Advancing methods for the biodemography of aging within social contexts

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Abstract . Several social traits including status, integration, early-life adversity, and their interactions across the life course can predict health, reproduction, and mortality in humans. Accordingly, individual sociality plays a fundamental role in the emergence of phenotypes driving the evolution of aging. Recent work placing human social gradients on a biological continuum with other species provides a useful evolutionary context for aging questions, but there is still a need for a unified evolutionary framework for sociality, health, and aging. Here, we first summarize current challenges to disentangle the effects of the social environment on human life courses. Next, we review recent advances in comparative biodemography and propose a biodemographic perspective to address socially driven health phenotype distributions and their evolutionary consequences using a nonhuman primate population. This new comparative approach uses evolutionary demography to address the joint dynamics of populations, sociality, phenotypes, and life history parameters. The long-term goal is to advance our understanding of the link between individual sociality, population-level outcomes, and the evolution of aging.

1. Introduction

The social environment shapes human life courses, and can generate strong associations between sociality, health, and longevity. For example, higher social status predicts longer lifespan (Adler et al., 1993; Chetty et al., 2016; Hajat et al., 2011; Lantz et al., 2010; Sapolsky, 2004; Wilkinson and Marmot, 2003), greater social support predicts healthier aging (Antonucci et al., 2019; Béland et al., 2005; Holt-Lunstad et al., 2010), and early life social adversity predicts higher mortality risk (Anda et al., 2006; Ferraro et al., 2016; Hughes et al., 2017). However, disentangling the effects of the social environment on human life courses remains challenging due to multiple uncontrolled (e.g., incongruencies in self-reported health; non-random attrition) and unknown confounding factors (e.g., biased survey information). Comparative approaches can both provide evidence concerning the evolutionary origins of the social determinants of human health and aging, and provide a model for the intricate interactions and potential feedback loops between sociality and aging (Carey and Judge, 2001; Lucas and Keller, 2020). This review argues that studies on the comparative biodemography of aging can advance our understanding of the link between individual sociality, population-level demographic outcomes, and the evolution of aging in humans. For this, we define senescence as a decline in function with age and differentiate it from health statuses which we define as deviations from such expected mean decline. We introduce conceptual frameworks for the evolutionary demography of aging within social contexts, discuss why current challenges in human health and aging studies call for comparative approaches, and describe a unifying methodological framework for the biodemography of aging that links current research in the social determinants of health to evolutionary demography approaches to the fundamental rules of life history evolution.

1.1 The biodemography of human aging within social contexts

Mortality in human populations has been delayed substantially in recent years (Vaupel, 2010). Senescence, the process of aging, has been slowed down or postponed largely due to progress in public-health efforts, access to education, socioeconomic mobility, and cultural changes in lifestyles (Achey, 2016; Cundiff et al., 2017; Oeppen and Vaupel, 2002; Riley, 2001; Vable et al., 2019), rather than strong selection on genetic factors (Christensen et al., 2006; Hjelmborg et al., 2006; McGue et al., 1993). Yet, accumulating evidence shows that there are persistent health inequalities within today's aging populations as well, highlighting the importance of mechanistic questions regarding how and why variability in the aging process across individuals emerges and is maintained, and how individual sociality and health influences such process (Crimmins and Vasunilashorn, 2016; Gutin and Hummer, 2021).

The emerging field of biodemography integrates such sociality factors in moving towards a full understanding of the evolutionary roots of health and aging (Hooper et al. 2014). In particular, the biodemography of aging incorporates biological theory and methods on ecological and evolutionary processes with traditional demographic approaches to better understand the dynamics of health and mortality within populations (Baudisch, 2015; Carnes, 2007; Christensen, 2008; Gavrilov and Gavrilova, 2015; Vaupel, 2004; Wachter, 2008; Yashin et al., 2016). Biodemography also incorporates theories of life history trade-offs, allowing us to quantify dynamics between survival and reproduction (Tuljapurkar et al., 2020). This interdisciplinarity encourages an alliance between the social and the biological sciences that expands beyond traditional demographic structures (e.g., age, race/ethnicity, socioeconomic status) as it provides novel opportunities to address how these structures are linked to the underlying pathways that modulate health (Arbeev et al., 2019; Crimmins and Vasunilashorn, 2016; Giuliani et al., 2018; Palma-Gudiel et al., 2020). These advances occurred in concert with work by social scientists who incorporated a life course perspective into studies of health inequality (Dannefer, 2003, 1987; Ferraro et al., 2009; Ferraro and Shippee, 2009; Morton and Ferraro, 2020). In just the past few years, evidence has continued to accumulate concerning the role that structural inequality (e.g., discrimination, racism) and associated factors shaping the social environment (e.g., poverty, stress) have on major disparities in health (e.g., Jackson and Engelman, 2022; Morton and Ferraro, 2020; Noren Hooten et al., 2022; Sauerteig et al., 2022; Williams et al., 2019). Such evidence shapes paradigms in biodemography and the social sciences (e.g., "the gerontological imagination", Ferraro 2018). It is now time to parallel these efforts with methods for the quantification of the effect of individual sociality on health phenotypes, and how these associations translate into the evolutionary dynamics of human aging.

2. Current challenges in modeling the social determinants of health and aging call for comparative approaches

Socially and economically disadvantaged persons experience a higher accumulation of risk factors (low income: Bor et al., 2017; Hirai et al., 2012; migrants: Riosmena et al., 2014; racial minorities: Shah et al., 2020;

Wallace, 2015; Williams and Chiquita, 1995) and increased mortality (Chetty et al., 2016; National Center for Health Statistics, 2016). Yet, common approaches to modeling health trajectories (e.g., growth curve models, latent class models) often report similar health profiles between socially disadvantaged and advantaged groups (Brown et al., 2012; Gueorguieva et al., 2009; Markides and Coreil, 1986) or favorable health trajectories in traditionally marginalized groups (i.e., Migrant Effect and the Hispanic Paradox; Franzini et al., 2001; Markides and Rote, 2019; Quiñones et al., 2011). This divergence between evidence of cumulative risk and increased mortality on the one hand, and methodological approaches that model average health trajectories of disadvantaged groups on the other, suggests that current forecasting methods for predicting the progression of individual health may fail to capture critical aspects of human sociality and thus not accurately capture human health trajectories (Engelman and Jackson, 2019). Another issue when modeling the social determinants of human health and aging concerns limitations in handling missing data when this missing data is not random. As individuals age and their health deteriorates, longitudinal studies suffer non-random reductions in the number of participants due to mortality and other sources of attrition (Vaupel, 2010). Thus, many studies of human health and aging may have biases in that robust individuals will remain in the study into very old age, whereas those who die earlier or have unknown fates will not be included (Jackson et al., 2019). Finally, survey responses – a common method in human studies – are influenced by many other factors such as the personal perceptions of respondent and interviewers (Courtenay, 2000; Davis et al., 2010; Dowd and Zajacova, 2010; Gunasekara et al., 2012; Salazar, 1990; Sorlie et al., 1992; Williams and Chiquita, 1995) that can limit our understanding of the causal mechanisms of individual health and consequent aging. We argue that animal models for the social dimensions of health and aging can therefore provide a new and valuable opportunity to test novel biodemographic perspectives on analyzing individual health and improve methods to forecast health over the life course that can be applied to humans.

2.1 Challenge 1: untying individual health forecasting from gradualist assumptions

A typical view of senescence is that individual health deteriorates with increasing age. Such a process can be described by mixed-effects regression methods through an intercept (i.e., baseline measure of health) and a slope (i.e., rate of health change over time; DiPrete and Eirich, 2006). Although these methods allow for individual variation in baseline levels (i.e., random intercepts) and in the rate of change (e.g., random slopes, quadratic terms, exponential functions), they operate under the assumption that health changes smoothly and gradually as individuals age. In doing so, forecasts from these methods do not align with empirical evidence demonstrating associations between cumulative disadvantage and late life outcomes, and this modeling approach may not fully capture within-person variability in health (Fig 1, survey data). In particular, the smoothing of mean health trajectories across social groups may not capture the effect of the social environment on individual health and consequent aging because this approach may underestimate the accumulation of poor health outcomes in socially disadvantaged persons (Engelman and Jackson 2019; Fig 1, mixed-effects).

In contrast to the gradualist assumptions of many models, empirical evidence suggests that human health can show periods of stability, slight deterioration, and then recovery from health insults (Bolano et al., 2019; Gill et al., 2010; Guilley et al., 2008; Keown, 2003). As life progresses through time, individuals may remain in the same health status (i.e., stasis) or transition among health states before death. That is, health does not decline gradually and homogeneously with no reversals. This highlights a crucial aspect of human health dynamics that accurate forecasting models must capture. In line with this, Engelman and Jackson (2019) proposed a new approach to health history forecasting by describing individual health trajectories as a punctuated equilibrium pattern where individuals experience periods of long-term stability interrupted by sudden changes in health status or mortality. The authors argue that while gradual approaches appeal to an intuitive reasoning about health change, such a modeling choice produces a mean health change that is not representative of the changes experienced by most of the individuals comprising the population.

One way to capture such health dynamics are multi-state models (Namboodiri and Suchindran, 2013; Schoen, 2006) and sequence analysis (Abbott and Tsay, 2000). These models describe discrete health states and transition probabilities among these states, and more accurately capture the health trajectories observed in real populations (Engelman and Jackson, 2019). We also argue that multi-state models describing changes across age as a Markov process may also provide a much-needed reconciliation between deterministic and stochastic processes when modeling individual health that would be otherwise obscured by the smoothing of health trajectories in gradualist approaches (Figure 1, multi-state).

2.2 Challenge 2: Addressing data missing not at random

Another key issue with human studies is that they likely underestimate the extent of poor health in aging populations given limited approaches to handle missing data (Jackson et al., 2019; Jackson and Engelman, 2022). Selective dropout at very old ages, especially among unhealthy and socially disadvantaged persons, is common (Badawi et al., 1999; Coste et al., 2013; Duim and Lima Passos, 2020; Mirowsky and Reynolds, 2000; Purdie et al., 2002; Van Beijsterveldt et al., 2002; Young et al., 2006) and can result in the selection of robust individuals in late life. Moreover, many approaches to research on health across the life course do not account for competing risks of mortality, health change, and attrition across groups. This conceals persistent socially driven health inequities in late life because the privileged sector often suffers a higher accumulation of health penalties due to longer lives (Jackson and Engelman, 2022).

As the limitations of missing data have been increasingly recognized, methods addressing missing data at random have become more widely used (e.g., multiple imputation maximum likelihood; Graham, 2009). However, these methods cannot remove the bias associated with data missing not at random (Goldberg et al., 2021). In contrast, multi-state models provide flexibility in the number of meaningful life states describing individual trajectories, allowing us to incorporate temporary missingness as a discrete state in the model (Engelman and Jackson, 2019). Here, temporary missingness becomes a life state that individuals can transition into if they leave the study, or out of if they return to the study. Multi-state models are thus powerful tools that make it possible to empirically quantify the likelihood that a particular person belonging to a health state will leave and return to the sample. Because mortality (i.e., absorbing state) and other types of attrition can also be easily distinguished and incorporated, multi-state models explicitly account for the contribution of different types of missing data to the cohort's health experiences (Engelman and Jackson, 2019).

2.3 Challenge 3: Recognizing the limitations of survey data

Survey research and self-reported health are common elements of human health and aging studies addressing the impact of social inequalities (Black et al., 2017). Surveys have proven to be a reliable general tool for quickly producing empirical data from large representative samples, but these data also have significant disadvantages. For example, response rates are hard to control, and the data produced can lack many important details about the topic under investigation (Kelley et al., 2003). When used longitudinally (e.g., cohort studies), survey research suffers from other limitations due to the potential for significant changes in individual's responsiveness over time, as well as in the consistency of respondents in their replies to public health-relevant questions when asked again at a later time (ethnic origin: Johnson 1974; patterns of abuse: Abramsky et al., 2022; Loxton et al., 2019; smoking: Kaestle, 2015; substance use: Broman et al., 2022; suicidal attempts: Hart et al., 2013). In general, there may be systematic differences in the ability of individuals to self-evaluate their own health across time (Black et al., 2017; Vuolo et al., 2014). Associations between self-reported health and objective health, as measured by biological risk factors, may also differ across socially stratified groups (Dowd and Zajacova, 2010; Layes et al., 2012). Conversely, interviewer effects also contribute significantly to biases in survey research, as respondents may be predisposed to provide socially desirable responses to the interviewer (Davis et al., 2010; Salazar, 1990). Interviewers also contribute to misclassification of race and ethnic groups (Massey 1980; Williams and Chiquita, 1995); biased assumptions of health among old persons (Thorslund and Wärneryd, 1990); biases in age, race, and gender perceptions (as reviewed by Davis et al., 2010); and can be affected by their level of experience interviewing people (Salazar, 1990). Taken together, these data limitations may contribute to the census miscount of socially stratified groups that ultimately affects reported rates of health conditions (Williams and Chiquita, 1995). Thus, both survey and interviewer data can result in biases in our ability to evaluate the accuracy of models quantifying the effects of the social environment on human health and consequent life courses.

2.4 Social animal models for the biodemography of aging

The biological pathways from social adversity to health and longevity, together with the proximate physiological and molecular mechanisms that shape these changes, are now being revealed (Cavigelli and Caruso, 2015; Snyder-Mackler et al., 2020; Shively and Wilson, 2016). Yet, the need for a unified evolutionary framework for the social determinants of health and aging across species remains. Animal models provide several advantages relative to human studies, as they allow us to record the specific nature of social relationships through direct observations without complex processes of human cultural evolution (Mesoudi and Thornton, 2018). Animal models allow us to measure the natural course of health deterioration and recovery with no interventions or significant confounding factors that may impact human outcomes (Challenge 1; Blumstein et al., 2018). Animal models also allow us to quantify nonrandom mortality risks given that each individual's endpoint is known (Challenge 2). Finally, animal models allow us to evaluate the accuracy of health and aging forecasting models using systematic data collection methods impossible to implement in most human studies, such as survey-based research (Challenge 3; Colman, 2018). Thus, animal models provide comparative approaches that could become our gateway to explore the evolutionary origins of the social determinants of human aging and how this relates to health: whether and how our closest relatives are similarly shaped by social gradients, and why certain aging trajectories across the tree of life are shared by some but not others (Jones et al., 2014). We recognize that our human concept of aging cannot be directly transferred to numerous species, especially within social contexts, but we also emphasize that this represents an opportunity and not an occasion for disengagement (Cohen, 2018).

A call to advance studies on cross-species comparisons of social environments and their effects on health, longevity, and life histories was enthusiastically made almost a decade ago when the National Research Council of the National Academies prompted a discussion about sociality, hierarchy, and health within a comparative biodemographic perspective (Committee on Population National Research Council, 2014). Since then, several advances in our understanding of the social mechanisms of aging have highlighted the complex dynamics between social relationships and life outcomes, as well as the need to study animals with long lifespans if we intend to understand the extraordinary longevity of humans (Colchero et al., 2016; Korb and Heinze, 2021). In this section, we review recent comparative reports on the evolution of aging within social contexts that followed such call.

While many mechanistic questions on the evolution of increased longevity remain unanswered, both physiological and social mechanisms appear to shape mortality schedules across species (Lucas and Keller, 2020; Noren Hooten et al., 2022; Snyder-Mackler et al., 2020). Evidence that sociality is associated with long lives across the tree of life has been accumulating, partly due to the recent focus of aging researchers on eusocial insects (Johnson and Carey 2014) and the counterintuitive observation that those who reproduce more also have exceptionally long lives (i.e., absence of the fecundity/longevity trade-off; Dixon et al., 2014; Heinze and Giehr, 2021; Korb et al., 2021; Kramer et al., 2021; Negroni et al., 2021; Rau and Korb, 2021; Tasaki et al., 2021). Here, the evolution of a reproductive division of labor confers strong advantage to reproductive individuals through increased survival. Transcriptome analyses revealed that experimental reproductive activation in worker honeybees increased survival through a reduction in risk of disease and increased oxidative stress resistance (Kennedy et al., 2021). Similar patterns of resilience to oxidative stress were observed in leaf-cutting ant workers (Majoe et al., 2021) and the ant *Temnothorax rugatulus* (Korb et al., 2021) after experimental loss of the nest's queen. This is especially intriguing because leaf-cutting ant workers, for example, do not produce fertile offspring. Thus, such findings raise important questions regarding the evolution of improved health trajectories in queenless workers (Majoe et al., 2021).

By expanding comparative studies beyond eusocial insects, we gain further insights into whether and how multiple social dimensions including status, integration, and early life environments shape health and aging trajectories across a physiological and cognitive complexity gradient (Marmot and Sapolsky 2014). For example, social status in a cooperative breeder population of Seychelles warblers is associated to the pace of aging through a reduction in telomere attrition (a marker of cellular senescence) among dominant females, likely due to reduced costs of parental care trading-off against increased senescence (Hammers et al., 2019).

The observation that breeders receiving help in raising the young age more slowly than the helpers has been observed across several taxa (Berger et al., 2018; Downing et al., 2021), although causality or associations to health remain unknown. In primates, evidence from genome-wide and multi-region transcriptomic studies show that social status affects immune regulation and aging producing evidence of antiviral phenotypes (Snyder-Mackler et al., 2016; 2018) and younger relative transcriptional ages (Chiou et al., 2022) in high-status females. However, associations among social status, health, and aging are often sex-specific and context-dependent. High-status male baboons exhibit up-regulation in inflammation and immune defense-related genes, but such traits may have been present in these males before moving up in the hierarchy (Lea et al., 2018). This complex causal relationship between socioenvironmental factors and aging trajectories was further highlighted by Anderson et al. (2021), who found that high-status males were predicted to be older than their chronological ages with respect to a DNA methylation-based age predictor ('epigenetic clock'). High-status meerkats similarly show higher rates of both telomere attrition and survival (Cram et al., 2018). While such accelerated aging may be indicative of costs associated to higher reproductive effort in high social status individuals, this raises questions regarding the role, if any, of other social dimensions on epigenetic age across populations.

Social networks metrics, such as how integrated and connected an individual is to others in the network, have recently emerged as an important domain for understanding aging and mortality processes (Silk 2014). Social network statistics have open the opportunity to deconstruct sociality into the types of social connections that predict longevity (Ellis et al., 2019). Individuals with strong connections and central roles in the network, or those that are highly integrated, exhibit lower risks of mortality. This is potentially mediated through social security (Montero et al., 2020), mutualistic behaviors (Archie et al., 2014; Cheney et al., 2016; Ellis et al., 2019; Lehmann et al., 2015), stronger social support (Nuñez et al., 2015), and better access to social information (Ellis et al., 2017). Whether these associations between an individual's social integration and connectedness and their life trajectory are equally conserved at old ages requires more attention. Using physiological and anatomical markers of immunity in an adult population of rhesus macaques which included aging individuals, Pavez-Fox et al. (2021) found associations between social integration and low white blood cell counts suggesting links between social integration and inflammation markers. On the other hand, increased social support through higher pack size in cooperative grey wolves was found to offset individual costs of disease (Almberg et al., 2015). The absence of an association between group size and increased senescence was also described for a socially foraging bat (Gager et al., 2016). These findings contradict long-standing hypothesized costs of group living (i.e., disease transmission, increased infection rates) and further highlights the need to revisit classical hypotheses on life history trade-offs in social animals.

Finally, several comparative studies echoing the potential role that the early life social environment has on compromising health and shaping the fate of individuals have emerged. An accumulation of adverse events early in life predicted longevity in baboons (Tung et al., 2016) and such adverse environment had intergenerational effects (Zipple et al., 2019). Early adversity was also found to elevate glucocorticoid levels in adult female baboons, a measure of stress response associated to health (Patterson et al., 2021; Rosenbaum et al., 2020). The mechanisms behind the relationship between early life adversity and health across the lifespan may involve physiological changes such as inflammation and disease risk (Kinnally et al. 2019)

These relationships between sociality, health and aging also involve complex interactions among them. Multiple species show shifts in patterns of social behavior and underlying psychological processes as individuals age (Kroeger et al., 2021; Machanda and Rosati, 2020; Siracusa et al., 2022) indicating that sociality trajectories are as varied as health and aging trajectories and likely modulated by social status, social organization, and sex. For example, while many primates show reductions in sociality during aging, in very long-lived chimpanzees older males have higher-quality relationships and are more gregarious by many metrics than are younger males, despite their lower social status (Rosati et al 2020). Thus, there are likely reciprocal causalities whereby longevity changes an individual's social patterns, which in turn impacts senescence (Carey and Judge, 2001; Lucas and Keller, 2020). Other, contrasting patterns have also been reported. Several mammal species have shown increased mortality risk in highly connected individuals (Blumstein et al., 2018; Thompson and Cords, 2018), in cooperatively breeding species versus non-cooperative ones (Vágási et al., 2021) and in individuals lacking social support (Begall et al., 2021), suggesting that benefits from social relations may not be universal across species (Blumstein et al., 2018). Together, these patterns highlight further the need for a foundational eco-evolutionary methodological framework to study health and aging within social contexts (Lange et al., 2022).

3. A comparative biodemographic perspective of health and aging withing social contexts

To advance our understanding of the biodemography of aging within social contexts, we need a unifying method linking current research in the social determinants of individual variability to evolutionary demography approaches to the fundamental rules of life history evolution. Here, we provide a general roadmap for accomplishing this using rhesus macaques living at the Cayo Santiago Biological Field Station as an example. Although we do not provide empirical data, our model formulation is based on realistic demographic and health phenotype metrics currently being collected in this population. Our methods can be applied across the entire spectrum of animal models, yet nonhuman primates provide unique advantages to gain insights into aging due to their complex social behavior with analogs of human health-relevant status disparities (Phillips et al., 2014).

3.1 Conceptual framework of evolutionary demography

Classical work on life history theory traces back to the foundations of evolutionary theory (Charlesworth, 1994; Hamilton, 1966; Stearns, 1992). In any given age-structured population, individuals have a survival rate and a fertility rate that both depend on age. The famous Lotka equation demonstrates that in this scenario the annual population growth rate, λ, is a function of age, survival and fertility. Because these three parameters make up a life history, the Lotka equation provided means to quantify associations between life history components and the corresponding values of λ that these associations yield. The realization that the population growth rate, λ, was a quantitative definition of population fitness – it is defined by fitness components – allowed a direct connection between life history theory and evolutionary theory (Hamilton 1966). Now, estimating changes in fitness λ produced by changes in the life history was made possible. For example, if changes are assumed to arise from random mutations, consequent changes in fitness can be interpreted as selection acting on the mutations (Charlesworth 1994). Crucially, such fitness changes can also be computed from λ and its partial derivatives (i.e., sensitivity; Caswell 2001). The definition of these quantitative associations between fitness and the life history directly linked individual phenotypes, to population and evolutionary dynamics setting the stage for the field of evolutionary demography.

Because of its flexible applicability grounded in general theory, many developments to this approach have been made for both ecological and evolutionary theory (Charlesworth 1994; Caswell 2001). More recent studies addressing the evolutionary demography of animal populations have focused on integral projection models (IPMs) as a flexible method to quantify population and evolutionary dynamics while accounting for continuous phenotypes (Levin et al., 2021). Since the development of IPMs (Easterling et al., 2000), studies addressing size-based demographics by structuring populations into a body size continuum have become common mostly in mammals and birds (Coulson, 2012; Levin et al., 2021; Merow et al., 2014; Rees et al., 2014), however few studies have attempted to incorporate social structures into the model (Kappeler et al., 2019; Paniw et al., 2021), while studies explicitly incorporating health structures have just started to emerge (Vincze et al., 2022).

3.2 Integral projection model for socially driven health dynamics in a nonhuman primate

Following the conceptual framework of evolutionary demography, if the evidence indicates that changes in the life history are being driven by sociality, then we argue that changes in fitness can be interpreted as selection acting on the socially driven life courses. Integral projection models allow us to quantitatively test this. IPMs are flexible population models that describe how a population structured by a continuous individual-level state variable (i.e., individual phenotype) changes in discrete time (Easterling et al., 2000). Their construction depends on four fundamental relationships that describe the associations between the phenotype and survival, the phenotype and fertility, the phenotype dynamics (e.g., ontogeny, growth) among survivors and the probability density distribution of offspring phenotypes given parental phenotypes (i.e., heritability; Coulson et al., 2010; Table 1). Importantly, IPMs are realistic as these relationships can vary with age, time and environments (Ellner and Rees, 2006). IPMs are also flexible as they can be extended to incorporate covariation between demographic rates, as well as their uncertainty, by including demographic parameters estimated in Bayesian frameworks (Elderd & Miller, 2016; Hernández-Pacheco et al. 2020; Plard et al., 2019).

For our purpose, individual sociality can be defined by any relevant metric such as social status or social integration as either categorical or continues variable, while individual phenotypes can be defined by any relevant continuous metric of individual health in the population of interest (e.g., biomarkers, body-mass index, cortisol levels). The rhesus macaques of the Cayo Santiago Biological Field Station live in a naturalistic environment with well-known demographics (Hernández-Pacheco et al., 2013) and exhibit a complex dominance hierarchy (i.e., social status or rank) involving relationships between both kin and unrelated individuals (i.e., social integration and connectedness; Ellis et al., 2019; Pfefferle et al., 2014). In particular, these monkeys are good comparative models for addressing questions about psychological health, physical health, and aging. Macaques share human-like social preferences for attending to socially relevant information (Burrows et al., 2009; Hoffman et al., 2007), can further reason about complex social information such as other's perceptual and goal states (Flombaum and Santos, 2005; Santos et al., 2006), and show important similarities with human reward-based decision-making (Santos and Platt, 2014). Lifespan trajectories of these cognitive traits show that older macaques exhibit declines in social attention (co-orienting with another individual), and adult females are more attentive to social information than males (Rosati et al., 2016). On the other hand, increased body condition defined by mass influences their overall health status (Bauer et al., 2011). Thus, to gain insights into the social determinants of health and the evolution of aging, we propose to structure our rhesus macaque population into proxies of both psychological (cognitive) health based on looking time metrics (Rosati et al., 2018) and physical health based on body mass. With this information, we can quantify the individual- and population-level demographic effects of changes in individual health across a sociality gradient using IPMs.

To describe the annual dynamics of the distribution of psychological and physical phenotypes across the socially stratified lifespan, we propose to build an IPM based on phenotype-demography associations evaluated with generalized linear models (Fig 2). Here, social stratification is defined by social status as a categorical variable of two levels, $s$and s' (e.g., high status, low status) and we assume such level remains constant throughout the life of individuals. We consider individuals tracked annually (Fig 2, individual life course from time$t$ to t +1). Thus, for a given individual, ontogenetic changes are defined by cognitive changes and gains or losses in body mass from one year to the next. In a given year, a monkey of sociality$s$, age a, and health z has a 1-year probability of survival given by a function $s_{s,a}(z)$, i.e., the fraction of s, a,z monkeys that survive from age a to age $a+1$ (Fig 2, health-survival function). Ontogenetic changes of survivors are described by a distribution $G_{s,a}(y|z)$, i.e., the fraction of$s$, a, and z monkeys that change health from z to $y$when transitioning from age a to $a+1$ (Fig 2, health-change function), where y represents the health phenotype z of surviving individuals one year later. Reproduction by monkeys of sociality s, age a, and health z will be described by$M_{s,a}(z)$, i.e., the fraction of s, a, z monkeys that produce an offspring (Fig 2, health-fertility function). Finally, inheritance is described by a function $D_{s,a}(y|z)$ that links the health of offspring y and parental health z according to parental age and sociality (Fig 2, health heritability function). For our population, the health-dependent demographic performance and population dynamics across social stratification will be the outcome of two demographic processes: survival and ontogenetic development,$P_{s,a}\,(y|z) = G_{s,a}\,(y|z)\, s_{s,a}(z)$, and reproduction,$F_{s,a}\,(y|z) = M_{a,s}(z) D_{s,a}(y|z)$. Thus, we propose the following general IPM formulation:

$$\mathbf{n}(s, a+1,\ y) = \int \left[P_{s,a}\,(y|z)\, F_{s,a}\,(y|z)\right] \mathbf{n}\,(s,a)\,\mathrm{dz}$$

where n is the population vector describing the total number of individuals of a given sociality, a given age, and a given health state at a given time. IPM analyses require the integral above to be discretized and ultimately be analyzed as traditional multi-state models based on Markov chains (Levin et al., 2021).

Multi-state models (i.e., matrix population models; Caswell 2001) yield a demographic equilibrium, and we can use them to compute the fitness λ, as well as the expected population distribution across health for individuals of a particular sociality and age (i.e., stable distribution; Fig 3). Similarly, for a given sociality and age class, we can estimate the expected contribution to births of an individual to the next generation given its current health state (i.e., reproductive value, Fig 3). Many of our model assumptions can be relaxed and adapted to the population of interest. Sociality metrics can be used in categorical (e.g., status) or continues (e.g., group size) forms and transitions among social categories can be included for populations showing social aging. Multiple heritability functions concerning sociality and health phenotypes can also be added. The variances around the health-demographic functions can also be integrated, and thus we can include estimates of variability around health change. Finally, this approach can be performed using single or two-sex models.

With this information on fitness λ, the stable population structure, and the reproductive value, we can evaluate phenotype-specific selection gradients on demographic and life history parameters through sensitivity analysis (Caswell 2001; Coulson et al. 2010). For example, we can evaluate whether the strength and direction of selection on health-demography function parameters (i.e., GLMs coefficients) and their variances, vary with sociality and aging. If there is high sensitivity of λ to the survival function parameters of high social status or highly integrated monkeys, then an appropriate conclusion is that there is a strong selection acting on the health-survival function parameters of these monkeys as these population metrics contribute more to fitness overall. On the other hand, low social status or poorly integrated individuals may experience a stronger selection on their health-fertility function parameters, given their expected shorter lifespan and potential selection for a faster reproduction. IPMs versatility also provides the novel opportunity of exploring the complex relationships between sociality, health and aging. For example, we can directly quantify shifts in the cognitive response and body mass distributions as individuals age and determine whether such shifts correspond to sociality and whether they have an influence on fitness (Fig 2; Fig 3). If individuals are likely to remain within a health state class throughout life (i.e., stasis), then we can use the IPM to ask whether the social environment is driving such state persistence. Given that IPMs can be used to calculate generation time and net reproductive rate, sensitivity analysis can also evaluate how changes in selection gradients affect these life history descriptors (Coulson et al., 2010). These important features of IPMs, within the multi-state framework, ultimately allows us to quantify the variability in individual health that underlies the observed prevalence of stability, deterioration, and recovery from disabilities (i.e., health states) among socially advantaged and disadvantaged subgroups (Fig 1, multi-state).

4. Conclusions

The social environment predicts health risks and mortality in humans and many other animals. Thus, new advances in the biodemography of aging require the consideration of social factors shaping the life course of people. Because most human health and aging studies depend on self-reports of health, several challenges to disentangle the role of sociality on human life courses remain. Animal models for the social dimensions of health and aging provide new perspectives on the evolution of aging that can be exploited within the methodological framework of evolutionary demography.

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References

Abbott, A., Tsay, A., 2000. Sequence analysis and optimal matching methods in sociology. Annu. Rev. Sociol. 29, 3–33.

Abramsky, T., Harvey, S., Mosha, N., Mtolela, G., Gibbs, A., Mshana, G., Lees, S., Kapiga, S., Stöckl, H.,

2022. Longitudinal inconsistencies in women's self-reports of lifetime experience of physical and sexual IPV: evidence from the MAISHA trial and follow-on study in North-western Tanzania. BMC Womens Health 22, 1–13. https://doi.org/10.1186/s12905-022-01697-y

Achey, R.L., 2016. Life Expectancy. J. Palliat. Med. 19, 468. https://doi.org/10.1089/jpm.2015.0452

Adler, N.E., Boyce, W.T., Chesney, M.A., Folkman, S., Syme, S.L., 1993. Socioeconomic Inequalities in Health: No Easy Solution. JAMA 269, 3140–3145. https://doi.org/10.1001/jama.1993.03500240084031

Almberg, E.S., Cross, P.C., Dobson, A.P., Smith, D.W., Metz, M.C., Stahler, D.R., Hudson, P.J., 2015. Social living mitigates the costs of a chronic illness in a cooperative carnivore. Ecol. Lett. 18, 660–667. https://doi.org/10.1111/ele.12444

Anda, R.F., Felitti, V.J., Bremner, J.D., Walker, J.D., Whitfield, C., Perry, B.D., Dube, S.R., Giles, W.H., 2006. The enduring effects of abuse and related adverse experiences in childhood: A convergence of evidence from neurobiology and epidemiology. Eur. Arch. Psychiatry Clin. Neurosci. 256, 174–186. https://doi.org/10.1007/s00406-005-0624-4

Anderson, J.A., Johnston, R.A., Lea, A.J., Campos, F.A., Voyles, T.N., Akinyi, M.Y., Alberts, S.C., Archie, E.A., Tung, J., 2021. High social status males experience accelerated epigenetic aging in wild baboons. Elife 10, 1–22. https://doi.org/10.7554/ELIFE.66128

Antonucci, T.C., Ajrouch, K.J., Webster, N.J., Zahodne, L.B., 2019. Social relations across the life span: scientific advances, emerging issues, and future challenges. Annu. Rev. Dev. Psychol. 1, 313–336. https://doi.org/10.1146/annurev-devpsych-121318-085212

Arbeev, K.G., Ukraintseva, S. V., Bagley, O., Zhbannikov, I.Y., Cohen, A.A., Kulminski, A.M., Yashin, A.I., 2019. "Physiological Dysregulation" as a Promising measure of robustness and resilience in studies of aging and a new indicator of preclinical disease. J. Gerontol. A. Biol. Sci. 74, 462–468. https://doi.org/10.1093/gerona/gly136

Archie, E.A., Tung, J., Clark, M., Altmann, J., Alberts, S.C., 2014. Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. Proc. Royal Soc. B 281, 20141261. https://doi.org/10.1098/rspb.2014.1261

Badawi, M.A., Eaton, W.W., Myllyluoma, J., Weimer, L.G., Gallo, J., 1999. Psychopathology and attrition in the Baltimore ECA 15-year follow-up 1981-1996. Soc. Psychiatry Psychiatr. Epidemiol. 34, 91–98. https://doi.org/10.1007/s001270050117

Baudisch, A., 2015. Perspectives on the Biodemography of Longevity and Aging. KZfSS Kölner Zeitschrift für Soziologie und Sozialpsychologie 67, 425–439. https://doi.org/10.1007/s11577-015-0321-x

Bauer, S.A., Arndt, T.P., Leslie, K.E., Pearl, D.L., Turner, P. V., 2011. Obesity in rhesus and cynomolgus macaques: A comparative review of the condition and its implications for research. Comp. Med. 61, 514–526.

Begall, S., Nappe, R., Hohrenk, L., Schmidt, T.C., Burda, H., Sahm, A., Szafranski, K., Dammann, P., Henning, Y., 2021. Life expectancy, family constellation and stress in giant mole-rats (*Fukomys mechowii*). P. Philos. Trans. R. Soc 376. https://doi.org/10.1098/rstb.2020.0207

Béland, F., Zunzunegui, M.V., Alvarado, B., Otero, A., Del Ser, T., 2005. Trajectories of cognitive decline and social relations. J. Gerontol. B Psychol. Sci. 60, 320–330. https://doi.org/10.1093/geronb/60.6.P320

Berger, V., Lemaître, J.F., Allainé, D., Gaillard, J.M., Cohas, A., 2018. Early and adult social environments shape sex-specific actuarial senescence patterns in a cooperative breeder. Am. Nat. 192, 525–536. https://doi.org/10.1086/699513

Black, N., Johnston, D.W., Shields, M.A., Suziedelyte, A., 2017. Who provides inconsistent reports of their health status? The importance of age, cognitive ability and socioeconomic status. Soc. Sci. Med. 191, 9–18. https://doi.org/10.1016/j.socscimed.2017.08.032

Blumstein, D.T., Williams, D.M., Lim, A.N., Kroeger, S., Martin, J.G.A., 2018. Strong social relationships are associated with decreased longevity in a facultatively social mammal. Proc. Royal Soc. B 285. https://doi.org/10.1098/rspb.2017.1934

Bolano, D., Berchtold, A., Bürge, E., 2019. The Heterogeneity of Disability Trajectories in Later Life: Dynamics of Activities of Daily Living Performance Among Nursing Home Residents. J. Aging Health 31, 1315–1336. https://doi.org/10.1177/0898264318776071

Bor, J., Cohen, G.H., Galea, S., 2017. Population health in an era of rising income inequality: USA, 1980–2015. The Lancet 389, 1475–1490. https://doi.org/10.1016/S0140-6736(17)30571-8

Broman, M.J., Bista, S., Broman, C.L., 2022. Inconsistency in Self-Reporting the Use of Substances over Time. Subst. Use Misuse 57, 1356–1364. https://doi.org/10.1080/10826084.2022.2083168

Brown, T.H., O'Rand, A.M., Adkins, D.E., 2012. Race-Ethnicity and Health Trajectories: Tests of Three Hypotheses across Multiple Groups and Health Outcomes. J.. Health Soc Behav. 53, 359–377. https://doi.org/10.1177/0022146512455333

Burrows, A.M., Waller, B.M., Parr, L.A., 2009. Facial musculature in the rhesus macaque (Macaca mulatta): Evolutionary and functional contexts with comparisons to chimpanzees and humans. J. Anat. 215, 320–334. https://doi.org/10.1111/j.1469-7580.2009.01113.x

Carey, J.R., Judge, D.S., 2001. Principles of biodemography with special reference to human longevity. Population; An English selection 13:9–24.

Carnes, B.A., 2007. Senescence viewed through the lens of comparative biology. Ann N Y Acad Sci. 1114:14–22.

Caswell, H., 2001. Matrix population models: construction, analysis and interpretation. 2nd edition. Sunderland, MA: Sinauer Associates, Inc.

Cavigelli, S.A., Caruso, M.J., 2015. Sex, social status and physiological stress in primates: The importance of social and glucocorticoid dynamics. Philos. Trans. R. Soc. 370. https://doi.org/10.1098/rstb.2014.0103

Charlesworth, B., 1994. Evolution in Age-Structured Populations. Cambridge, Cambridge University Press.

Cheney, D.L., Silk, J.B., Seyfarth, R.M., 2016. Network connections, dyadic bonds and fitness in wild female baboons. R. Soc. Open Sci. 3. https://doi.org/10.1098/rsos.160255

Chetty, R., Stepner, M., Abraham, S., Lin, S., Scuderi, B., Turner, N., Bergeron, A., Cutler, D., 2016. The association between income and life expectancy in the United States, 2001-2014. JAMA 315, 1750–1766. https://doi.org/10.1001/jama.2016.4226

Chiou, K.L., DeCasien, A.R., Rees, K.P. et al., 2022. Multiregion transcriptomic profiling of the primate brain reveals signatures of aging and the social environment. Nat Neurosci. https://doi.org/10.1038/s41593-022-01197-0

Christensen, K., 2008. Human biodemography: Some challenges and possibilities for aging research. Demographic Res. 19, 1575–1586. https://doi.org/10.4054/DemRes.2008.19.43

Christensen, K., Johnson, T.E., Vaupel, J.W., 2006. The quest for genetic determinants of human longevity: Challenges and insights. Nat. Rev. Genet. 7, 436–448. https://doi.org/10.1038/nrg1871

Cohen, A.A., 2018. Aging across the tree of life: The importance of a comparative perspective for the use of animal models in aging. Biochim. Biophys. Acta Mol. Basis. Dis. 1864, 2680–2689. https://doi.org/10.1016/j.bbadis.2017.05.028

Colchero, F., Rau, R., Jones, O.R., Barthold, J.A., Conde, D.A., Lenart, A., Nemeth, L., Scheuerlein, A., Schoeley, J., Torres, C., Zarulli, V., Altmann, J., Brockman, D.K., Bronikowski, A.M., Fedigan, L.M., Pusey, A.E., Stoinski, T.S., Strier, K.B., Baudisch, A., Alberts, S.C., Vaupel, J.W., 2016. The emergence of longevous populations. Proc. Natl. Acad. Sci. USA 113, E7681–E7690. https://doi.org/10.1073/pnas.1612191113

Colman, R.J., 2018. Non-human primates as a model for aging. Biochim. Biophys. Acta Mol. Basis Dis. 1864, 2733–2741. https://doi.org/10.1016/j.bbadis.2017.07.008

Committee on Population; Division of Behavioral and Social Sciences and Education; National Research Council. Sociality, Hierarchy, Health: Comparative Biodemography: A Collection of Papers. Weinstein M, Lane MA, editors. Washington (DC): National Academies Press (US); 2014 Sep 22. PMID: 25254285.

Coste, J., Quinquis, L., Audureau, E., Pouchot, J., 2013. Non response, incomplete and inconsistent responses to self-administered health-related quality of life measures in the general population: Patterns, determinants and impact on the validity of estimates - a population-based study in France using the MOS S. Health Qual Life Outcomes 11. https://doi.org/10.1186/1477-7525-11-44

Coulson, T., 2012. Integral projections models, their construction and use in posing hypotheses in ecology. Oikos 121, 1337–1350. https://doi.org/10.1111/j.1600-0706.2012.00035.x

Coulson, T., Tuljapurkar, S., Childs, D.Z., 2010. Using evolutionary demography to link life history theory, quantitative genetics and population ecology. J. Anim. Ecol. 79, 1226–1240. https://doi.org/10.1111/j.1365-2656.2010.01734.x

Courtenay, W.H., 2000. Constructions of masculinity and their influence on men's well-being: a theory of gender and health. Soc. Sci. Med. 50, 1385–401. https://doi.org/10.1016/s0277-9536(99)00390-1

Cram, D.L., Monaghan, P., Gillespie, R., Dantzer, B., Duncan, C., Spence-Jones, H., Clutton-Brock, T., 2018. Rank-Related Contrasts in Longevity Arise from Extra-Group Excursions Not Delayed Senescence in a Cooperative Mammal. Curr. Biol. 28, 2934-2939.e4. https://doi.org/10.1016/j.cub.2018.07.021

Crimmins, E.M., Vasunilashorn, S.M., 2016. Chapter 3 - Biodemography: Adding Biological Insight into Social, Economic, and Psychological Models of Population and Individual Health Change with Age, in: George, L.K., Ferraro, K.F. (Eds.), Handbook of Aging and the Social Sciences (Eighth Edition). Academic Press, San Diego, pp. 55–75. https://doi.org/https://doi.org/10.1016/B978-0-12-417235-7.00003-2

Cundiff, J.M., Boylan, J.M., Pardini, D.A., Matthews, K.A., 2017. Moving up matters: Socioeconomic mobility prospectively predicts better physical health. Health Psychology. https://doi.org/10.1037/hea0000473

Dannefer, D., 2003. Cumulative Advantage/Disadvantage and the Life Course: Cross-Fertilizing Age and Social Science Theory. J Gerontol B Psychol Sci Soc Sci. 58, 327–337. https://doi.org/10.1093/geronb/58.6.S327

Dannefer, D., 1987. Aging as intracohort differentiation: Accentuation, the Matthew effect, and the life course. Sociol. Forum 2, 211–236. https://doi.org/10.1007/BF01124164

Davis, R.E., Couper, M.P., Janz, N.K., Caldwell, C.H., Resnicow, K., 2010. Interviewer effects in public health surveys. Health Educ. Res. 25, 14–26. https://doi.org/10.1093/her/cyp046

DiPrete, T.A., Eirich, G.M., 2006. Cumulative advantage as a mechanism for inequality: A review of theoretical and empirical developments. Annu. Rev. Sociol. 32, 271–297. https://doi.org/10.1146/annurev.soc.32.061604.123127

Dixon, L., Kuster, R., Rueppell, O., 2014. Reproduction, social behavior, and aging trajectories in honeybee workers. Age (Omaha) 36, 89–101. https://doi.org/10.1007/s11357-013-9546-7

Dowd, J.B., Zajacova, A., 2010. Does self-rated health mean the same thing across socioeconomic groups? Evidence from biomarker data. Ann. Epidemiol. 20, 743–749. https://doi.org/10.1016/j.annepidem.2010.06.007

Downing, P.A., Griffin, A.S., Cornwallis, C.K., 2021. Hard-working helpers contribute to long breeder lifespans in cooperative birds. Philos. Trans. R. Soc. 376. https://doi.org/10.1098/rstb.2019.0742

Duim, E., Lima Passos, V., 2020. Highways to Ageing - Linking life course SEP to multivariate trajectories of health outcomes in older adults. Arch. Gerontol. Geriatr. 91, 104193. https://doi.org/10.1016/j.archger.2020.104193

Easterling, M.R., Ellner, S.P., Dixon, P.M., 2000. Size-specific sensitivity: Applying a new structured population model. Ecology 81, 694–708. https://doi.org/10.1890/0012-9658(2000)081[0694:SSSAAN]2.0.CO;2

Elderd, B.D., Miller, T.E.X., 2016. Quantifying demographic uncertainty: Bayesian methods for Integral Projection Models (IPMs). Ecol. Monogr. 86, 125–144.

Ellis, S., Franks, D.W., Nattrass, S., Cant, M.A., Weiss, M.N., Giles, D., Balcomb, K.C., Croft, D.P., 2017. Mortality risk and social network position in resident killer whales: sex differences and the importance of resource abundance. Proc. Biol. Sci. 284. https://doi.org/10.1098/rspb.2017.1313

Ellis, S., Snyder-Mackler, N., Ruiz-Lambides, A., Platt, M.L., Brent, L.J.N., 2019. Deconstructing sociality: The types of social connections that predict longevity in a group-living primate. Proc. Royal Soc. B 286. https://doi.org/10.1098/rspb.2019.1991

Ellner, S.P., Rees, M., 2006. Integral projection models for species with complex demography. Am. Nat. 167, 410–428. https://doi.org/10.1086/499438

Engelman, M., Jackson, H., 2019. Gradual Change, Homeostasis, and Punctuated Equilibrium: Reconsidering Patterns of Health in Later Life. Demography 56, 2323–2347. https://doi.org/10.1007/s13524-019-00826-x

Ferraro, K.F., 2018. The gerontological imagination: An integrative paradigm of aging. Oxford University Press.

Ferraro, K.F., Schafer, M.H., Wilkinson, L.R., 2016. Childhood Disadvantage and Health Problems in Middle and Later Life: Early Imprints on Physical Health? Am. Sociol. Rev. 81, 107–133. https://doi.org/10.1177/0003122415619617

Ferraro, K.F., Shippee, T.P., 2009. Aging and cumulative inequality: How does inequality get under the skin? Gerontologist 49, 333–343. https://doi.org/10.1093/geront/gnp034

Ferraro, K.F., Shippee, T.P., Schafer, M.H., 2009. Cumulative inequality theory for research on aging and the life course. Handbook of Theories of Aging 413–434. https://doi.org/10.1017/S000748530002229X

Flombaum, J.I., Santos, L.R., 2005. Rhesus monkeys attribute perceptions to others. Curr. Biol. 15, 447–52. https://doi.org/10.1016/j.cub.2004.12.076

Franzini, L., Ribble, J.C., Keddie, A.M., 2001. Understanding the Hispanic paradox. Ethn. Dis. 11, 496–518.

Gager, Y., Gimenez, O., O'Mara, M.T., Dechmann, D.K.N., 2016. Group size, survival and surprisingly short lifespan in socially foraging bats. BMC Ecol. 16, 1–12. https://doi.org/10.1186/s12898-016-0056-1

Gavrilov, L.A., Gavrilova, N.S., 2015. New Developments in the Biodemography of Aging and Longevity. Gerontology 61, 364–371. https://doi.org/10.1159/000369011

Gill, T.M., Gahbauer, E.A., Han, L., Allore, H.G., 2010. Trajectories of Disability in the Last Year of Life. NEJM 362, 1173–1180. https://doi.org/10.1056/nejmoa0909087

Giuliani, C., Garagnani, P., Franceschi, C., 2018. Genetics of human longevity within an eco-evolutionary nature-nurture framework. Circ. Res. 123, 745–772. https://doi.org/10.1161/CIRCRESAHA.118.312562

Goldberg, S.B., Bolt, D.M., Davidson, R.J., 2021. Data missing not at random in mobile health research: Assessment of the problem and a case for sensitivity analyses. J. Med. Internet. Res. 23, 1–18. https://doi.org/10.2196/26749

Graham, J.W., 2009. Missing data analysis: Making it work in the real world. Annu. Rev. Psychol. 60, 549–576. https://doi.org/10.1146/annurev.psych.58.110405.085530

Gueorguieva, R., Sindelar, J.L., Falba, T.A., Fletcher, J.M., Keenan, P., Wu, R., Gallo, W.T., 2009. The impact of occupation on self-rated health: Cross-sectional and longitudinal evidence from the health and retirement survey. J. Gerontol. B Psychol. Sci. Soc. Sci. 64, 118–124. https://doi.org/10.1093/geronb/gbn006

Guilley, E., Ghisletta, P., Armi, F., Berchtold, A., D'Epinay, C.L., Michel, J.P., De Ribaupierre, A., 2008. Dynamics of frailty and ADL dependence in a five-year longitudinal study of octogenarians. Res. Aging 30, 299–317. https://doi.org/10.1177/0164027507312115

Gunasekara, F.I., Carter, K., Blakely, T., 2012. Comparing self-rated health and self-assessed change in health in a longitudinal survey: Which is more valid? Soc. Sci. Med. 74, 1117–1124. https://doi.org/10.1016/j.socscimed.2011.11.038

Gutin, I., Hummer, R.A., 2021. Social Inequality and the Future of US Life Expectancy. Annu. Rev. Sociol. 47, 501–520. https://doi.org/10.1146/annurev-soc-072320-100249

Hajat, A., Kaufman, J.S., Rose, K.M., Siddiqi, A., Thomas, J.C., 2011. Long-term effects of wealth on mortality and self-rated health status. Am. J. Epidemiol. 173, 192–200. https://doi.org/10.1093/aje/kwq348

Hamilton, W.D., 1966. The Moulding of Senescence by Natural Selection. J. Theor. Biol. 12, 12-45.

Hammers, M., Kingma, S.A., Spurgin, L.G., Bebbington, K., Dugdale, H.L., Burke, T., Komdeur, J., Richardson, D.S., 2019. Breeders that receive help age more slowly in a cooperatively breeding bird. Nat. Commun. 10, 1–10. https://doi.org/10.1038/s41467-019-09229-3

Hart, S.R., Musci, R.J., Ialongo, N., Ballard, E.D., Wilcox, H.C., 2013. Demographic and clinical characteristics of consistent and inconsistent longitudinal reporters of lifetime suicide attempts in adolescence through young adulthood. Depress Anxiety 30, 997–1004. https://doi.org/10.1002/da.22135

Heinze, J., Giehr, J., 2021. The plasticity of lifespan in social insects. Philos. Trans. R. Soc. 376, 0–2. https://doi.org/10.1098/rstb.2019.0734

Hernández-Pacheco, R., Plard, F., Grayson, K.L., Steiner, U.K., 2021. Demographic consequences of changing body size in a terrestrial salamander. Ecol. Evol. 11:174–185.

Hernández-Pacheco, R, Rawlins, R.G., Kessler, M.J., et al., 2013. Demographic variability and density-dependent dynamics of a free-ranging rhesus macaque population. Am. J. Primatol. 75:1152–1164.

Hirai, H., Kondo, K., Kawachi, I., 2012. Social determinants of active aging: Differences in mortality and the loss of healthy life between different income levels among older japanese in the ages cohort study. Curr. Gerontol. Geriatr. Res 2012. https://doi.org/10.1155/2012/701583

Hjelmborg, J.B., Iachine, I., Skytthe, A., Vaupel, J.W., McGue, M., Koskenvuo, M., Kaprio, J., Pedersen, N.L., Christensen, K., 2006. Genetic influence on human lifespan and longevity. Hum. Genet. 119, 312–321. https://doi.org/10.1007/s00439-006-0144-y

Hoffman, K.L., Gothard, K.M., Schmid, M.C.C., Logothetis, N.K., 2007. Facial-Expression and Gaze-Selective Responses in the Monkey Amygdala. Curr. Biol. 17, 766–772. https://doi.org/10.1016/j.cub.2007.03.040

Holt-Lunstad, J., Smith, T.B., Layton, J.B., 2010. Social relationships and mortality risk: A meta-analytic review. PLoS Med. 7. https://doi.org/10.1371/journal.pmed.1000316

Hooper, P.L., Gurven, M., Kaplan, H.S., 2014. Social and economic underpinnings of human biodemography M. Weinstein, M.A. Lane (eds.), Sociality, Hierarchy, Health: Comparative Biodemography: A Collection of Papers, National Academies Press, Washington, DC, pp. 169-196

Hughes, K., Bellis, M.A., Hardcastle, K.A., Sethi, D., Butchart, A., Mikton, C., Jones, L., Dunne, M.P., 2017. The effect of multiple adverse childhood experiences on health: a systematic review and meta-analysis. Lancet Public Health 2, e356–e366. https://doi.org/10.1016/S2468-2667(17)30118-4

Jackson, H., Engelman, M., 2022. Deaths, Disparities, and Cumulative (Dis)Advantage: How Social Inequities Produce an Impairment Paradox in Later Life. J. Gerontol. A Biol. Sci. 77, 392–401. https://doi.org/10.1093/gerona/glab181

Jackson, H., Engelman, M., Bandeen-Roche, K., 2019. Robust Respondents and Lost Limitations: The Implications of Nonrandom Missingness for the Estimation of Health Trajectories. J. Aging Health 31, 685–708. https://doi.org/10.1177/0898264317747079

Johnson, C.E., 1974. Consistency of reporting ethnic origin in the current population survey. US Dep. Commerce Tech. Pap. No. 31, Washington, DC: Bur Census

Johnson, B., Carey, J.R., 2014. Hierarchy and connectedness as determinants of health and longevity in social insects, in Sociality, Hierarchy, Health: Comparative Biodemography: A Collection of Papers (National Academies Press, 2014), pp. 269–293.

Jones, O.R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C.G., Schaible, R., Casper, B.B., Dahlgren, J.P., Ehrlén, J., García, M.B., Menges, E.S., Quintana-Ascencio, P.F., Caswell, H., Baudisch, A., Vaupel, J.W., 2014. Diversity of ageing across the tree of life. Nature 505, 169–173. https://doi.org/10.1038/nature12789

Kaestle, C.E., 2015. Age of smoking milestones: Longitudinal inconsistencies and recanting. J. Adolesc. Health 56, 382–388. https://doi.org/10.1016/j.jadohealth.2014.12.005

Kappeler, P.M., Clutton-Brock, T., Shultz, S., Lukas, D., 2019. Social complexity: patterns, processes, and evolution. Behav. Ecol. Sociobiol. 73, 1–6. https://doi.org/10.1007/s00265-018-2613-4

Kelley, K., Clark, B., Brown, V., Sitzia, J., 2003. Good practice in the conduct and reporting of survey research. IJQHC 15, 261–266. https://doi.org/10.1093/intqhc/mzg031

Kennedy, A., Herman, J., Rueppell, O., 2021. Reproductive activation in honeybee (Apis mellifera) workers protects against abiotic and biotic stress. Philos. Trans. R. Soc. 376. https://doi.org/10.1098/rstb.2019.0737

Keown, D., 2003. Patterns of functional decline At the End of Life, in: Buddhism & Bioethics. Palgrave Macmillan UK, London, pp. 139–187. https://doi.org/10.1007/978-1-349-23981-8_3

Kinnally, E.L., Martinez, S.J., Chun, K., Capitanio, J.P., Ceniceros, L.C. Early Social Stress Promotes Inflammation and Disease Risk in Rhesus Monkeys. Sci Rep. 2019;9. pmid:31110226

Korb, J., Heinze, J., 2021. Ageing and sociality: Why, when and how does sociality change ageing patterns? Philos. Trans. R. Soc. 376. https://doi.org/10.1098/rstb.2019.0727

Korb, J., Meusemann, K., Aumer, D., Bernadou, A., Elsner, D., Feldmeyer, B., Foitzik, S., Heinze, J., Libbrecht, R., Lin, S., Majoe, M., Kuhn, J.M.M., Nehring, V., Negroni, M.A., Paxton, R.J., Séguret, A.C., Stoldt, M., Flatt, T., 2021. Comparative transcriptomic analysis of the mechanisms underpinning ageing and fecundity in social insects. Philos. Trans. R. Soc. 376. https://doi.org/10.1098/rstb.2019.0728

Kramer, B.H., Nehring, V., Buttstedt, A., Heinze, J., Korb, J., Libbrecht, R., Meusemann, K., Paxton, R.J., Séguret, A., Schaub, F., Bernadou, A., 2021. Oxidative stress and senescence in social insects: A significant but inconsistent link? Philos. Trans. R. Soc. 376. https://doi.org/10.1098/rstb.2019.0732

Kroeger, S.B., Blumstein, D.T., Martin, J.G.A., 2021. How social behaviour and life-history traits change with age and in the year prior to death in female yellow-bellied marmots. Philos. Trans. R. Soc. 376. https://doi.org/10.1098/rstb.2019.0745

Lange, E.C., Zeng, S., Campos, F.A., Li, F., Tung, J., Archie, E.A., Alberts, S.C., 2022. Early life adversity and adult social relationships have independent effects on survival in a wild animal model of aging. bioRixv 1–35.

Lantz, P.M., Golberstein, E., House, J.S., Morenoff, J., 2010. Socioeconomic and behavioral risk factors for mortality in a national 19-year prospective study of U.S. adults. Soc. Sci. Med. 70, 1558–1566. https://doi.org/10.1016/j.socscimed.2010.02.003

Layes, A., Asada, Y., Kepart, G., 2012. Whiners and deniers - What does self-rated health measure? Soc. Sci. Med. 75, 1–9. https://doi.org/10.1016/j.socscimed.2011.10.030

Lea, A.J., Akinyi, M.Y., Nyakundi, R., Mareri, P., Nyundo, F., Kariuki, T., Alberts, S.C., Archie, E.A., Tung, J., 2018. Dominance rank-associated gene expression is widespread, sex-specific, and a precursor to high social status in wild male baboons. Proc. Natl. Acad. Sci. USA 115, E12163–E12171. https://doi.org/10.1073/pnas.1811967115

Lehmann, J., Majolo, B., McFarland, R., 2015. The effects of social network position on the survival of wild Barbary macaques, Macaca sylvanus. Behav. Ecol. 27, 20–28. https://doi.org/10.1093/beheco/arv169

Levin, S.C., Childs, D.Z., Compagnoni, A., Evers, S., Knight, T.M., Salguero-Gómez, R., 2021. ipmr: Flexible implementation of Integral Projection Models in R. Methods Ecol. Evol. 12, 1826–1834. https://doi.org/10.1111/2041-210X.13683

Loxton, D., Powers, J., Townsend, N., Harris, M.L., Forder, P., 2019. Longitudinal inconsistency in responses to survey items that ask women about intimate partner violence. BMC Med Res. Methodol. 19, 1–8. https://doi.org/10.1186/s12874-019-0835-4

Lucas, E.R., Keller, L., 2020. The co-evolution of longevity and social life. Funct. Ecol. 34, 76–87. https://doi.org/10.1111/1365-2435.13445

Machanda, Z.P., Rosati, A.G., 2020. Shifting sociality during primate ageing: Shifting sociality during primate aging. Philos. Trans. R. Soc. 375. https://doi.org/10.1098/rstb.2019.0620rstb20190620

Majoe, M., Libbrecht, R., Foitzik, S., Nehring, V., 2021. Queen loss increases worker survival in leaf-cutting ants under paraquat-induced oxidative stress. Philos. Trans. R. Soc. 376. https://doi.org/10.1098/rstb.2019.0735

Markides, K.S., Coreil, J., 1986. The health of Hispanics in the southwestern United States: An epidemiologic paradox. Public Health Reports 101, 253–265.

Markides, K.S., Rote, S., 2019. The Healthy Immigrant Effect and Aging in the United States and Other Western Countries. Gerontologist 59, 205–214. https://doi.org/10.1093/geront/gny136

Marmot, M.G., Sapolsky, R., 2014. Of baboons and men: Social circumstances, biology, and the social gradient in health, in Sociality, Hierarchy, Health: Comparative Biodemography: A Collection of Papers, National Academies Press, pp. 365–388.

Massey, J.T., 1980. A comparison of interviewer observed race and respondent reported race in the National Health Interview Survey. In Proceedings of the American Statistical Association (pp. 425-428). Washington, DC: American Statistical Association.

McGue, M., Vaupel, J.W., Holm, N.V., 1993. Harvald, B. Longevity is moderately heritable in a sample of Danish twins born 1870–1880. J. Gerontol. A 48, B237–B244.

Mesoudi, A., Thornton, A., 2018. What is cumulative cultural evolution? Proc. Royal Soc. B. 285:20180712.

Merow, C., Dahlgren, J.P., Metcalf, C.J.E., Childs, D.Z., Evans, M.E.K., Jongejans, E., Record, S., Rees, M., Salguero-Gómez, R., Mcmahon, S.M., 2014. Advancing population ecology with integral projection models: A practical guide. Methods Ecol. Evol. 5, 99–110. https://doi.org/10.1111/2041-210X.12146

Mirowsky, J., Reynolds, J.R., 2000. Age, depression, and attrition in the national survey of families and households. Sociol. Methods Res. https://doi.org/10.1177/0049124100028004004

Montero, A.P., Williams, D.M., Martin, J.G.A., Blumstein, D.T., 2020. More social female yellow-bellied marmots, Marmota flaviventer, have enhanced summer survival. Anim. Behav. 160, 113–119. https://doi.org/10.1016/j.anbehav.2019.12.013

Morton, P.M., Ferraro, K.F., 2020. Early Social Origins of Biological Risks for Men and Women in Later Life. J. Health Soc. Behav. 61, 503–522. https://doi.org/10.1177/0022146520966364

Namboodiri, K., Suchindran, C.M., 2013. Life table techniques and their applications. Academic Press.

National Center for Health, 2016. National Center for Health Statistics. Health, United States 2015: with Special Feature on Racial and Ethnic Health Disparities.

Negroni, M.A., MacIt, M.N., Stoldt, M., Feldmeyer, B., Foitzik, S., 2021. Molecular regulation of lifespan extension in fertile ant workers. Philos. Trans. R. Soc. 376. https://doi.org/10.1098/rstb.2019.0736

Noren Hooten, N., Pacheco, N.L., Smith, J.T., Evans, M.K., 2022. The accelerated aging phenotype: The role of race and social determinants of health on aging. Ageing Res. Rev. 73, 101536. https://doi.org/10.1016/j.arr.2021.101536

Nuñez, C.M.V., Adelman, J.S., Rubenstein, D.I., 2015. Sociality increases juvenile survival after a catastrophic event in the feral horse (Equus caballus). Behav. Ecol. 26, 138–147. https://doi.org/10.1093/beheco/aru163

Oeppen, J., Vaupel, J.W., 2002. Broken Limits to Life Expectancy. Science 296, 1029–1031. https://doi.org/10.1126/science.1069675

Palma-Gudiel, H., Fañanás, L., Horvath, S., Zannas, A.S., 2020. Psychosocial stress and epigenetic aging, 1st ed, Int. Rev. Neurobiol. Elsevier Inc. https://doi.org/10.1016/bs.irn.2019.10.020

Paniw, M., Cozzi, G., Sommer, S., Ozgul, A., 2021. Demographic processes in socially strutured populations, in: Salguero-Gómez, R. and Gamelon, M. (eds.), Demographic methods across the tree of life. Oxford, Oxford Uiversity Press, pp. 341-350.

Patterson, S.K., Hinde, K., Bond, A.B., Trumble, B.C., Strum, S.C., Silk, J.B., 2021. Effects of early life adversity on maternal effort and glucocorticoids in wild olive baboons. Behavioral Ecol. Sociobiol. 75: 114.

Pavez-Fox, M.A., Negron-Del Valle, J.E., Thompson, I.J., Walker, C.S., Bauman, S.E., Gonzalez, O., Compo, N., Ruiz-Lambides, A., Martinez, M.I., Platt, M.L., Montague, M.J., Higham, J.P., Snyder-Mackler, N., Brent, L.J.N., 2021. Sociality predicts individual variation in the immunity of free-ranging rhesus macaques. Physiol. Behav. 241. https://doi.org/10.1016/j.physbeh.2021.113560

Pfefferle, D., Kazem, A.J.N., Brockhausen, R.R., Ruiz-Lambides, A. V., Widdig, A., 2014. Monkeys Spontaneously Discriminate Their Unfamiliar Paternal Kin under Natural Conditions Using Facial Cues. Curr. Biol. 24, 1806–1810. https://doi.org/10.1016/j.cub.2014.06.058

Phillips, K.A., Bales, K.L., Capitanio, J.P., Conley, A., Czoty, P.W., ’t Hart, B.A., Hopkins, W.D., Hu, S.L., Miller, L.A., Nader, M.A., Nathanielsz, P.W., Rogers, J., Shively, C.A., Voytko, M. Lou, 2014. Why primate models matter. Am. J. Primatol. 76, 801–827. https://doi.org/10.1002/ajp.22281

Plard, F., Turek, D., Gruebler, M.U., Schaub, M., 2019. Ipm2: Towards better under-standing and forecasting of population dynamics. Ecol. Monogr., 89, e01364.

Purdie, D.M., Dunne, M.P., Boyle, F.M., Cook, M.D., Najman, J.M., 2002. Health and demographic characteristics of respondents in an Australian national sexuality survey: Comparison with population norms. J. Epidemiol. Community Health (1978) 56, 748–753. https://doi.org/10.1136/jech.56.10.748

Quiñones, A.R., Liang, J., Bennett, J.M., Xu, X., Ye, W., 2011. How does the trajectory of multimorbidity vary across black, white, and mexican americans in middle and old age? J Gerontol B Psychol Sci Soc Sci. 66 B, 739–749. https://doi.org/10.1093/geronb/gbr106

Rau, V., Korb, J., 2021. The effect of environmental stress on ageing in a termite species with low social complexity. Philos. Trans. R. Soc. 376. https://doi.org/10.1098/rstb.2019.0739

Rees, M., Childs, D.Z., Ellner, S.P., 2014. Building integral projection models: A user's guide. J. Anim. Ecol. 83, 528–545. https://doi.org/10.1111/1365-2656.12178

Riley, J.C., 2001. Rising Life Expectancy: A Global History. Cambridge, Cambridge University Press.

Riosmena, F., Everett, B.G., Rogers, R.G., Dennis, J.A., 2014. Negative acculturation and nothing more? cumulative disadvantage and mortality during the immigrant adaptation process among Latinos in the United States. International Migration Review 49, 443–478. https://doi.org/10.1111/imre.12102

Rosati, A.G., Arre, A.M., Platt, M.L., Santos, L.R., 2018. Developmental shifts in social cognition: socio-emotional biases across the lifespan in rhesus monkeys. Behav. Ecol. Sociobiol. 72, 163. https://doi.org/10.1007/s00265-018-2573-8

Rosati, A.G., Arre, A.M., Platt, M.L., Santos, L.R., 2016. Rhesus monkeys show human-like changes in gaze following across the lifespan. Proc. Royal Soc. B 283. https://doi.org/10.1098/rspb.2016.0376

Rosati, A.G., Hagberg, L., Enigk, D.K., Otali, E., Emery Thompson, M., Muller, M.N., Wrangham, R.W., Machanda, Z.P., 2020. Social selectivity in aging wild chimpanzees. Science, 370: 473-476

Rosenbaum, S., Zeng, S., Campos, F.A., Gesquiere, L.R., Altmann, J., Alberts, S.C., Li, F., Archie, E.A., 2020. Social bonds do not mediate the relationship between early adversity and adult glucocorticoids in wild baboons. Proc. Natl Acad. Sci. USA 117:052–20 062.

Salazar, M.K., 1990. Interviewer bias. How it affects survey research. AAOHN J 38, 567–72. https://doi.org/10.1177/216507999003801203

Santos, L.R., Nissen, A.G., Ferrugia, J.A., 2006. Rhesus monkeys,*Macaca mulatta* , know what others can and cannot hear. Anim. Behav. 71, 1175–1181. https://doi.org/10.1016/j.anbehav.2005.10.007

Santos, L.R., Platt, M.L., 2014. Evolutionary Anthropological Insights into Neuroeconomics. Neuroeconomics 109–122. https://doi.org/10.1016/b978-0-12-416008-8.00007-3

Sapolsky, R.M., 2004. Social Status and Health in Humans and Other Animals. Annu. Rev. Anthropol. 33, 393–418. https://doi.org/10.1146/annurev.anthro.33.070203.144000

Sauerteig, M.R., Ferraro, K.F., Bauldry, S., 2022. Life Course Stressors and Functional Limitations in Later Life among White, Black, and Hispanic Adults: Deleterious, Hardening, or Benign? J. Gerontol. B Psychol. Sci. Soc. Sci. 77, 249–259. https://doi.org/10.1093/geronb/gbab066

Stearns, S.C., 1992. The Evolution of Life Histories. Oxford, Oxford University Press.

Schoen, R., 2006. Dynamic Multistate Models. Dynamic Population Models. Springer, Dordrecht. 161-202.

Shah, M., Sachdeva, M., Dodiuk-Gad, R.P., 2020. COVID-19 and racial disparities. J. Am. Acad. Dermatol .83, e35. https://doi.org/10.1016/j.jaad.2020.04.046

Shively, C.A., Wilson, M.E., 2016. Social Inequalities in Health in Nonhuman Primates, The Biology Gradient. Switzerland, Springer International Publishing.

Silk, J.B., 2014. Evolutionary perspectives on the links between close social bonds, health, and fitness. In Sociality, Hierarchy, Health: Comparative Biodemography, in: Weinstein, M., Lane, M.A. (Eds.), pp. 121–143. National Academies Press, Washington.

Siracusa, E.R., Higham, J.P., Snyder-Mackler, N., Brent, L.J.N., 2022. Social ageing: Exploring the drivers of late-life changes in social behaviour in mammals. Biol. Lett. 18. https://doi.org/10.1098/rsbl.2021.0643

Snyder-Mackler, N., Burger, J.R., Gaydosh, L., Belsky, D.W., Noppert, G.A., Campos, F.A., Bartolomucci, A., Yang, Y.C., Aiello, A.E., O'Rand, A., Harris, K.M., Shively, C.A., Alberts, S.C., Tung, J., 2020. Social determinants of health and survival in humans and other animals. Science 368. https://doi.org/10.1126/SCIENCE.AAX9553

Snyder-Mackler, N., Sanz, J., Kohn, J.N., Brinkworth, J.F., Morrow, S., Shaver, A.O., Grenier, J.C., Pique-Regi, R., Johnson, Z.P., Wilson, M.E., Barreiro, L.B., Tung, J., 2016. Social status alters immune regulation and response to infection in macaques. Science 354, 1041–1045. https://doi.org/10.1126/science.aah3580

Snyder-Mackler, N., Sanz, J., Kohn, J.N., Voyles, T., Pique-Regi, R., Wilson, M.E., Barreiro, L.B., Tung, J., 2018. Social status alters chromatin accessibility and the gene regulatory response to glucocorticoid stimulation in rhesus macaques. Proc. Natl. Acad. Sci. U.S.A. 116, 1219–1228.

Sorlie, P.D., Rogot, E., Johnson, N.J., 1992. Validity of demographic characteristics on the death certificate. Epidemiology 3, 181–184. https://doi.org/10.1097/00001648-199203000-00018

Tasaki, E., Takata, M., Matsuura, K., 2021. Why and how do termite kings and queens live so long? Philos. Trans. R. Soc. 376. https://doi.org/10.1098/rstb.2019.0740

Thompson, N.A., Cords, M., 2018. Stronger social bonds do not always predict greater longevity in a gregarious primate. Ecol. Evol. 8, 1604–1614. https://doi.org/10.1002/ece3.3781

Thorslund, M., Wärneryd, B., 1990. Surveying the elderly about health, medical care and living conditions. Some issues of response inconsistency. Arch Gerontol.. Geriatr. 11, 161–173. https://doi.org/10.1016/0167-4943(90)90009-U

Tuljapurkar, S., Zuo, W., Coulson, T., Horvitz, C., Gaillard, J.M., (2020). Skewed distributions of lifetime reproductive success: Beyond mean and variance. Ecology Letters, 23, 748– 756.

Tung, J., Archie, E.A., Altmann, J., Alberts, S.C., 2016. Cumulative early life adversity predicts longevity in wild baboons. Nat Commun 7, 11181. https://doi.org/10.1038/ncomms11181

Vable, A.M., Gilsanz, P., Kawachi, I., 2019. Is it possible to overcome the “long arm” of childhood socioeconomic disadvantage through upward socioeconomic mobility? J. Public Health (Oxf) 41, 566–574. https://doi.org/10.1093/pubmed/fdz018

Vágási, C.I., Vincze, O., Lemaître, J.F., Pap, P.L., Ronget, V., Gaillard, J.M., 2021. Is degree of sociality associated with reproductive senescence? A comparative analysis across birds and mammals. Philos. Trans. R. Soc. 376. https://doi.org/10.1098/rstb.2019.0744

Van Beijsterveldt, C.E.M., Van Boxtel, M.P.J., Bosma, H., Houx, P.J., Buntinx, F., Jolles, J., 2002. Predictors of attrition in a longitudinal cognitive aging study: The Maastricht Aging Study (MAAS). J. Clin. Epidemiol. 55, 216–223. https://doi.org/10.1016/S0895-4356(01)00473-5

Vaupel, J.W., 2010. Biodemography of human ageing. Nature 464, 536–542. https://doi.org/10.1038/nature08984

Vaupel, J.W., 2004. The Biodemography of Aging. Population and Development Review

30, Supplement: Aging, Health, and Public Policy (2004), pp. 48-62.

Vincze, O., Colchero, F., Lemaître, JF. et al., 2022. Cancer risk across mammals. Nature 601, 263–267. https://doi.org/10.1038/s41586-021-04224-5

Vuolo, M., Ferraro, K.F., Morton, P.M., Yang, T.Y., 2014. Why Do Older People Change Their Ratings of Childhood Health? Demography 51, 1999–2023. https://doi.org/10.1007/s13524-014-0344-3

Wachter, K.W., 2008. Biodemography comes of Age. Demographic Res. 19, 1501–1512. https://doi.org/10.4054/DemRes.2008.19.40

Wallace, S.P., 2015. Equity and social determinants of health among older adults. Generations, 38, 6–11.

Wilkinson, R., Marmot, M., 2003. Social Determinants of Health The Solid Facts, in: Chronic Illness Care. Springer International Publishing, Cham, pp. 435–449. https://doi.org/10.1007/978-3-319-71812-5_36

Williams, D.R., Chiquita, C., 1995. US Socioeconomic and Racial Differences in Health: Patterns and Explanations. Annu. Rev. Sociol. 21, 349–386. https://doi.org/10.1146/annurev.soc.21.1.349

Williams, D.R., Lawrence, J.A., Davis, B.A., 2019. Racism and Health: Evidence and Needed Research. Annu. Rev. Public Health 40, 105–125. https://doi.org/10.1146/annurev-publhealth-040218-043750

Yashin, A.I., Stallard, E., Land, K.C. 2016. Biodemography of aging: determinants of healthy life span and longevity. Springer

Young, A.F., Powers, J.R., Bell, S.L., 2006. Attrition in longitudinal studies: Who do you lose? Aust N Z J Public Health 30, 353–361. https://doi.org/10.1111/j.1467-842X.2006.tb00849.x

Zipple, M.N., Archie, E.A., Tung, J., Altmann, J., Alberts, S.C., 2019. Intergenerational effects of early adversity on survival in wild baboons. Elife 8, 1–14. https://doi.org/10.7554/eLife.47433.001

Table 1 . Basic demographic information for the construction of integral projection models (IPMs). The construction of IPMs depends on four fundamental relationships (phenotype-demographic functions) that describe the associations between the phenotype and survival, the phenotype and the ontogeny of the phenotype (change) among survivors, the phenotype and fertility, and the probability density distribution of offspring phenotypes given parental phenotypes (i.e., heritability). Variables in bracket represent those in the proposed IPM.

Vital Rates	**Dependency at present time (t)**	**Proposed dependencies**
Survival	State, age	Sociality [s], health [z], age [a]
Phenotype ontogeny (state change)	State, age	Sociality [s], health [z], age [a]
Number of offspring	State, age	Sociality [s], health [z], age [a]
Kind of offspring (state distribution)	Inheritance – parental state, parental age	Parental sociality [s], parental health [z],

Fig 1. Comparison of mixed-effects regression and multi-state model predictions of individual health histories from simulated survey data. Survey data: colored trajectories represent 10 randomly chosen individual histories from the total pool of trajectories. Mixed-effects: black trajectories represent 10 randomly chosen predicted individual histories from the total pool of trajectories (gray). For this, the survey data (gray dots) was modeled using a linear mixed-effect model. Multi-state model: black trajectories represent 10 randomly chosen predicted individual histories from the total pool of trajectories (gray). For this, the survey data (gray dots) was discretized into five health states and modeled using a 5 x 5 matrix population model.

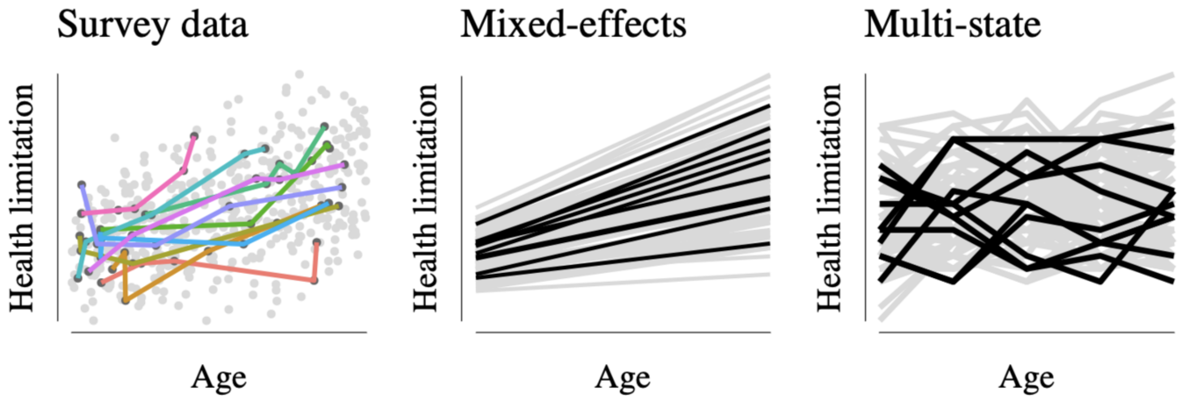


Figure 1: This is a caption

Fig 2. Comparison of mixed-effects regression and multi-state model predictions of individual health histories from simulated survey data. Survey data: colored trajectories represent 10 randomly chosen individual histories from the total pool of trajectories. Mixed-effects: black trajectories represent 10 randomly chosen predicted individual histories from the total pool of trajectories (gray). For this, the survey data (gray dots) was modeled using a linear mixed-effect model. Multi-state model: black trajectories represent 10 randomly chosen predicted individual histories from the total pool of trajectories (gray). For this, the survey data (gray dots) was discretized into five health states and modeled using a 5 x 5 matrix population model.

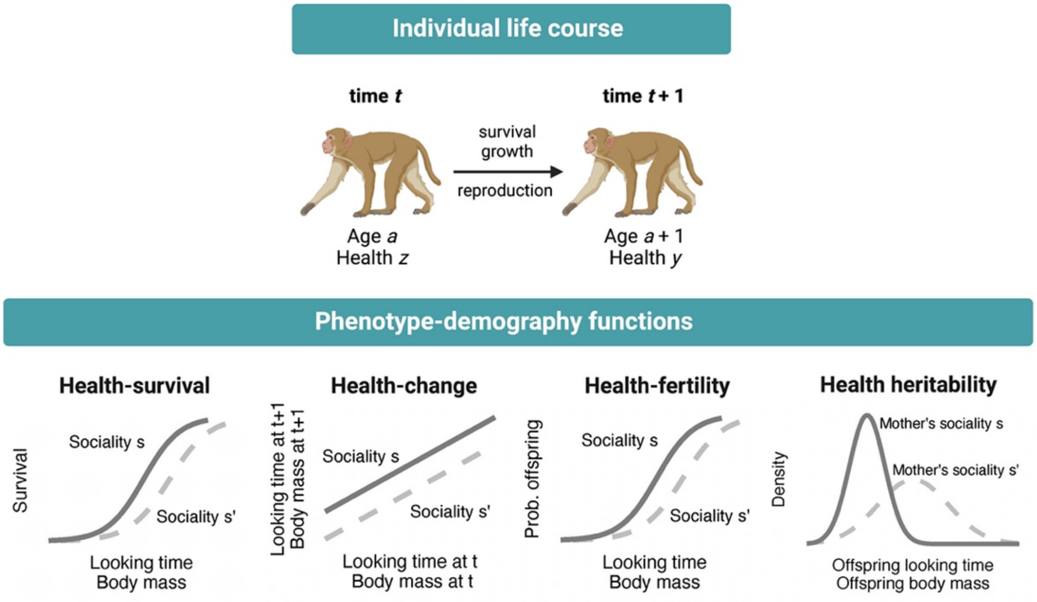
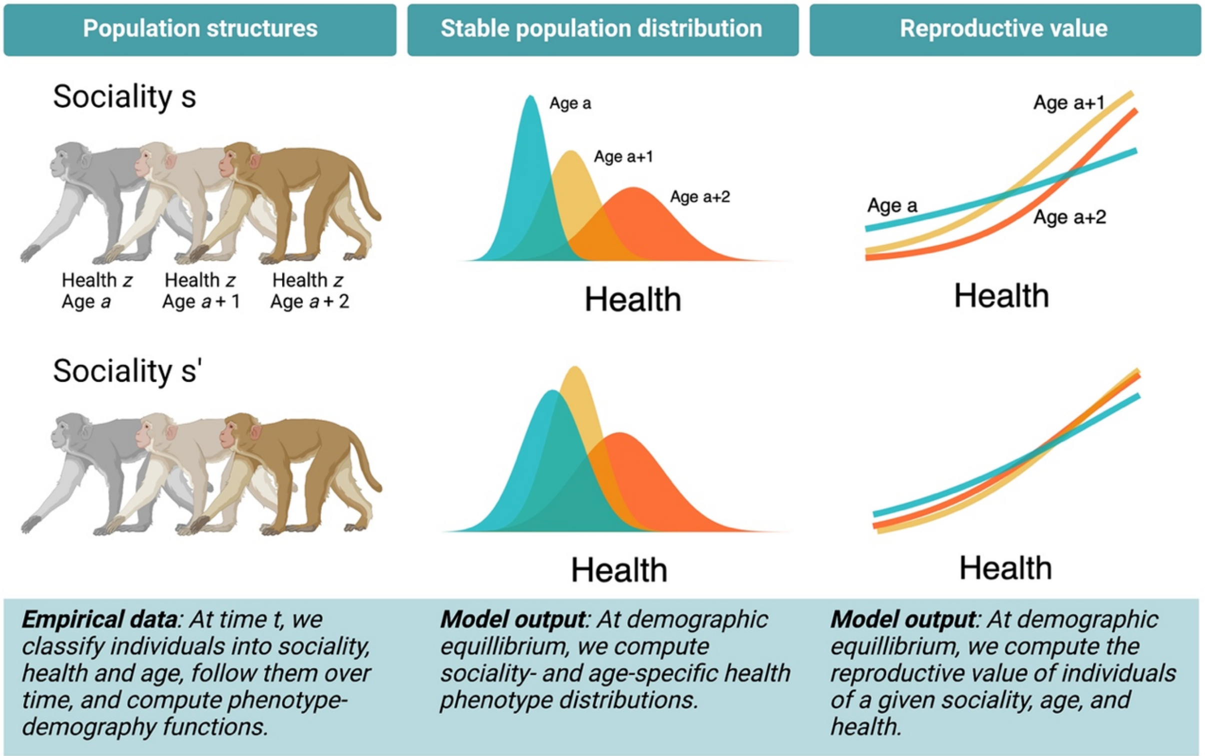


Fig 3. Integral projection model output across population health and age structures needed to evaluate phenotype-specific selection gradients on demographic and life history parameters through sensitivity analysis. Sociality is defined by social status as a categorical variable of two levels, s and s'. Sex structure is not shown.



***Empirical data**: At time t, we classify individuals into sociality, health and age, follow them over time, and compute phenotype-demography functions.*

***Model output**: At demographic equillibrium, we compute sociality- and age-specific health phenotype distributions.*

***Model output**: At demographic equillibrium, we compute the reproductive value of individuals of a given sociality, age, and health.*