

Sex-specific senescence in body mass of a monogamous and monomorphic mammal: the case of Alpine marmots

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Abstract Sex-specific senescence has been commonly reported in highly dimorphic and polygynous species. However, whether between-sex differences in senescence occur in monogamous and monomorphic species is poorly known. In this study, we used an extensive dataset of 20 years of mass measurements on free-ranging male and female Alpine marmots (*Marmota marmota*), a medium-sized, long-lived, social and hibernating mammal, to assess sex-specific patterns of senescence in body mass. We tested for the occurrence of both a decrease in body mass scaled to absolute age (called chronological senescence) and a decrease in body mass scaled to individual age at death (called terminal decline). Whereas males showed evidence of both chronological senescence and terminal decline in body mass, females did not show any detectable senescence in body mass. This unexpected between-sex difference of senescence in a species subject to weak sexual selection might be shaped either by costs of an asymmetric intra-sex competition for mates or by costs of social thermoregulation.

Keywords Ageing · Individual heterogeneity · *Marmota marmota* · Terminal decline · Sexual selection

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Introduction

Senescence is usually defined as a within-individual process caused by deterioration in molecular and physiological functions (Medawar 1952; Williams 1957; Hamilton 1966), which increases probabilities of both mortality and unsuccessful reproduction of individuals as they age (Monaghan et al. 2008). However, senescence appears to be a highly heterogeneous process. The magnitude of senescence depends on the focal trait and species, on the environmental conditions, and even on the focal individual, leading to a “mosaic ageing” pattern (sensu Walker and Herndon 2010; Ricklefs 2010a). According to this mosaic ageing, an accumulation of physiological deterioration in a given individual occurs at different locations, times and rates, generating a complex pattern of ageing which can only be assessed by using long-term monitoring of individuals from birth to death. Some factors have been identified as structuring this mosaic ageing both between and within species. For instance, the rate of ageing increases with decreasing generation time (Jones et al. 2008; Ricklefs 2010b) and with increasing population density during early life (Nussey et al. 2007).

In most theoretical and empirical studies performed to date, senescence has been perceived as a chronological decline in demographic performance with age (called ageing; see Ricklefs 2010a for a recent review on actuarial senescence) starting from the age at first reproduction (Hamilton 1966). Alternatively, McNamara et al. (2009) proposed that lifespan is not limited by time per se, but by physical deterioration over time. Senescence could then involve a physiological decline that occurs at different ages in different individuals. Thus, the decline period is indexed to the age of death, beginning at some fixed interval of time prior to death (Coulson and Fairweather 2001; Hayward

et al. 2009). Such a terminal decline is usually investigated using years before death (YBD: age at death minus age; Martin and Festa-Bianchet 2011) instead of age, and has been reported to occur in females of several vertebrate species (Rattiste 2004; Weladji et al. 2006; Nussey et al. 2011) since the pioneering work by Coulson and Fairweather (2001). Hence, senescence can be scaled to both absolute age and age at death [see Martin and Festa-Bianchet 2011 for a recent case study on female bighorn sheep (*Ovis canadensis*)]. The two facets of senescence translate, at the population level, into different age-specific patterns. Provided that confounding effects of individual heterogeneity are accounted for, chronological senescence at the individual level necessarily leads to an age-dependent decline in performance at the population level. Conversely, terminal decline, which also corresponds to an age-dependent decline in performance at the individual level (i.e. by definition death occurs at the oldest age an individual reaches), often leads to an age-independent decline in performance at the population level.

Several long-term longitudinal studies have reported evidence of senescence for different life history traits in populations of wild vertebrates (e.g. McNulty et al. 2009 and Lecomte et al. 2010 for foraging ability, Monaghan et al. 2008 and Hayward et al. 2009 for immune system and physiology, Owens and Bennett 2002 and Gaillard et al. 2003 for survival in birds and large herbivores, respectively, and Descamps et al. 2007, Nussey et al. 2009 and Sharp and Clutton-Brock 2010 for reproductive traits of red squirrels (*Sciurus vulgaris*), red deer (*Cervus elaphus*), and meerkats (*Suricata suricatta*), respectively). However, except for a recent detailed analysis of senescence in females of three ungulate species (Nussey et al. 2011), reports of senescence in body mass from longitudinal studies in mammals are anecdotal [see, e.g., Bérubé et al. 1999 in bighorn sheep, Bowen et al. 2006 and Proffitt et al. 2007 in grey (*Halichoerus grypus*) and Weddell (*Lep-*tonychotes weddellii*) seals, respectively, and Derocher and Stirling 1994 in polar bears (*Ursus maritimus*)] and mostly focused on females only [but see Garel et al. 2009 and Mason et al. 2011 in Alpine chamois (*Rupicapra rupicapra*)]. Males may have different senescence patterns than females as suggested for mammals where the rate of senescence increases with sexual selection among males (Clutton-Brock and Isvaran 2007). Males with demanding mating tactics, allocating a high amount of energy in searching and securing mates, have higher body deterioration with age than females, visible through a higher loss of body mass either within or among years towards the end of life (Bowen et al. 2006; Galimberti et al. 2007; Hoffman et al. 2010). Overall, the relative importance of chronological senescence and terminal decline and whether it differs between sexes remain open questions.*

Alpine marmots (*Marmota marmota*) are socially monogamous mammals that live in family groups typically composed of a dominant pair, sexually mature and immature subordinates of both sexes, and juveniles of the year (Perrin et al. 1993). They are cooperative social breeders hibernating in groups from mid-October until early April. Body mass, which strongly influences the demography of several species (Murie and Boag 1984; Bérubé et al. 1999; Galimberti et al. 2007; Raveh et al. 2010), is a reliable indicator of individual demographic performance in marmots. In North American polygynous sciurids, heavy males have access to a larger number of mates (Raveh et al. 2010) and have a higher survival rate (Armitage et al. 1976; Ozgul et al. 2010) than light ones. Body mass confers winter survival advantages because body fat accumulated during summer provides the only source of energy for hibernation (Bibikow 1968; Armitage 2003). This is particularly true in Alpine marmots where animals may lose up to 30 % of their fall body mass during the course of hibernation (Arnold 1990).

Taking advantage of long-term individually based monitoring, we investigated whether chronological senescence (i.e. an age-dependent process at the population level) and/or terminal decline (i.e. a process most often age-dependent at the individual level) shape within-individual variation in body mass over the lifetime in the Alpine marmot after accounting for the confounding effects of individual heterogeneity (Vaupel et al. 1979; van de Pol and Verhulst 2006). As senescence is pervasive in vertebrate life history traits (Gaillard and Bonenfant 2008), we expected body mass of male and female marmots to exhibit either chronological senescence or terminal decline. According to life history theory, the intensity of sexual selection should be low in monogamous species with a weak sexual size dimorphism (Andersson 1994). With males being only 5 % larger than females (this study) and displaying social monogamy, Alpine marmots should rank close to the low end of intensity of sexual selection. We therefore expected the type and the magnitude of senescence to be similar in both sexes, contrary to what has been reported in highly polygynous and dimorphic species subject to strong sexual selection (Clutton-Brock and Isvaran 2007).

Materials and methods

Study population and data collection

The population of Alpine marmots is monitored since 1990 in La Grande Sassièrè Nature Reserve at an elevation of 2,300 m a.s.l. (French Alps, 45°29'N, 6°59'E). From 1990 to 2010, Alpine marmots have been caught each year from

early April to mid-July. Marmots were trapped using two-door live-capture traps baited with dandelion (*Taraxacum densleonis*) (see Cohas et al. 2007 for further details). Once trapped, individuals were tranquillized with Zolétil 100 (0.1 ml kg^{-1}), and individually marked with a unique numbered ear tag and a transponder (TrovanTM, Germany). Captured marmots were sexed, weighed, and measured for several morphological variables. As dominant individuals of a family group monopolise reproduction by suppressing reproduction of subordinates through aggressive behaviour (Arnold and Dittami 1997; Hackländer et al. 2003), reproductive status (and thereby social status of individuals) was assigned from scrotal development for males and from pregnancy or lactation status for females. However, as extra-pair paternity can occur in the studied population (Cohas et al. 2006), we used daily observations of scent marking and aggressive behaviours to confirm the dominance status of individuals.

Only individuals monitored throughout their adult lifespan were included in the analysis. As senescence should not occur prior to the age at first reproduction (Hamilton 1966), we restricted the analysis to potentially reproductive marmots (i.e. 3 years of age and older; Schwartz and Armitage 2005) when full adult body mass is reached. Subordinates, once they have reached sexual maturity at 2 years of age, start to disperse to establish dominance and to breed the following year (so at 3 years of age). Immigrant individuals that established their dominance in our study site were thus included in the analysis and an age of 3 years was assigned to them when they started to breed on the study site (Lardy et al. 2011). However, during dispersal, sexually mature subordinates could have either died or ended up establishing as dominant outside the study area (see Cohas et al. 2007). Subordinates were thus no longer monitored and were removed from the dataset. Therefore, only dominant marmots, which stay on the same territory for their entire life and potentially reproduce once a year, were included in the analysis. The probability for an individual to become dominant again after being evicted is extremely low. The eviction of a dominant marmot by a challenger results in severe injuries or forces the evicted dominant to hibernate alone the following winter, leading to its death (Allainé and Theuriau 2004; Lardy et al. 2011). We considered that all individuals evicted from dominance died the following winter because these marmots did not re-establish in another territory, nor became subordinate in our study site and were never seen again. Hence, an individual was considered as living its last year when seen as dominant before eviction, during its last event of reproduction, or the year prior to its observed death (Lardy et al. 2011).

We collected 414 age-specific body mass measures on 131 dominant marmots (70 males and 61 females) aged

between 3 and 16 years of age collected from 1990 to 2011 for males and from 1992 to 2011 for females. Longevity was known for 82 individuals. Thirty-four individuals (34) were sampled only once after the age of 3 (mostly still-young individuals) and 97 individuals were sampled between 2 and 10 times during the 1990–2011 period with an average of 3.45 ± 1.76 times per individual (in different years). Thirty-four individuals (34) out of those 97 were captured more than once within a given year, with an average of 2.12 ± 0.38 captures per year.

Statistical analysis

Intra-annual variation in body mass

Alpine marmots hibernate socially (i.e. each family group in the same burrow) between fall and early spring (Arnold 1990), and spend the active season accumulating enough fat for both surviving during hibernation and initiating reproduction the following year (Schwartz and Armitage 2005). Hibernation thus involves a cyclic pattern of body mass variation within a year that might confound age-specific body mass gain. To account for this process, we investigated the pattern of body mass gain within a year. In the case of marmots and other hibernating sciurids, males and females have markedly different patterns of body mass gain during the growing season in relation with reproduction (Boswell et al. 1994; McWhirter 1991). Shortly after hibernation, mating occurs and males spend a lot of time and energy to defend their territory and monopolize their female (Boswell et al. 1994; McWhirter 1991). In contrast, female body mass gain can be affected by reproductive status because after 30 days of gestation they spend most of the next several weeks underground caring for dependent young, which reduces feeding time (McWhirter 1991). This lactation and young raising period is the most demanding period in terms of energy (Clutton-Brock et al. 1989).

To account for such marked between-sex differences in dynamics of body mass over time generated by differential energy expenditure and feeding behaviour, we first explored the time variation of body mass gain during summer with a Generalized Additive Mixed Model (Woods 2006) for each sex separately and using the date of capture within a year as the smoothed predictor (Ozgul et al. 2010; Electronic Supplementary Material). We chose to perform separate analyses for each sex to decrease model complexity because body mass varied according to sex-specific factors (e.g. gestation status in females). For females, we used the date of capture in interaction with a three-level factor (non-reproducing, pregnant, or lactating) to account for the effect of the reproductive phase and status on female body mass. Although dominant marmots reproduce

on an annual basis, they can skip or fail reproduction one year depending on environmental and social conditions. For males, we used capture date to model time variation in body mass within the season. To support our choice to analyse sexes in two different models, we tested, although no such effect was expected to occur, the effect of reproductive status (non-reproducing vs. reproducing) on male summer body mass gain. Additionally, for both sexes, the year of capture and the orientation of the marmot territory (either in the valley or oriented south) were included in the model as fixed effects (Allainé et al. 1998). We did not include elevation or social status because the variation in elevation among territories was negligible at our study site and because we restricted the analysis to mature adults of the same social status (i.e. dominant). Marmot identity was included as a random effect on the intercept to account for problems of both individual heterogeneity and pseudo-replication (sensu Hurlbert 1984). We fitted one model for each sex called “baseline model” before testing for chronological ageing and terminal decline of body mass.

Age-dependent senescence and terminal decline

We tested for the occurrence of chronological senescence by adding age effects to the sex-specific baseline model. We used Akaike Information Criterion (AIC) for model selection, considering the random effect as one parameter (Vaida and Blanchard 2005). We retained the model with the lowest AIC as the best model describing our data. When the difference in AIC between competing models was less than 2, we retained the simplest model (Burnham and Anderson 2002). AIC weight (w_i) was calculated for each model, giving its relative likelihood to be the best among the set of tested models. Age was included either as a linear, quadratic, smoothed term (using penalized regression splines in GAMM) or discrete factor to account for possible non-linear effects of age on body mass. We also fitted piecewise models where body mass was held constant up to a threshold age and from which body mass started to decrease. To fix the threshold value, we used the deviance profile of a model with a varying threshold (see Ulm 1989). We selected the threshold age at the lowest deviance and added one extra parameter to calculate the AIC of the piecewise models. To assess the proportion of variation accounted for by a given model of age-specific body mass we performed an analysis of deviance (ANO-DEV; Skalski et al. 1993). ANODEV compares three models: the full age-dependent model including age as a discrete factor, the focal age-dependent model (e.g. linear, quadratic, smoothed term or piecewise regression of body mass on age), and the age-independent model (i.e. baseline model) to quantify how much of the age-specific variation in body mass is accounted for by any age nested models.

To test for terminal decline, we tested the changes in body mass using a two-level factor “last year of life”, indicating whether or not the body mass was measured during the individual’s last year before death (see Weladji et al. 2006; Reed et al. 2008; Martin and Festa-Bianchet 2011; Nussey et al. 2011). This variable allowed us to compare the population average body mass during adulthood (constant until the individual starts to age) to body mass of individuals in their last year of life. This last variable can be combined with age to assess whether senescence involves a decline of mass scaled to the absolute age (i.e. chronological senescence), a decline of mass scaled to individual age at death (i.e. terminal decline), or both. We included marmot longevity in our models of body mass following van de Pol and Verhulst’s (2006) recommendations to account for individual heterogeneity. As heavier individuals are expected to live longer, not accounting for selective disappearance could mask senescence (Vaupel et al. 1979; van de Pol and Verhulst 2006).

Sex-specific pattern of senescence

To investigate for sex-specific differences in senescence patterns, we compared chronological age and terminal decline between sexes and tested the null hypothesis that coefficients are equal using Wald tests (Agresti 2002). Parameter estimates of senescence and associated standard errors were extracted from sex-specific models and compared with a Wald test. This method allows testing for differences according to a fixed factor when one cannot compute an explicit test from nested models, while taking into account the uncertainty around parameter estimates (Agresti 2002).

We performed all analyses using R 2.10.1 (R Development Core Team 2008) using the function `gamm` in the “`mgcv`” library for Generalized Additive Mixed Models (Woods 2006). Estimates are given as mean \pm 1 SE.

Results

Intra-annual variation in body mass

Mean annual body mass varied over years in both sexes (from 1990 to 2011 for males: $F = 2.6$, $df = 21$, 173.48, $p < 0.01$; and from 1992 to 2011 for females: $F = 2.67$, $df = 19$, 189.51, $p < 0.01$). Reproductive status, as expected, had no effect on male summer body mass gain (difference in AIC values for models with and without interaction of reproductive status with date: $\Delta AIC < 2$), supporting our choice to fit separate models for each sex. Therefore, the model for males only included a non-linear

effect of date, describing a low increase in body mass at the beginning of the season followed by a strong increase during May–July (smoothed term: $F = 71.64$, $df = 2.51$, 173.48 , $p < 0.01$; see Electronic Supplementary Material). In contrast, the time variation of female body mass gain differed according to reproductive status (see Electronic Supplementary Material). Non-reproducing females showed a non-linear increase in body mass, starting later and at a lower rate than males during May–July (smoothed term: $F = 13.92$, $df = 2.04$, 189.51 , $p < 0.01$). Pregnant females had a constant body mass during gestation from April 15 to May 30 (smoothed term: $F = 1.17$, $df = 1$, 189.51 , $p = 0.28$). Lactating females started to increase their body mass once the young were born (between May 20 and July 15). Body mass of lactating females increased linearly during May–June, at a lower rate than males, and decreased slightly from the end of June to July 15th when the pups emerge from the burrow (smoothed term: $F = 18.78$, $df = 3.45$, 189.51 , $p < 0.01$).

No effect of territory orientation was detected on body mass in both sexes (valley versus south: males: -73.14 ± 79.74 , $F = 0.84$, $df = 1$, 172.53 , $p = 0.36$; females: 20.48 ± 94.43 , $F = 0.05$, $df = 1$, 188.52 , $p = 0.82$). Likewise, we did not detect any effect of the two-way

interactions between the orientation, year, reproductive status and date of capture.

Longevity had no effect on body mass for male or female marmots (slope for males: 4.32 ± 24.58 , $F = 0.03$, $df = 1$, 115.76 , $p = 0.87$; slope for females: 20.41 ± 20.54 , $F = 0.99$, $df = 1$, 118.93 , $p = 0.32$) indicating that marmots living longer were not heavier at a given age than shorter-lived individuals. As including longevity restricted the dataset to individuals of known longevity (284 observations on 81 individuals), we only presented results obtained from the entire dataset (individuals of known age, 414 observations on 131 individuals; Table 1).

Chronological senescence and terminal decline

Male and female marmots showed different age-specific patterns of variation in body mass (Table 1; Fig. 1). We found a clear decline in male body mass with increasing age. The quadratic model accounted for 65 % of the observed variation in body mass with age, while the threshold model accounted for 58 % (ANODEV; Table 1; Fig. 1a). Average adult male body mass was $3,893 \pm 230$ g between 3 and 8 years of age (predicted average at the mean capture date), and decreased by about 75.0 ± 34.2 g per

Table 1 Modeling age-specific pattern of body mass variation in male and female Alpine marmots (*Marmota marmota*) (La Grande Sassièrre, French Alps) using Generalized Additive Mixed Models (GAMMs)

Model	Males				Females			
	$n = 198$ (70 individuals)				$n = 216$ (61 individuals)			
	k	ΔAIC	w_i	ANODEV	k	ΔAIC	w_i	ANODEV
Base	23	9.27	0.01	–	22	1.65	0.15	–
Age	24	11.26	0.00	0.00	23	2.42	0.10	0.06
Age ²	25	7.08	0.02	0.65	24	4.23	0.04	0.06
<i>F</i> (Age)	33	13.62	0.00	–	33	0.00	0.33	–
Threshold (8 years)	25	5.51	0.04	0.58	24	3.65	0.05	0.00
<i>s</i> (Age)	24	10.17	0.00	0.25	23	4.42	0.04	0.06
Last year of life (LYL)	24	5.99	0.03	–	23	3.60	0.05	–
Age + LYL	25	6.86	0.02	–	24	4.38	0.04	–
Age + Age ² + LYL	26	0.00	0.58	–	25	6.20	0.01	–
<i>F</i> (Age) + LYL	34	4.36	0.07	–	34	1.56	0.15	–
Threshold + LYL	26	3.52	0.10	–	25	5.59	0.02	–
<i>s</i> (Age) + LYL	25	3.34	0.11	–	24	6.32	0.01	–
Age × LYL	26	5.58	0.04	–	25	11.66	0.00	–

The baseline model (*base*: including year of capture as a factor for both sexes, date of capture for males and date of capture in interaction with reproductive status—non-reproducing, pregnant, lactating—for females) accounts for seasonal variation in body mass of both sexes. *Age* corresponds to a linear relationship between mass and age, *Age*² to a quadratic relationship with mass, *F* (*Age*) to the full age-dependent model (including age as a discrete factor), *Threshold* to the best piecewise regression model linking age and mass, *s* (*Age*) to a model linking mass and a smoothed term of age (using penalized regression splines in GAMM), and *Last year of life* (*LYL*) to a relationship between mass and whether or not the individual is in its last year before death (see text for further details). The best model of age is in bold and the best model overall is in bold and italics. Model selection has been performed using Akaike Information Criterion (AIC), and ΔAIC is the difference between each model AIC and the best model. Akaike weights (w_i) correspond to the relative likelihood of a model to be the best among the set of models tested. *Base* and *F* (*Age*) are used to calculate ANODEV providing the percentage of the age-specific variation in body mass explained by the model, they therefore have no associated value. k is the model number of parameters

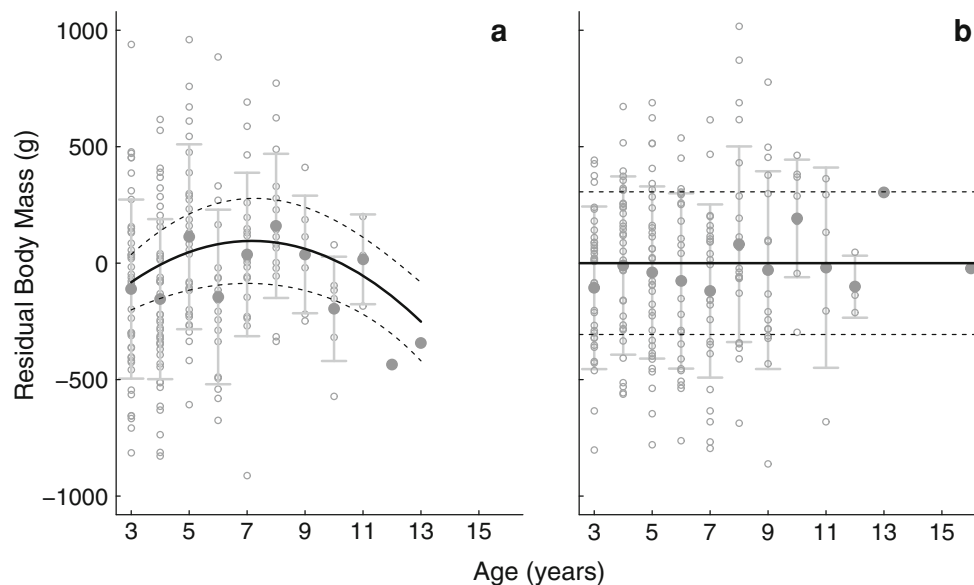


Fig. 1 Sex-specific body mass variation of Alpine marmots (*Marmota marmota*) with age (once accounted for capture date, year and reproductive status—for females only). **a** Male body mass. *Thick line* is the prediction of the quadratic model (i.e. the best model) with

standard error within *dotted lines*. **b** Female body mass. The best model suggests little influence of age on body mass (i.e. constant model, with standard error within *dotted lines*). For both sexes, *grey dots* represent mean body mass variation per age

year (Fig. 1a) from 8 years of age onwards, leading the oldest individuals to lose about 10 % of their adult mass at the end of their life.

Consistent with the terminal decline hypothesis, males lost body mass during their last year of life (Table 1; Fig. 2). Observed variation in male body mass was satisfactorily explained by both absolute age and last year of life ($AIC_w = 0.58$). The best model describing male marmots body mass included both a quadratic effect of age (age 146.20 ± 50.41 , $F = 9.19$, $df = 1$, 170.79 , $p < 0.01$; age² -10.20 ± 3.74 , $F = 8.21$, $df = 1$, 170.79 , $p < 0.01$, Fig. 1) and a terminal decline ($F = 8.29$, $df = 1$, 170.79 , $p < 0.01$; Fig. 2; Table 1). Males lost 161.5 ± 58.1 g in their last year of life, corresponding to about 5 % of their mass. There was no obvious link between age and last year of life (-39.24 ± 23.75 , $F = 2.92$, $df = 1$, 170.58 , $p = 0.09$) indicating that the magnitude of the terminal decline was not much amplified at old ages.

Contrary to males, female body mass did not change with absolute age (linear age: 13.38 ± 12.46 , $F = 1.15$, $df = 1$, 188.76 , $p = 0.28$; Fig. 1b). The baseline model outperformed all other age-dependent models, including the full age-dependent model (all $\Delta AIC < 2$; Table 1). The average mass of females (predicted at the mean capture date) across the entire life span was $3,641 \pm 140$ g for non-reproducing females and $3,696 \pm 147$ g for reproducing females. In addition, female body mass did not show any evidence of terminal decline (estimated slope of 13.14 ± 56.75 , $F = 0.054$, $df = 1$, 188.48 , $p = 0.82$; Fig. 2). Adding longevity in the models did not improve the model fit.

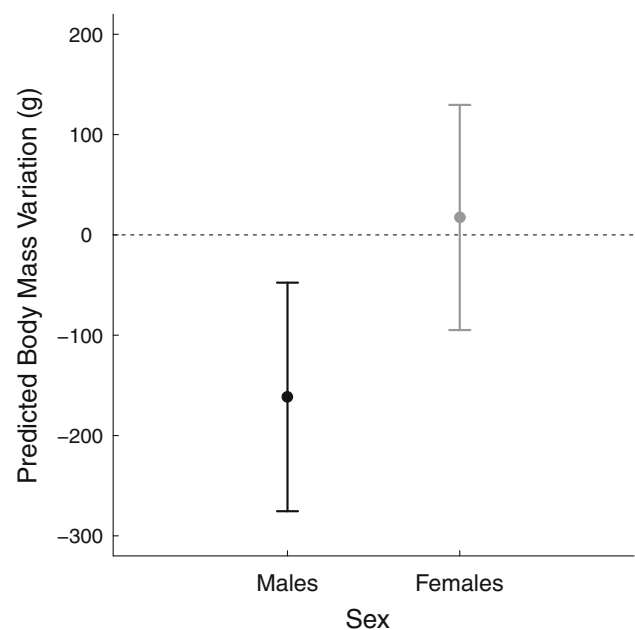


Fig. 2 Predicted body mass variation of male and female marmots in their last year of life once effects of capture date, reproductive status (for females only), year and chronological age (for males only) are accounted for (see text for further details). Models predictions (*dots*) and confidence intervals (*error bars*) are represented in *black* for males and in *grey* for females. The best model for males included a quadratic effect of age and a terminal loss of body mass. This last year effect was detected for males only

To confirm the robustness of our results independently of the few very old marmots, we removed the oldest individuals of both sexes (the only individual of 13 years

for males and the two individuals of 13 and 16 years of age for females) and replicated our analyses. All results remained qualitatively unchanged.

Sex-specific pattern of senescence

We found between-sex difference of body mass variation with chronological age (comparison of the second order polynomial terms of males and females: $z = -2.03$, $p = 0.04$), while the difference of terminal decline between sexes was lower but close to statistical significance (comparison of the “last year of life” effect for males and females: $z = -1.89$, $p = 0.06$).

Discussion

While evidence for senescence in mass has been previously reported in mammals (see Nussey et al. 2011 for a recent detailed analysis in female ungulates), previous studies focused on females and did not look for possible between-sex differences in ageing patterns. One noticeable exception is the study of Mason et al. (2011), that recently analysed age-specific variation in mass for Alpine chamois of both sexes and only found evidence of senescence in males. However, they did not look for combined effects of chronological age and terminal decline. We found clear evidence of chronological senescence of body mass in male marmots, a medium-sized social and hibernating mammal, but not in females (Fig. 1). Based on our current understanding of life history evolution and sexual selection theory (Clutton-Brock and Isvaran 2007), this finding was unexpected for a monogamous and monomorphic species (average body mass of 3.9 and 3.7 kg at mean capture date for adult males and females, respectively).

From 8 years of age onwards, the body mass of males decreased slowly until the last year of life during which a marked terminal decline occurred (Figs. 1a, 2). By contrast, the body mass of females remained quite constant throughout their lifetime (Figs. 1b, 2). Overall, our results clearly demonstrate that the onset of chronological senescence in body mass occurs earlier (at least for marmots older than 8 years of age) and with a much higher intensity in males than in females. As body mass markedly influences reproductive success and survival of marmots (Armitage et al. 1976; Armitage 2003; Ozgul et al. 2010), we expect those fitness components to show senescence in males of this species, as reported in both sexes in several vertebrates (survival: Owens and Bennett 2002 in birds, Gaillard et al. 2003 in large herbivores, Ricklefs 2010a in captive and wild vertebrates; reproductive performance: Bertran et al. 2009 in seabirds, Nussey et al. 2009 in red deer).

While between-sex differences of ageing rates is the rule for different life history traits in a wide diversity of taxa

including insects (Zajitschek et al. 2009), birds (Lecomte et al. 2010) and mammals (Clutton-Brock and Isvaran 2007), the mechanisms involved have not yet been identified (Bonduriansky et al. 2008). The intensity of sexual selection has been proposed to be a driver of the greater actuarial senescence reported in males of highly polygynous and/or dimorphic species (Clutton-Brock and Isvaran 2007). In the case of Alpine marmots, it could explain the chronological senescence in body mass we observe among males, even if the sexual size dimorphism is weak. The cost of territoriality is higher for males, as the annual probability for a dominant Alpine marmot of being replaced is about 8 % for females and 11 % for males (Arnold 1990). Moreover, despite being monomorphic and socially monogamous, subordinates of the family group are potential competitors and dominants of both sexes try to suppress their reproduction (Arnold and Dittami 1997; Hackländer et al. 2003). Dominant males also have to compete with males from outside the family that try to gain extra-pair copulations and evict them (Goossens et al. 1998; Cohas et al. 2006; Lardy et al. 2012). The ability of dominant males to monopolise reproduction is inversely related to the number of subordinate males in the group (Cohas et al. 2006; Lardy et al. 2012). This unavoidable competition with subordinates and intruders is energetically costly for dominant males, which have to defend their territory and their female, beyond the mating period, during the whole active season (Arnold and Dittami 1997; Lardy et al. 2012), and seems to lead to long-term detrimental effect on summer mass gain of dominant males (Arnold and Dittami 1997). Hence, as an individual ages, its body mass will consistently decrease, therefore reducing its capacity to maintain dominance.

The occurrence of a terminal decline of body mass of males indicates that some particular events occur at short notice before the animal dies. This finding seems consistent with the “terminal illness” hypothesis proposed by Coulson and Fairweather (2001), taking the form of an increased winter mass loss with ectoparasite load, and thereby a decreased winter survival in marmots. However, Arnold and Lichtenstein (1993) did not find that the parasite load in Alpine marmots was greater for older individuals, and the terminal illness hypothesis is thus unlikely to explain between-sex differences of terminal decline.

Alternatively, and similarly to chronological senescence, an increase in intra-sexual competition might be involved in the terminal loss of body mass that usually precedes loss of dominance and death in marmots (Arnold and Dittami 1997; Allainé and Theuriau 2004; Lardy et al. 2012). The energy allocated by dominants in controlling subordinate reproduction and monopolising breeding increases with the number of subordinate males in the group (Cohas et al. 2006; Lardy et al. 2012). Hence, male reproductive senescence has the potential to foster conflicts between dominant

males and their competitors, young males being able to mate successfully with the dominant females only when the dominant male has impaired competitive abilities, as reported in feral fowl (*Gallus gallus*) (Dean et al. 2010). Therefore, the intense intra-sexual competition that takes place at the beginning of the mating season (which corresponds to the emergence from hibernation) might accelerate body mass loss and lead to death of male marmots (Allainé and Theuriau 2004; Lardy et al. 2012). The rate of intra-sexual competition for territory and reproduction seems to be less important for females, which do not lose mass the year prior to death (Lardy 2012).

However, the rather sudden decline of mass we reported in male marmots might also involve an environmentally driven cause of death. Although we lack measurements of body mass at the exact time of entry in and emergence from hibernation, we suggest that winter survival and body condition at emergence could shape the observed sex-specific mass loss, either chronological or terminal, we reported here. Hibernation leads to decreased mortality and longer lifespan (Wilkinson and South 2002; Turbill et al. 2011) but also to costs in social species in relation to social thermoregulation (Armitage 2003; Zervanos and Salsbury 2003). As male marmots spend more energy in hibernation than do females (Arnold 1988, 1993; Zervanos and Salsbury 2003) they might pay the cost of being more active in social thermoregulation, in terms of somatic maintenance, by suffering more pronounced decline in body mass. We call for further investigation into that interesting avenue of research for comparative ageing.

Our findings of different senescence patterns between sexes point out the complexity of senescence mechanisms in free-ranging mammals. Our study of the monogamous and social Alpine marmot suggests that the mechanisms underlying between-sex differences in senescence might strongly differ depending on the species' life history. Moreover, contrasted environmental conditions among populations might also generate differential senescence rates in life history traits. Further studies will be required to assess the magnitude of variation in senescence rate across populations within a given species.

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References

Agresti A (2002) Categorical data analysis, 2nd edn. Wiley, Hoboken
 Allainé D, Theuriau F (2004) Is there an optimal number of helpers in Alpine marmot family groups? *Behav Ecol* 15:916–924

- Allainé D, Graziani L, Coulon J (1998) Postweaning mass gain in juvenile alpine marmots *Marmota marmota*. *Oecologia* 113:370–376
- Andersson MB (1994) Sexual selection. Princeton University Press, New Jersey
- Armitage KB (2003) Marmots (*Marmota monax* and allies). In: Feldhamer GA, Thompson BC, Chapman JA (eds) Wild mammals of North America: biology, management and conservation, 2nd edn. John Hopkins University Press, Baltimore, pp 188–210
- Armitage KB, Downhower JF, Svendsen GE (1976) Seasonal changes in weights of marmots. *Am Midl Nat* 96:36–51
- Arnold W (1988) Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). *J Comp Physiol B* 158: 151–156
- Arnold W (1990) The evolution of marmot sociality: II. costs and benefits of joint hibernation. *Behav Ecol Sociobiol* 27: 239–246
- Arnold W (1993) Social evolution in marmots and the adaptive value of joint hibernation. *Verh Dtsch Zool Ges* 86:79–93
- Arnold W, Dittami J (1997) Reproductive suppression in male Alpine marmots. *Anim Behav* 53:53–66
- Arnold W, Lichtenstein AV (1993) Ectoparasite loads decrease the fitness of Alpine marmots (*Marmota marmota*) but are not a cost of sociality. *Behav Ecol* 4:36–39
- Berman M, Gaillard JM, Weimerskirch H (2009) Contrasted patterns of age-specific reproduction in long-lived seabirds. *Proc R Soc Lond B* 276:375–382
- Bérubé CH, Festa-Bianchet M, Jorgenson JT (1999) Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology* 80:2555–2565
- Bibikow DI (1968) Die Murmeltiere. Die neue Brehm Bücherei. Ziemsen, Wittenberg Lutherstadt
- Bonduriansky R, Maklakov A, Zajitschek F, Brooks R (2008) Sexual selection, sexual conflict and the evolution of ageing and life span. *Funct Ecol* 22:443–453
- Boswell T, Woods SC, Kenagy GJ (1994) Seasonal changes in body mass, insulin, and glucocorticoids of free-living golden-mantled ground squirrels. *Gen Comp Endocr* 96:339–346
- Bowen WD, Iverson SJ, McMillan JI, Boness DJ (2006) Reproductive performance in grey seals: age-related improvement and senescence in a capital breeder. *J Anim Ecol* 75:1340–1351
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York
- Clutton-Brock TH, Isvaran K (2007) Sex differences in ageing in natural populations of vertebrates. *Proc R Soc Lond B* 274: 3097–3104
- Clutton-Brock TH, Albon SD, Guinness FE (1989) Fitness costs of gestation and lactation in wild mammals. *Nature* 337:260–262
- Cohas A, Yoccoz NG, Allainé D (2006) Extra-pair paternity in the monogamous Alpine marmot (*Marmota marmota*): the roles of social setting and female mate choice. *Behav Ecol Sociobiol* 59:597–605
- Cohas A, Bonenfant C, Gaillard JM, Allainé D (2007) Are extra-pair young better than within-pair young? A comparison of survival and dominance in Alpine marmot. *J Anim Ecol* 76:771–781
- Coulson JC, Fairweather JA (2001) Reduced reproductive performance prior to death in the black-legged kittiwake: senescence or terminal illness? *J Avian Biol* 32:146–152
- Dean R, Cornwallis CK, Lovlie H, Worley K, Richardson DS, Pizzari T (2010) Male reproductive senescence causes potential for sexual conflict over mating. *Curr Biol* 20:1192–1196
- Derocher AE, Stirling I (1994) Age-specific reproductive performance of female polar bears (*Ursus maritimus*). *J Zool* 234:527–536

- Descamps S, Boutin S, Berteaux D, Gaillard JM (2007) Female red squirrels fit Williams' hypothesis of increasing reproductive effort with increasing age. *J Anim Ecol* 76:1192–1201
- Gaillard JM, Bonenfant C (2008) Vertebrate ageing: an evolutionary process with a genetic basis? *Curr Biol* 18:R130–R131
- Gaillard JM, Loison A, Festa-Bianchet M, Yoccoz NG (2003) Ecological correlates of life span in populations of large herbivorous mammals. In: Carey JR, Tuljapurkar S (eds) *Life span: evolutionary, ecological and demographic perspectives*. Population Council, New York, pp 39–56
- Galimberti F, Sanvito S, Braschi C, Boitani L (2007) The cost of success: reproductive effort in male southern elephant seals (*Mirounga leonina*). *Behav Ecol Sociobiol* 62:159–171
- Garel M, Loison A, Jullien JM, Dubray D, Maillard D, Gaillard JM (2009) Sex-specific growth in Alpine chamois. *J Mammal* 90:954–960
- Goossens B, Graziani L, Waits LP, Farand E, Magnolon S, Coulon J, Bel MC, Taberlet P, Allainé D (1998) Extra-pair paternity in the monogamous Alpine marmot revealed by nuclear DNA microsatellite analysis. *Behav Ecol Sociobiol* 43:281–288
- Hackländer K, Möstl E, Arnold W (2003) Reproductive suppression in female Alpine marmots, *Marmota marmota*. *Anim Behav* 65:1131–1140
- Hamilton WD (1966) The moulding of senescence by natural selection. *J Theor Biol* 12:12–45
- Hayward AD, Wilson AJ, Pilkington JG, Pemberton JM, Kruuk LEB (2009) Ageing in a variable habitat: environmental stress affects senescence in parasite resistance in St Kilda soay sheep. *Proc R Soc Lond B* 276:3477–3485
- Hoffman CL, Higham JP, Mas-Rivera A, Ayala JE, Maestriperi D (2010) Terminal investment and senescence in rhesus macaques (*Macaca mulatta*) on Cayo Santiago. *Behav Ecol* 21:972–978
- Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54:187–211
- Jones OR, Gaillard JM, Tuljapurkar S, Alho JS, Armitage KB, Becker PH, Bize P, Brommer J, Charmantier A, Charpentier M, Clutton-brock TH, Dobson FS, Festa-Bianchet M, Gustafsson L, Jensen H, Jones CG, Carl G, Lilland T, McCleery R, Merilä J, Neuhaus P, Nicoll MAC, Norris K, Oli MK, Pemberton J, Pietiäinen H, Ringsby TH, Roulin A, Saether BE, Setchell JM, Sheldon BC, Thompson PM, Weimerskirch H, Wickings EJ, Coulson T (2008) Senescence rates are determined by ranking on the fast–slow life-history continuum. *Ecol Lett* 11:664–673
- Lardy S (2012) Evolutionary consequences of intra-sexual competition in social species: the example of the Alpine marmot *Marmota marmota*. PhD dissertation, University of Lyon, Villeurbanne
- Lardy S, Cohas A, Figueroa I, Allainé D (2011) Mate change in a socially monogamous mammal: evidences support the “forced divorce” hypothesis. *Behav Ecol* 22:120–125
- Lardy S, Cohas A, Desouhant E, Tafani M, Allainé D (2012) Paternity and dominance loss in male breeders: the cost of helpers in a cooperatively breeding mammal. *PLoS ONE* 7:1–6
- Lecomte VJ, Sorci G, Cornet S, Jaeger A, Faivre B, Arnoux E, Gaillard M, Trouvé C, Besson D, Chastel O, Weimerskirch H (2010) Patterns of aging in the long-lived wandering albatross. *Proc Natl Acad Sci USA* 107:6370–6375
- Martin JGA, Festa-Bianchet M (2011) Age-independent and age-dependent decreases in reproduction of females. *Ecol Lett* 14:576–581
- Mason THE, Chirichella R, Richards SA, Stephens PA, Willis SG, Apollonio M (2011) Contrasting life histories in neighbouring populations of a large mammal. *PLoS ONE* 6:e28002
- McNamara JM, Houston AI, Barta Z, Scheuerlein A, Fromhage L (2009) Deterioration, death and the evolution of reproductive restraint in late life. *Proc R Soc Lond B* 276:4061–4066
- McNulty DR, Smith DW, Vucetich JA, Mech LD, Stahler DR, Packer C (2009) Predatory senescence in ageing wolves. *Ecol Lett* 12:1347–1356
- McWhirter RB (1991) Effects of reproduction activity and foraging behaviour of adult female columbian ground-squirrels. *Can J Zool* 69:2209–2216
- Medawar PB (1952) *An unsolved problem of biology*. Lewis, London
- Monaghan P, Charmantier A, Nussey DH, Ricklefs RE (2008) The evolutionary ecology of senescence. *Funct Ecol* 22:371–378
- Murie JO, Boag DA (1984) The relationship of body weight to overwinter survival in columbian ground-squirrels. *J Mammal* 65:688–690
- Nussey DH, Metherell B, Moyes K, Donald A, Guinness FE, Clutton-Brock TH (2007) The relationship between tooth wear, habitat quality and late-life reproduction in a wild red deer population. *J Anim Ecol* 76:402–412
- Nussey DH, Kruuk LEB, Morris A, Clements MN, Pemberton JM, Clutton-Brock TH (2009) Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. *Am Nat* 174:342–357
- Nussey DH, Coulson T, Delorme D, Clutton-Brock TH, Pemberton JM, Festa-Bianchet M, Gaillard JM (2011) Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. *Ecology* 92:1936–1947
- Owens IPF, Bennett PM (2002) *Evolutionary ecology of birds: life histories, mating systems, and extinction*. Oxford series in ecology and evolution, Oxford University Press, Oxford
- Ozgul A, Childs DZ, Oli MK, Armitage KB, Blumstein DT, Olson LE, Tuljapurkar S, Coulson T (2010) Coupled dynamics of body mass and population growth in response to environmental change. *Nature* 466:482–485
- Perrin C, Allainé D, Le Berre M (1993) Socio-spatial organization and activity distribution of the Alpine marmot *Marmota marmota*: preliminary results. *Ethology* 93:21–30
- Proffitt KM, Garrot RA, Rotella JJ, Wheatley KE (2007) Environmental and senescent related variations in weddell seal body mass: implications for age-specific reproductive performance. *Oikos* 116:1683–1690
- R Development Core Team (2008) *R: a language and environment for statistical computing*. R Project, Vienna
- Rattiste K (2004) Reproductive success in presenescent common gulls (*Larus canus*): the importance of the last year of life. *Proc R Soc Lond B* 271:2059–2064
- Raveh S, Heg D, Dobson FS, Coltman DW, Gorrell JC, Balmer A, Neuhaus P (2010) Mating order and reproductive success in male Columbian ground squirrels (*Urocitellus columbianus*). *Behav Ecol* 21:537–547
- Reed TE, Kruuk LEB, Wanless S, Frederiksen M, Cunningham EJA, Harris MP (2008) Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are associated with varying costs of early reproduction. *Am Nat* 171:E89–E101
- Ricklefs RE (2010a) Insights from comparative analyses of aging in birds and mammals. *Aging Cell* 9:273–284
- Ricklefs RE (2010b) Life-history connections to rates of aging in terrestrial vertebrates. *Proc Natl Acad Sci USA* 107:10314–10319
- Schwartz OA, Armitage KB (2005) Weather influences on demography of the yellow-bellied marmot (*Marmota flaviventris*). *Oikos* 265:73–79
- Sharp SP, Clutton-Brock TH (2010) Reproductive senescence in a cooperatively breeding mammal. *J Anim Ecol* 79:176–183
- Skalski JR, Hoffman A, Smith SG (1993) Testing the significance of individual- and cohort-level covariates in animal survival studies. In: Lebreton JD, North PM (eds) *Marked individuals in the study of bird populations*. Birkhäuser Verlag, Basel, pp 9–28

- Turbill C, Bieber C, Ruf T (2011) Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proc R Soc Lond B* 278:3355–3363
- Ulm K (1989) On the estimation of threshold values. *Biometrics* 45:1324–1326
- Vaida F, Blanchard S (2005) Conditional Akaike information for mixed effects models. *Biometrika* 92:351–370
- van de Pol M, Verhulst S (2006) Age-dependent traits: a new statistical model to separate within- and between-individual effects. *Am Nat* 167:766–773
- Vaupel JW, Manton KG, Stallard E (1979) The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography* 16:439–454
- Walker LC, Herndon JG (2010) Mosaic aging. *Med Hypotheses* 74:1048–1051
- Weladji RB, Gaillard JM, Yoccoz NG, Holand Ø, Myrseth A, Loison A, Nieminen M, Stenseth NC (2006) Good reindeer mothers live longer and become better in raising offspring. *Proc R Soc Lond B* 273:1239–1244
- Wilkinson GS, South JM (2002) Life history, ecology and longevity in bats. *Aging Cell* 1:124–131
- Williams GC (1957) Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 11:398–411
- Woods SN (2006) *Generalized additive models: an introduction with R*. Chapman & Hall, London
- Zajitschek F, Bonduriansky R, Zajitschek SRK, Brooks RC (2009) Sexual dimorphism in life history: age, survival, and reproduction in male and female field crickets *Teleogryllus commodus* under seminatural conditions. *Am Nat* 173:792–802
- Zervanos SM, Salsbury CM (2003) Seasonal body temperature fluctuations and energetic strategies in free-ranging eastern woodchucks (*Marmota monax*). *J Mammal* 84:299–310