from the survival analysis of our studied population.

RESULTS

Goodness-of-fit tests.—The overall goodness-of-fit (GOF) test of the Cormack–Jolly–Seber model (i.e., the fully time-dependent model) was statistically significant ($\chi^2 = 159.58$, $d.f. = 79$, $P < 0.01$) due to transience detected by the 3SR component test or also called the Brownie–Robson test ($\chi^2 = 93.55$; $d.f. = 22$, $P < 0.01$). Individuals considered as transients were in fact pups that did not survive to their 1st hibernation and were thus captured only once. A 2nd GOF test was thus run on a dataset from which the 1st occasion of capture for individuals caught as pups was removed. The overall GOF test was no longer statistically significant ($\chi^2 = 28.87$, $d.f. = 56$, $P = 0.99$) nor was the transience test (test 3SR; $\chi^2 = 21.55$, $d.f. = 22$, $P = 0.49$). Yet, taking into account age classes in the baseline model solved the initial problem of apparent transience.

Baseline model.—After selection using AIC (see [Supporting Information S1](#)), the baseline model was

$$p^s(a_1; a_2; a_3; a_{4-7}) + t + \text{sex} \Phi^s(a_1 * \text{helpm}; a_2; a_3; a_{4-7}) + t E^s a_3; a_4; a_{5-7} p^D(a_3; a_{4-7}) + t + \text{sex} \Phi^D(a_3; a_{4-7}) + t \Psi^{SD} a_1; a_{7-17}; a_2; a_3; a_{4-7}$$

Survival varied over time, between status, and age classes. Dominant adults had a higher survival (0.773 ± 0.016) than subordinate adults (0.550 ± 0.024), which can result from natal dispersal of subordinates outside the study site ([Magnolon 1999](#)) that cannot be distinguished from death.

Age-specific survival.—Dominant alpine marmots displayed clear evidence of senescence in survival ([Table 2](#)). Both linear and quadratic models performed poorly compared to the baseline model. Our results rather showed a threshold pattern of survival where survival remained constant until a threshold age and declined thereafter ([Fig. 1](#)). Three threshold models received strong support with an age at the onset of senescence at 6, 7, and 8 years of age, respectively. As these models provided similar fit, we performed a model-averaging procedure to estimate the constant survival during early ages and the rate of actuarial senescence, and thereby age-specific survival estimates. Survival remained constant at 0.79 ± 0.02 from 3 years of age until the threshold age (in females: 0.82 ± 0.02 ; in males: 0.78 ± 0.02) until 6 years of age and then declined to 0.31 at 16 years of age ($\beta_{\text{averaged}} = -0.25$; [Fig. 1](#); see [Supporting Information S2](#)). Neither early adulthood survival nor the rate of senescence differed between sexes ([Table 2](#)). As expected, the

number of individuals monitored decreased with increasing age, which led error bars from the full dependent age model to be larger for old than for young individuals, especially in males.

DISCUSSION

Survival starts to decrease from 6 to 8 years of age in dominant alpine marmots, which is quite similar to the value obtained from the model in [Péron et al. \(2010\)](#) based on the covariation among early life history traits across bird and mammal species. Indeed, model in [Péron et al. \(2010\)](#) predicts an onset of actuarial senescence of marmots at 6.5 years of age. However, as most marmots start reproducing at 3 years of age, the onset of actuarial senescence of alpine marmots is delayed compared to the theoretical assumption that actuarial senescence should start at the age at 1st reproduction ([Williams 1957](#); [Hamilton 1966](#)). Although the age-specific survival patterns we report in alpine marmots does not fit with theoretical expectations, several iteroparous species showed similar patterns (e.g., [Stolen and Barlow 2003](#); [Toïgo et al. 2007](#); [Descamps et al. 2008](#); [Bronikowski et al. 2011](#)). Our case study on alpine marmots thus contributes to the growing empirical evidence supporting that the synchrony between the age at 1st reproduction and the age at the onset of senescence is rather the exception than the rule. Finally, contrary to our expectation based on senescence patterns observed in body mass, the rate of actuarial senescence did not differ between sexes.

The absence of sex difference in the strength of actuarial senescence we report for alpine marmots does not support the expected “live fast, die young” life history strategy expected to be displayed by males ([Bonduriansky et al. 2008](#)). Indeed, our finding markedly contrasts with studies of other mammal species that reported earlier or stronger senescence in males compared to females (e.g., [Gaillard et al. 2003](#); [Lemaître and Gaillard 2013](#)). However, these studies included polygynous species for which reproductive effort is much greater in males than in females ([Clutton-Brock and Isvaran 2007](#); [Bonduriansky et al. 2008](#); but see [Greiner et al. 2013](#)). In polygynous species, the intensity of sexual selection is expected to drive the magnitude of sex differences in actuarial senescence ([Clutton-Brock and Isvaran 2007](#); but see [Tidière et al. 2014](#)). On the contrary, in monogamous species, like the alpine marmot, the intrasexual competition is similar in both sexes and sex-specific differences in ageing should not be marked in monogamous species ([Bonduriansky et al. 2008](#)), which is supported by several empirical studies ([Clutton-Brock and Isvaran 2007](#); [Larson et al. 2016](#)).

In females, the onset of actuarial senescence is consistent with the onset of senescence reported for reproductive success (approximately 8 years of age—[Berger et al. 2015](#)) but markedly differs from the senescence pattern reported in body mass (with an absence of senescence—[Tafari et al. 2013](#)). In males, no information on age-specific variation in reproduction is available but body mass starts to decrease from about 8 years of age, which is consistent with the onset of actuarial senescence we report here. Surprisingly, alpine marmots displayed

Table 1.—Abbreviations used in model notations.

| Abbreviations | Meanings |
|---------------|---|
| P | Recapture probability |
| Φ | Survival probability |
| Φ^D | Survival probability of dominant individuals |
| $1 - \Phi$ | Mortality probability (encompassing both mortality and dispersal probabilities for individuals older than 2 years of age) |
| Ψ | State transition probability (conditional on survival) |
| E | Event probability (probability of successful reproduction) |
| Subscript | |
| a_1 | Age from 0 to 1 year |
| a_2 | Age from 1 to 2 years |
| a_{x-y} | Age from x to y |
| $a_{x+...+y}$ | Age classes $x+...+y$ |
| <i>Sex</i> | Sex |
| T | Time effect (years) |
| * | Interactive effects |
| + | Additive effects |
| <i>Helpm</i> | Number of male helpers present during the 1st hibernation |
| Superscript | |
| S | Subordinate status |
| D | Dominant status |
| † | Dead |

Table 2.—Model selection for the effects of age on survival of dominant alpine marmots (*Marmota marmota*) marked from 1990 to 2013 ($N = 242$). Φ^D corresponds to survival of dominant individuals. T_i corresponds to a constant survival until the threshold age (i) followed by a linear decline of survival with increasing age. $\Phi_{a_2-16}^D$ corresponds to a linear decrease of survival from age 2 to age 16. $\Phi_{a_2+\dots+a_{16}}^D$ corresponds to the full age-dependent model. All other parameters (transition, capture, and reproduction) are fixed as in the baseline model. AIC_c = Akaike Information Criterion corrected for small sample sizes; k = number of identifiable parameters; ΔAIC_c = difference in AIC_c between the candidate model and the model of the set with the lowest AIC_c ; $AIC_w = AIC_c$ weight. The selected model including an age effect is in bold and is highlighted with gray shading, and the competitive candidate models are in bold.

| Model notation | Deviance | k | AIC | ΔAIC | AIC_w |
|---|-----------------|------------|-----------------|--------------|-------------|
| $\Phi_{t_8}^D + t$ | 6,108.39 | 113 | 6,334.39 | 0 | 0.25 |
| $\Phi_{t_7}^D + t$ | 6,108.48 | 113 | 6,334.48 | 0.09 | 0.24 |
| $\Phi_{t_6}^D + t$ | 6,110.36 | 113 | 6,336.36 | 1.97 | 0.09 |
| $\Phi_{t_7}^D * sex + t$ | 6,106.55 | 115 | 6,336.55 | 2.16 | 0.08 |
| $\Phi_{t_8}^D * sex + t$ | 6,106.56 | 115 | 6,336.56 | 2.17 | 0.08 |
| $\Phi_{t_9}^D + t$ | 6,110.78 | 113 | 6,336.78 | 2.39 | 0.07 |
| $\Phi_{t_6}^D * sex + t$ | 6,108.38 | 115 | 6,338.38 | 3.99 | 0.03 |
| $\Phi_{t_5}^D + t$ | 6,112.54 | 113 | 6,338.54 | 4.15 | 0.03 |
| $\Phi_{a_2-16}^D + t$ | 6,112.80 | 113 | 6,338.8 | 4.41 | 0.03 |
| $\Phi_{t_9}^D * sex + t$ | 6,109.08 | 115 | 6,339.08 | 4.69 | 0.02 |
| $\Phi_{t_{10}}^D + t$ | 6,113.97 | 113 | 6,339.97 | 5.58 | 0.01 |
| $\Phi_{t_5}^D * sex + t$ | 6,110.55 | 115 | 6,340.55 | 6.16 | 0.01 |
| $\Phi_{a_2-16}^D + \Phi_{a_2-16}^D + t$ | 6,110.64 | 115 | 6,340.64 | 6.25 | 0.01 |
| $\Phi_{a_2-16}^D * sex + t$ | 6,110.89 | 115 | 6,340.89 | 6.5 | < 0.01 |
| $\Phi_{t_5}^D * sex + t$ | 6,112.42 | 115 | 6,342.42 | 8.03 | < 0.01 |
| $\Phi_{t_{11}}^D + t$ | 6,116.44 | 113 | 6,342.44 | 8.05 | < 0.01 |
| $\Phi_{t_{14}}^D + t$ | 6,117.74 | 113 | 6,343.74 | 9.35 | < 0.01 |
| $\Phi_{t_{15}}^D + t$ | 6,117.94 | 113 | 6,343.94 | 9.55 | < 0.01 |
| $\Phi_{t_{12}}^D + t$ | 6,118.39 | 113 | 6,344.39 | 10 | < 0.01 |
| $\Phi_{a_2-16}^D * sex + \Phi_{a_2-16}^D * sex + t$ | 6,108.67 | 118 | 6,344.67 | 10.28 | < 0.01 |
| $\Phi_{t_{13}}^D + t$ | 6,118.81 | 113 | 6,344.81 | 10.42 | < 0.01 |
| $\Phi_{t_{11}}^D * sex + t$ | 6,115.03 | 115 | 6,345.03 | 10.64 | < 0.01 |
| $\Phi_{t_{14}}^D * sex + t$ | 6,115.89 | 115 | 6,345.89 | 11.5 | < 0.01 |
| $\Phi_{t_{15}}^D * sex + t$ | 6,116.68 | 115 | 6,346.68 | 12.29 | < 0.01 |
| $\Phi_{t_{12}}^D * sex + t$ | 6,117.14 | 115 | 6,347.14 | 12.75 | < 0.01 |
| $\Phi_{t_{13}}^D * sex + t$ | 6,117.53 | 115 | 6,347.53 | 13.14 | < 0.01 |
| $\Phi_{a_2+}^D + t$ | 6,097.49 | 127 | 6,351.49 | 17.1 | < 0.01 |
| $\Phi_{a_2+}^D * sex + t$ | 6,077.17 | 142 | 6,361.17 | 26.78 | < 0.01 |

sex differences in body mass senescence, which involves the decline of body mass with increasing age in males but only a last year effect in females (Tafari et al. 2013), whereas no sex difference occurred in the rate of actuarial senescence. Two possible explanations may explain this pattern. First, in the alpine marmot, the senescence in body mass is independent of the senescence in other traits, as expected if fitness-related traits show heterochrony in their senescence patterns (Nussey et al. 2013). Such variable patterns of senescence have been recently reported in Soay sheep (*Ovis aries*) across 20 phenotypic traits (Hayward et al. 2015). Second, the senescence in body mass has implications for senescence in fitness traits, but could target reproduction rather than survival in marmots. As males consume more energy than do females during hibernation (Arnold 1986, 1988), sex differences in body mass could result from highest costs of hibernation in males and one can speculate that this may potentially strengthen reproductive senescence (i.e., the decline of reproductive output, including probability

to give birth, litter size, or offspring size, with increasing age). However, in monogamous species such as the alpine marmot in which reproduction of dominant males is strongly associated to that of females and the loss of dominance (reproduction) is associated to death in both sexes (Lardy et al. 2011), it is not easy to understand why reproductive senescence could be stronger in males than in females. However, assessing sex differences in reproductive senescence is required to assess a potential heterochrony of senescence among demographic traits.

The pattern of actuarial senescence in alpine marmots we report could result from the high level of sociality of this species. In cooperative breeders, individuals in the family group help, warn, defend, or check the territory, which leads to decrease environmentally driven mortality (Komdeur 2010). Moreover, in cooperative breeders, both dispersal and reproduction are delayed for several years (Koenig et al. 1992). Additionally, helpers may contribute to decrease the reproductive effort of dominant individuals (Crick 1992). Cooperative

breeding influences biological times (i.e., by delaying age at 1st reproduction) and leads the species-specific pace of life to slow down, which might ultimately delay the onset of actuarial senescence (e.g., Jones et al. 2008). Indeed, the released energy costs of reproduction for breeders offered by helpers can be allocated in somatic maintenance and can potentially delay senescence (Bourke 2007). At the intraspecific level, the evidence for associations between sociality and actuarial senescence is scarce (e.g., Paquet et al. 2015). Although further investigation is required, we suggest that a high level of sociality should delay the onset of actuarial senescence in cooperative breeders.

Moreover, hibernation is also expected to shape the actuarial senescence pattern in alpine marmots. Hibernation is an energy-saving tactic that strongly affects life history strategies (Turbill et al. 2011). Thus, from a comparative analysis across mammals, Turbill et al. (2011) showed that hibernation slows down the pace of life. In particular, they found that small hibernating mammals have longer maximum longevity (50% greater), survive better over the winter (by 15%), reproduce at slower rates, mature at older ages, and have longer generation times than nonhibernating mammals of similar size. In other words, hibernation slows down the pace of life. As senescence is strongly linked with the pace of life (Jones et al. 2008), hibernation should also strongly impact senescence patterns. In Alpine marmots, all members of the family group hibernate altogether. Males enter first at each cycle in eutheria phases and warm the hibernaculum, providing heat for the other members of the family group. The phenomenon is called social thermoregulation (sensu—Arnold 1990). The energy saved during the winter through social thermoregulation during hibernation could thus be reallocated into somatic maintenance. Social thermoregulation during hibernation could thus also shape senescence in alpine marmots. However, further research is required to know whether such reallocation mechanisms allowed by hibernation takes place in the alpine marmot.

We showed that actuarial senescence does occur in dominant alpine marmots of both sexes from about 6 years of age. The alpine marmot displays a delayed senescence relatively to the age at 1st reproduction that might come from the sociality of this species and/or the social thermoregulation during hibernation, an energy-saving strategy. The absence of sex differences in senescence patterns we report on alpine marmots could be associated with the weak intensity of sexual selection experienced by monogamous species.

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Alpine marmot’s life cycle and selection of the multievent baseline model.

Supporting Information S2.—Model averaging.

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