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How social behaviour and life-history traits change with age and in the year prior to death in female yellow-bellied marmots

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Studies in natural populations are essential to understand the evolutionary ecology of senescence and terminal allocation. While there are an increasing number of studies investigating late-life variation in different life-history traits of wild populations, little is known about these patterns in social behaviour. We used long-term individual based data on yellow-bellied marmots (*Marmota flaviventer*) to quantify how affiliative social behaviours and different life-history traits vary with age and in the last year of life, and how patterns compare between the two. We found that some social behaviours and all life-history traits varied with age, whereas terminal last year of life effects were only observed in life-history traits. Our results imply that affiliative social behaviours do not act as a mechanism to adjust allocation among traits when close to death, and highlight the importance of adopting an integrative approach, studying late-life variation and senescence across multiple different traits, to allow the identification of potential trade-offs.

This article is part of the theme issue 'Ageing and sociality: why, when and how does sociality change ageing patterns?'

1. Introduction

Senescence is the irreversible accumulation of damage with increasing age, leading to deteriorating cellular and physiological function and eventual death [1,2]. Thus, the impact that age has on performance and function late in life has been the focus of many recent studies in natural populations (reviewed by the authors in [3,4]). There is substantial variation in how traits change late in life. Some traits undergo a gradual decrease over several years, as is usually expected for senescence, while others show an abrupt decrease in trait value close to death, potentially signalling a more general physiological collapse, for example, owing to terminal illness [5]. By contrast, there are also positive effects of age later in life, which can be attributed to increasing experience or maturity [6,7], social aspects (e.g. dominance position, [8]; number of helpers, [9]), terminal investment [10] and/or terminal allocation (*sensu* [11]), which unlike terminal investment does not necessarily imply fitness costs. Because observed patterns can differ among traits, it is important to study a suite of factors rather than a single trait in isolation (see [12–14]). Doing so permits the detection of different processes that contribute to the same senescence patterns and to identify potential trade-offs that would not have otherwise been detected [13,15].

Most senescence studies in natural populations have focused on survival and reproduction (reviewed by Nussey *et al*. [3]), the two core traits related

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to fitness [16]. However, there are a growing number of studies that test for age-dependent decreases in other traits that underlie survival and reproduction, including body mass (e.g. [17,18]), physiological traits (i.e. traits related to the immune system, [13,19,20]; traits related to stress hormones: [19,21]), and behaviour (e.g. foraging, [19,22–24]; dispersal, [25]). Terminal effects, typically estimated through the so-called last year of life effects, have most frequently been tested in studies on reproduction (e.g. [5,14,26–29]) and body mass (e.g. [17,18,30]). What stands out is that comparatively few studies in natural populations have quantified late-life variation in behavioural traits (but see [31]), with studies on social behaviour being particularly uncommon. This is surprising because sociality is known to impact longevity [32,33] and has known benefits and costs associated with it [34]. It is possible that studies on such traits are rare because behaviour has not typically been considered part of the senescence process [31].

Living in groups may protect animals from predation [35], permitting them to allocate less time to antipredator vigilance and more time to other fitness-related activities [36]. However, group living also exposes animals to more parasites and pathogens [37]. Such disease challenges may drive the evolution of compensatory social responses such as allogrooming [38]. While it is commonly assumed that sociality is associated with decreased extrinsic mortality and hence increased longevity, this is not always seen [33]. Nonetheless, in humans [32] and a variety of other social mammals (e.g. [39–41]), those with stronger social relationships do live longer lives. Interestingly, and while social relationships may vary over the course of an individual's lifetime [42], less is known about patterns of senescence. Overall, we know very little about late-life variation in social behaviour of free-living non-primate mammals and how this variation compares to patterns observed in life-history traits.

One challenge with studying late-life variation across multiple traits in natural systems is that it requires detailed longitudinal data for many individuals with known lifespans. We capitalized on a long-term study of free-living, individually marked yellow-bellied marmots (*Marmota flaviventer*), a long-lived rodent species with lifespans up to 16 years in the wild (D. T. Blumstein 2021, unpublished observations) and annual adult survival probabilities of 72–80% [43]. We know that traits reflecting social networks in the marmots are heritable [44] and can negatively impact longevity [45]; and, while we know that older females are less social [42], we are aware of no previous studies that have specifically focused on late-life variation in social behaviour. As for life-history traits, we know that stress hormone levels (faecal glucocorticoid metabolites), which negatively affect marmot survival [46], are negatively associated with age [47], as is vigilance behaviour, but only when adults are in good body condition [48]. In addition, separate studies have found evidence in support of senescence in reproduction and body mass [18,49], and of a terminal decrease in body mass [18]. To date, age-related variation in traits related to immune response has not been investigated in yellow-bellied marmots.

Here, we analyse late-life variation in 11 social network traits and five life-history traits (reproduction, body mass, stress hormone levels, immune response and vigilance behaviour), to determine whether social behaviour varies with age and close to death, and how the observed patterns compare to those in life-history traits. We focused on females, for which there were adequate data available for all traits. If social behaviour is costly (as suggested by Blumstein *et al.* [45]), we expect gradual and/or terminal decreases in sociality late in life based on the senescence hypothesis, whereas benefits gained through social behaviour may compensate costs or even lead to animals being more social [33]. For life-history traits, we expect stress hormone levels and immune response to be higher at older ages and/or later in life, and body mass, reproduction and vigilance to decrease either gradually, terminally or both.

2. Methods

(a) Study system

Yellow-bellied marmots were studied along a 5 km stretch of the Upper East River Valley, CO, USA (38°57′ N, 106°59′ W; 2900 m elevation; [43]), in and around the Rocky Mountain Biological Laboratory in Gothic. Most individuals live in colony groups with a harem-polygynous mating system, where they share a territory with other related adult females, yearlings, juveniles and the resident adult male. Colony locations in our study area are classified as either up-valley or down-valley sites, depending on whether they were in the higher or lower elevation sections of the valley [50]; most individuals do not move between them.

(b) Live-trapping data collection

Every year between 1962 and 2018, from mid-May to mid-September, we regularly live trapped marmots at known burrow locations. At first capture, individuals were marked with uniquely numbered ear tags and a dorsal fur symbol (which was refreshed when required), to allow identification across years and during observations from afar, respectively. Females in our dataset were first caught as juveniles or yearlings and are thus of known age.

Females have at most one litter per year. We recorded reproductive status during trapping events and assigned offspring to their mothers through behavioural observations, and since 2002, confirmed maternity via genetic analyses (98% matching), based on a likelihood approach of 8–12 microsatellite loci at 95% trio confidence level (see methods in [51]). Pups are born underground and first emerge weaned and fully independent in late June or July [43]. Once offspring emerged, we intensified our trapping efforts to mark them within one to two weeks. New pups are unlikely to be missed, as all colonies are very closely monitored during the pup emergence season. We used the number of weaned offspring to quantify reproductive success.

An individual's body mass was measured at every capture, using a handling bag and digital scales. To compare body mass across years, for each individual, we standardized measures taken at various dates to 15 August (late-season body mass is important in predicting overwinter survival) using best linear unbiased predictors (following [52,53]; also see [54]).

Faecal samples were collected and immediately stored on ice whenever marmots defecated in the trap or during handling, and later frozen at −20°C. Faecal glucocorticoid metabolites (henceforth 'glucocorticoids') were then extracted from faecal samples and quantified yearly following established protocols and by using a validated assay [55].

As a proxy metric for immune response, we chose the quotient of the absolute neutrophil and lymphocyte counts (i.e. N : L ratio), a measure that is commonly used as an indicator for immunological challenges and physiological stress [56–58]. We collected 2–3 ml blood from the femoral vein of captured marmots, and stored samples in vacutainers containing heparin or ethylenediamine tetraacetic acid on ice until being processed in the laboratory. We made thin film blood smears within 2 h of collecting the samples [48]. Slides were stained with a Thermo Fisher Scientific Hema 3 Stat Pack. The N : L ratio was then calculated using a standard procedure that entailed counting neutrophils, lymphocytes, basophils and monocytes until 100 cells were counted or 30 min passed, whichever came first [59].

(c) Observational data collection

Near daily colony observations from 2002 to 2018 were conducted from mid-April to mid-September, from 7.00 to 10.00 and from 16.00 to 19.00, when marmots are most active and during periods when it was not raining or snowing; vigilance observations were not conducted when it was excessively windy. Observations were conducted by trained observers from distances that did not interfere with marmot activity using binoculars and 15–45× spotting scopes.

If a female was not observed during a given season, she was recorded as dead because adults have an annual recapture probability of greater than 98% (see multistate mark–recapture analyses, [51,60]). Indeed, given the intensive monitoring regime and site fidelity in adult females, an unobserved female is almost certainly dead. The exact cause of mortality is usually unknown, and we are thus looking at all-cause mortality. Based on the year of death, we were also able to estimate lifespan (i.e. age of last observation) and the last year of life (LYL), which describes the year prior to the year of death.

To quantify vigilance while foraging, we conducted 2 min focal animal observations during which we noted the following behavioural transitions: foraging in a bipedal or quadrupedal position, bipedal or quadrupedal looking (henceforth 'vigilance'), locomotion and out of sight [48,61]. Observations were dictated into handheld recorders and later scored in JWATCHER 1.0 [62]. Observers were trained to identify all behaviours in the ethogram and then to quantify them using JWATCHER until their intra-observer reliability was greater than or equal to 0.95.

We used all-occurrence sampling to record affiliative social interactions between marmots. These included behaviours such as greeting each other, allogrooming, sitting in close proximity, playing and foraging together (ethogram in [63]). Following Blumstein *et al*. [45], we used the same 11 social network statistics (i.e. indegree, outdegree, betweenness centrality, incloseness, outcloseness, local clustering, global clustering, negative average shortest path, eigenvector centrality, instrength and outstrength; for further details, see [64–66]) to estimate sociality for individuals with at least 5 yearly observations.

Indegree and outdegree describe how many other individuals a subject receives interactions from and initiates interactions with, respectively. Betweenness centrality is the proportion of shortest path lengths in the network between all pairs of individuals that are connected to a given individual. Closeness measures how close an individual is to all other individuals in the network through both direct and indirect relationships. Incloseness and outcloseness describe the number of received and initiated interactions, respectively. Clustering represents network cliquishness and is calculated by dividing an individual's actual number of relationships by the total possible number that it could form with adjacent neighbours in theory. We specifically used local clustering, which refers to an individual's embeddedness in the network, and global clustering, which describes network density around a certain individual. The average shortest path is measured as the average number of social network members that a given individual needs to go through in order to contact another individual in the network, and thus represents the efficiency of information transfer. We used the additive inverse of average shortest path (i.e. 'negative average shortest path') to facilitate interpretation of this variable alongside the other traits. Eigenvector centrality describes an individual's connectedness in the network, and it also takes indirect relationships among its neighbours into account. Finally, instrength and outstrength describe received and initiated interactions, respectively, where strength is calculated as the frequency (sum of weights) of interactions between an individual and its adjacent neighbours. For all traits, a larger value is interpreted as being more social. Additional detail on these data can be found in Blumstein *et al*. [45].

(d) Statistical analyses

To test for changes in sociality with age and in the year before death, for each social network trait except instrength, outstrength and negative average shortest path, we fitted a generalized linear mixed-effects model (GLMM) with a binomial error distribution. Instrength and outstrength were fitted in GLMMs assuming a Poisson distribution. For negative average shortest path, we fitted a linear mixed-effects model (LMM) with Gaussian error function. To test if age and proximity to death influence social behaviour, we included second-order orthogonal polynomials for age, and a two-level factor for LYL (yes versus no) as fixed effects. To control for environmental effects on sociality, and potential environmental dependence of age and LYL effects on sociality, we also fitted valley as two-level factor (up versus down), and two-way interactions between valley and age (linear and quadratic), and valley and LYL.

To test for changes in life-history traits with age and in the year before death, we fitted LMMs with Gaussian distribution for glucocorticoids and body mass, and GLMMs with a Poisson error structure for the number of offspring and N : L ratio, and a binomial distribution for vigilance. The model for N : L ratio was fitted with neutrophil count as the response and the log of lymphocyte count as an offset variable [67], which allows us to adequately evaluate the variation in the N : L ratio while retaining the Poisson distribution for neutrophil count.

The models for life-history traits also included fixed effects of age (second-order orthogonal polynomials), a two-level factor for LYL and valley, and two-way interactions between valley and age and valley and LYL. In addition, to control for potential reproductive suppression (as previously reported in yellow-bellied marmots, [68]; and Alpine marmots, *Marmota marmota*; [69]), and density dependence of age and LYL effects on reproduction and vigilance, we fitted the number of adult females within a colony in each year (henceforth 'density'), and the interaction of density with age and LYL as covariates. Models for faecal glucocorticoids, N : L ratio and vigilance further included fixed effects of day of year and time of day, to account for seasonal and daily variation in those response variables, respectively. Finally, to account for potential seasonal and daytime dependence of age and LYL effects on glucocorticoids, N : L ratio and vigilance, we fitted interactions of day of year and time of day with age and with LYL.

To confirm that negative quadratic age effects indeed described a decrease in a trait at old ages, rather than an increase at young ages followed by a plateau (and vice versa for positive quadratic age effects), we refitted models on subsets of the data, including only observations at older ages (7+ years) and only a linear age effect. To facilitate model convergence and allow for comparison across traits, all continuous predictors were scaled and centred with a mean of 0 and a variance of 1. All models included random effects of female identity, year and female year of birth to account for non-independence of repeated observations of individuals, years and cohorts, respectively. We also included an observation-level random effect in the Poisson-distributed models to account for overdispersion [67], as indicated by the ratio of residual deviance to residual degrees of freedom (ratios of 4.13, 3.71, 1.75 and 21.8 for instrength, outstrength, number of offspring and N : L ratio, respectively).

Models were fitted with the glmer and lmer functions from the package lme4 [70] in R v. 3.6.3. [71]. To avoid biasing estimates in our models, non-significant interactions ($p > 0.05$) were backwards eliminated based on ANOVA type III tests, but otherwise full models with non-significant fixed effects were retained [72]. Fitting age as orthogonal polynomials allowed us to independently test and interpret linear and quadratic age effects within the same model [73].

Because individual heterogeneity and selective disappearance are known to cause biases in longitudinal and cross-sectional analyses of age [74,75], we also fitted a series of additional models with data subsets that comprised females that reached a lifespan of at least 6 years. These models yielded qualitatively similar results to the models fitted to the full datasets, leading us to conclude that population-level age effects can be interpreted at the individual level. Selective disappearance biases in the data structure were minimized by only including individuals from cohorts that were almost completely extinct (maximum 1 or 2 surviving individuals) in the analyses.

3. Results

(a) Data summary

Datasets ranged in size between 133 and 1315 data points (electronic supplementary material, table S1). Female age ranged between 2 and 14 years across all datasets, except for social network traits and N : L ratio, where the maximum age was 12 years. The median female age was 4.0 in the vigilance dataset, 3.5 in the body mass dataset and 3.0 in all other datasets. Details regarding the structure of each individual dataset are listed in the electronic supplementary material, table S1.

(b) Effects of age and last year of life

Age was significantly associated with 5 out of 11 social network traits (figure 1*a–k*; electronic supplementary material, table S2), namely local clustering, global clustering, eigenvector centrality, outstrength and instrength. We found a positive linear effect of age for local clustering, and a positive quadratic effect of age for global clustering (figure 1; electronic supplementary material, tables S2–S4). Local clustering (i.e. how embedded an individual is in the network) increased with age (figure 1*f*), and global clustering (i.e. network density) decreased prior to about age 5 and then increased at older ages (figure 1*g*). We also found a negative linear effect of age for both eigenvector centrality (i.e. influence) and instrength (i.e. received interactions), and a negative linear and a positive quadratic effect of age for outstrength (i.e. initiated interactions; figure 1; electronic supplementary material, tables S2 and S5–S7), showing that eigenvector centrality and instrength decreased with age, whereas oustrength decreased at younger ages and increased in old age (figure 1*i–k*). Contrary to our expectations, there was no significant change in any of the social network traits in the year preceding death compared to earlier years (electronic supplementary material, tables S2–S13).

On the other hand, there were significant age-related changes in all life-history traits (figure 1*l–p*; electronic supplementary material, table S2). Specifically, there was an interaction between valley and quadratic age for glucocorticoids and between valley and linear and quadratic age for body mass. Body mass increased with age, with a greater increase in the down-valley environment, and at older ages, both glucocorticoids and body mass decreased, but only down-valley (figure 1*l,m*; electronic supplementary material, tables S2, S14 and S15). We also found a linear positive and a negative quadratic age effect for both number of offspring and N : L ratio (figure 1; electronic supplementary material, tables S2, S16 and S17). Both traits increased prior to about age 7 or 8 and then decreased in old age (figure 1*n,o*). For vigilance, we found an interaction between season and linear age (figure 1; electronic supplementary material, table S18), showing that vigilance increased with increased age, but more so later in the season (figure 1*p*). Models fitted to data subsets truncated at age 6 confirmed quadratic age effects in the main models, except for N : L ratio, suggesting that part of the negative quadratic age effect describes increases at young ages followed by a plateau, rather than a decrease at old ages.

We further found significant changes in body mass, number of offspring and vigilance in the last year of life (electronic supplementary material, tables S2, S15, S16 and S18). Specifically, we found a negative LYL effect for body mass, showing that body mass was lower in the last year of life compared to previous years (electronic supplementary material, table S14). For the number of offspring, we found an interaction of density with LYL, showing that the number of offspring was lower in the last year of life, even more so at greater colony densities (electronic supplementary material, table S16). Finally, for N : L ratio and vigilance, we found interactions of season with LYL, showing that N : L ratio was higher and vigilance lower in the least year of life compared to previous years, more so later in the season (electronic supplementary material, tables S2, S17 and S18).

4. Discussion

Little is known about late-life variation in social behaviour, and how it compares to patterns observed in life-history traits. Our study yields two important insights regarding late-life variation in social behaviour. First, sociality varies with age (i.e. effects can stretch out over a long time), and we provide a rare example for potential senescence in affiliative social behaviour. Second, there does not appear to be enough variation in such traits to allow terminal adjustment of affiliative behaviours at the end of life in favour of other important life-history traits. Yet, life-history traits show striking complementary patterns prior to death, suggesting that changes in other behaviours (vigilance and foraging) may be used to compensate for detrimental late-life effects.

(a) Age-dependent patterns

The frequency of received interactions, as well as an individual's influence decreased with increasing age, while initiated interactions, network density and embeddedness within its network (i.e. cliquishness) increased. The increase in trait values for initiated interactions, network density and embeddedness potentially reflect that older females have larger matrilines (related females; [43]). Negative effects of age on social network traits, showing that older females are less social, have previously been reported [42,45], and are in line with our expectation that sociality is costly. However, the increase in initiated interactions suggests that old females might compensate for increasing social isolation as shown by the decrease in received interactions and influence on the network.

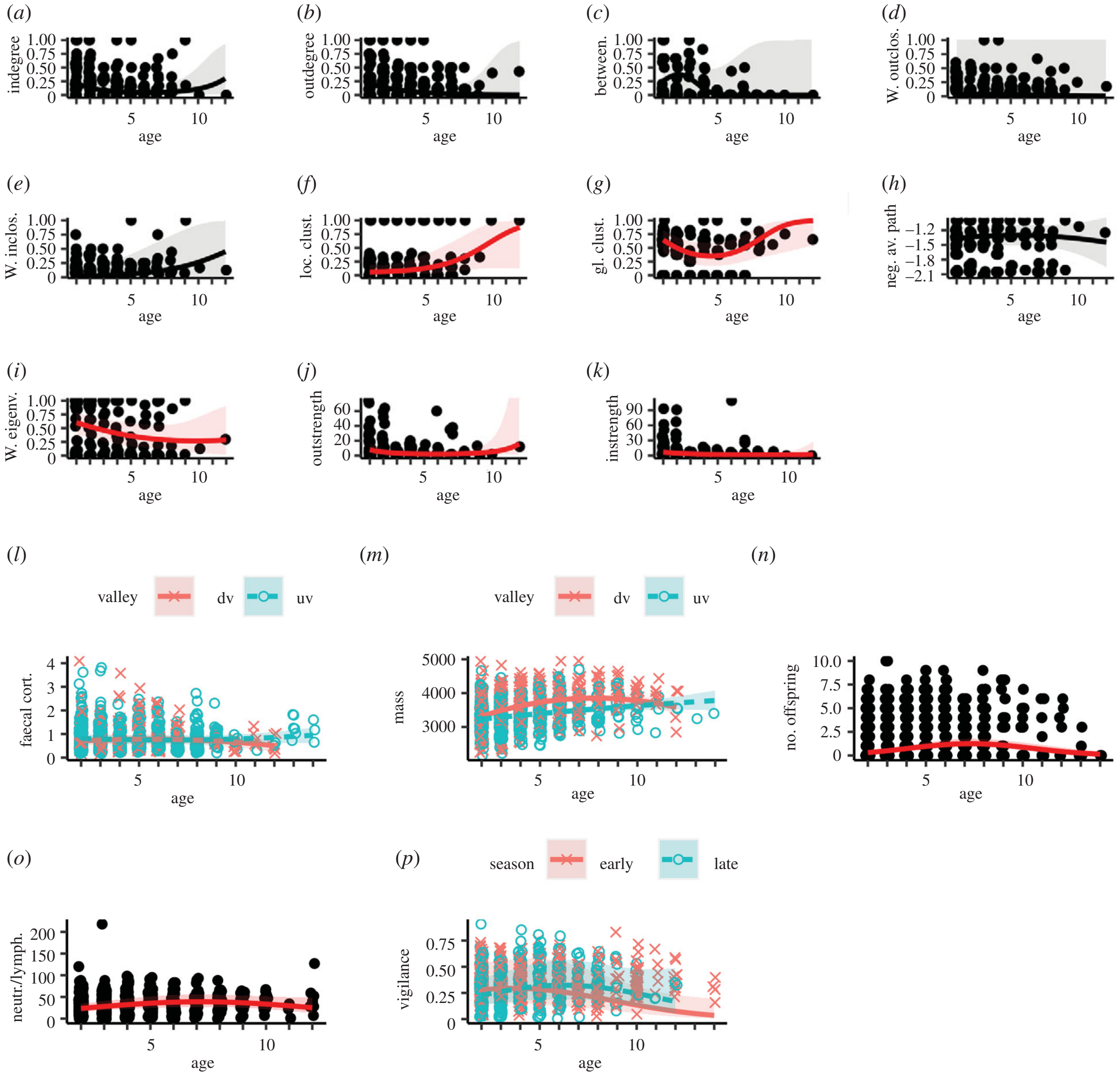

Figure 1. Relationships between age and (*a–k*) social network traits and (*l–p*) life-history traits. Colour indicates significant ($p < 0.05$) relationships of age with a respective trait. In (*l*,*m*), there is an interaction of age with valley, represented through different colours (orange) down-valley and (blue) up-valley. In (*p*), there is an interaction of age with day of year (i.e. season), and while season is a continuous variable, it is shown in (orange) early and (blue) late-season categories for illustration purposes. Shaded areas indicate prediction approximated confidence intervals and points show raw data.

In life-history traits, patterns of age-dependent variation were largely consistent with the senescence hypothesis, while exhibiting a high degree of synchrony [14,76]. The number of offspring increased in early years of adult life, followed by a decrease later in life. The age-dependent decrease is in line with previous studies on reproductive senescence [4]. Early-life increases could be owing to individuals becoming better at acquiring or allocating resources (i.e. increasing experience; [6,77]). Results for immune response, measured as N : L ratio, suggested a similar pattern to that of offspring number, although there was no significant decrease in old age. Vigilance increased with age, more so later in the season, possibly because pups are present. Body mass increased with age in both environments, with a greater increase down-valley, and at old ages, both body mass and stress hormones decreased, but only down-valley. The absence of senescence in body mass up-valley has previously been reported [18] and may reflect physiological constraints in a harsher environment [78], where females exhibit little senescence because they have little mass to lose. Interestingly, however, stress hormone levels also tended to increase at older ages up-valley, suggesting that patterns in these two traits may be linked. One possible explanation is that old females living in the harsher (i.e. more stressful) environment may not be in good enough condition to reproduce. Various studies show that chronic stress is linked to reduced reproductive performance (e.g. [79,80]), and stress levels are indeed known to impact reproduction in the marmots [81].

(b) Terminal effects

Contrary to our expectation, there was no significant change in social behaviour in the last year of life compared to earlier years. This suggests that a change in social behaviour at the end of an individual's life is unlikely to provide a performance advantage, or that it acts as a marker for general physiological collapse. By contrast, we found that life-history traits exhibited terminal effects in all traits except stress hormone levels. The absence of elevated stress hormones in the last year of life compared to the rest of life supports the idea that some stress effects are more likely to be chronic, though it is possible that terminal stress responses occur over shorter timescales and last year of life effects do not capture such variation.

Body mass and number of offspring decreased in the year prior to death, consistent with a general physiological collapse at the end of life. A terminal decrease in body mass is likely to be a good indicator for impending death, given that marmots with a low body mass late in the season (i.e. at entry to hibernation) are unlikely to survive the winter [82,83]. We also found a greater decrease in the number of offspring at higher colony densities, suggesting that females may be reproductively suppressed [68], or provide alloparental care [84] when they are close to dying and not able to produce many pups of their own. These hypotheses remain to be explicitly tested.

Resources late in life could also be allocated to other important functions, such as immune responses. We found a terminal increase in N : L ratio, which was more pronounced later in the season. This suggests increased allocation to immune function towards the end of life, possibly involving a trade-off with reproduction or other traits [85], and matches the physiological collapse indicated by body mass and reproduction. The results for vigilance behaviour also match those of the other life-history traits that exhibited terminal effects. Vigilance decreased in the last year of life and more as the season progressed. Later in the season, females may take greater risks and reduce vigilance in favour of time spent foraging [48,86]. Females are likely to require more food to compensate for their deteriorating physiological condition and increased energetic expenses on behalf of the immune system [85], as indicated by the terminal decrease in body mass and litter size and the terminal increase in N : L ratio.

5. Conclusions

We found that age affected both social behaviour and life-history traits, whereas terminal effects in the last year of life were only observed in the latter. This leads us to conclude that social relationships are relatively stable in the last year of life, whereas in life-history traits, terminal effects are almost the rule. It may be easier to adjust major performance traits in favour of one another, as reproduction and other life-history traits are more likely to be directly energetically constrained compared to sociality. We should emphasize that yellow-bellied marmots, while social, are not obligately social, and rates of social interactions are substantially lower than in highly social species (e.g. primates). Owing to the low rate of interactions, which normally decline as the year progresses, we estimated every individual's social network traits once per year. Because behaviours are highly dynamic and can change throughout the season, we might have missed changes in sociality that played out over shorter timescales, within a season, that might be important in the last year of life.

Overall, our results imply that changes in social behaviour at old ages reflect a shift in social interaction dynamics with a decrease in received and an increase in initiated interactions, suggesting social isolation by others and compensation. Once an individual is close to dying, it has comparatively low body mass and litter size, and is apparently more immunologically challenged, thus it should focus on allocating more time to foraging, which probably comes at the expense of vigilance. Indeed, acquisition of resources is fundamental in determining possibilities of allocation to other traits [87]. Further work that directly investigates associations between vigilance and major performance traits would allow us to gain a better understanding of the patterns observed here. Thus, an exciting avenue of research would be to investigate whether age and sociality interact to impact senescence trajectories in life-history traits, and thus whether sociality can dampen senescence effects in those traits.

Ethics. Marmots were studied under annual permits issued by the Colorado Division of Wildlife (TR-917). All procedures were approved under research protocol ARC 2001-191-01 by the University of California Los Angeles Animal Care Committee on 13 May 2002, and renewed annually.

Data accessibility. The data and code are available through the open science framework: https://doi.org/10.17605/OSF.IO/DVAZJ.

Authors' contributions. The study was designed by S.B.K., J.G.A.M. and D.T.B. All authors collected the data. S.B.K. and J.G.A.M. analysed the data. S.B.K. wrote the manuscript, with contributions and critical revisions by D.T.B. and J.G.A.M.

Competing interests. We declare we have no competing interests.

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