The manifestations and interdependence of social and physiological aging in wild female Assamese macaques (*Macaca assamensis*)

Dissertation

for the award of the degree "Doctor of Philosophy (Ph.D.)"

Division of Mathematics and Natural Sciences

of the Georg-August-Universität Göttingen

within the doctoral program Behavior and Cognition (BeCog)

of the Georg-August University School of Science (GAUSS)

Submitted by

Baptiste Sadoughi

From Paris, France

Göttingen, 2023

Thesis Committee

Prof. Dr. Julia Ostner

Behavioural Ecology, Georg-August-Universität Göttingen, and Primate Social Evolution, German Primate Centre, Leibniz Institute for Primate Research, Göttingen

PD. Dr. Oliver Schülke

Behavioural Ecology, Georg-August-Universität Göttingen, and Primate Social Evolution, German Primate Centre, Leibniz Institute for Primate Research, Göttingen

Prof. Dr. Susann Boretius

Functional Imaging Laboratory, German Primate Center, Leibniz Institute for Primate Research, Göttingen

Members of the Examination Board

Reviewer: Prof. Dr. Julia Ostner

Second Reviewer: Prof. Dr. Susann Boretius

Further members of the Examination Board

Dr. Verena Behringer

Endocrinology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Göttingen

Prof Dr. Rolf Daniel

Genomic and Applied Microbiology and Göttingen Genomics Laboratory, Institute of Microbiology and Genetics, Georg-August-Universität Göttingen

Prof. Dr. Julia Fischer

Cognitive Ethology Laboratory, German Primate Center, Leibniz Institute for Primate Research, and Department for Primate Cognition, Georg-August-Universität Göttingen

Prof. Dr. Peter Kappeler

German Primate Center, Behavioral Ecology Unit, Leibniz Institute of Primate Biology, Göttingen, and Department of Sociobiology and Anthropology, Georg-August-Universität Göttingen

Date of the oral examination: 9th of May 2023

Summary

Aging is a multifaceted process which increases the probability of death, and although there can be only one outcome, the ways to get there are diverse. Accumulating evidence of aging in natural animal populations has shed light on this diversity, both across and within species, but we still have little knowledge of the opportunities, constraints and trade-offs faced by individuals as they go through this ultimate life-history stage. Specifically, it remains unclear which individual traits exhibit signs of aging, how individuals may adjust their behavior in response to physiological decay, and how, together, these changes may ultimately contribute to whole-organism aging. As such, investigating age-related changes in social behavior and physiological functions is imperative to reach a more holistic understanding of aging.

A key issue in addressing social and physiological aging is the strong association between sociality and health. Social bonds, social integration, and exposure to social adversity are important predictors of health and lifespan across mammals. As some of the physiological mechanisms underlying the connections between sociality and health are uncovered, it becomes especially clear that aging of one component may influence aging in the other. Yet, the interdependences between sociality and physiology have seldom been addressed in the study of aging, due partly to a lack of detailed data on social behavior in natural populations of long-lived species. Another difficulty arises from the need to assess physiology via markers measured from non-invasively collected samples. Finally, although aging is an individual-level process, demographic and cohort effects can influence the patterns of aging uncovered in cross-sectional studies, which calls for a longitudinal approach.

In this thesis, I investigate age-related changes in social and physiological traits in wild female Assamese macaques (*Macaca assamensis*) to address key questions at the crossroad of aging, sociality, and health in natural animal populations: Does social behavior exhibit age-related changes? Which physiological systems, at the interface with sociality, should be investigated for age-related changes? Does social aging influence the manifestations of aging in physiological traits, and vice versa? Can biomarkers of energetic state provide means of non-invasively investigating the physiological constraints on social behavior under field conditions? To investigate these issues in the female Assamese macaques, I use extensive behavioral data, and a review of the mechanisms linking sociality and health in non-human primates, after which I focus on the HPA axis and the gut microbiome as key physiological systems. Finally, I validated the non-invasive measurement of markers of metabolic activity in macaques to offer perspective to explore the causal path from physiology towards sociality.

My results show that female Assamese macaques experience both social and physiological aging. Females decreased their social engagement and reduced the size of their grooming network with advancing age. This phenomenon could not be explained by a lack of opportunities to interact and was not associated with a greater tendency to focus on preferred partners with age. In addition to within-individual age effects, cross-sectional aging dynamics were influenced by demographic processes consistent with the selective disappearance of poorly socially connected individuals. Together, these results highlight the contribution of within-individual and demographic processes to group-level social aging and do not support increasing social selectivity as the primary driver of social disengagement in this population.

For physiological traits, I find trait-specific aging patterns, across and within traits. HPA axis activity assessed from fecal glucocorticoid concentrations was not associated with age, neither before nor after accounting for the strength of individuals' strong bonds. The taxonomic diversity of the gut bacterial community was not associated with age, and age was not a consistent predictor of gut bacterial composition across individuals. However, the gut bacterial composition exhibited a personal signature which became less stable and increasingly personalized with age. A decrease in the social transmission of gut bacteria may have contributed to, but was not sufficient to explain, the age-related patterns uncovered here.

The validation of markers of metabolic activity was conducted via a food restriction experiment in captive macaques and assessed urinary concentrations of triiodothyronine and cortisol. Both hormones exhibited the predicted change with a decrease in triiodothyronine and an increase in cortisol during the restriction phase of the experiment. Furthermore, variation in urinary triiodothyronine concentrations correlated positively with variation in body mass. Concentrations of urinary triiodothyronine were reasonably robust to many issues associated with collection of samples under field conditions, making it a suitable non-invasive marker of energetic state in macaques.

In conclusion, in female Assamese macaques, age is associated with progressive social disengagement and modifications in several aspects of the gut bacterial communities, whereas glucocorticoid concentrations appear constant over adulthood. The characterization of consistent aging patterns across individuals in a population is a necessary step in understanding the opportunities, constraints, and potential trade-offs that individuals face. As such, my thesis contributes to the growing field of biogerontology. Future research should investigate how individuals differ from the average trajectories and consider potential age-specific optima, in a diversity of systems, to advance our understanding of the links between sociality, health, and aging.

Table of Contents

Chapter 1

General introduction

Demographics changes are foreseen as major societal challenges within the next decades, as the population is rapidly getting older. With increasing life-expectancy, two billion people are predicted to be over 60 in 2050 (United Nations, 2017), creating the need for care and medical assistance on a scale not yet experienced. The lengthening of lifespan underlying this demographic revolution is not matched by an equal increase in healthspan, the number of years of life free from diseases (Partridge et al., 2018), and is associated with increasing loneliness among the elders (Müller and Ellwardt, 2022), which urges to address the physiological, psychological, and social dimensions of aging.

Finding a clear definition for aging is however not straightforward, and consequently, there is a long tradition of debates on the best way to characterize pathological, normal, as opposed to successful aging (Bulterijs et al., 2015; Rowe and Kahn, 1987; Stowe and Cooney, 2015). In any case, there should be an agreement on the phenotypic traits to investigate for age-related changes. One solution offered to us to broaden our thinking is to consider aging in its entire diversity by moving beyond humans to adopt a comparative perspective.

Indeed, our very conception of aging is focused on humans and model organisms for human aging (Mikuła-Pietrasik et al., 2021). To better understand the variation in life-history and aging trajectories from an evolutionary standpoint, we need interdisciplinary approaches studying long-lived species, ideally under natural conditions. To investigate the link between sociality, health, and aging, the study of a range of species with complex social systems will be imperative. In this thesis, I investigate social and physiological manifestations of aging in a wild population of Assamese macaques (*Macaca assamensis*). In this first chapter, I briefly present the concept of aging from an evolutionary perspective and illustrate how aging translates into decreasing survival and reproduction. Then, I introduce the manifestations of aging in other traits because we know much less here, which is why my work focuses on age-related changes in social behavior, hormonal systems, and the gut microbiome. In the third part, I emphasize on the interdependence between sociality and physiology tied through the sociality-health nexus, and how it relates to aging. In the last part, I detail the aims and approaches followed in this thesis.

1.1 Evolution of aging

Aging, or senescence, is the deterioration of physiological functions that leads to an increased probability of death and a decrease in reproductive success with advancing age (Kirkwood and Austad, 2000; Maklakov and Chapman, 2019). The phenomenon is so ubiquitous in our immediate environment that it may seem inevitable, yet aging represents an evolutionary paradox. As natural selection favors the traits of those organisms that contribute the most offspring to the next generation, aging should be selected against. The key to this paradox is that the strength of natural selection weakens with age, because deleterious traits that preferentially affect the fitness of individuals with the least reproductive value are not strongly selected against (Haldane, 1941; Hamilton, 1966; Medawar, 1952; Williams, 1957). Williams (1957) was the first to suggest an explanation for the decrease in reproductive value with age, which for him was that external age-independent causes of mortality inevitably reduce the probability that any organism will rear offspring over time. Several non-mutually exclusive mechanistic theories have emerged from this understanding, suggesting that age-related declines result from the accumulation of deleterious mutations (Mutation Accumulation: Medawar, 1952), from pleiotropic alleles that are beneficial in early life but detrimental in late life (Antagonistic Pleiotropy: Williams, 1957), and from trade-offs between investment in soma repair and reproductive effort (Disposable Soma: Kirkwood, 1977). Although reassessment of Hamilton's mathematical formulation of aging (Hamilton, 1966) has demonstrated that the decline in reproductive value is not due to extrinsic mortality, as postulated by Williams, but to the decreasing proportion of older age classes in the population over time (Moorad et al., 2019; Wensink et al., 2017; Williams et al., 2006), early contributions provided the evolutionary foundation for what has since become biogerontology.

Research on laboratory model organisms has led to major advances in our understanding of the molecular and cellular drivers of aging, including for example genomic instability, telomere attrition, and loss of proteostatis (López-Otín et al., 2013). Experiments on fruit flies (*Drosophila melanogaster*), nematode worms (*Caenorhabditis elegans*), yeast (*Saccharomyces cerevisiae*), and mice (*Mus musculus*) have demonstrated that lifespan can be extended by the mutation of single genes, caloric restriction, and drugs like metformin (Fontana and Partridge, 2015; López-Otín et al., 2013; Mikuła-Pietrasik et al., 2021). At the same time, several long-held assumptions have been challenged by accumulating evidence. For example, the concept of oxidative damage as a fundamental cause for aging is slowly being abandoned (Gladyshev, 2014; Selman et al., 2012; Speakman et al., 2015), the decoupling of reproductive performance and survival in fruit flies and nematodes is forcing nuances in the Disposable Soma theory (Cohen et al., 2020; Maklakov and Chapman, 2019), and positive

correlations between early and late-life performance support the notion of 'positive pleiotropy' (Maklakov et al., 2015).

The early emphasis placed on the contribution of extrinsic mortality to the declining strength of natural selection led Medawar and his successors to assume that only humans and domestic animals would senesce, whereas wild animals would seldom reach this stage (Kirkwood and Austad, 2000; Medawar, 1952). Possibly because of the focus on model organisms and their contribution to our understanding of human aging, the diversity of aging has only recently been recognized thanks to a more comparative perspective (Cohen, 2018; Jones et al., 2014). Evidence that some organisms do not age, even among those with distinct germ lines and soma, such as turtles and tortoises (da Silva et al., 2022), has questioned the rationale underlying the theories of aging (Jones et al., 2014) and contributed to nuance the contribution of extrinsic mortality to aging. The burst in the field of aging in non-model animal systems at the turn of the century was quickly followed by increasing research on aging in wild vertebrate populations (Nussey et al., 2013), and more recently plants (Gaillard and Lemaître, 2020; Roach and Carey, 2014). The original formulation predicting shorter lifespan and earlier onset of senescence under high (random) extrinsic mortality (broadly summarized by a 'fast pace of life' (Healy et al., 2019; Jones et al., 2008) has been extended to integrate how demographics and individual traits, such as population density (Abrams, 1993), condition-dependent mortality (Williams et al., 2006; Williams and Day, 2003), and the counterbalancing force of increasing fecundity with age (da Silva et al., 2022; Gaillard and Lemaître, 2020; Jones et al., 2014) interact to shape patterns of senescence in naturally occurring populations (Ronget et al., 2017).

Of course, it is important to bear in mind that beyond average aging trajectories, organisms exhibit immense heterogeneity (Alpert et al., 2019; Badal et al., 2020; Johnson et al., 2022), which allows to investigate sources of deviations between an individual's expected (i.e., chronological) and realized (i.e., biological) age (Arneson et al., 2022; Hannum et al., 2013; Horvath, 2013; Johnson et al., 2022). Although biological age may closely depict changes occurring within each individual, assessing biological age is technically complex and still out of reach for most research especially in wildlife (Arneson et al., 2022), so chronological age is used throughout the literature reviewed below and in the present work. Having outlined the current consensus on the evolutionary roots of aging and the diversity of patterns, it is necessary to ask which are the broadly conserved manifestations of aging at the population and individual levels.

1.2 Manifestations of aging

In the following section, I will present how aging manifests itself with regards to mortality and reproduction, the two concepts most widely studied, but I will also highlight the need to consider aging

in other traits, both across and within species if we are to answer some of the most pressing challenges in the field of biogerontology (Gaillard and Lemaître, 2020).

1.2.1 Aging in life-history traits

Actuarial senescence is the most common operational definition of aging which focuses on describing the increase in mortality with age (Gaillard and Lemaître, 2020; Monaghan et al., 2008). The phenomenon is found in organisms as phylogenetically distant as bacteria, insects and mammals (Jones et al., 2014, 2008), but exhibit marked variation between and within taxa. Comparisons can only be made using common metrics, and in practice, actuarial senescence has been studied either through lifespan or age-dependent mortality rates (Ronget and Gaillard, 2020). Lifespan expresses the pace of aging and allows to compare short-lived to long-lived species, whereas age-specific mortality expresses the shape of aging and is modeled by continuous statistical functions such as the Gompertz or the Weinbull laws (Ronget and Gaillard, 2020). Maximum lifespan, life expectancy at birth (i.e., mean age at death reached by individuals in the population), or 90% longevity (i.e., age at which 90% of the individuals have died) are all metrics for the pace of aging, each of which has advantages and shortcomings (Ronget and Gaillard, 2020). Maximum lifespan is currently available for a wide range of taxa and is nowadays easily accessible in public databases (e.g., AnAge, De Magalhães and Costa, 2009), but has been criticized for its sensitivity to outliers (Ronget and Gaillard, 2020). Life expectancy and 90% longevity are more robust metrics but require more detailed data on wild populations and call for long-term field research (Clutton-Brock and Sheldon, 2010).

Together, these metrics have revealed a number of insights, like the fact that lifespan and aging rate may differ between sexes (Bronikowski et al., 2022; Clutton-Brock and Isvaran, 2007; da Silva et al., 2022), with females living longer and aging more slowly than males in most (but not all) mammals (Lemaître et al., 2020b), including humans (Austad, 2006; Colchero et al., 2016); that some species exhibit no signs of aging, irrespective of their lifespan (da Silva et al., 2022; Reinke et al., 2022); and that the rate of aging is slower in species protected from extrinsic mortality, either by physical shields (e.g., turtles) or specific habitats, namely aerial (e.g., birds and bats), underground (e.g., mole rats), or arboreal (e.g., primates) (Reinke et al., 2022; Ricklefs, 2010; although see Moorad et al., 2019). Whether disparities between taxa or sexes result from differences in genetic content or from local environmental conditions is actively debated (Austad and Fischer, 2016; Bronikowski et al., 2022; Gaillard and Lemaître, 2020; Lemaître et al., 2020b). For example, across vertebrates, shorter male lifespan and faster aging appear to be mostly confined to polygynous species where males are under strong sexual selection (Clutton-Brock and Isvaran, 2007; Tidière et al., 2015; but see Lemaître et al., 2020b). However, this finding may not be a universal pattern, as shown by the example that in roe

deer (*Capreolus capreolus*), a polygynous ungulate, longer female lifespan is not observed in all populations (Garratt et al., 2015), highlighting the role of local environmental pressures in shaping actuarial senescence.

Due to the direct relationship between reproduction and fitness, reproductive aging is often investigated alongside the link between aging and mortality (Nussey et al., 2013), also in light of a human-focus interest on post-reproductive lifespan (Croft et al., 2015). Fertility (Aubry et al., 2009; Martin and Festa-Bianchet, 2011), miscarriage (Fogel et al., 2023), litter or clutch size (St. Lawrence et al., 2022; Tidière et al., 2018), interbirth interval (Campos et al., 2022; Hoffman et al., 2010), probability to wean offspring (Catry Paulo et al., 2006), and offspring survival to maturity (Bouwhuis et al., 2009; Campos et al., 2022; Hoffman et al., 2010) have all been found to decline with age in taxa as distantly related as meerkats (*Suricata suricatta*) (Sharp and Clutton-Brock, 2010), kittiwakes (*Rissa tridactyla*) (Aubry et al., 2009), albatrosses (*Thalassarche chrysostoma*) (Catry Paulo et al., 2006), non-human primates (Campos et al., 2022; Hoffman et al., 2010; Tidière et al., 2018), yellow-bellied marmots (*Marmota flaviventer*) (St. Lawrence et al., 2022), and bighorn sheep (*Ovis canadensis*) (Martin and Festa-Bianchet, 2011). The decline in reproductive success with aging is found in both sexes, for example in wandering albatrosses (*Diomedea exulans*), where father's age is associated with lower fledging success (Lecomte et al., 2010), and ruffed lemurs (*Varecia sp.*), where mother's age is negatively correlated to offspring survival (Tidière et al., 2018). The deterioration in reproductive function is not necessarily linear with age but may exhibit accelerated decline in the last years of life, or may vary independently of chronological age, rather decreasing with respect to an individual age at death (Martin and Festa-Bianchet, 2011; Reed et al., 2008). Actuarial and reproductive senescence may also appear to be decoupled if individuals increase their terminal investment in reproduction at the end of life (Duffield et al., 2017; Hoffman et al., 2010). Overall, reproductive senescence occurs in the majority of free- or semi-free ranging female mammals and birds studied to date (Vágási et al., 2021).

To summarize, evidence of actuarial and reproductive senescence in non-human animal populations has contributed to bridge some of the ultimate gaps between aging, fitness, and natural selection. Often studies have investigated survival or reproduction, and combining them is a first important step, but ultimately it is necessary to investigate the other traits underlying an organism's ability to survive challenges, mobilize energy, and invest in reproduction as they may be themselves subjected to aging.

1.2.2 Manifestations of aging in other traits

"[…] while we now have fairly accurate knowledge of demographic senescence patterns in the wild, at least in mammals and birds, we know much less about age-specific changes in other biological parameters associated with physiology, life history or behaviour." Gaillard and Lemaitre 2020, p.5

When studying aging, we must bear in mind that survival results from a mixture of extrinsic and intrinsic mortality, and that both are likely to depend, at least to some extent, on the performance of many morphological, physiological, and behavioral traits. Similarly, the declining reproductive performance observed across a wide range of taxa calls for an investigation of somatic functions over age, while acknowledging that decoupled reproductive and somatic aging exists, for example among species with extended post-reproductive lifespan (Alberts et al., 2013; Croft et al., 2015). Furthermore, the preconception that aging occurs synchronously within individuals is being challenged by both conceptual and empirical work (Fay et al., 2021; Hayward et al., 2015; Moorad and Ravindran, 2022), allowing to explore patterns of aging in various traits to infer on the strength of selection pressure applied. Finally, if the aim is to learn from comparative research to inform human medicine, then healthspan will be better approximated by other systems than by comparing taxa based solely on the shape of actuarial and reproductive senescence. Some of the best documented traits to date are physiology and sociality (Gaillard and Lemaître, 2020; Nussey et al., 2013; Partridge et al., 2018; van den Beld et al., 2018).

1.2.2.a Physiological aging

One of the most studied physiological markers of aging is body mass because variations in body mass provide important cues about the organism's state of energy balance, and loss of body mass has been associated with lower fertility and higher mortality risk (Denryter et al., 2022; Gaillard et al., 2000; Kroeger et al., 2018; Nussey et al., 2011). Age-related loss of body mass is documented in birds (Catry Paulo et al., 2006), ungulates (Nussey et al., 2011), primates (Altmann et al., 2010; Emery Thompson et al., 2020b; Hämäläinen et al., 2014), yellow-bellied marmots (Kroeger et al., 2021), and can be gradual or accelerated preceding death (Kroeger et al., 2021; Nussey et al., 2011). Decreases in fat and muscle may be caused by reduced feeding ability owing to tooth wear, declining physical strength in aerial and arboreal species, or hunting skills (Altmann et al., 2010; Catry Paulo et al., 2006; Frankish et al., 2020; Hämäläinen et al., 2015a; Lecomte et al., 2010; MacNulty et al., 2009; Pelletier and Festa-Bianchet, 2004). However, old individuals can overcome age-related deterioration in more favorable environments (Kroeger et al., 2021, 2018) or by investing relatively more resources towards the maintenance of body mass (Kroeger et al., 2021; Nussey et al., 2011). At least among mammals and birds, the general trend points to decreasing body mass post sexual maturity being modulated by the

ability of old individuals to prioritize energy allocation to body condition. Despite its value, measurement of body mass is not possible in all situations (e.g., research on large mammals), so biomarkers allowing more direct assessment of energy balance could be particularly informative. Biomarkers of energy mobilization, energy intake and metabolic activity, such as thyroid hormones, are especially promising (Behringer et al., 2018; Girard-Buttoz et al., 2011; Heistermann et al., 2006) and could contribute to assess age-related changes in body condition, although this requires to first establish their link to energy balance and their suitability to conditions associated with field research.

More recently, other age-related physiological changes have also been documented, encompassing a wide range of immunological, hormonal, and microbiome systems. Multidimensional physiological data aggregated into a single metric have demonstrated a common pattern of physiological dysregulation with advancing age in humans and several captive non-human primates (Cohen et al., 2013; Dansereau et al., 2019; Kraft et al., 2020). The changes underlying this dysregulation are especially pronounced among immune cells, with a decline of immune activity referred to as immunosenescence, translating into reduced innate immunity through decreased phagocytosis and natural killer cell activity (Blacher et al., 2022; Linehan and Fitzgerald, 2015), altered inter-cellular chemokine signaling (Blacher et al., 2022; Metcalf et al., 2020), depletion in the pool of naïve lymphocytes associated to an accumulation of deficient clones (Alpert et al., 2019; Linehan and Fitzgerald, 2015), and overall heightened pro-inflammatory profiles (Franceschi et al., 2017; Müller et al., 2017; Watowich et al., 2022). Among hormonal systems, age is associated with marked changes in glucose homeostasis, insulin resistance, and the hypothalamic-pituitary-peripheral organ axes (Clegg et al., 2013; van den Beld et al., 2018). Strikingly, the microorganisms communities residing in the mouth, gut, genitalia, and on the skin exhibit decreasing diversity and stability as humans age (Badal et al., 2020; Bana and Cabreiro, 2019; Bosco and Noti, 2021; Ghosh et al., 2022; O'Toole and Jeffery, 2015) even though they are not part of the soma *per se*.

These findings are just some examples of the profound physiological changes occurring with age and which contribute to age-related delayed wound healing, increased risk for several types of cancer and cardiovascular diseases, and greater frailty (i.e., general decline in health and disease resistance) (Clegg et al., 2013; Lemaître et al., 2020a; Linehan and Fitzgerald, 2015). The adaptive value of some of those processes are, however, still debated. For example, some have argued that age-related increase in inflammation, negatively coined as inflammaging (Franceschi et al., 2017), may be the most efficient defense against pathogens in a context of depleted humoral immunity (Fulop et al., 2016). Broadening the scope to other species will likely reveal informative on the correlates of physiological changes with advancing age. As such, evidence of immunosenescence in wildlife is accumulating (Cheynel et al., 2017; Nussey et al., 2013, 2012; Peters et al., 2019). However, most investigations have been cross-

sectional with the risk that selective disappearance of individuals with poor immune defenses biases profiles measured at old age when survival co-varies with immune functions (Nussey et al., 2008; van de Pol and Wright, 2009). One noticeable longitudinal study found that Soay sheep (*Ovis aries*) exhibit a gradual decline in antibody titers with age before a sharp drop predicting death in the following winter (Froy et al., 2019), providing rare evidence for a fitness correlate of immunosenescence in the wild. On the contrary, longitudinal immune profiles in common terns (*Sterna hirundo*) did not match expected immunosenescence (Bichet et al., 2022).

Investigating physiological aging in free-ranging animal populations requires the use of non-invasive methods whenever handling or blood sampling raises practical or ethical concerns, which limits the range of available biomarkers. In this context, the study of hormonal profiles and gut microbiome appear especially promising. The development of methods to measure hormones from urine and feces has opened up many possibilities for the investigation of physiology in wildlife (Higham, 2016). Validated measurements of steroid hormones (Heistermann et al., 2004) and biomarkers of immune activation (Behringer et al., 2017; Heistermann and Higham, 2015) are beginning to provide insights into reproductive (Altmann et al., 2010) and immunological (Cooper et al., 2022; Dibakou et al., 2020; Müller et al., 2017) aging.

Recently, the gut microbiome has become a major target in both human and animal aging research. The gut microbiome consists of the community of *Bacteria*, microbial eukaryotes, *Archaea,* and viruses residing in the gastrointestinal tract and engaging in continuous interactions with each other and the host (Björk et al., 2019; Miller et al., 2018). This ecosystem's composition is highly dynamic, shaped by competitive and cooperative microbial interactions (Coyte et al., 2015), as well as host-microbes interactions. The gut microbiome affects host health by conditioning immune responses, metabolic processes, and neurological functions, while host dynamics in turn impact microbial communities (Björk et al., 2019; Ezenwa et al., 2012; Miller et al., 2018; Sherwin et al., 2019). Disrupting this often mutualistic relationship can lead to dysbiosis, which is increasingly implicated in metabolic, digestive, and age-related diseases (Askarova et al., 2020; Badal et al., 2020; Bana and Cabreiro, 2019; Ghosh et al., 2020, 2022; Popkes and Valenzano, 2020; Ragonnaud and Biragyn, 2021; P. Smith et al., 2017). Consequently, gut microbiome health has been introduced as a new hallmark of aging (López-Otín et al., 2023; Schmauck-Medina et al., 2022), with potential as an early diagnostic tool for frailty (Jackson et al., 2016; Renson et al., 2020). As an example, 'gut clocks' gathering information on microbiome diversity, taxonomic and metabolic composition outperform epigenetic clocks in detecting age-related diseases and frailty (Ratiner et al., 2022). A less diverse and less stable gut bacterial composition, as well as enriched energy-related pathways have been described in older human patients (Badal et al., 2020; Bana and Cabreiro, 2019; Ghosh et al., 2022). However, the relationship between age and the

gut microbiome depends on cultural, environmental, and lifestyle variables which prohibits the generalization of patterns in WEIRD panels (de la Cuesta-Zuluaga et al., 2019; Lloyd-Price et al., 2016; Yatsunenko et al., 2012). Furthermore, "dysbiosis" has a broad definition that encompasses various scenarios, including the shift in dominant microbial groups, the microbial composition seen in sick patients, or any differences in the abundance of specific microbial taxa between a healthy state and a state of interest (Berg et al., 2020; Hooks and O'Malley, 2017). Finally, it remains unclear whether aging of the host *per se* is the cause for these changes, as gut bacterial composition is extremely sensitive to lifestyle-linked factors (often) associated with aging (e.g., reduced caloric intake, medication use).

Fecal samples can be used to non-invasively assess gut microbiome communities, making them suitable for wild animal research. Investigations in natural populations have revealed that gut microbial composition is influenced by seasonal cycles, diet, sex, and host genetics (Grieneisen et al., 2020; Hicks et al., 2018; Huang et al., 2022; Murillo et al., 2022a; Trosvik et al., 2018), and undergoes significant changes during early development (Baniel et al., 2022; Petrullo et al., 2021). The influence of host aging has received comparatively little attention (Björk et al., 2019). Furthermore, investigations have focused mostly on gut microbial diversity and composition similarity across hosts (Janiak et al., 2021; Perofsky et al., 2017; Reese et al., 2021), which only provide partial insight into this dynamic and complex ecosystem. Which features of the gut microbiome exhibit aging and whether these changes are conserved across species, are central questions left unanswered.

To summarize, the sheer number of physiological traits associated with senescence imply that it is very unlikely that a single consistent pattern of physiological senescence will ever emerge. Nevertheless, one take-home message from wildlife research is that life under natural conditions is compatible with the slow deterioration of, at least some, physiological functions. Which of these functions are under the most pressure from natural selection is still unclear (Hayward et al., 2015; Moorad and Ravindran, 2022). Although not necessarily fatal, declining physiological traits nevertheless impose constraints which must be mitigated, and it is therefore important to understand how individuals cope with these changes.

1.2.2.b Social aging

Behavior plays a key role in allowing individuals to adapt to physiological changes, by altering their activity budget (Corr, 2003; Frankish et al., 2020; Rathke and Fischer, 2021; Veenema et al., 1997), roaming strategies (Frankish et al., 2020; Froy et al., 2018), and diet selection (Galbany et al., 2011; Logan and Sanson, 2002; Venkataraman et al., 2014), which in turn may contribute to age-structured spatial distribution at the population level (Albery et al., 2022; Frankish et al., 2020; Froy et al., 2018; Lecomte et al., 2010). As such, behavioral changes represent another trait that 'ages'. These changes

not only concern behavior centered on self, but further extend to social interactions in group living species. Flexible behavioral strategies can then serve to mitigate decreasing physical competitive ability (Fischer et al., 2004), as seen in aging male non-human primates, who may switch to more opportunistic mating strategies, invest in affiliative interactions with females as an alternative to costly mate-guarding activity (Silk et al., 2020), provide more parental care (Silk et al., 2020), or engage increasingly in coalitions with other males (Berghänel et al., 2011; Rathke et al., 2017).

A striking feature of social behavior among aging humans is a general tendency to decrease social engagement with advancing age, which may translate into reduced time spent social, decreasing social network size, or both (Cornwell et al., 2021; Lang et al., 1998; Lang and Carstensen, 1994; Mor-Barak and Miller, 1991; Müller and Ellwardt, 2022; Röhr et al., 2020; Zheng and Chen, 2020). Several competing theories, mostly coming from psychological research rooted in human social psychology, have attributed this decline in turn to increasing lack of interest in the social world (Cumming and Henry, 1961), increasing frailty (reviewed in Müller and Ellwardt, 2022), and gradual shift towards more emotionally-rewarding relationships (Charles and Carstensen, 2010), and suggested models for successful aging based on the maintenance of physical activity, social engagement, or the achievement of age-specific goals (Antonucci et al., 2014; Carstensen, 2019; Cumming and Henry, 1961; Freund et al., 2021; Rowe and Kahn, 1997, 1987). Recently, evidence of social withdrawal among non-human mammals has broadened our appreciation of social aging (Machanda and Rosati, 2020; Siracusa et al., 2022a), offering an opportunity to test the involvement of cognitive and psychological mechanisms in social withdrawal (e.g., increasing social selectivity, decreased motivation) (Almeling et al., 2016; Nakamichi, 2003, 1984; Rathke et al., 2022; Rathke and Fischer, 2021, 2020; Rosati et al., 2018, 2016; Rosati and Santos, 2017), and to anchor social aging in broader life-history theories (e.g., kin selection, competitive exclusion) (Albery et al., 2022; Kroeger et al., 2021; Siracusa et al., 2022b). On the downside, most studies on social aging are cross-sectional or fail to account for potential cohort effects, which emphasizes the need to investigate social aging with longitudinal approaches (Nussey et al., 2008; Rohrer and Murayama, 2023).

It is becoming clear that 'aging' refers to a collection of biological changes which increase the risk of mortality. Which traits show aging, and which do not? Which trait-specific declines best translate into whole-organism aging? These are unresolved questions that would require, as a first step, finer characterizations of aging in a variety of traits. Captive animals have provided critical insights into physiological aging, that need to be confirmed in their wild counterparts using validated non-invasive markers of energetic state and inflammation, and by investigating the gut microbiome. The importance of social behavior in mediating age-related constraints is becoming increasingly clear, calling for a more

holistic view of aging. Investigating these issues in natural populations will provide a better picture of the trade-offs associated with the type of environment in which aging patterns have evolved.

1.3 Interdependences in aging systems

Above, I briefly described how some of the changes in behavioral and physiological traits that occur with age ultimately contribute to declining performance in survival and reproduction. Although I presented those systems independently, evidence points to their interdependence, which suggests that aging in one system may precede and promote aging in another. Notably, physiological functions are major building blocks of an organism's health state, which has been repeatedly linked to sociality in animals, including humans (Kappeler et al., 2015; Ostner and Schülke, 2018; Snyder-Mackler et al., 2020). As sociality and physiology are interdependent, i.e., social behavior impacts physiology and vice versa, determining the independent influence of age on sociality and age on physiology can be challenging. I will discuss the current state of knowledge on these complex links in the following section.

1.3.1 Sociality and health

A first important consequence of group living is heightened exposure to pathogens (Kappeler et al., 2015). Body contact and mouth-to-hand interactions, such as grooming, promote the acquisition of parasites from social partners, and consequently, more socially connected and more central individuals in a network face higher parasitism (Briard and Ezenwa, 2021). Even in the absence of direct contact, individuals can become infected by picking up parasites from contaminated soil (Friant et al., 2016; Müller-Klein et al., 2019). This implies that the markers of immune and endocrine activity discussed above will be partly influenced by the social position of individuals through the link between sociality and parasitism (Defolie et al., 2020). Social transmission of microorganisms applies not only to viral and gastrointestinal parasites, but also to gut microbes (Sarkar et al., 2020). Shared environments and close interactions facilitate the horizontal transmission of microbes (Ezenwa et al., 2012; Sarkar et al., 2020; Sherwin et al., 2019), which homogenizes microbial compositions within populations (Björk et al., 2022; Perofsky et al., 2017; Rudolph et al., 2022), especially between strongly connected individuals (Murillo et al., 2022b; Raulo et al., 2021; Sarkar et al., 2020). Therefore, age-related changes in gut microbiome composition must integrate age-related changes in social behavior.

The frequency of social contact and number of social partners are quantitative aspects of sociality influencing physiology through the sociality-parasitism link, but qualitative aspects are also important. In humans, competitive, agonistic, and more broadly stressful, interactions elicit the activation of immune and neuroendocrine processes (Cohen et al., 2012; Hostinar et al., 2014). Experience of social

adversity translates into low-grade inflammation, increased prevalence of cardiovascular, endocrine, cancer and gastrointestinal diseases (Bergmann et al., 2014; Cole et al., 2007; Fuligni et al., 2009; Guarner and Rubio-Ruiz, 2015; Kiecolt-Glaser et al., 2010; Miller et al., 2011; Rohleder, 2014; Snyder-Mackler et al., 2020; Tamashiro et al., 2011). Strong evidence for the causal influence of sociality on these biological processes has been provided by experiments with animal models (Adams et al., 1985; Capitanio et al., 1998; Cohen et al., 1992; Hawkley and Capitanio, 2015; Shively et al., 2009, 1997; but see Zane et al., 2021). For example, experimentally manipulated low dominance rank predicted dampened anti-viral response in favor of a pro-inflammatory immune phenotype in female rhesus macaques (*Macaca mulatta*) (Snyder-Mackler et al., 2016), and greater susceptibility to cold infections in male long-tailed macaques (*Macaca fascicularis*) (Cohen et al., 1997). Conversely, a positive social environment provided by the presence of strongly bonded partners has a beneficial effect on individual health and disease resistance (Ezenwa et al., 2016b), due to a subjective feeling of integration and an effective partner support (Cohen et al., 2015, 1992; Cohen and Wills, 1985; Donovan et al., 2018; Hennessy et al., 2009; Hostinar et al., 2014; Young et al., 2014). Therefore, assessing aging of neuroendocrine functions requires integrating different aspects of sociality.

Investigations of the links between sociality and neuroendocrine activity in wildlife have relied largely on the non-invasive measurements of glucocorticoids since they are excreted unchanged or as metabolites in several matrices (e.g., saliva, feathers, hair, feces, and urine), some of which can be collected non-invasively. Activation of the hypothalamic-pituitary-adrenal axis triggers the secretion of glucocorticoids (GCs) involved in maintaining homeostasis in response to predictable (e.g., seasonal migration) and unpredictable (e.g., predator attack, major injury) events, the latter being commonly referred to as stressors (McEwen and Wingfield, 2003; Romero et al., 2009). GC concentrations are often elevated after agonistic interactions (Wittig et al., 2016; Young et al., 2014) or at times of heightened competition (Petrullo et al., 2022a; Sadoughi et al., 2021b), and are lowered by friendly interactions (Wittig et al., 2016) and in those benefiting from greater social support (Brent et al., 2011; Fürtbauer et al., 2014), illustrating the value of measuring GCs concentrations to investigate the physiological correlates of sociality in wildlife (Beehner and Bergman, 2017).

A critical difference between humans (and animal models) and wildlife may be the consequences of repeated HPA axis activation. In humans and animal models, repeated elevations of GCs outside of the physiological range are thought to cause wear and tear on the organism (Allostatic Load: McEwen and Wingfield, 2003; Reactive Scope: Romero et al., 2009), lowering the capacity to cope with stressor over time and leading to deleterious outcomes (Charmandari et al., 2005; Sapolsky, 2004; Sapolsky et al., 2002). Whether the social activation of HPA axis in natural living environments is associated to some of the chronic stress effects seen in humans is strongly debated (Beehner and Bergman, 2017; Bonier

et al., 2009a; Dickens and Romero, 2013; MacDougall-Shackleton et al., 2019; Schoenle et al., 2021; Scott et al., 2012; Vitousek et al., 2019b).

This debate is important for our understanding of the relationship between age and GCs. In humans and animal models, age-related changes in GCs are thought to result from the gradual accumulation of damage (Glucocorticoid Cascade Hypothesis: Sapolsky et al., 2002). Studies have documented several age-related changes in the diurnal rhythm, baseline, and stress-induced levels of GCs (Dodt et al., 1991; Ferrari et al., 2001; Goncharova et al., 2019; Goncharova and Lapin, 2002; Gust et al., 2000, 2000; Nathanielsz et al., 2020; Otte et al., 2005; Reul et al., 1991, 1991; Sapolsky, 1992a; Touitou et al., 1983; Van Cauter et al., 1996, 1996; Yang et al., 2017), some stronger in women than in men (Born et al., 1995; Otte et al., 2005; Van Cauter et al., 1996). Nevertheless, the picture is far from clear, with many examples reporting no changes or changes in only some aspects of GC physiology (Born et al., 1995; Dodt et al., 1991; Goncharova et al., 2019; Goncharova and Lapin, 2002; Harris and Saltzman, 2013; Nathanielsz et al., 2020; Yang et al., 2017; Zambrano et al., 2015), and most studies contrasting profiles between two groups rather than evaluating changes over as much of adulthood as possible. In the wild, the relationship between age and GCs has been considered in relation to GC-mediated trade-offs between reproduction and stress-responsiveness in birds (Heidinger et al., 2010; Lendvai et al., 2015; Schoenle et al., 2021; Vitousek et al., 2019b). Individuals are thought to down-regulate HPA axis activity or sensitivity to GCs when the value of current reproduction is higher than future reproduction (Angelier et al., 2007; Elliott et al., 2014). In mammals, which typically display a higher rate of physiological aging than birds (Ricklefs, 2010), no clear pattern has yet emerged, with increased (Altmann et al., 2010; Campos et al., 2021; Charpentier et al., 2018; Emery Thompson et al., 2020a; Pavitt et al., 2016, 2015), decreased (Maestripieri and Georgiev, 2016), or unchanged GCs (Gesquiere et al., 2011) with age. Crucially, only three studies accounted for social traits (Campos et al., 2021; Charpentier et al., 2018; Emery Thompson et al., 2020a), and none tried to disentangle changes that may arise from demographics rather than aging processes.

In summary, social relationships have multiple and complex influences on physiology, resulting in important inter-individual differences in health. All of these mechanisms likely contribute to the association between greater social support and lower mortality risks in humans and other animals (Archie et al., 2014; Holt-Lunstad et al., 2015; Kajokaite et al., 2022; Maestripieri and Georgiev, 2016; Marescot et al., 2018; Marmot and Sapolsky, 2014; Ostner and Schülke, 2018; Silk et al., 2010; Snyder-Mackler et al., 2020; Thompson, 2019). Despite an overall clear benefit of sociality, notable exceptions point to context dependence, suggesting that relationships imposed by habitat saturation or unstable bonds are detrimental to survival (Blumstein et al., 2018; Thompson and Cords, 2018). These links between sociality and physiology are also scrutinized in explaining differences in lifespan not only

within but also between species, as comparative data indicate that eusocial insects and social mammals live longer than their asocial counterparts (Zhu et al., 2023; but see Lucas and Keller, 2020 for critical discussion across species).

However, whether the benefits and shortcomings of sociality are experienced uniformly across the lifespan is unknown. To date, few studies have attempted to contrast the contribution of social network size to survival or health across life stages. One study in humans found social network size to impact the health of the young and the elderly more compared to middle-aged subjects (Yang et al., 2016), whereas another study in humans and one in macaques found the opposite (Brent et al., 2017; Holt-Lunstad et al., 2015). Age-dependent benefits of sociality can arise in cross-sectional studies if those reaching old ages are especially robust, or if benefits of sociality earlier in life determine the susceptibility to hazards later on (De Nys et al., 2017). To make progress, it is necessary to investigate age-related changes in sociality in longitudinal studies across more diverse contexts, and where possible, to account for age-specific optima when studying sociality-physiology dynamics.

1.3.2 Physiology and sociality

The previous section illustrates how social stimuli trigger neuroendocrine responses and may influence vital physiological functions. Evidence demonstrates that neuroendocrine responses can in turn play a strong role in modulating behavior (Raulo and Dantzer, 2018). Elevations in GCs appear to inhibit proactive social behavior while promoting pair-bonding and cooperation among group members (Raulo and Dantzer, 2018). Another example of reversed causality between physiology and sociality is the influence of skin and gland microbial communities on the host's olfactory signaling with conspecifics, susceptible to affect recognition and bonding (Ezenwa et al., 2012; Müller-Klein et al., 2019; Poirotte et al., 2017; Sherwin et al., 2019).

Physiological conditions that lead to deteriorating health or poorer physical condition may impact social integration and social status, or cause individuals to withdraw from their social environment (Kröger et al., 2015). However, little effort has been devoted to the causal influence of frailty on sociality, with mixed results. In humans, physical decline appears to have less impact on the social lives of older people compared to cognitive decline, because subjects effectively shift the composition of their network to family members or receive increasing support from extended networks, while opportunities to compensate for the loss of distant network ties seems absent when cognition declines (Aartsen et al., 2004; Cornwell, 2009; Li and Zhang, 2015). However, others have found no influence of subjective, physiological, or cognitive health on social network size (Mor-Barak and Miller, 1991). In other mammals, declining locomotor skills, sensory system acuity, cognitive functions, and the physiological changes reviewed above, are all thought to contribute to decreasing social engagement

with age (Machanda and Rosati, 2020; Siracusa et al., 2022a), although direct causal evidence is lacking.

The links within the sociality-physiology-health nexus are complex and possibly include self-reinforcing loops, with individuals having access to poorer social resources experiencing more rapid declining health, which in turn results in further social withdrawal. To improve our understanding of how the causes and effects of the social environment on individual health transcend into variation in aging processes, and how health and aging in turn impact social behavior, long-term, holistic studies of social animals under natural conditions that include detailed information on life-history, social environment, physiology, immune function, and frailty will be imperative.

1.4 This thesis

1.4.1 Study species

Assamese macaques (*Macaca assamensis*) are cercopithecine primates native to South and South-East Asia (Schülke et al., 2011; Thierry, 2007), and the population studied at the Phu Khieo Wildlife Sanctuary (PKWS) in Thailand inhabits the species' southern-eastern range. Assamese macaques are primarily arboreal, exhibit female philopatry with male dispersal, and live in female-bonded multi-male-multi-female social groups (Ostner et al., 2013; Richter et al., 2016; Schülke et al., 2011). Female social structure is organized into matrilines of adjacently ranked kin, with mostly stable dominance relationships across and within matrilines. Juvenile and subadult males emigrate from their natal group between roughly three to seven years of age and migrate repeatedly throughout their life. Dominance among males is achieved according to competitive ability, which may rely on the combination of individual quality and the formation of alliances (Schülke et al., 2010). Due to male dispersal, knowledge about female life-history trajectories is more complete, and ages in females can be estimated with more certainty, which is why this thesis focuses on female aging.

Assamese macaques are seasonal breeders with the vast majority of births occurring over three months, and a maximum spread from the first to the last birth of six months (Fürtbauer et al., 2010; Touitou et al., 2021a). Female fertility is concealed and receptivity is synchronized, contributing to a low paternity skew (Sukmak et al., 2014). Gestation lasts on average 164 days and interbirth intervals are bimodally distributed around one and two years (Fürtbauer et al., 2010). This pattern arises because females reproducing early in a birth season are more likely to resume cyclicity and conceive at the end of the next mating season, while females giving birth late in the birth season skip the next mating season. Female Assamese macaques are relaxed-income breeders relying on energy stored in a season of high food abundance several months before their fertile periods (Touitou et al., 2021a).

Lactation is timed to periods of high food availability, during which conception success is enhanced by food availability (Heesen et al., 2013), and nutritional requirements of gestation are met by behavioral, dietary, and physiological adaptations (Touitou et al., 2021a). Females' first live birth coincides with growth cessation around six years of age (Anzà et al., 2022), and therefore first conception marks the transition to adulthood for this thesis.

Adult males and females form differentiated and lasting social bonds within and across sexes (Haunhorst et al., 2016; Kalbitz et al., 2016; Macdonald, 2014) which are known to be beneficial. In males, same-sex bonds enhanced coalitionary support (Schülke et al., 2010) and both same- and opposite-sex bonds increase male siring success (Ostner et al., 2013; Schülke et al., 2010). In females, female-female bonds provide increased feeding tolerance (Heesen et al., 2014), while male-female bonds are associated with higher levels of male support and increased foraging efficiency (Haunhorst et al., 2017). Therefore, females may be under strong pressure to maintain social investment into old age. Power asymmetries, owing to dominance rank among females, govern access to male partners (Haunhorst et al., 2020) and to feeding sites (Heesen et al., 2015, 2014), which lower-ranking females mitigate by adopting flexible feeding strategies (Heesen et al., 2015, 2014, 2013) rather than trading grooming for rank-related benefits (Macdonald et al., 2013).

The population has been followed since 2005, and for this thesis, I included data on physiology and social behavior collected from 2010 to 2020, spanning about half of the average adulthood of female macaques (Brent et al., 2017; Johnson and Kapsalis, 1995). Although very few individuals have complete life records, combined cross-sectional and longitudinal analyses offer an opportunity to address central issues surrounding social and physiological aging over a timespan associated with noticeable physical aging within individual (**Figure 1**).

Figure 1. Physical aging in a female Assamese macaque from 2006 to 2020 (left to right).

1.4.2 Aims and hypotheses

The general aim of this thesis was to investigate the social and physiological manifestations of aging in wild female Assamese macaques, and by doing so, contribute to pressing questions about the prevalence and characterization of aging across traits in a long-lived species (**Figure 2**). To address these issues, I collected behavioral data on adult female-female social interactions, and incorporated data from the long-term project at PKWS in my analysis. To investigate physiological aging non-invasively, I collected fecal samples to sequence bacterial 16S rRNA genes to reconstruct the composition of individual gut bacterial communities, validated the measurement of hormonal markers for the assessment of physiological response to energy shortage, and continued the long-term collection of fecal samples for GC metabolites analysis.

After this first chapter, introducing essential notions and pressing questions in the study of aging, I divided my investigations into five chapters. In doing so, special attention was paid to considering the interdependence between sociality and physiology. Although the work presented cannot directly test causal relationships, hypotheses are inevitably formulated following causal pathways. The first four chapters presented follow a progression from sociality towards physiology, while the fifth chapter offers perspective to explore the reverse path from physiology towards sociality.

To start on the social end of the sociality-health nexus, Chapter 2 of this thesis focuses on age-related changes in social relationships among adult females. In non-human animals, sociality is a loose term describing the position of an individual within its social environment inferred from spatial associations, affiliative, and agonistic interactions among group members (Hinde, 1976; Silk and Kappeler, 2017). Group living animals can form differentiated relationships between pairs of individuals creating group-level social network structures and dynamics. Social status and affiliative relationships are the most commonly studied dimensions of sociality, and the second is further subdivided into integration assessed by the number of ties, and bonding assessing relationships quality and arranged into strong bonds and weak ties (Schülke et al., 2022; Silk et al., 2018). Evidence from captive non-human primate populations suggests that individuals decrease the size of their social network with age but may at the same time partially offset the costs of social isolation by increasing selectivity for strongly bonded partners (Almeling et al., 2016). The benefits of sociality, and more specifically female-female relationships, identified in this population may be decisive to cope with external pressures and thereby constrain the social expression of aging. The aim of this study was to investigate whether females manifest social aging under natural predation and environmental pressures, and to test whether changes would be consistent with theories of social selectivity.

Moving along the sociality-health nexus, Chapter 3 of this thesis reviews the many links between sociality and health with a focus on primates. The aim is to provide a comprehensive summary of the mechanisms best documented and to point to innovative research perspectives, some of which are addressed further in this thesis.

Chapter 4 focuses on one hormonal system, the HPA axis. Previous investigations have shown that reproductive state, climatic conditions, and social interactions correlate with GC concentrations in female Assamese macaques (Fürtbauer et al., 2014; Touitou et al., 2021b). However, it remains unclear whether GC profiles shift across the lifetime, and whether those changes could be attributed to endocrinological aging or be rather mediated by social aging. In a longitudinal analysis of the long-term hormonal database, I investigate the relationship between age and GCs concentrations measured in feces (fGCs). The first aim is to test for an increase in fGCs consistent with the 'Glucocorticoid Cascade Hypothesis', while accounting for circannual variations in fGCs dictated by climatic conditions and the influence of reproductive state. To disentangle the influence of age from the potential confounding effects of social decline (cf. Chapter 2), I examine whether any association between age and fGCs persists after controlling for social bonding and dominance status.

Chapter 5 investigates age-related modifications in the composition of gut bacterial communities using a set of complementary metrics based on data collected over one and a half years and analyzed cross-sectionally. The gut microbiome undergoes profound modifications with age in humans and is scrutinized for its contribution to both healthy and pathological aging. Whether those modifications are features of a widely shared transitions from adulthood to late-life or merely the consequence of modern human lifestyle is unknown because age-related changes in the gut microbiome are strikingly understudied in other natural mammalian populations. Thereby, I test the often-cited loss of gut bacterial diversity with age, the causal relationship between diversity and stability, and the age-structuring of gut bacterial composition. I further investigate whether sociality mediates changes in gut microbiome to assess the interdependence between social and physiological aging.

After exploring aging via the sociality-health nexus from sociality to physiology, Chapter 6 opens on the perspective to explore the influence of physiological aging on social aging. In this introductory chapter, I highlighted the need for biomarkers of energetic status and body condition, so Chapter 6 is a contribution to the development of non-invasive markers of metabolic response. Urine samples originally collected for the validation of C-peptide in captive macaques (Girard-Buttoz et al., 2011) were analyzed for concentrations of triiodothyronine and cortisol. Both hormones contribute to trade-offs between energy mobilization and allocation, but their profiles have not been simultaneously

investigated under controlled conditions nor linked to variation in body mass, which are necessary steps prior to their application in field research as biomarkers of aging.
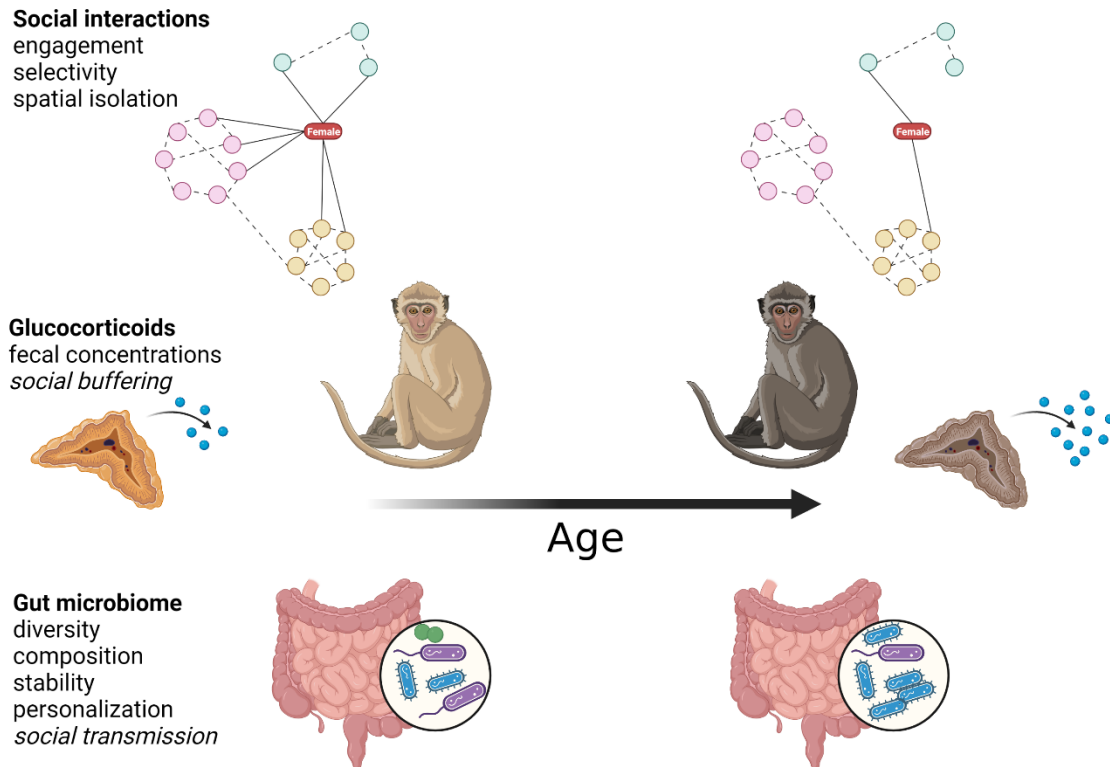
Figure 2. Overview of the physiological and social traits investigated for age-related changes in this thesis. Traits are in bold, components belonging to one trait are in plain text, and those bridging between two traits are in italic. Created in BioRender.com.

Chapter 2

Social network shrinking is explained by active and passive effects but not increasing selectivity with age in wild macaques

Baptiste Sadoughi [a,b,c], Roger Mundry [c,d,e], Oliver Schülke [a,b,c], Julia Ostner [a,b,c]

[a]Department of Behavioral Ecology, Johann-Friedrich-Blumenbach Institute for Zoology and Anthropology, Georg-August-Universität Göttingen, Kellnerweg 6, D-37077 Göttingen, Germany

[b]Research Group Primate Social Evolution, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

[c]Leibniz ScienceCampus Primate Cognition, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

[d]Cognitive Ethology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany

[e]Department for Primate Cognition, Georg-August-Universität Göttingen, Germany

Abstract

Evidence of social disengagement, network narrowing, and social selectivity with advancing age in several non-human animals challenges our understanding of the causes of social ageing. Natural animal populations are needed to test whether social ageing and selectivity occur under natural predation and extrinsic mortality pressures, and longitudinal studies are particularly valuable to disentangle the contribution of within-individual ageing from the demographic processes that shape social ageing at the population level. Data on wild Assamese macaques (*Macaca assamensis*) were collected between 2013 and 2020 at the Phu Khieo Wildlife Sanctuary, Thailand. We investigated the social behavior of 61 adult females observed for 13,270 hours to test several mechanistic hypotheses of social ageing and evaluated the consistency between patterns from mixed-longitudinal and within-individual analyses. With advancing age, females reduced the size of their social network, which could not be explained by an overall increase in the time spent alone, but by an age-related decline in mostly active, but also passive, behavior, best demonstrated by within-individual analyses. A selective tendency to approach preferred partners was maintained into old age but did not increase. Our results contribute to our understanding of the driver of social ageing in natural animal populations and suggest that social disengagement and selectivity follow independent trajectories during ageing.

Keywords

Introduction

The world's human population is ageing rapidly, reaching an estimated 2 billion people over the age of 60 by 2050 (United Nations, 2017). This challenge to societal organizations and health care systems, can be better met by promoting healthier ageing. One of the keys to healthy ageing may lie in the positive influence of strong social integration on health (Evans et al., 2019; Snyder-Mackler et al., 2020). Concerns therefore arise from research showing that people reduce the size of their social network and their level of social engagement with age (Müller and Ellwardt, 2022). The causes and consequences of this reduction in social engagement are still actively debated (Evans et al., 2019; Müller and Ellwardt, 2022).

Several causal models for reduced social engagement are anchored in the framework of age-related losses (e.g., activity and social exchange theories, reviewed in (Müller and Ellwardt, 2022)). Accordingly, individuals experiencing frailty, sickness, or loss of social value with age are unable to maintain their social engagement due to physiological constraints, exclusion by younger generations, or diminished self-perception. Although in one case physiological decline translates into social decline while in the other exclusion hampers social engagement, in both cases, the reduction in network size and in time spent socially engaged is considered detrimental to wellbeing. However, reduced network size may also result from the tendency of older people to actively focus on preferred partners and positive relationships (e.g., socioemotional selectivity and convoy model theories, (Antonucci et al., 2014; Charles and Carstensen, 2010)). Recently, evidence is accumulating for decreasing social engagement in non-human animals (Albery et al., 2022; Hrdy and Hrdy, 1976; Nakamichi, 1991; Picq, 1992; Rathke and Fischer, 2021; Thompson González et al., 2021; Veenema et al., 1997) and particularly for social selectivity among non-human primates (Almeling et al., 2016; Rosati et al., 2020; Schino and Pinzaglia, 2018; Siracusa et al., 2022b).

The social selectivity in human self-reports can be translated into several predictions for observational studies quantifying animal interaction networks (figure 1). Differences arise from a need to test social features relevant to the study species, and because socioemotional selectivity theory remains vague about how exactly selectivity is expressed at the interaction level. Older individuals may focus their interactions on preferred partners and maintain their overall level of social engagement (Rosati et al., 2020; Siracusa et al., 2022b), with engagement in preferred partners compensating for the loss of more distant relationships (figure 1A). Alternatively, individuals may reduce their overall engagement (figure 1B), while maintaining a constant level of engagement with preferred partners (Lang and Carstensen, 1994; Veenema et al., 1997), possibly due to a loss of interest in less preferred partners. Finally, they may decrease their engagement in all relationships, but less so with preferred partners (figure 1C)

(Lang et al., 1998). While increasing selectivity would account for a reduction in network size in the first and second scenarios, the third suggests that another level of constraint is at play.
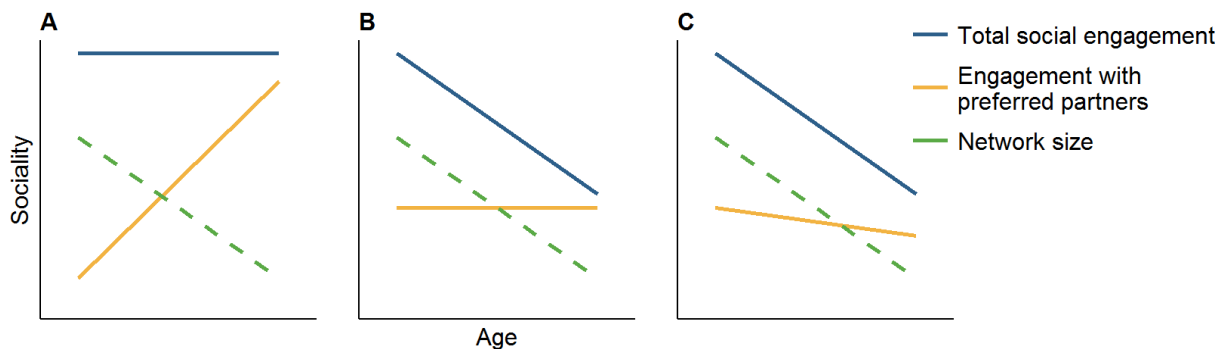
Figure 1. Social selectivity with age can manifest in different ways. (**A**) Social engagement does not change with advancing age, but individuals increasingly prioritize their preferred partners leading to a reduction in network size. (**B**) Social engagement decreases with advancing age but reduction in network size allows individuals to maintain constant engagement with their preferred partners. (**C**) Social engagement decreases with age imposing a reduction in network size and engagement with preferred partners, which may still be prioritized relatively to the other potential partners.

Although the socioemotional *selectivity* hypothesis focusses on the motivation of the ageing individual in explaining changes in social network and engagement, these changes could also result from several other mechanisms. First, since spatial proximity is a prerequisite for close range interactions, age-structured spatial distribution may account for age-related social patterns (Albery et al., 2022). Individuals who spend relatively more time alone will have fewer opportunities for social engagement, and this may arise from differences in either social or non-social traits (e.g., travelling more slowly, foraging in a different area, or spending more time on the ground). Therefore, it is important to test whether *spatial segregation* could drive social interactions on lower scales. Second, individuals may engage in fewer interactions if they experience avoidance or exclusion by others. Crucially, active behaviors typically viewed as actor-driven, such as lower rates of approaching others, may also stem from exclusion. Therefore, actor-centered measures should be complemented with metrics that focus on the partners. Third, older individuals may be unable, or lack the motivation, to socialize leading to a general disengagement from social interactions across partners in the absence of increasing focus on preferred partners, despite preserved opportunities to do so. Distinguishing between the different hypotheses is a necessary first step in better understanding the drivers and consequences of social ageing. As no behavior in isolation provides necessary support for one or the other mechanism, investigations should aim to identify the most consistent pattern and a set of minimum necessary conditions.

Age-associated changes in a sample population can result from within-individual ageing or from the selective disappearance of individuals at a younger age based on the feature investigated or other correlated traits (Hämäläinen et al., 2014). Selective disappearance effects could be strong enough to mask or bias within-individual trajectories leading to erroneous conclusions about ageing (Hämäläinen et al., 2014). As sociality often influences health and survival (Ostner and Schülke, 2018; Snyder-Mackler et al., 2020), less socially integrated individuals could be more likely to be missing from a cohort, particularly among older individuals, creating an apparent association between age and social traits. In the wild, biases due to selective disappearance are of even greater concern, because predation and fatal accidents are more likely to affect individuals in poorer body condition or more peripheral to the group. Captive and food-provisioned populations, which are less likely subject to selective disappearance have provided compelling evidence for social ageing across (Machanda and Rosati, 2020) and within individuals (Siracusa et al., 2022b) although patterns may be exacerbated by extreme lifespan and comorbidities (e.g., obesity) that are absent in the wild. Longitudinal data can address this issue by partitioning variance that occurs within individuals versus across individuals (van de Pol and Wright, 2009), and thus provide a more accurate picture of ageing than purely cross-sectional (i.e., one observation per subject over a given age span) or mixed-longitudinal (i.e., consisting of repeated observations over a limited age range for each individual) studies. In this context, longitudinal data on wild animal populations are particularly relevant to determine the occurrence, drivers, and consequences of social ageing.

Here, we investigated social ageing in a long-term study population of Assamese macaques (*Macaca assamensis*) living in their natural environment at Phu Khieo Wildlife Sanctuary in Thailand (De Moor et al., 2020). We focused on females, the philopatric sex in macaques, for which longitudinal social data and more precise age estimates were available. In this population, close female-female affiliative relationships provide benefits such as enhanced tolerance at feeding sites and access to spatially more central positions that may be associated with reduced predation risk (Heesen et al., 2015; Ostner and Schülke, 2018). In the wild, females must travel daily with their group and experience multiple energetic challenges throughout the year and throughout their lives (Touitou et al., 2021b, 2021a), which may exacerbate physiological and physical constraints on sociality compared to captive populations. In this context, two competing predictions can be made. If dynamics in the wild parallel findings from captive populations, we predict that females will reduce their active social engagement in favor of increasing social selectivity with age. On the contrary, if social integration is closely linked to survival, individuals will exhibit no signs of social ageing, and patterns at the population level will suggest an increase in social traits due to selective disappearance. Using data on female-female interactions collected over eight years across five social groups, we first aimed to exclude the

possibility that (a) spatial segregation would explain age-related changes of closer range interactions by testing for an increase with age in the time females spent alone. From there on, we tested three hypotheses for social ageing using directed social behaviors to weight the contribution of the partner's and the ageing subject's behavior. If older females are being excluded, we would expect (b) a decrease with age in the frequency of being approached by others, the number of partners grooming the female, and the time spent receiving grooming. Older females may drive age-related social changes either by becoming increasingly selective or by disengaging from social interactions more generally. In both cases, we would first predict (c) females to actively groom a decreasing number of social partners. Increasing or constant time spent grooming with the remaining partners would be consistent with increasing selectivity (figure 1A,B). In case of decreasing time spent engaging, contrasting the slopes for preferred and all partners will tell whether increased selectivity is observed (figure 1C). In the absence of evidence for selectivity, the concomitant decrease in the number of partners and the time spent actively interacting with them would suggest social disengagement, which would be further supported by a decrease in the frequency at which females approached others. For all analyses, we report both mixed-longitudinal and within-individual trends, and (d) discuss evidence for inconsistencies.

Methods

Study site and study subjects

We studied a population of Assamese macaques living in their natural environment at Phu Khieo Wildlife Sanctuary (PKWS, 16°05'-35'N, 101°20'-55'E, >1600 km^2), part of the more than 6500km² Western Isaan Forest Complex in Northeastern Thailand (Touitou et al., 2021b). These Assamese macaques are seasonal breeders living in hill evergreen forests, with a mating season spanning over the dry season from October to February and births spread from March to August with a peak in mid-May (Fürtbauer et al., 2010).

Each study group was composed of adult females, their immature offspring, and several adult and subadult males for a total group size between 28 and 98 macaques, with fluctuations resulting from male immi- and emigration, births, deaths, and group splits. This study focused on adult females, with females considered adult from the mating season of their first conception (usually at 5.5 years of age) (Anzà et al., 2022). Year of birth was either known from witnessed birth or inferred by experienced members of the research team based on morphological comparison with individuals of known age. The age distribution had a median[IQR] of 10[7–16] years and a range of 4 to 30, consistent with the

low survival probability beyond 25 and the maximum documented lifespan in semi-free captive populations of other macaque species (Brent et al., 2017; Johnson and Kapsalis, 1995).

Behavioral data collection

Data were collected on two groups between January 2013–September 2014, and three groups from January 2015–July 2019, October 2019–March 2020, and October 2020–March 2021 (figure S1). Observations were assigned to the mating or birth season of the corresponding year, creating a season-year time unit (e.g., data collected from October 2019 through February 2020 belonged to the season-year 'mating 2019').

During 40min continuous focal animal protocols (Altmann, 1974) we recorded all instances of dyadic grooming interactions between adult females along with the identity of the actor and the receiver. Approaches within 1.5m of another adult female were also recorded, with the identity of the initiator and receiver. Dyadic agonistic interactions (including aggressions or spontaneous submissions) were recorded during focal animal protocols and *ad libitum*. Over the study period, 61 adult females were observed for a total of 13,270 hours (median[IQR] = 216[85–332] hours per female, figure S2). Females were observed up to 14 season-years (10[4–13] season-years per female), for 24[19–32] hours per season-year, and per season-year we observed 39[33–44] females.

In addition, from January 2015 through March 2021 the identity of group members within 5m of the focal individual were recorded instantaneously every 10min during focal animal protocols. A total of 81,969 such instantaneous data points were recorded during 21,722 focal animal protocols (median[IQR] = 5[2–5] scans per focal follow) from 58 females. For the proximity dataset, females were observed 10[6–11] season-years.

Sociality metrics

Grooming out- and instrength, out- and indegree

From the adult female social network with tie weight reflecting the duration of directed grooming interactions in a group-season-year, we determined two dyad level metrics reflecting grooming given to and received from a specific adult female partner and four node level metrics of directed grooming behavior (out- and instrength, out- and indegree (Sosa et al., 2021)) (see also Sosa et al., 2021 for an introduction to social network terminology). Strength and degree are direct sociality measures which have been extensively scrutinized for their link to fitness in primates and other mammals (Ellis et al., 2019; Ostner and Schülke, 2018) and pertain to different social strategies (Schülke et al., 2022).

Grooming given to a partner was determined as the time (sec/hour) grooming a female partner divided by dyadic observation time (i.e., divided by the sum of observation time for each member of the dyad during which the other member of the dyad was also present and adult). Similarly, grooming received from a partner was determined as the time receiving grooming from that partner divided by dyadic observation time. The resulting dyad-level metrics indicate the strength of directed ties for every pair of females in a group. Individual-level grooming outstrength (given) and instrength (received) were determined as the sum of all female dyadic outgoing and ingoing weighted ties, respectively, allowing to compare females according to their overall engagement. We determined outdegree and indegree (figure S3) as the number of unique female partners an individual groomed and was groomed by, irrespective of the duration of the interactions.

Selective approach based on tie strength

To test for increasing selectivity with advancing age, we assessed whether females increasingly approached those partners they shared a stronger tie with. We calculated a dyadic sociality index (DSI) for every pair of females in a group based on the time spent in 1.5m proximity, time spent grooming, the frequency of approach given, and the frequency of grooming given (Silk et al., 2013), irrespective of which partner initiated the interaction. The value for each behavior in a pair was corrected for dyadic observation time and further divided by the average of all dyadic measures in the group for that behavior (cf. equation in supplementary material). For each season-year, the index was calculated based on interactions in all previous season-years, so we refer to it as a cumulated DSI. If females are selective, we expected that greater cumulated DSI would predict longer, or more frequent, interactions directed towards the partner in the next season-year, and if females are increasingly selective this association between past and future interactions to strengthen with age.

Approaching and being approached by other adult females

The number of times a focal female approached or was approached by another adult female into 1.5m was determined per season-year. For one female in one season-year, focal data were collected over only one day. This female-season-year was excluded from the analysis. Females directed approximately 1.0 approaches/hour (median[IQR] = 20[11–35] approaches per season-year of roughly 25h of observations) and received 1.3 approaches/hour (27[18–44] approaches per season-year).

Proportion time alone

For each instantaneous proximity record, we determined whether the focal female was within 5m proximity of at least one other adult female. The one female-season-year excluded from the approaches was also excluded here for the same reason. Out of 81,969 data points, 62,842 were

recorded with no other female in proximity. With a median[IQR] of 168[134–230] data points collected per female-season-year, the proportion of records spent alone was 0.77[0.71–0.83] per female.

Control variables

To control for social status, dominance Elo scores were determined from winner-looser agonistic interactions (Neumann et al., 2011), and female's Elo score at the end of each season-year or on the last day observed were extracted (see supplementary material for details). To account for possible effects of reproductive state, females giving birth in a given birth season were defined as reproductively active during the preceding mating season and the respective birth season (coded as a binary variable with reference set to not reproductively active). About half of the females were reproductively active per season-year (median[IQR] = 0.56[0.45 − 0.67]). Finally, we calculated the number of available partners in each season-year-group as the (number of females in the group − 1, 11[9 − 14]).

Statistical analysis

Response variable and model structures are detailed below. Full model formulae and sample sizes can be found in the supplementary material. Shortened model results for the effect of within-individual age are presented in the main text, while detailed results and mixed-longitudinal model results are provided in tables S1–10.

Grooming outstrength and grooming instrength

The influence of age on outstrength and instrength in the grooming network was modelled with Gaussian error distribution. To improve homogeneity of the distribution of residuals, we applied a square root transformation on the response variables.

Outdegree and indegree

The number of partners an individual was observed grooming and being groomed by, i.e., degree (Sosa et al., 2021), is not adequately modelled with a Poisson or Normal error distribution because it is biased by sampling effort and reaches an upper limit imposed by group size. To overcome this limitation, we modelled degree as a binomial probability to observe a directed tie from any actor towards any receiver over age with binomial error distribution including an offset for the log of dyadic observation time.

Selective approach based on tie strength

We first aimed to investigate selectivity by testing whether cumulated DSI would be associated with how long females groomed each partner in the next season. However, as the number of partners and time spent giving grooming sharply decreased with age (cf. Results), data lacked resolution. Therefore, we used the number of approaches given to each partner, a more frequent behavior even at old ages, as the response. Approach directed towards a given partner was modelled with a negative binomial error distribution including an offset for dyadic observation time in the season-year.

Approaching and being approached by other adult females

The tendency of females to engage in social interactions, irrespective of partner identity, was modelled as the count of approaches towards and by others, respectively, with a negative binomial error distribution including an offset for the log of female's observation time.

Proportion time alone

The influence of age on the proportion of instantaneous data points an individual was observed alone was modelled with a beta error distribution weighted for the number of records during a given female-season-year. To allow convergence, group was included as a fixed and not a random effect.

General statistical considerations

All analyses were conducted with Generalized Linear Mixed Models in R with RStudio (R Core Team, 2021 version 4.0.4; RStudio Team, 2022 version 2022.07.02+576). All models included the covariate female age as the key predictor and we furthermore included fixed effects of Elo score as well as reproductive status and season and their two-way interactions, differentiating females who did or did not conceive, did or did not give birth in each mating or birth season, respectively, to control for their effects. The (number of females in the group − 1) was also included as a fixed effects to account for variation in the availability of partners across season-years. The interaction of actor's age and cumulated DSI was included in the model assessing selective approach. To avoid pseudo-replication, models of grooming outstrength, grooming instrength, approaching others, being approached by others, and time alone included female identity, group, and season-year as random intercept effects. Models on grooming outdegree, grooming indegree, and selective approach, included the identity of the actor, the identity of the receiver, the identity of the dyad, group, and season-year as random intercept effects. Covariates were z-transformed, and factors were dummy coded and centered when included as random slopes. Within and average individual age terms were scaled by mean-centering and then dividing by the standard deviation of raw age to facilitate model convergence and comparisons across models. For all models, we started from a maximal random slopes structure best suited to maintain type 1 error rate at the nominal 5% level (Barr et al., 2013). When model

convergence failed, we inspected the parameters for the correlations among random intercepts and slopes and removed seemingly unidentifiable correlations close to +1 or -1 (Matuschek et al., 2017). Furthermore, we removed random slopes with the lowest estimated variance sequentially until a model converged.

Assessing result robustness to uncertainty about age

Studying wild animal populations implies a degree of uncertainty regarding several individual attributes. As age is central to the present study, we evaluated whether results were robust to possible errors regarding the date of birth assigned to individuals by assigning to each female a symmetric range of possible years around our best estimated year of birth (see supplementary material for details). Results showed that limited uncertainty regarding females' year of birth would not compromise the conclusions of the present study (figure S6).

Investigating selective disappearance and its possible influence on the relationship between age and sociality

All individuals are subject to age-related changes in physiology, cognition, and possibly social behavior. Within-individual ageing represents changes in the response as an individual grows older, whereas between-individual ageing represents the association between age and the response at the level of the sample population under study. In a situation where individuals' death is not random but statistically associated to the response variable (i.e., selective disappearance, with or without causality), a between-individual effect is measured even without within-individual ageing. For example, more social individuals may be better buffered against external or intrinsic sources of mortality (e.g., predation), resulting in the 'selective disappearance' of less social individuals at an earlier age. Within-individual centering is advocated to remove this confound, because it separates the within and between-individual effect of age into two independent variables (van de Pol and Verhulst, 2006; van de Pol and Wright, 2009; Westneat et al., 2020) (see supplementary material for details). Eleven females died during the study (median[IQR] = 21[15–27] years old).

To investigate whether selective disappearance influenced the relationship between age and sociality, we reran all models after applying within-individual centering. To identify the slopes of within and between-individual ageing, a first set of models included within-individual age and average age. A second set of models included the raw age and the average age to assess the significance of the difference between the within and between-individual slopes, indicated by the p-value of the average age term (see supplementary material for details).

Results

(a) Spatial segregation as a possible driver of changes in social interactions with advancing age

Regardless of age, females were typically observed without another adult female within 5m of them. The proportion of time spent alone showed a marginal 3% increase in mixed-longitudinal analyses. This was not consistent within-individual, which we express for a female on average 15 years old and ageing from 11 to 19 over the eight-year study period. The predicted proportion time alone showed a small 8% decrease within-individual, associated with large uncertainty (table 1 and S1, figure 2A,B). This suggests that with advancing age, females did not spend more time alone, spatially segregated without any partner to interact with. This condition being fulfilled, we next investigated whether passive and active social behaviors changed with age.

Table 1. Estimated slopes for the effect of increasing age within and between individuals on the social behavior investigated (see supplementary table S2-10 for full model results). Hypotheses tested are increasing spatial segregation, exclusion by partners, increasing social selectivity, and disengagement.

Hypothesis	Response	Within-individual effect				Between-individual effect				Slope difference	Supported
		$\beta_{within\text{-}age} \pm SE$	CI_{lower}	CI_{upper}	P	$\beta_{average\ age} \pm SE$	CI_{lower}	CI_{upper}	P	$P_{(average - within)}$	
spatial segregation	proportion time alone	-0.291 ±0.187	-0.623	0.049	0.127	0.083 ±0.028	0.023	0.140	0.005	0.072	N
exclusion	being approached	0.317 ±0.092	0.163	0.495	0.003	0.030 ±0.027	-0.019	0.083	0.261	0.013	N
exclusion	grooming instrength	-0.720 ±0.453	-1.623	0.193	-0.592	0.536 ±0.152	0.234	0.861	0.007	0.253	N
exclusion	grooming indegree	-0.661 ±0.232	-1.067	-0.217	0.008	0.144 ±0.060	0.025	0.256	0.006	0.004	Y
disengagement/ selectivity	grooming outdegree	-0.937 ±0.204	-1.349	-0.516	<0.001	-0.311 ±0.050	-0.407	-0.210	<0.001	0.007	Y
disengagement/ selectivity	grooming outstrength	-2.564 ±0.509	-3.590	-1.582	<0.001	-1.162 ±0.197	-1.527	-0.803	<0.001	0.026	Y
increased selectivity	selective approach	-0.130 ±0.147	-0.427	0.172	0.375	-0.085 ±0.037	-0.163	-0.019	0.030	0.786	(N)
disengagement	approaching others	-0.414 ±0.139	-0.647	-0.158	0.004	-0.082 ±0.036	-0.148	-0.019	0.037	0.036	Y

The significance of the difference between within and between-individual age slopes is indicated by the p-value of the estimate of average individual age in a model including both raw and average individual age terms and suggests selective disappearance.

(b) Contribution of social exclusion to patterns of social ageing

The mixed-longitudinal and within-individual analyses revealed that age was associated with a higher tendency to be approached, with a predicted increase of 54% approaches received per hour from 11 to 19 years (table 1 and S1, figure 2C,D). Age did not affect the time females spent receiving grooming from female partners (instrength, figure 2D,E). Finally, the number of partners grooming the subject (indegree) appeared to be relatively constant in the mixed-longitudinal analysis, with females being

groomed by an average of six partners. However, this result was not representative of the clear 43% decrease in indegree within individuals (figure 2E,F). To place this in a socially relevant context, figure 2G,H depicts this probability also as a count of partners (i.e., degree) by multiplying age-specific probabilities for each tie by 12, which is the median female group size in this study. Therefore, at least one aspect of passive sociality, here the number of partners grooming the subject, decreased with advancing age, whereas the patterns across all three passive behaviors investigated provided only mixed evidence for the social exclusion of aging females.
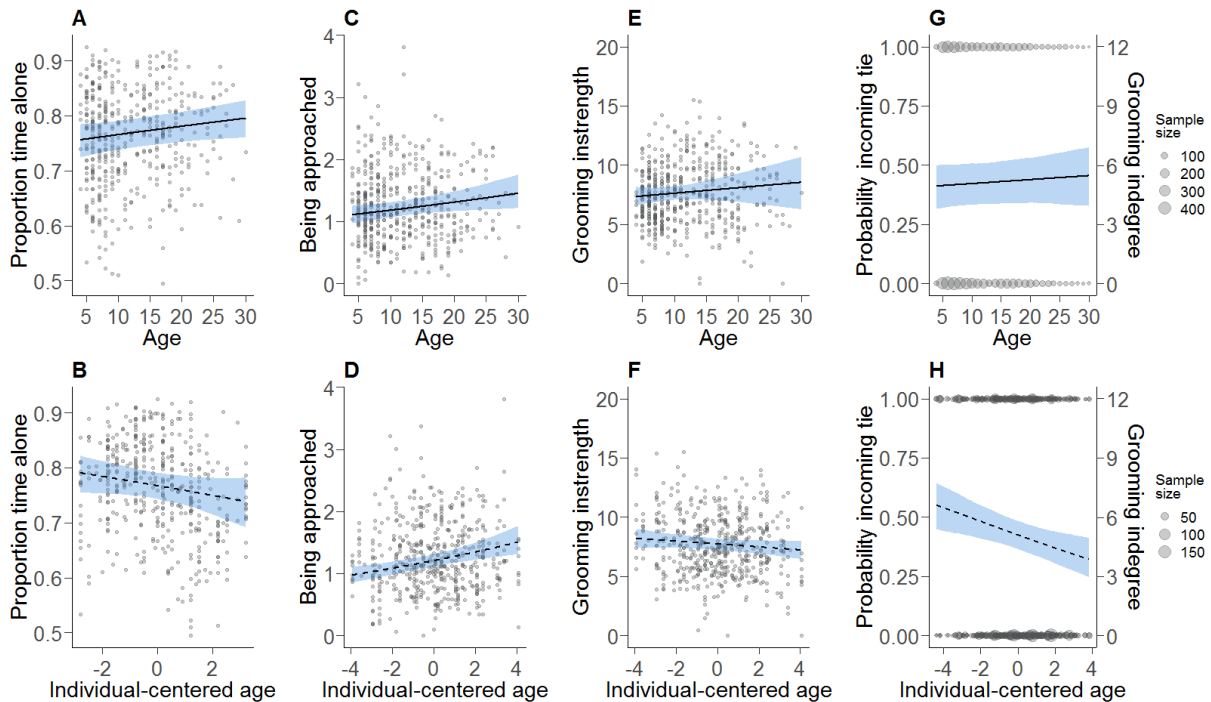
Figure 2. (**A**) Time spent alone slightly increased with age in the mixed-longitudinal analysis (**B**) and did not change within-individual. The possibility that older individuals were being excluded was not supported by (**C,D**) the increasing frequency of being approach, and (**E,F**) the absence of change in grooming received. In mixed-longitudinal analysis, (**G**) the number of partners grooming the subject (indegree) remained relatively unchanged which contrasted with (**H**) a sharp decrease within-individual. Degree is modelled as the probability to observe a directed tie between a female and every other female in her social group (left axis). To facilitate interpretation, this probability is expressed on the right axis as a count of partners for a group size of 12 adult females with equal observation time. Age is expressed in years in the upper row and frequency is given per hour.

(c) Testing increasing selectivity and increasing disengagement with advancing age

To disentangle scenarios of social selectivity, it is necessary to consider the number of partners a female is actively interacting with, the overall engagement across all partners, and interactions

directed to preferred partners (scenarios A-C; figure 1). Older females were less likely to groom other females, leading to a marked 61% decrease in the probability to observe a specific outgoing tie for a female ageing from 11 to 19 years of age (table 1-S1). Grooming outstrength, a measure of total engagement in grooming given, was also negatively correlated with age, showing a reduction by 48% (figure 3C,D). These patterns were consistent between mixed-longitudinal and within-individual analyses and indicated that network narrowing, i.e., the reduction in grooming partners, was not compensated by increased investment in remaining partners, which is incompatible with scenario A of selectivity (figure 1).

We modelled the frequency at which a female approached each partner in a season-year as a function of her age and cumulated previous DSI with the partner. In the mixed-longitudinal model, the slope for age was negative, the slope for cumulated previous DSI positive, and the interaction of the two not significant (table S1). Therefore, females were selective as they approached those partners more with whom they had shared a stronger tie in the past (figure G), an effect that was not moderated by age. The model differentiating between within- and between-individual effect corroborated these results; previous relationship strength was a positive predictor of approaching a partner that was not affected by age changes within the individual (table S8). In summary, females exhibited a decreasing frequency of approaches towards partners, even those with whom they had a higher cumulative DSI. Despite this decrease, they maintained a selective inclination towards stronger ties, thereby refuting scenario B in favor of scenario C. We note that effects of cumulative DSI were quite small and conclude that these time series analyses provided some evidence for relatively constant, but not increasing, selectivity across the lifespan.

These findings indicate that the decrease in both the number of partners groomed and the time spent grooming did not align with a concurrent tendency to focus on a few specific partners. Instead, it appeared that females actively withdrew from social interactions. This hypothesis was further supported by the net reduction in the frequency with which females approached others, irrespective of the partner's identity (table 1-S1). Data showed that a female on average 15 years old would have decreased approaches towards others from 1 to 0.56 per hour over eight years (figure 3E,F).
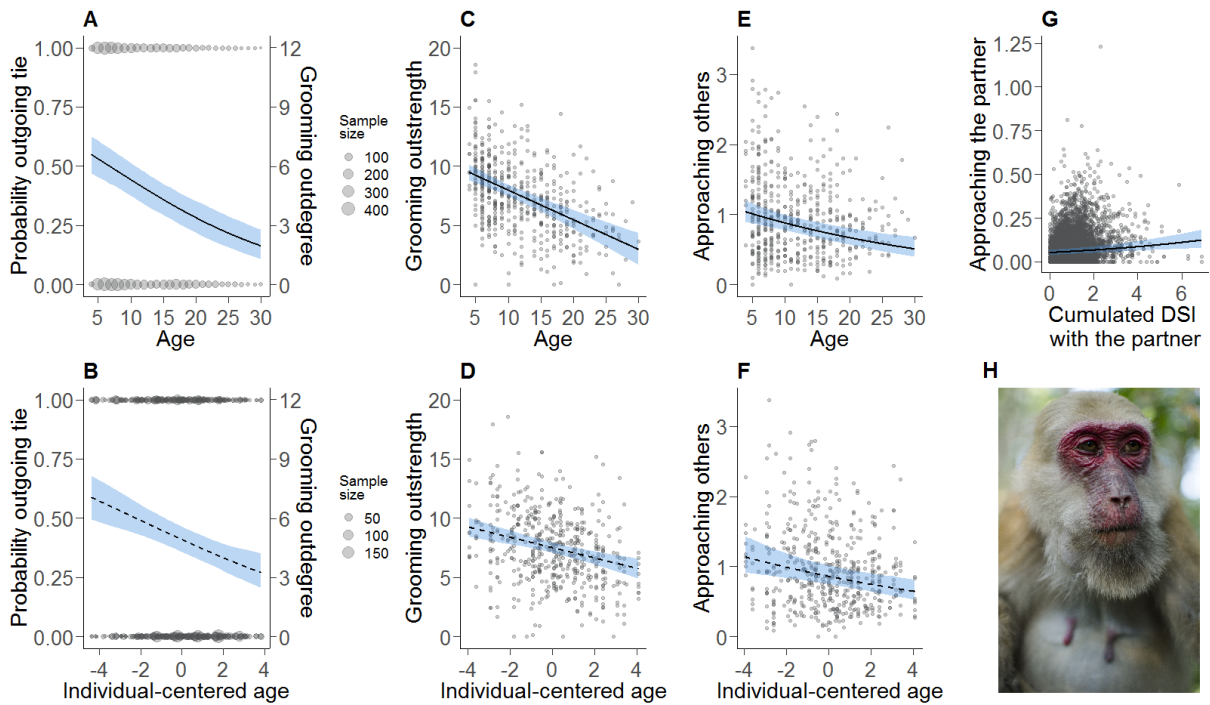
Figure 3. Age was associated with (**A,B**) a reduction in the number of partners females groomed (outdegree). Degree is modelled as the probability to observe a directed tie between a female and every other female in her social group (left axis). To facilitate interpretation, this probability is expressed on the right axis as a count of partners for a group size of 12 adult females with equal observation time. (**C,D**) Grooming outstrength, i.e., total grooming given across all partners, decreased with age. (**E,F**) The frequency with which females approached others decreased with age. (**G**) The frequency of approaches directed at specific partners increased with increasing cumulated dyadic sociality index estimated based on past interactions. (**H**) Nineteen-year-old female Assamese macaque from the study population. Age is expressed in years in the upper row and frequencies are given per hour.

(d) Comparison of within-individual and between-individual effects

Most conclusions drawn from mixed-longitudinal analyses were confirmed at the individual level. Yet, mixed-longitudinal effects tended to underestimate age-related changes in social behaviour, and in some cases, diverged from within-individual dynamics. These inconsistencies are better understood when comparing within-individual and between-individual effects. For grooming outdegree, grooming outstrength, and approaching others, both within- and between-individual slopes were significant and negative, but the between-individual effect sizes were much smaller than the within-individual effects (table 1). More surprisingly, within-individual ageing was associated with a decline in the number of partners grooming the subject, in contrast to a tendency to increase across individuals. This suggests that the between-individual effect masked the decrease experienced by individuals with age when the

pattern was investigated mixed-longitudinally without differentiating within and between-individual effects. These results together suggest that individuals with fewer grooming partners, grooming and approaching others less, i.e., less social, are underrepresented at older ages. We note, however, that the significant difference in the slope of within and between-individual effects on the frequency of being approached by others would suggest the opposite, namely that more social individuals died at an earlier age (although the between-individual effect for this variable was far from significant). Finally, within- and between-individual slopes did not differ for selective approach, instrength, and time spent alone, although here again between effects were small compared to within-individual changes.

Discussion

This study provides evidence for social ageing among females of a wild population of Assamese macaques. By investigating changes in several social behaviors with age, we tested four hypotheses on drivers of social ageing. With advancing age, females did not spend more time alone isolated from others, providing no support for increasing spatial segregation with age. Yet, as females aged, they approached others less frequently, groomed fewer partners, and spent less time grooming others. Females were socially selective by approaching more often those partners they shared a stronger tie with, and this tendency was maintained, but not increasingly expressed, into old age. Finally, females were not less frequently approached or groomed by others, but received grooming from increasingly fewer partners as they aged, consistent with some aspects of social exclusion. Together, these results provide evidence for the contribution of both active and passive processes in the reduction of a female's social network and engagement with advancing age. Furthermore, age effects were weaker between than within individuals, and consequently, age-related changes identified by mixed-longitudinal analyses did not always match true ageing effects. Here, we first discuss what could explain such active and passive social changes, then what these results bring to comparative ageing in light of the social selectivity hypothesis, before ending with a consideration of the implications of studying ageing longitudinally.

Changes experienced with advancing age are not limited to the social domains and most evidence in wildlife shows alterations in body condition and reproductive function (Gaillard and Lemaître, 2020; Siracusa et al., 2022a). For example, ageing females may modify their activity budget, reducing social time to free time for resting and feeding (Nakamichi, 1991; Pavelka, 1990; Veenema et al., 1997). An increase in time spent resting could explain a decrease in time spent actively grooming others and in the number of partners groomed but would not be sufficient to explain a decrease in the number of partners grooming the ageing subject as recipients of grooming are resting. Additionally, changes in the activity budget may be reflected in different spatial distributions (Emery Thompson et al., 2020b).

Although ageing was not associated with increasing time spent alone, older females may remain within 5m proximity to others while engaging in other activities, like feeding, without initiating grooming interactions. Indeed, age was associated with a tendency to approach others into 1.5m less often, suggesting that females were less motivated to interact with those around them or that they found themselves close to others when the context was not favorable to grooming.

Active social behavior may also decrease if older individuals experience a decline in the ability to digest food and extract energy due to reduced gut integrity, disruption of gut microbiome communities, or infection with macroparasites (e.g., helminths) (Mitchell et al., 2017; Sadoughi et al., 2022a). Such gastrointestinal disorders may further influence passive social behavior if group members detect signs of infections (e.g., lethargy or modified fecal odors) and avoid infected conspecifics, as shown in mandrills and Barbary macaques (Müller-Klein et al., 2019; Poirotte et al., 2017). In this population of female Assamese macaques, age is associated with an increased abundance in the gut of several pro-inflammatory bacterial taxa and the oldest females have a lower stability of gut bacterial composition (Sadoughi et al., 2022b), which could impact gut health and contribute to both the active and passive decrease in grooming partners. The linear relationships between age and the social traits observed here do not exclude the possibility of an additional age-independent deterioration among the oldest which could more closely match physiological decline. For example, body mass decreases linearly with age to a point where it drops more rapidly before death in ungulates and yellow-bellied marmots (Kroeger et al., 2021; Nussey et al., 2011). We did not test for non-linear effects and a larger sample size of subjects at old ages is needed to test whether non-human primates experience accelerated social decline in late life.

Social disengagement could also arise from external, rather than internal frailty-related, constraints, if ageing females find themselves in increasingly unfavorable social environments. Non-human primates often show a preference to interact with close kin (De Moor et al., 2020; Siracusa et al., 2022b; Veenema et al., 1997) or individuals of similar age (Rosati et al., 2020; Veenema et al., 1997). The availability of such partners will depend on stochastic demographic events like group splits or the death of same-aged individuals which then constrains the ability to focus on preferred partners. However, current evidence does not suggest that kin availability decreases with age in cercopithecines (Ellis et al., 2022; Silk et al., 2006), and we did not examine the influence of the death of a close partner because, with the exception of spousal death in humans (Wrzus et al., 2013), affiliative networks in humans (Cornwell et al., 2021), non-human primates (Fedurek et al., 2022; Siracusa et al., 2022b), and ungulates (Albery et al., 2022) appear to be resilient to partner loss. In summary, investigations of within-individual changes in non-social behavior and health appear as the most fruitful follow-up to pinpoint the causes for active and passive social ageing in this population.

Although frailty and declining motivation may contribute to decreasing social engagement with age, prevailing socioemotional (SES) theories of ageing tend to emphasize increasing selectivity in partner choice as a driver of age-related network narrowing (Antonucci et al., 2014; Charles and Carstensen, 2010; Cornwell et al., 2021; Müller and Ellwardt, 2022). According to SES theories, among humans changes in network composition and size result from greater priority given to maintaining emotionally positive relationships over acquiring new information, leading subject to discard less valued relationships. Evidence for a greater investment in two-sided rather than one-sided grooming partners (Rosati et al., 2020), reduced interest in non-social compared to social information (Almeling et al., 2016), and an increase in the proportion of kin in the network in non-human primates suggest that preferential interest may shift with age in other species too. How could such a shift account for the reduction in social engagement and network size with age in several species (Albery et al., 2022; Almeling et al., 2016; Rathke and Fischer, 2021; Schino and Pinzaglia, 2018) remained unclear, especially because similar social patterns are expected irrespective of whether social selectivity or general decline is assumed (figure 1). We have proposed several scenarios of selectivity, with two (A and B) considering selectivity as a driver of network narrowing and reduction in overall time spent social. Contributing to answering this question, our findings corroborate the reduction in network size and social engagement with age, and further provide evidence that these changes occur within individuals, emphasizing the social dimension of ageing in wild populations. However, selectivity did not account for this decline, which echoes previous evidence of concomitant decrease in grooming given and preserved selective interest in cues from preferred partners in another primate (Almeling et al., 2016), and contrasts with patterns more closely related to scenario A (Rosati et al., 2020; Siracusa et al., 2022a). In the latter two cases, overall time spent social did not decrease with age. However, this would likely not explain the differences between findings, as the scenarios proposed in figure 1 decouple overall time spent social from the expression of selectivity. Taken together, these results suggest that selectivity and engagement may be two social dimensions that remain independent into old age at a time when other constraints lead the ageing subject to disengage from most social interactions.

One of the aims of the social selectivity hypothesis of ageing was to suggest a counter narrative to previous theories considering social disengagement as a detrimental process. Older individuals may not experience detrimental consequences of social disengagement if partners continue investing in them. In Assamese macaques, remaining partners appeared to compensate for the decrease in the number of partners grooming the subject, resulting in mostly constant grooming received. The overall time spent grooming from combined active and passive processes nevertheless decreased with age (Figure S6). Although decreasing social engagement with age may be described with loaded terms such

as "decline" or "disengagement", the consequences of such disengagement may be beneficial, which has not been conclusively tested yet. There is repeated evidence that the effect of social bonds and integration on physiology and health is modulated by individual dominance status (Brent et al., 2011), reproductive state (Crockford et al., 2008), sex or dominance status of the social partner (Fürtbauer et al., 2014; Sapolsky, 1992b), or by context-dependencies, such as timing to mating season or group-level social stability (Sapolsky, 2005). Similarly, the social or emotional benefits derived from social interactions could differ across the lifespan, resulting in several age-specific optima. This hypothesis has only rarely been directly addressed, and results are inconclusive (Brent et al., 2017; Holt-Lunstad et al., 2015; Yang et al., 2016). Describing how social bond strength, social status, and broader social integration vary for specific age-classes will be a necessary first step requiring large enough cohorts at different ages. It is further important to formulate hypotheses regarding which social system or environmental conditions should favor increasing, or conversely decreasing, benefits of sociality with age.

Critical to the study of ageing in wild populations, the comparison of mixed-longitudinal and within-individual effects of age revealed that changes within-individual were partially confounded by demographic processes at the population level. For example, the decrease in the number of partners grooming the subjects was only discovered using a longitudinal analysis. The difference between the within-individual (i.e., senescence) and between-individual (i.e., demographic) effects of age on social traits would suggest selective disappearance of females that groomed and were groomed by fewer grooming partners and groomed overall less. In other free-ranging populations selective disappearance was demonstrated for lighter individuals in ungulates (Nussey et al., 2011) and mouse lemurs (Hämäläinen et al., 2014), poorer breeders in great tits (Bouwhuis et al., 2009), and subordinates in meerkats (Cram et al., 2018), but not in rhesus macaques (Siracusa et al., 2022b) and wolves (MacNulty et al., 2009). It has to be noted though that in the Assamese macaques between-individual effects were generally small perhaps because sampling was limited across the within-individual age range (Westneat et al., 2020). The oldest subjects were already mid-aged adults at the beginning of the study, which implies that age at the start and at the end of the study are not independent. A more direct test of selective disappearance is achieved if all individuals enter the study at the same age and are followed until death (Nussey et al., 2008). More confidence can be placed into the estimates of the within-individual slopes which are robust to model choices (Westneat et al., 2020).

What could explain the disappearance at younger ages of females with fewer grooming partners, approaching others less, but being approached more? Social integration has been positively linked to survival in mammals (Kappeler et al., 2015; Silk et al., 2010; Snyder-Mackler et al., 2020), in part mediated by enhanced access to food resources (Kajokaite et al., 2022), more central positions within

groups associated with lower predation-related mortality (Cram et al., 2018; Hrdy and Hrdy, 1976; van Noordwijk and van Schaik, 1987), resistance to disease (Sadoughi et al., 2022a), and buffering against adverse social and abiotic environments (Archie et al., 2014; Campos et al., 2021; Young et al., 2014). In this population, females mitigate intra-group competition by distancing themselves when feeding, which may come at the expense of an increased predation risk (Heesen et al., 2015). However, time spent alone only increased slightly across individuals with advancing age, suggesting that those more frequently observed alone were also on average older, inconsistent with increased mortality from predation at the periphery. Females also navigate feeding competition by preferentially attending food patches with females with whom they frequently groom (Heesen et al., 2014), which could lead to sociality-dependent energy intake and survival of those with better body condition (Hämäläinen et al., 2014), whereas frequency of being approached could increase if females are more frequently displaced during those feeding bouts. This is entirely speculative, and we would therefore predict the value of these social bonds to be especially high during gestation and late lactation when females increase feeding to meet their energetic requirements (Touitou et al., 2021a), which could be tested by assessing the relationship between social integration and timing of death in the population.

The possible coexistence of senescence and selective disappearance in shaping age-sociality dynamics is critical for interpreting the results of previous mixed-longitudinal studies. Active engagement in social interactions, measured either as grooming given or a combination of grooming and approaching others, was found to decrease [15,8,10–12,17,14,females: 13 and 82] or remain stable [male chimpanzees: 13,16] in several non-human primates with age. Passive engagement was found to increase [one of two social groups: 10, males: 82], decrease [12,17,females: 82,males: 13,one of two social groups: 10], or stay stable [15,16,females: 13]. Finally, studies reporting undirected measures of social engagement found a decrease (Archie et al., 2014; Nakamichi, 1991; Veenema et al., 1997) (or a decreasing trend (Silk, 1994)) or no change (Borries and Koenig, 2008; Pavelka, 1990; van Noordwijk and van Schaik, 1987) with age. Combining all metrics (and counting sexes from the same study separately), 12 out of 17 studies report at least one negative relationship between social engagement and age. Under the (extreme) assumption of no social senescence, the negative correlation between age and social engagement in four wild and eight captive studies would be caused by the selective disappearance of highly socially engaged individuals. Alternatively, assuming some degree of senescence, the absence of a relationship between age and sociality in three wild and two captive populations could have arisen from the selective disappearance of poorly connected individuals. Although speculative, it seems more plausible that unaccounted selective disappearance contributes to discrepancies between studies by masking social senescence.

In conclusion, this study highlights that social ageing occurs in wild primates and, in conjunction with demographic effects, contributes to age-related variation in social behavior. As females aged, they engaged less frequently in social interactions which led to a narrowing of their social network despite evidence for selectivity in partner choice. Possibly because of such disengagement, fewer partners interacted with females as they grew older. This effect was partially confounded by demographic trends, compatible with selective disappearance, further highlighting the need to account for demographic effects, a critical point in both animal and human biogerontology research (Bouwhuis et al., 2009; Cornwell et al., 2021; Lang et al., 1998). Complete life-course trajectories are almost impossible to collect in humans, and mixed-longitudinal studies are biased by selective mortality and sensitive to self-perception and memory recollection biases when surveys are used (Lang et al., 1998; Müller and Ellwardt, 2022). In this context, longitudinal data collected through systematic direct observation of animal populations represent a valuable contribution to social ageing research.

Supplementary material

Supplementary methods

Cumulated dyadic sociality index

A dyadic sociality index (Silk et al., 2013) was calculated for every pair of females in a group in each season-year based on the time spent in 1.5m proximity, time spent grooming, the frequency of

approach given, and the frequency of grooming given, irrespective of which partner initiated the interaction, across all previous season-years.

$$cumulated\ DSI_{xy} = \frac{\sum_{i=1}^{d} \frac{f_{ixy}}{\bar{f}_{iz}}}{d}$$

with d being the number of behaviors contributing to the index, here four, f_{ixy} being the rate of behavior i for dyad xy (i.e., count or time spent interacting divided by dyadic observation time), and $\bar{f}_{iz}$ being the average rate for the behavior i across all pairs xy from group z.

Control variables

Dominance Elo scores

Based on the direction of submission and aggression recorded during focal follows and *ad libitum*, we determined the winner of each dyadic female-female conflict (including spontaneous submission, Ostner et al., 2008) and computed group-specific Elo scores with the package Elo_rating version 0.46.11 (functions elo_seq and elo_plot with k = 100 and a starting value of 1,000) (Neumann et al., 2011). Undecided conflicts (8% of records) were counted as half a win for each participant following the package's default setting. Female's Elo score at the end of a season (30th of September for the previous birth and 1st of March for the previous mating season) or on the last day observed (four females who died or disappeared during a season) were extracted. The correlation between female age and Elo score was low (Pearson's rho = 0.24; Kendall's tau-b = 0.13; n = 517, p < 0.001, package stats version 4.0.4 (R Core Team, 2021), figure S4).

Reproductive status

Macaques do not exhibit menopause, but may experience extended interbirth intervals with advancing age (Nakamichi, 1991; van Noordwijk and van Schaik, 1987). If reproductive status influences sociality, the effect of age on sociality may be partially mediated by or confounded with reproductive status (Thompson González et al., 2021). To account for possible effects of reproductive states, females giving birth were defined as reproductively active in the given birth and preceding mating season (coded as a binary variable with reference level set to not reproductively active). About half of the females were reproductively active per season-year (median[Q1–Q3] = 0.56[0.45 − 0.67]).

Statistical analysis

The package *lme4* version 1.1-30 (Bates et al., 2015) was used for models with an error distribution being Gaussian (function lmer), binomial (function glmer, family argument set to binomial), or negative

binomial (function glmer.nb). Beta models were fitted with the package *glmmTMB* version 1.1.4 (Brooks et al., 2017) (function glmmTMB). We fitted Gaussian models with identity link, binomial and beta model with a logit link, and negative binomial models with a log link function (McCullagh and Nelder, 1989). P-values on individual terms in Gaussian models were obtained using the Satterthwaite approximation implemented in the package *lmerTest* version 3.1-3 (Kuznetsova et al., 2017), and for other models with the function drop1. The 95% confidence intervals of model estimates were determined by means parametric bootstrapping (N = 1,000 bootstraps; package *glmmTMB* function simulate; package *lme4* function bootMer).

Assessing models for issues or violations of assumptions

There were no issues with or violations of assumptions in any of the models. All models were of good stability as assessed by excluding levels of random factors one at a time and comparing the estimates of models fitted to the derived subsets with those derived for the full dataset. Furthermore, in none of the negative binomial and beta models the response variable was overdispersed given the model (dispersion parameter: binomial models: grooming outdegree = 0.79; grooming indegree = 0.77; negative binomial models: approaches towards others = 0.94; approaches by others = 0.99; beta models; time alone = 1.12, selective approach = 0.90). None of the Gaussian models revealed a deviation from the assumptions of normally distributed and homogeneous residuals (packages *performance* version 0.9.2 function check_model, and DHARMA version 0.4.5 (Hartig, 2022; Lüdecke et al., 2021)), and collinearity also was no issue in any of the models (vif function in package *car* version 3.1-0 (Fox and Weisberg, 2018), max VIF = 2.28).

Model sample sizes

Model	No. females	No. female-season-years	No. dyads (when applicable)	No. social groups
Grooming outstrength	61	518	-	5
Grooming instrength	61	518	-	5
Grooming outdegree	61	7004	539	5
Grooming indegree	61	7004	539	5
Selective approach	55	5926	470	5
Approaching others	61	517	-	5
Being approach by others	61	517	-	5
Proportion time alone	58	451	-	4

Model pseudocode formulae

The pseudocodes below follow the syntax of the package *lme4* (Bates et al., 2015). For clarity, A * B means the two main effects and their interactions, the character| stands in front of the random effects factor, and || means that correlation between random slopes and the random intercept were excluded within a given random effects factor. The model formulae presented include the raw age term used in mixed-longitudinal analyses, which was replaced by a within-individual centered age term and a between-individual age term in longitudinal analyses.

Grooming outstrength:

lme4::lmer(sqrt(outstrength) ~ age actor + Elo score actor + reproductive state actor * season + nfemale +

 (1 + age actor + Elo score actor + reproductive state actor + season + nfemale || actor) +

 (1 + age actor + Elo score actor + reproductive state actor * season || group) +

 (1 + age actor + Elo score actor + reproductive state actor || season_year),

 REML = FALSE,

 control = lmerControl(optimizer="bobyqa", optCtrl = list(maxfun=100000)))

Grooming instrength:

lme4::lmer(sqrt(instrength) ~ age receiver + Elo score receiver + reproductive state receiver * season +nfemale+

 (1 + age receiver + Elo score receiver + reproductive state receiver * season + nfemale |receiver) +

 (1 + age receiver + Elo score receiver + reproductive state receiver * season |group) +

 (1 + age receiver + Elo score receiver + reproductive state receiver |season_year),

 REML = FALSE,

 control = lmerControl(optimizer="bobyqa", optCtrl = list(maxfun=100000)))

Grooming outdegree:

lme4::glmer(degree ~ age actor + Elo score actor + reproductive state actor * season + nfemale +

 offset(log(dyads_obs_time/3600)) +

 (1 + age actor + Elo score actor + reproductive state actor * season + nfemale || actor) +

 (1 + age actor + Elo score actor + reproductive state actor * season || group) +

 (1 + age actor + Elo score actor + reproductive state actor * season || dyad) +

 (1 + age actor + Elo score actor + reproductive state actor * season + nfemale || receiver) +

 (1 + age actor + Elo score actor + reproductive state actor|| season_year),

family = binomial,

control = glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun=100000000)))

Grooming indegree:

lme4::glmer(degree ~ age receiver + Elo score receiver + reproductive state receiver * season + nfemale +

offset(log(dyads_obs_time/3600)) +

(1 + age receiver + Elo score receiver + reproductive state receiver * season + nfemale || receiver) +

(1 age receiver + Elo score receiver + reproductive state receiver * season || group) +

(1 + age receiver + Elo score receiver + reproductive state receiver * season || dyad) +

(1 + age receiver + Elo score receiver + reproductive state receiver * season + nfemale | actor) +

(1 + age receiver + Elo score receiver + reproductive state receiver || season_year),

family = binomial,

control = glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun=100000000)))

Selective approach:

glmmTMB::glmmTMB(approach towards partner ~ age actor * cumuDSI previous season + Elo score actor +
reproductive state actor * season + nfemale +

offset(log(dyads_obs_time/3600) +

(1 + age actor + cumuDSI previous season + Elo score actor + reproductive state actor + season + nfemale
+ reproductive state actor + season || actor) +

(1 + age actor + cumuDSI previous season + Elo score actor + reproductive state actor + season + nfemale
|| receiver) +

(1 + age actor + cumuDSI previous season + Elo score actor + reproductive state actor + season || dyad)
+

(1 + age actor + cumuDSI previous season + Elo score actor + reproductive state actor + season || group)
+

(1 + age actor + cumuDSI previous season + Elo score actor + reproductive state actor || season_year),

family = nbinom2(link = "log"))

Approaching others:

lme4::glmer.nb(Approaching others ~ age + season * reproductive state + Elo score + nfemale +

offset(log(obs_time/3600)) +

(1 + age + season + reproductive state + Elo score + nfemale | female) +

(1 + age + season * reproductive state + Elo score || group) +

    (1 + age + reproductive state + Elo score | season_year),

    control = glmerControl(optCtrl = list(maxfun=100000)))

Being approached by others:

lme4::glmer.nb(Being approached by others ~ age + season * reproductive state + Elo score + nfemale +

    offset(log(obs_time/3600)) +

    (1 + age + season + reproductive state + Elo score + nfemale | female) +

    (1 + age + season * reproductive state + Elo score || group) +

    (1 + age + reproductive state + Elo score | season_year),

    control = glmerControl(optCtrl = list(maxfun=100000)))

Proportion time alone:

glmmTMB::glmmTMB(Proportion time alone ~ age + season * reproductive state + Elo score + group +female +

    (1 + age + Elo score + reproductive state * season + nfemale || female) +

    (1 + age + Elo score + group.ms2 + group.mst + group.sst + reproductive state || season_year),

    family = beta_family,

    weights = (data$weight/sum(data$weight))*nrow(data),

    control = glmmTMBControl(optimizer = "nlminb", optCtrl = list(iter.max=10000, eval.max=10000)))

The weighting term was defined such that $weight = \frac{x}{X} \times n$ with x total number of records during a given female-season-year, X the sum of x across all female-season-years, and n total sample size.

Assessing result robustness to uncertainty about age

Studying wild animal populations implies a degree of uncertainty regarding several individual attributes. As age is central to the present study, we tested whether results were robust to possible error regarding the date of birth assigned to individuals. We assigned to each female a symmetric range of possible years around our best estimated year of birth. Among the 61 females, 12 had an uncertainty of several years, 10 had uncertainty of one year, and 39 had an age known within a few days or weeks. For each model, year of birth was randomly sampled from a normal distribution with a mean set to the best estimated year and a standard deviation of $sd = \frac{max-min}{4}$. The procedure was repeated 1,000 times and the respective full model was fitted to each data set obtained. The distribution of the estimated coefficients for the slope of age was inspected for evidence of large variability. Results

showed that limited uncertainty regarding females' year of birth would not compromise the conclusions of the present study (figure S6).

Estimating within and between–individual ageing

All individuals are subject to age-related changes in physiology, cognition, and possibly social behavior. In standard linear mixed models, the influence of age (expressed as a fixed effect) on the response results from a combination of within and between-individual processes. Within-individual ageing represents changes in the response as an individual grows older, whereas between-individual ageing represents the association between age and the response at the level of the sample population under study. In a situation where individuals' death is not random but statistically associated to the response variable (i.e., selective disappearance, with or without causality), a between-individual effect is measured even without within-individual ageing. For example, more social individuals may be better buffered against external or intrinsic sources of mortality (e.g., predation), resulting in the 'selective disappearance' of less social individuals at an earlier age. Within-individual centering is advocated to remove this confound, because it separates the within and between-individual effect of age into two independent variables (van de Pol and Verhulst, 2006; van de Pol and Wright, 2009; Westneat et al., 2020).

Within-individual age centering involves subtracting the mean age at which the individual was observed from the age associated to each data point. Equation (1) including a fixed effect for age turns into (2).

$$y_{ij} = \beta_0 + \beta_1 age_{ij} + u_{0j} + e_{0ij} \tag{1}$$

with age_{ij} being the age at measurement i for individual j, a population intercept β_0, the slope for age β_1, an individual random intercept u_{0j} and residual error e_{0ij}.

$$y_{ij} = \beta_0 + \beta_\omega(age_{ij} - \overline{age}_j) + \beta_B \ \overline{age}_j + u_{0j} + e_{0ij} \tag{2}$$

with age_j being the mean age for individual j, β_ω being the within-individual effect, and β_B being the between–individual effect of age on y.

However, this procedure is not a one fits all solution (Fay et al., 2022; van de Pol and Wright, 2009; Westneat et al., 2020). First, within and between-individual estimates are only accurate if the (unknown) underlying biological process actually matches the assumed mathematical relation (Westneat et al., 2020). Second, when the direction of the two slopes differs, the between-individual estimate is biased towards the within-individual estimate (Westneat et al., 2020). Finally, it has already been shown that the accuracy of β_B diminishes when within-individual variance is high (van de Pol and

Verhulst, 2006), but it remains unclear how many within-individual measurements are needed to accurately estimate β_ω. In this study, individuals were observed on average over 10 season-years. Whether or not this allows to effectively partition the effects of age is unknown given the complexity associated with any natural animal system (cf. figure S7, which shows that in the present case the models are in good agreement with the observed data, and therefore capture the observed behaviors well). Therefore, we chose to present results in the main text based on the pooled effect of age (equation 1). To investigate the potential mismatch between within and between-individual ageing effects, we also report results using within-individual centering (equation 2).

Whenever the two effects (within- and between-individual age) appear to act in opposite direction, or in the same direction with fairly different magnitude, it suggests that selective disappearance of highly or poorly social individuals contributes to the age-associated social changes observed. Testing for a significant difference between the slopes is achieved by modifying equation (2) into

$$y_{ij} = \beta_0 + \beta_\omega age_{ij} + (\beta_B - \beta_\omega)\ \overline{age}_j + u_{0j} + e_{0ij} \qquad (3)$$

with the slope associated to the between-individual effect $\overline{age}_j$ now expressing the difference between the slopes of the within and between-individual effect in (2) (equation 3).

Supplementary figures
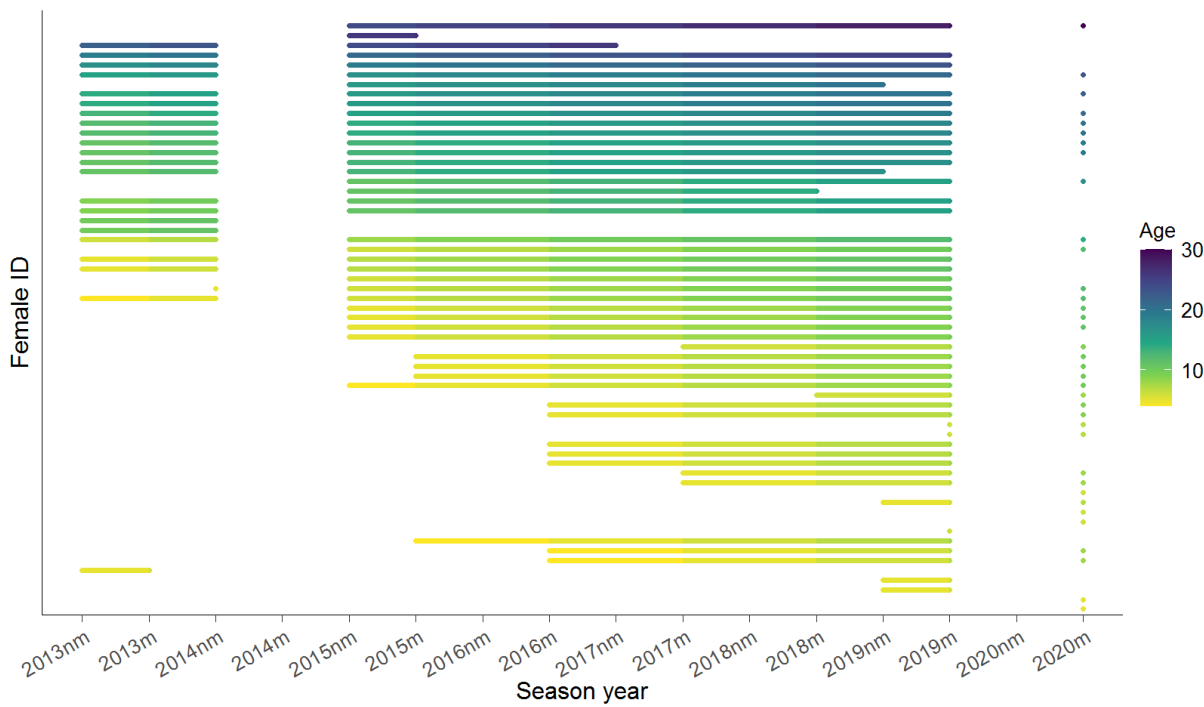
Figure S1. Season-years for which the study females were observed, with continuous sampling represented by lines connecting observations. Age is displayed with a color gradient, and females are ordered by increasing mean age on the y-axis.
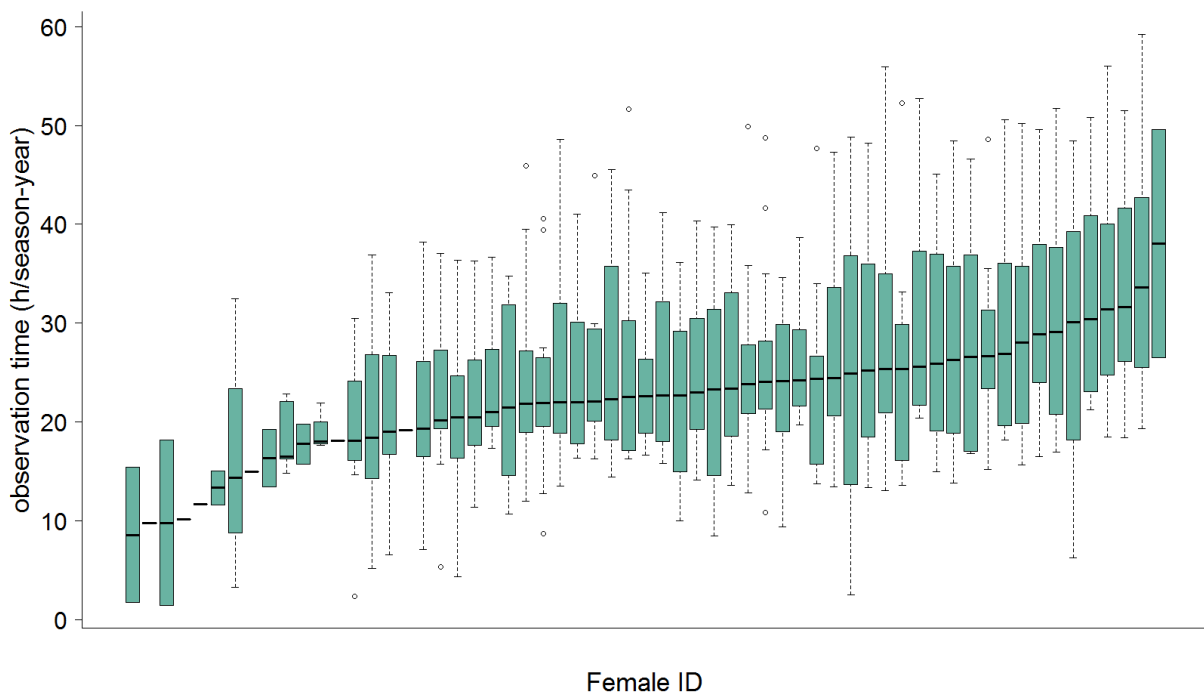
Figure S2. Hours of focal observation time per female per season-year. Females are ordered on the x-axis by ascending median focal observation time. Boxes represent the interquartile range (IQ), which contains the middle 50% of the records. Vertical lines extend from the upper and lower edges of the

box to the highest and lowest values which are no greater than 1.5 times the IQ range, and a line across the box indicates the median. Circles represent outliers.
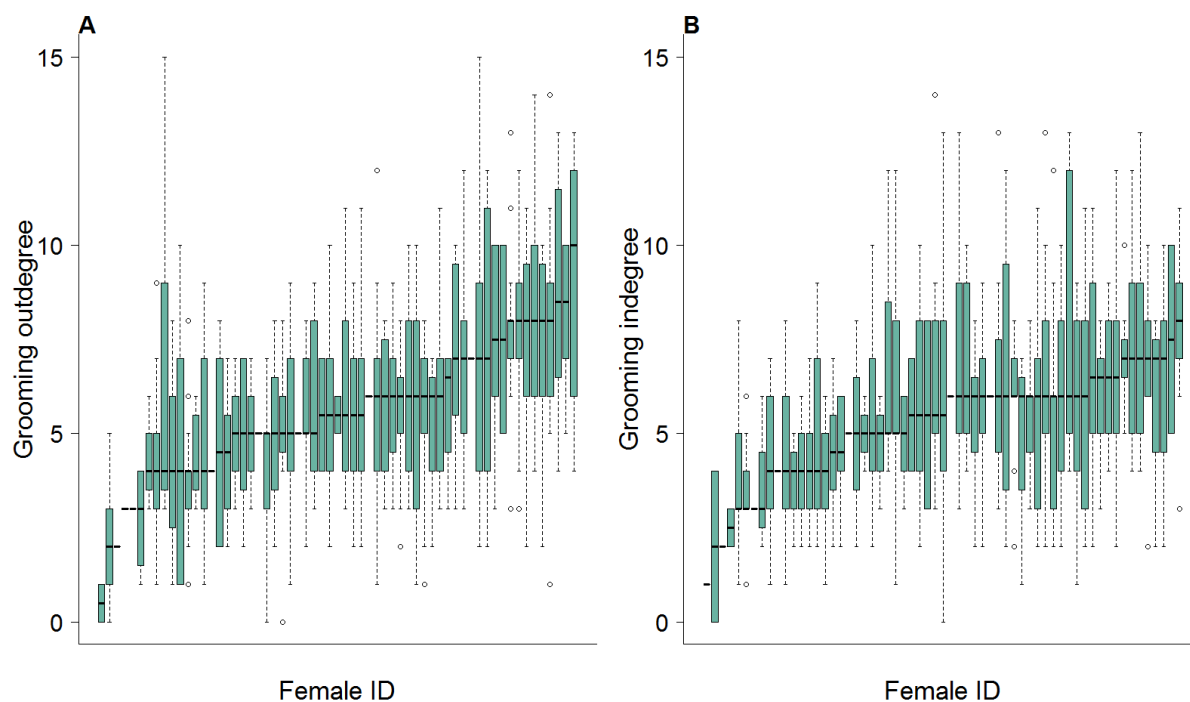
Figure S3. Number of unique partners a female (**A**) groomed (outdegree) and (**B**) was groomed by (indegree). Observations correspond to a count over a season-year. Females are ordered on the x-axis by ascending median of the response. Boxes represent the interquartile range (IQ), which contains the middle 50% of the records. Vertical lines extend from the upper and lower edges of the box to the highest and lowest values which are no greater than 1.5 times the IQ range, and a line across the box indicates the median. Circles represent outliers.
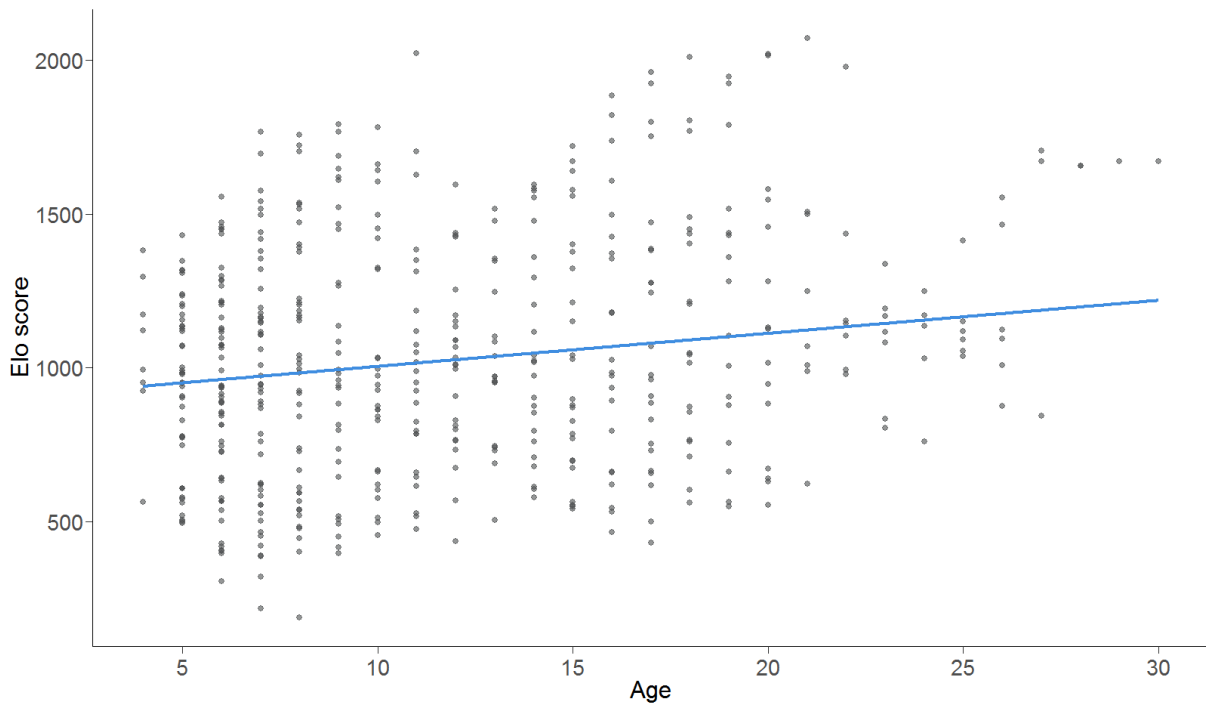
Figure S4. Estimated relationship between age and Elo score obtained from a linear mixed model with Gaussian error distribution including female identity, group, and season-year to account for non-independence among data. Age is expressed in years.
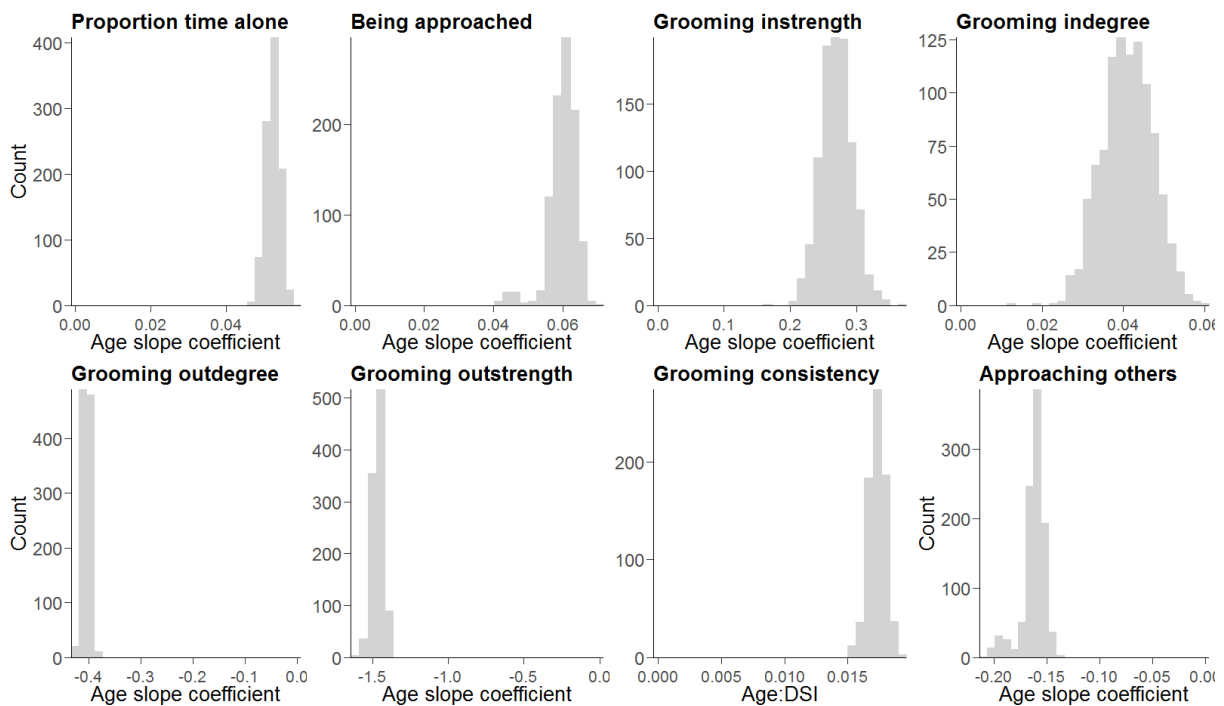
Figure S5. Distribution of the estimated slopes for age accounting for uncertainty regarding true individual's age. Female age was drawn from a normal distribution with mean = estimated age and standard deviation = (range of uncertainty/4). Random sampling was performed 1,000 times. The

respective response variable is specified as the title following denomination in Table 1. Estimated slopes are far from approaching zero for all models providing adequate confidence in the results.
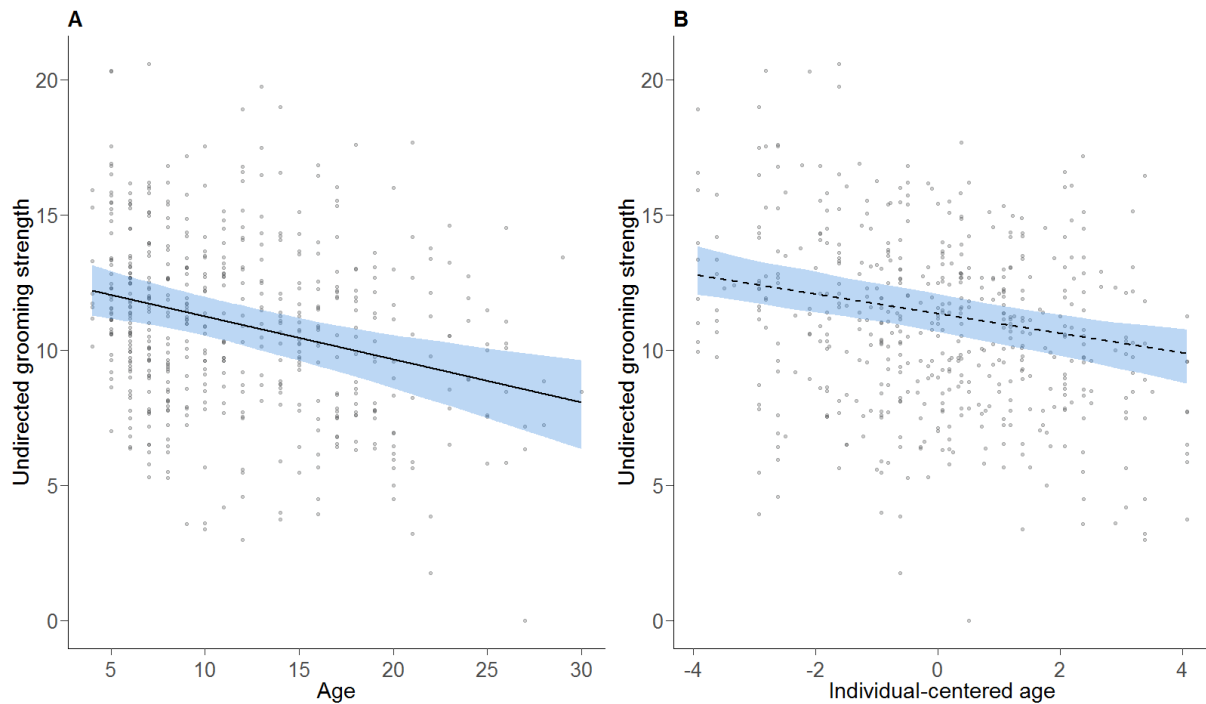
Figure S6. Undirected grooming strength decreased with age in both (**A**) mixed-longitudinal and (**B**) within-individual analyses. Undirected grooming strength is calculated from summing for each female all undirected dyadic ties to her grooming partners, with each dyadic tie calculated as the duration of grooming given and received corrected for dyadic observation time of the grooming partners.

Supplementary tables

Table S1. Mixed-longitudinal estimated slopes for the social behaviors investigated over age. Age was z-transformed in all models. Detailed model results including estimated slopes for the covariates Elo score and number of females, and the interaction between reproductive status and season are presented in Tables S1-S9. Hypotheses tested are increasing spatial segregation, increasing social selectivity, disengagement, and exclusion by partners.

Hypothesis	Response	$\beta_{age} \pm SE$	CI_{lower}	CI_{upper}	$P_{(age)}$
spatial segregation	proportion time alone	0.052 ±0.025	0.005	0.099	0.040
exclusion	being approached	0.061 ±0.027	0.011	0.110	0.032
exclusion	grooming instrength	0.273 ±0.283	-0.371	0.846	0.475
exclusion	grooming indegree	0.039 ±0.058	-0.064	0.147	0.387
disengagement/ selectivity	grooming outdegree	-0.402 ±0.059	-0.520	-0.292	<0.001
disengagement/ selectivity	grooming outstrength	-1.465 ±0.184	-1.843	-1.072	<0.001
increased selectivity	selective approach	-0.103 ±0.038	-0.177	-0.027	0.010
disengagement	approaching others	-0.161 ±0.040	-0.224	-0.083	0.002

Table S2. Detailed results for the model of proportion time spent alone. (**A**) Estimates for slopes with standard error, 95% confidence interval, test statistic, degrees of freedom, and p-values, are provided for fixed effects alongside (**B**) the estimated standard deviations for random effects intercepts and random slopes. Reference levels were set as reproductive status = not reproductively active, season = mating and group = mot.

A

Fixed term	Est.	SE	CI_{lower}	CI_{upper}	Df	Test stat.	P
intercept	1.336	0.113	1.103	1.555	-	-	-
within-individual age	-0.291	0.187	-0.623	0.049	1	2.334	0.127
between-individual age	0.083	0.028	0.023	0.140	1	7.979	0.005
Elo score	-0.121	0.026	-0.173	-0.072	1	18.192	<0.001
season	-0.154	0.146	-0.454	0.120	-	-	-
reproductive status	0.073	0.054	-0.025	0.174	-	-	-
season * reproductive status	-0.373	0.077	-0.514	-0.218	1	12.337	<0.001
nfemale	-0.119	0.114	-0.346	0.105	1	1.112	0.292
group ms2	-0.264	0.158	-0.539	0.009	3	5.415	0.144
group mst	0.070	0.172	-0.272	0.402	-	-	-
group sst	-0.209	0.108	-0.409	-0.013	-	-	-

B

Grouping factor	Random intercept or slope	SD
female	intercept	0.111
female	Elo score	0.079
female	season	0.077
female	reproductive status	0.042
female	nfemale	<0.001
season-year	intercept	0.214
season-year	Elo score	0.001
season-year	reproductive status	0.092
season-year	group ms2	<0.001
season-year	group mst	0.144
season-year	group sst	0.147

Within and between-individual age were standardized by mean centering and divided by the standard deviation of raw age. Within-individual age mean = 0, between-individual age mean = 11.88, raw age sd = 6.

Table S3. Detailed results for the model of being approached by others. (**A**) Estimates for slopes with standard error, 95% confidence interval, test statistic, degrees of freedom, and p-values, are provided for fixed effects alongside (**B**) the estimated standard deviations for random effects intercepts and random slopes. Reference levels were set as reproductive status = not reproductively active and season = mating.

A

Fixed term	Est.	SE	CI_{lower}	CI_{upper}	Df	Test stat.	P
intercept	0.141	0.085	-0.018	0.282	-	-	-
within-individual age	0.317	0.092	0.163	0.495	1	8.559	0.003
between-individual age	0.030	0.027	-0.019	0.083	1	1.263	0.261
Elo score	-0.052	0.028	-0.102	0.000	1	3.371	0.066
season	0.011	0.120	-0.177	0.223	-	-	-
reproductive status	-0.195	0.071	-0.314	-0.064	-	-	-
season * reproductive status	0.568	0.111	0.382	0.743	1	9.991	0.002
nfemale	0.001	0.025	-0.048	0.056	1	0.003	0.960

B

Grouping factor	Random intercept or slope	SD
female	intercept	0.137
female	Elo score	0.065
female	season	0.077
female	reproductive status	0.039
female	nfemale	0.047
group	intercept	<0.001
group	Elo score	<0.001
group	season	<0.001
group	reproductive status	<0.001
group	season * reproductive status	0.131
season-year	intercept	0.132
season-year	Elo score	0.010
season-year	reproductive status	0.119

Within and between-individual age were standardized by mean centering and divided by the standard deviation of raw age. Within-individual age mean = 0, between-individual age mean = 11.88, raw age sd = 5.85.

Table S4. Detailed results for the model of instrength. (**A**) Estimates for slopes with standard error, 95% confidence interval, test statistic, degrees of freedom, and p-values, are provided for fixed effects alongside (**B**) the estimated standard deviations for random effects intercepts and random slopes. Reference levels were set as reproductive status = not reproductively active and season = mating.

A

Fixed term	Est.	SE	CI$_{lower}$	CI$_{upper}$	Df	Test stat.	P
intercept	7.615	0.340	6.852	8.350	-	-	-
within-individual age	-0.720	0.453	-1.623	0.193	36.599	-0.442	0.661
between-individual age	0.536	0.152	0.234	0.861	47.872	2.841	0.007
Elo score	0.222	0.142	0.222	-0.084	2.276	1.185	0.345
season	0.294	0.427	-0.603	1.245	-	-	-
reproductive status	-0.765	0.402	-1.599	0.035	-	-	-
season * reproductive status	1.479	0.565	0.271	2.595	3.139	2.059	0.128
nfemale	0.492	0.170	0.110	0.910	9.579	2.229	0.051

B

Grouping factor	Random intercept or slope	SD
receiver	intercept	0.606
receiver	Elo score	0.250
receiver	season	0.917
receiver	reproductive status	0.729
receiver	nfemale	0.479
group	intercept	0.320
group	Elo score	0.125
group	season	0.441
group	reproductive status	0.267
group	season * reproductive status	0.362
season-year	intercept	0.413
season-year	Elo score	0.113
season-year	reproductive status	0.730

Within and between-individual age were standardized by mean centering and divided by the standard deviation of raw age. Within-individual age mean = 0, between-individual age mean = 11.86, raw age sd = 5.85.

Table S5. Detailed results for the model of indegree. (**A**) Estimates for slopes with standard error, 95% confidence interval, test statistic, degrees of freedom, and p-values, are provided for fixed effects alongside (**B**) the estimated standard deviations for random effects intercepts and random slopes. Reference levels were set as reproductive status = not reproductively active and season = mating.

A

Fixed term	Est.	SE	CI$_{lower}$	CI$_{upper}$	Df	Test stat.	P
intercept	-4.425	0.167	-4.757	-4.122	-	-	-
within-individual age	-0.661	0.232	-1.067	-0.217	1	7.005	0.008
between-individual age	0.144	0.060	0.025	0.256	1	7.631	0.006
Elo score	-0.005	0.051	-0.102	0.099	1	0.010	0.922
season	0.350	0.187	-0.014	0.692	-	-	-
reproductive status	-0.078	0.125	-0.305	0.141	-	-	-
season * reproductive status	0.320	0.199	-0.043	0.648	1	1.922	0.166
nfemale	-0.368	0.093	-0.578	-0.182	1	10.531	0.001

B

Grouping factor	Random intercept or slope	SD
actor	intercept	0.326
actor	Elo score	0.128
actor	season	0.133
actor	reproductive status	0.363
actor	season * reproductive status	0.534
actor	nfemale	0.233
receiver	intercept	<0.001
receiver	Elo score	<0.001
receiver	season	0.142
receiver	reproductive status	0.203
receiver	season * reproductive status	<0.001
receiver	nfemale	0.134
dyad	intercept	1.132
dyad	Elo score	<0.001
dyad	season	0.637
dyad	reproductive status	<0.001
dyad	season * reproductive status	<0.001
group	intercept	0.135
group	Elo score	<0.001
group	season	<0.001
group	reproductive status	<0.001
group	season * reproductive status	0.068
season-year	intercept	0.225
season-year	Elo score	<0.001
season-year	reproductive status	0.141

Within and between-individual age were standardized by mean centering and divided by the standard deviation of raw age. Within-individual age mean = 0, between-individual age mean = 11.70, raw age sd = 5.71.

Table S6. Detailed results for the model of grooming outdegree. (**A**) Estimates for slopes with standard error, 95% confidence interval, test statistic, degrees of freedom, and p-values, are provided for fixed effects alongside (**B**) the estimated standard deviations for random effects intercepts and random slopes. Reference levels were set as reproductive status = not reproductively active and season = mating.

A

Fixed term	Est.	SE	CI$_{lower}$	CI$_{upper}$	Df	Test stat.	P
intercept	-4.657	0.162	-4.933	-4.348	-	-	-
within-individual age	-0.937	0.204	-1.349	-0.516	1	18.393	<0.001
between-individual age	-0.311	0.050	-0.407	-0.210	1	30.182	<0.001
Elo score	0.021	0.042	-0.063	0.103	1	0.238	0.626
season	0.427	0.184	0.088	0.783	-	-	-
reproductive status	0.278	0.126	0.046	0.511	-	-	-
season * reproductive status	0.070	0.150	-0.249	0.349	1	0.215	0.643
nfemale	-0.362	0.095	-0.517	-0.191	1	11.792	0.001

B

Grouping factor	Random intercept or slope	SD
actor	intercept	0.095
actor	Elo score	<0.001
actor	season	<0.001
actor	reproductive status	0.150
actor	season * reproductive status	0.399
actor	nfemale	0.108
receiver	intercept	<0.001
receiver	Elo score	<0.001
receiver	season	0.132
receiver	reproductive status	<0.001
receiver	season * reproductive status	0.436
receiver	nfemale	0.072
dyad	intercept	1.141
dyad	Elo score	<0.001
dyad	season	0.663
dyad	reproductive status	0.177
dyad	season * reproductive status	<0.001
group	intercept	0.0115
group	Elo score	<0.001
group	season	0.052
group	reproductive status	0.121
group	season * reproductive status	<0.001
season-year	intercept	0.231
season-year	Elo score	<0.001
season-year	reproductive status	<0.001

Within and between-individual age were standardized by mean centering and divided by the standard deviation of raw age. Within-individual age mean = 0, between-individual age mean = 11.70, raw age sd = 5.71.

Table S7. Detailed results for the model of grooming outstrength. (**A**) Estimates for slopes with standard error, 95% confidence interval, test statistic, degrees of freedom, and p-values, are provided for fixed effects alongside (**B**) the estimated standard deviations for random effects intercepts and random slopes. Reference levels were set as reproductive status = not reproductively active and season = mating.

A

Fixed term	Est.	SE	CI_{lower}	CI_{upper}	Df	Test stat.	P
intercept	6.239	0.339	5.537	6.893	-	-	-
within-individual age	-2.564	0.509	-3.590	-1.582	32.031	-4.830	<0.001
between-individual age	-1.162	0.197	-1.527	-0.803	59.527	-5.703	<0.001
Elo score	0.210	0.229	-0.229	0.642	4.829	0.944	0.390
season	1.215	0.486	0.192	2.226	-	-	-
reproductive status	1.432	0.305	0.809	2.023	-	-	-
season * reproductive status	-0.390	0.390	-1.199	0.415	440.961	-1.013	0.312
nfemale	0.311	0.177	-0.051	0.651	58.665	1.739	0.087

B

Grouping factor	Random intercept or slope	SD
actor	intercept	0.988
actor	Elo score	0.355
actor	season	0.753
actor	reproductive status	<0.001
actor	nfemale	0.449
group	intercept	2.098
group	Elo score	0.238
group	season	0.489
group	reproductive status	0.257
group	season * reproductive status	<0.001
season-year	intercept	0.449
season-year	Elo score	0.247
season-year	reproductive status	<0.001

Within and between-individual age were standardized by mean centering and divided by the standard deviation of raw age. Within-individual age mean = 0, between-individual age mean = 11.86, raw age sd = 5.85.

Table S8. Detailed results for the model on selective approach. The interaction of age and cumulated DSI was non-significant and removed from the model (estimate ±SE = 0.017 ±0.015, p = 0.244). (**A**) Estimates for slopes with standard error, 95% confidence interval, test statistic, degrees of freedom, and p-values, are provided for fixed effects alongside (**B**) the estimated standard deviations for random effects intercepts and random slopes. Reference levels were set as reproductive status = not reproductively active and season = mating.

A

Fixed term	Est.	SE	CI$_{lower}$	CI$_{upper}$	Df	Test stat.	P
intercept	-2.879	0.154	-3.189	-2.592	-	-	-
within-individual age	-0.130	0.147	-0.427	0.172	1	0.786	0.377
between-individual age	-0.085	0.037	-0.163	-0.019	1	4.737	0.023
cumuDSI previous season	0.090	0.019	0.053	0.130	1	17.763	<0.001
Elo score	0.377	0.060	0.263	0.505	1	12.027	<0.001
season	-0.001	0.123	-0.234	0.232	-	-	-
reproductive status	-0.150	0.058	-0.277	-0.031	-	-	-
season * reproductive status	0.513	0.079	0.361	0.667	1	18.216	<0.001
nfemale	-0.220	0.059	-0.341	-0.089	1	13.426	<0.001

B

Grouping factor	Random intercept or slope	SD
actor	intercept	0.196
actor	cumuDSI previous season	0.038
actor	Elo score	<0.001
actor	season	0.081
actor	reproductive status	0.122
actor	nfemale	0.068
receiver	intercept	0.167
receiver	Elo score	0.262
receiver	season	0.133
receiver	reproductive status	0.060
receiver	nfemale	0.127
dyad	intercept	0.246
dyad	cumuDSI previous season	0.059
dyad	Elo score	0.085
dyad	season	0.153
dyad	reproductive status	0.042
group	intercept	0.261
group	Elo score	0.065
season_year	intercept	0.189
season_year	cumuDSI previous season	0.020
season_year	Elo score	0.020
season_year	reproductive status	0.114

Table S9. Detailed results for the model of approaching others. (**A**) Estimates for slopes with standard error, 95% confidence interval, test statistic, degrees of freedom, and p-values, are provided for fixed effects alongside (**B**) the estimated standard deviations for random effects intercepts and random slopes. Reference levels were set as reproductive status = not reproductively active and season = mating.

A

Fixed term	Est.	SE	CI$_{lower}$	CI$_{upper}$	Df	Test stat.	P
intercept	-0.271	0.117	-0.454	-0.053	-	-	-
within-individual age	-0.414	0.139	-0.647	-0.158	1	8.254	0.004
between-individual age	-0.082	0.036	-0.148	-0.019	1	4.332	0.037
Elo score	0.355	0.037	0.293	0.415	1	16.655	<0.001
season	0.113	0.147	-0.127	0.351	-	-	-
reproductive status	-0.043	0.074	-0.176	0.089	-	-	-
season * reproductive status	0.337	0.101	0.157	0.503	1	7.433	0.006
nfemale	0.115	0.058	0.024	0.218	1	5.028	0.025

B

Grouping factor	Random intercept or slope	SD
female	intercept	0.179
female	Elo score	0.047
female	season	0.046
female	reproductive status	0.114
female	nfemale	0.061
group	intercept	0.122
group	Elo score	<0.001
group	season	<0.001
group	reproductive status	<0.001
group	season * reproductive status	<0.001
season-year	intercept	0.186
season-year	Elo score	0.033
season-year	reproductive status	0.136

Within and between-individual age were standardized by mean centering and divided by the standard deviation of raw age. Within-individual age mean = 0, between-individual age mean = 11.88, raw age sd = 5.85.

Table S10. Assessing the difference in within and between-individual age estimated effects on the social behavior investigated. Models are based on equation (3) including the main term for age and individual average-age. The estimated slope and significance test assigned to the between-age effect represents the difference in the slopes of the within and between-individual effects, allowing to test for selective disappearance. Raw age was z-transformed and between-individual age mean-centered and scaled to the standard deviation of raw age in all models.

Hypothesis	Response	β_{age} ±SE	P	$\beta_{average\ age}$ ±SE	P
spatial segregation	proportion time alone	-0.281 ±0.181	0.127	0.374 ±0.204	0.072
exclusion	being approached	0.317 ±0.093	0.003	-0.287 ±0.105	0.013
exclusion	grooming instrength	-0.720 ±0.453	0.668	1.257 ±0.515	0.253
exclusion	grooming indegree	-0.661 ±0.232	0.008	0.804 ±0.258	0.004
disengagement/ selectivity	grooming outdegree	-0.937 ±0.204	<0.001	0.626 ±0.227	0.007
disengagement/ selectivity	grooming outstrength	-2.564 ±0.509	<0.001	1.402 ±0.586	0.026
increased selectivity	selective approach	-0.130 ±0.147	0.375	0.045 ±0.166	0.786
disengagement	approaching others	-0.414 ±0.139	0.004	0.332 ±0.157	0.036

Chapter 3

Parasites in a social world: Lessons from primates

Baptiste Sadoughi [a,b,c], Simone Anzà [a,b], Charlotte Defolie [d,e], Virgile Manin [f,g], Nadine Müller-Klein [h], Tatiana Murillo [e,i], Markus Ulrich [j], Doris Wu [j]

[a]Department of Behavioral Ecology, Johann-Friedrich-Blumenbach Institute for Zoology & Anthropology, Georg-August-Universität Göttingen, Göttingen, Germany

[b]Research Group Primate Social Evolution, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

[c]Leibniz Science Campus Primate Cognition, German Primate Center, Göttingen, Germany

[d]Department for Sociobiology/Anthropology, Johann-Friedrich-Blumenbach Institute for Zoology & Anthropology, Georg-August-Universität Göttingen, Göttingen, Germany

[e]Behavioral Ecology and Sociobiology Unit, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

[f]Department of Human Behavior, Ecology and Culture Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[g]Tai Chimpanzee Project Centre Suisse de Recherche Scientifique, Abidjan, Cote d'Ivoire

[h]Institute for Evolutionary Ecology and Conservation Genomics, Conservation Genomics and EcoHealth, Ulm University, Ulm

[i]Genomic and Applied Microbiology and Göttingen Genomics Laboratory Institute of Microbiology and Genetics, Georg-August-Universität Göttingen, Göttingen, Germany

[j]Epidemiology of Highly Pathogenic Microorganisms Robert Koch Institute, Berlin, Germany

Abstract

Social behavior and parasitism interconnect at all levels of sociality, from the community to the population and from the group down to the individual. This chapter explores key findings on the parasite-related costs and benefits of sociality, focusing on primates. The research spans across social networks, dominance and affiliative relationships, and individual behavior and physiology, highlighting established links between primate sociality and parasitism and identifying important gaps for future research. Given the use of nuanced conceptual frameworks and new analytical methods, combined with experimental studies and growing empirical data from long-term field projects, primates are a particularly exciting and helpful taxon for studying sociality-parasite interactions.

Keywords

Chapter 4

Investigation of glucocorticoid dynamics during aging in female Assamese macaques living in their natural habitat

Baptiste Sadoughi [a,b,c], Michael Heistermann [d], Durr-E-Ajam Riaz [a], Oliver Schülke [a,b,c], Julia Ostner [a,b,c]

[a]Department of Behavioral Ecology, Johann-Friedrich-Blumenbach Institute for Zoology and Anthropology, Georg-August-Universität Göttingen, Kellnerweg 6, D-37077 Göttingen, Germany.

[b]Research Group Primate Social Evolution, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany.

[c]Leibniz ScienceCampus Primate Cognition, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany.

[d]Endocrinology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany.

Abstract

Aging is often associated with dysfunction of the HPA axis in humans, thought to result from the mismatch between the classic vertebrate stress response and the constant social challenges arising in human daily life. This mismatch is thought to be shared with other non-human primates, and possibly other highly social species, navigating complex social interactions. Aging of the HPA axis in natural populations of non-human primates has been little studied, and the contribution of social factors to potential age-related changes is poorly understood. Non-invasive assessment of fecal glucocorticoid concentrations and social dynamics in wild female Assamese macaques (*Macaca assamensis*) over several years provided no evidence for age-related changes in endocrine function and did not implicate sociality as a mediator between age and HPA axis activity. These findings suggest that context-dependence, rather than a universal primate specificity, may be important in explaining age-related changes in HPA axis.

Keywords

Introduction

Glucocorticoids (GC) exert an extraordinary range of effects on the metabolism, reproductive system, immune function and behavior of vertebrates, and thereby contribute to important life-history events (e.g., growth and reproduction) (Crespi et al., 2013; Landys et al., 2006). The association between dysfunction of the HPA axis reactivity (whether blunted or enhanced) or HPA axis activation (relatively short pulses versus prolonged activation) and diseases has been demonstrated in humans and laboratory animal models (Charmandari et al., 2005; Sapolsky et al., 2000). Such findings have often been at odds with the scant evidence for detrimental effects of GCs in natural populations of birds and mammals (Beehner and Bergman, 2017; Bonier et al., 2009a; Schoenle et al., 2021). The rise in circulating concentrations of GCs in the face of experienced or anticipated stressors is influenced by the nature of the challenge. The greater the frequency, intensity, and the lower the predictability and level of control on the stressor, the stronger and more persistent the elevation in GCs (Sapolsky, 2021; Schoenle et al., 2018). Furthermore, the response orchestrated by GCs is predicted to be beneficial only if the downstream physiological adaptations effectively allow the organism to escape the challenge (Schoenle et al., 2018). A mismatch occurs when the stressor is unavoidable or must be dealt with by means not regulated by GCs. This mismatch is often cited when discussing the long-term consequences of social competition and hierarchies on the stress physiology of primates, including humans (Sapolsky, 2021). Individuals navigating unstable hierarchies, losing stable relationships, or experiencing harassment from dominants may exhibit prolonged HPA axis, potentially contributing to reduced survival and reproductive success (Abbott et al., 2003; Creel, 2001; Creel et al., 1996; Sapolsky, 2005; Scott et al., 2012; Thompson and Cords, 2018).

The manifestations of a lifetime of exposure to chronic social challenges are especially expected in old age because of the cumulative nature of the damage caused by repeated elevations of GCs on the brain and peripheral organs (Mizoguchi et al., 2003; Sapolsky et al., 2002). Loss of sensitivity to GC feedback results in a chronic elevation of baseline GCs, heightened responsiveness to acute stressors, and a blunted diurnal cyclicity with age (Born et al., 1995; Dodt et al., 1991; Ferrari et al., 2001; Goncharova et al., 2019; Goncharova and Lapin, 2002; Gust et al., 2000; Nathanielsz et al., 2020; Otte et al., 2005; Reul et al., 1991; Sapolsky, 1992b; Touitou et al., 1983; Van Cauter et al., 1996; Yang et al., 2017). However, very little data is available to corroborate the dysregulation of HPA activity outside of humans and captive non-human primates. In one population of yellow baboons, age was associated with reduced negative feedback and increased concentrations of baseline GCs, further manifested in increased fecal GCs (fGCs) in females but not males (Altmann et al., 2010; Sapolsky and Altmann, 1991). In a wild chimpanzee community urinary cortisol concentrations increased with age and diurnal

rhythmicity appeared blunted, although there was no evidence that the changes were mediated by sociosexual factors (Emery Thompson et al., 2020a).

We set out to investigate the relationship between age and fGCs in a long-term monitored population of Assamese macaques (*Macaca assamensis*). We focused on females for whom more precise age estimates were available and for whom we have previously documented a gradual social disengagement with progressing age (Chapter 2 of this thesis, *submitted*). Specifically, females decreased their active engagement in grooming interactions with age, which resulted in a decrease of the strength of the bonds with their top partners. As strongly bonded partners are important source of support in female cercopithecines (Ellis et al., 2019; Ostner and Schülke, 2018; Thompson, 2019), decreasing strength of the bonds with top partners could results in females facing higher level of adversity with age. In the present study, we investigate the influence of age and bond strength with the top partners, while controlling for environmental variables, to assess the contribution of social dynamics to patterns of fGcs over the life course. We predicted that an increase in fGCs with age, robust to intermittent changes in reproductive activity and sociality, would support an intrinsic aging of the HPA axis.

Methods

The study was carried out at the Phu Khieo Wildlife Sanctuary (PKWS, 16°05'–35'N, 101°20'–55'E, 1573 km^2), in northeastern Thailand, where a population of wild Assamese macaques fully habituated to human observers has been studied since 2005. Ambient temperature at the study site was automatically recorded by data loggers, allowing daily minimum temperatures to be computed. Fruit abundance at the study site was measured from tree species abundance in 45 botanical plots covering 21ha and monthly phenology scores from more than 650 trees representing important fruit sources (Heesen et al., 2013) and we extrapolated daily scores between consecutive monthly records. Temperature and fruit abundance were necessary here because GCs are secreted to promote catabolic activity during energy challenging conditions associated with low temperature or low energy intake (Sadoughi et al., 2021a; Touitou et al., 2021b).

Behavioral data and fecal samples were collected from adult females intermittently from 2010 to 2020. Years were divided into a mating (October to February) and a non-mating (March to September) seasons, giving unique season-year time periods. Females were observed for a mean of 6.0±2.9 season-years, with a range of to one to 11. Females were considered adult from the mating season of first conception (usually at 5.5 years of age) (Anzà et al., 2022) with ages known from witnessed births or inferred from comparisons with individuals of known age. Average (±SD) age was 11.9±5.5 years old, for a range of 4 to 29, covering most of the reported lifespan in populations of semi-free ranging

macaques (Brent et al., 2017; Johnson and Kapsalis, 1995). A detailed description of the behavioral protocol can be found in Chapter 2 of this thesis (Sadoughi et al. (*submitted*)). In brief, we followed groups from dawn to dusk using 40min continuous focal animal protocols (Altmann, 1974) to record all instances of dyadic grooming interactions between adult females along with the identity of the actor and the receiver. Dyadic agonistic interactions were collected during focal animal protocols and *ad libitum*, with the identity of the winner and loser. Based on 9404 hours of focal observation (27±9.3 hours per female per season-year), we calculated individual-level social metrics per season-year. The time spent grooming (both given and received) between two females was divided by dyadic observation time (i.e., divided by the sum of observation time for each member of the dyad during which the other member of the dyad was also present and adult). The resulting dyad metrics indicate the strength of ties for every pair of females in a group. For each female, we summed the three highest dyadic values to obtain an individual-level bond strength with the top partners. Dominance between adult females from the same group was determined from the direction of submission (e.g., silent bared teeth display, give ground) and aggression (e.g., open-mouth threat, chase), and computed as Elo scores with the package Elo_rating (functions elo_seq and elo_plot with k=100 and a starting value of 1,000) (Neumann et al., 2011). Undecided conflicts were counted as half a win for each participant following package default setting. Dominance relationships are highly stable within groups (function stab_elo, stability > 0.99) so we only extracted female's Elo scores at the end of each season (30th of September for the birth and 1st of March for the mating season) or on the last day observed (four females who died or disappeared during a season) and assigned the scores to all samples collected in the respective season.

Fecal samples were collected opportunistically throughout the day from clearly identified females and processed according to established protocols for storage and extraction in the field (Ostner et al., 2008; Shutt et al., 2012, 2007). Samples were shipped to the German Primate Center in Germany and kept frozen at -20°C until assayed using an in-house enzyme immunoassay validated for the measurement of 11β–hydroxyetiocholanolone a metabolite of GC in macaques (Heistermann et al., 2006). All samples were run in duplicates, and samples with intra-assay coefficients of variation (CVs) >10% between duplicates analyzed again. Average intra-assay CVs across assay plates based on high and low-concentration quality controls (QCs) were 9.1% and 11.5% respectively, while inter-assay CVs calculated across assay plates were 11.6% for high and 22.8% for low QCs. For each sample, we also determined whether the female was gestating, lactating, or non-gestating non-lactating (NGNL). Onset of gestation was determined *a posteriori* by subtracting the average gestation length (i.e., 164 days, Fürtbauer et al., 2010) from the date of parturition. If the exact date of parturition was unknown, we assigned the date of birth based on the last day we saw the mother not carrying an infant and on infant

morphology, and when the uncertainty was greater than two months (due to short interruptions in data collection), so we chose the peak of the birth season (15th of May, Fürtbauer et al., 2010; unpublished data) as birth date.

Analyses included two Linear Mixed Models (LMMs) in R with RStudio (R Core Team, 2021 version 4.0.4; RStudio Team, 2022 version 2022.07.02+576) using the package *lme4* (Bates et al., 2015). Covariates were z-transformed, and factors were dummy coded and centered when included as random slopes. The first model included the covariate for age, separated into within- and between-individual age terms (van de Pol and Verhulst, 2006; van de Pol and Wright, 2009) to disentangle individual aging from population level effect (e.g., selective disappearance). The factor term reproductive state (three levels), and the linear terms for daily fruit availability, daily minimum temperature, and the polynomial of daily minimum temperature were included as control variables because energy metabolic activity varies with reproductive state (Fürtbauer et al., 2014; Touitou et al., 2021b), and because caloric intake and temperature were found to correlate with urinary GCs in the population (Touitou et al., 2021b). The second model added to the first model the grooming strength to the female's top three adult female partners in the group, and dominance Elo score. Female ID, date of sample collection, and season-year were included as random effects terms in both models. The random slopes for within-individual age, Elo score, reproductive state, fruit availability and minimum temperature within ID and season-year, and for between-individual age within season-year were also included to maintain type I error rate at 5% and avoid false positive (Barr et al., 2013). The correlation of random intercept and slope were excluded from the second model to ease converge. Both models were of good stability as assessed by excluding levels of random effects factors one at a time and comparing the model estimates of models fitted to the derived subsets with those derived for the full dataset. The distribution of residuals followed a normal distribution and was homogeneous (packages *performance* function check_model), and collinearity was not an issue (vif function in package *car*, max VIF=3 excluding polynomial term, 3.2 when including it). The 95% confidence intervals of model estimates were determined by means of parametric bootstrapping (N=100 bootstraps; package *glmmTMB* function simulate). To avoid false positives when testing several predictors at once, we compared with Chi-square tests the first model to a model lacking within- and between-age terms, and the second model to a model lacking grooming strength and Elo scores. When full-reduced model comparisons were statistically significant, p-values on individual terms were obtained using the Satterthwaite approximation in the package lmerTest (Kuznetsova et al., 2017). P-values <0.05 were considered significant. Sample size was 2,752 samples.

Results

Daily minimum temperature ranged from 4.2 to 23.4°C (mean±SD=18.3±3.4°C), and daily fruit availability from 2.9 to 79.3 (28.5±17.6). Seven hundred thirty samples were collected from gestating females, 1358 from lactating females, and 664 from NGNL females, with one to 102 samples per female (47.5±27.0) with on average 7.9±3.9 samples per female per season-year. Concentrations of fGCs ranged from 21.0 to 3204.0 ng/g (mean±SD=180.3±145.1 ng/g).

The full-null model comparison for the model including only age and environmental control variables was not significant (χ^2=1.664, Df=2, p=0.435), providing no evidence for modifications of HPA axis activity during individual aging, nor support for a correlation of GCs and age at the population level (table 1A). As aging is associated with changes in social engagement, and as the support from closely bonded partners has been repeatedly linked to GCs dynamics in non-human primates, we included female's bond strength to her top partners and dominance status. The full-null model comparison was again not significant (χ^2=3.789, Df=2, p=0.150) (table 1B).

Table 1. Effects of age on the concentration of glucocorticoid metabolites (11β–hydroxyetiocholanolone) in feces (**A**) before and (**B**) after accounting for social factors. Covariates were z-transformed. P-values are not shown as full-reduced model comparisons were not significant.

A

Fixed term	Estimate	SE	95% CI$_{lower}$	95% CI$_{upper}$
intercept	5.23	0.08	5.08	5.38
within-age	0.13	0.09	-0.03	0.32
between-age	-0.02	0.03	-0.08	0.04
reproductive state (lactating)	-0.17	0.05	-0.27	-0.06
reproductive state (NGNL)	-0.07	0.06	-0.19	0.05
group (mst)	-0.16	0.07	-0.31	-0.01
group (oth)	0.01	0.08	-0.16	0.16
group (sst)	0.03	0.09	-0.18	0.20
group (stu)	-0.22	0.15	-0.55	0.18
daily fruit availability	0.16	0.12	-0.07	0.35
daily min temperature	0.00	0.03	-0.08	0.07
daily min temperature^2	-0.01	0.01	-0.03	0.02

B

Fixed term	Estimate	SE	95% CI$_{lower}$	95% CI$_{upper}$
intercept	5.20	0.08	5.02	5.36
within-age	0.09	0.09	-0.10	0.22
between-age	-0.01	0.03	-0.07	0.05
bond strength top partners	0.00	0.02	-0.03	0.04
Elo score	-0.06	0.03	-0.12	0.01
reproductive state (lactating)	-0.14	0.06	-0.23	-0.05
reproductive state (NGNL)	-0.06	0.05	-0.16	0.03
group (mst)	-0.13	0.07	-0.28	0.00
group (oth)	0.10	0.08	-0.09	0.27
group (sst)	0.01	0.09	-0.16	0.17
group (stu)	-0.16	0.17	-0.46	0.24
daily fruit availability	0.16	0.11	-0.08	0.36
daily min temperature	0.00	0.04	-0.07	0.08
daily min temperature^2	-0.02	0.01	-0.04	0.01
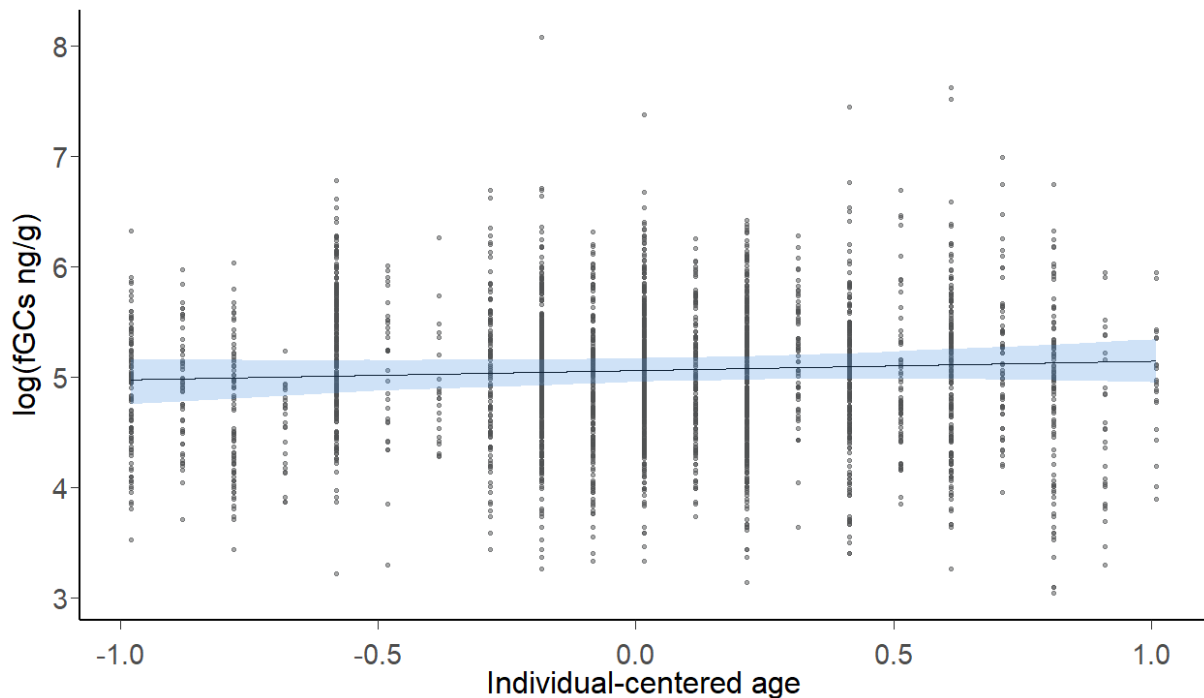
Figure 1. Individual centered age did not correlate with fecal glucocorticoid metabolites (fGCs) (estimated slope and confidence intervals extracted from model B in table 1).

Discussion

We found no evidence that within-individual age was associated with fGCs, suggesting no differences owing to aging. The between-individual age effect was not significant, suggesting that females on average older did not exhibit increased or decreased fGC concentrations compared to younger females. Therefore, cohort effects or selective disappearance could not explain the absence of within-individual age effects.

Despite great interest in understanding the contribution of HPA axis dysfunction to age-related pathologies in an aging human population, very few comparative studies have investigated the late-life course of GCs in other primates. Results are inconclusive, GCs increasing with age in female baboons (Altmann et al., 2010), and in both male and female chimpanzees (Emery Thompson et al., 2020a) irrespective of climatic and sociosexual dynamics, whereas no association was found in female rhesus (Maestripieri and Georgiev, 2016), golden lion tamarins (Bales et al., 2006), Barbary macaques (Shutt et al., 2007), and long–tailed macaques (van Schaik et al., 1991). Although the conclusion reached by some of these studies may be limited by small sample size and their cross-sectional design, results from our longitudinal analyses suggest that neither may be sufficient to explain a lack of age-related changes in GCs.

The relationship between social status, social integration (either measured by network size or bond strength) and fGCs is highly variable across the literature, even sometimes within species (Beehner and Bergman, 2017). An alternative interpretation of the results from humans, yellow baboons, chimpanzees, and captive non-human primates is that intense and frequent HPA triggering is required for age-related dysregulation of HPA axis to manifest. Evidence of increased baseline GCs with age in laboratory rodents (Sapolsky, 1992; Sapolsky et al., 2002) further supports that this dysregulation will arise under any (abnormally) chronically stressful environments. The results suggest that such stressful level of adversity is not encountered by female macaques living in their natural social and environmental conditions.

The 'coping hypothesis of aging' (Hämäläinen et al., 2015b) suggest that age-related dysfunction will only manifest under circumstances driving the greatest HPA activity. Consistent with this interpretation, GCs increased only during the dry season in female mouse lemurs (Hämäläinen et al., 2015b), and in mandrills the increase with age was magnified by lower rainfall and temperatures (Charpentier et al., 2018) (although note that age was not continuous but treated as dichotomic). On the contrary, age did not modify the association between cortisol and dominance status in chimpanzees (Emery Thompson et al., 2020a), although as social integration was not considered in the study, it remains possible that parallel age-related changes in affiliation strategies obscured the

relationship (Rosati et al., 2020). It would therefore seem that age-related changes in GCs are associated with the influence of environmental rather than social factors. The response of the HPA axis to variation in temperature and rainfall may therefore reflect the greater sensitivity to variation in thermoregulatory or energy needs in aging subjects, rather than enhanced responsiveness to social interactions. Late-life dynamics of the HPA axis are only beginning to be investigated in natural animal populations, and though studies have been mostly motivated by the search for features of a 'normal' primate aging, the present data suggest integrating context-dependence in GCs-age relationships is needed (Sapolsky, 2021; Schoenle et al., 2018; Vitousek et al., 2019a).

Funding

Acknowledgements

Chapter 5

Aging gut microbiota of wild macaques are equally diverse, less stable but progressively personalized

Baptiste Sadoughi [a,b,c,d], Dominik Schneider [c], Rolf Daniel [c], Oliver Schülke [a,b,d], Julia Ostner [a,b,d]

[a]Department of Behavioral Ecology, Georg-August Universität Göttingen, Göttingen, Germany

[b]Research Group Primate Social Evolution, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

[c]Genomic and Applied Microbiology and Göttingen Genomics Laboratory, Institute of Microbiology and Genetics, Georg-August Universität Göttingen, Göttingen, Germany

[d]Leibniz ScienceCampus Primate Cognition, German Primate Center, Göttingen, Germany

Abstract

Pronounced heterogeneity of age trajectories has been identified as a hallmark of the gut microbiota in humans and has been explained by marked changes in lifestyle and health condition. Comparatively, age-related personalization of microbiota is understudied in natural systems limiting our comprehension of patterns observed in humans from ecological and evolutionary perspectives. Here, we tested age-related changes in the diversity, stability, and composition of the gut bacterial community using 16S rRNA gene sequencing with dense repeated sampling over three seasons in a cross-sectional age sample of adult female Assamese macaques (*Macaca assamensis*) living in their natural forest habitat. Gut bacterial composition exhibited a personal signature which became less stable as individuals aged. This lack of stability was not explained by differences in microbiota diversity but rather linked to an increase in the relative abundance of rare bacterial taxa. The lack of age-related changes in core-taxa or convergence with age to a common state of the community hampered predicting gut bacterial composition of aged individuals. On the contrary, we found increasing personalization of the gut bacterial composition with age, indicating that composition in older individuals was increasingly divergent from the rest of the population. Reduced direct transmission of bacteria resulting from decreasing social activity may contribute to, but not be sufficient to explain, increasing personalization with age. Together, our results challenge the assumption of a constant microbiota through adult life in a wild primate. Within the limits of this study, the fact that increasing personalization of the aging microbiota is not restricted to humans, suggests the underlying process to be evolved instead of provoked only by modern lifestyle of and health care for the elderly.

Keywords

Chapter 6

Non-invasive assessment of metabolic responses to food restriction using urinary triiodothyronine and cortisol measurement in macaques

Baptiste Sadoughi [a,b,f], Cédric Girard-Buttoz [c], Antje Engelhardt [d], Michael Heistermann [e,+], Julia Ostner [a,b,f,+]

[a]Department of Behavioral Ecology, University of Goettingen, Göttingen, Germany

[b]Research Group Primate Social Evolution, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

[c]Department of Human Behavior, Ecology and Culture, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[d]Faculty of Science, School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool L3 3AF, UK

[e]Endocrinology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

[f]Leibniz ScienceCampus Primate Cognition, German Primate Center, Göttingen

[+]Equal contribution as last author

Abstract

Regulation of energy allocation and metabolic rate plays an important role in determining behavior and fitness in wild animals, calling for the validation of non-invasive markers of energetic condition. Recently, the thyroid hormone triiodothyronine (T3) has emerged as a promising marker as concentrations decrease to lower the metabolic rate during energetically challenging periods. However, it remains largely unclear whether T3 merely represents an alternative or provides additional information compared to other compounds involved in the regulation of energy acquisition and allocation, like cortisol and C-peptide, as few joint measurements have been conducted to date in non-invasively collected samples. We aimed to validate the non-invasive measurement of immunoreactive urinary total T3 (uTT3), in comparison to urinary cortisol (uCort) and urinary C-peptide (uCP), as a marker of metabolic response to variation in food intake in macaques, and to address a number of issues regarding the collection, storage and processing of samples which are important for application of uTT3 measurements under field conditions. We used daily samples and body mass measures from a prior food restriction-refeeding experiment over 4 weeks with six captive macaques and analyzed concentrations of uTT3 and uCort in samples collected prior to (fasting) and after morning feeding (non-fasting). Concentrations of uTT3 decreased in response to restriction in food supply and were also lower during weeks of food restriction compared to weeks of refeeding. Variation in uTT3 also correlated positively with variation in body mass and concentrations of uCP. As expected, uCort showed the reverse pattern, increasing during food restriction and decreasing following refeeding, but was not associated with variation in body mass. Generally, compared to fasting samples, concentrations were higher in post-morning feeding, i.e., non-fasting, samples for uTT3 but not uCort. Contamination of urine samples with fecal matter, but not soil, and exposure to UV light led to a decrease in uTT3. uTT3 was largely unaffected by repeated freeze-thaw cycles and by refrigeration for medium-term storage (2 days) but degraded substantially when stored at ambient temperature for the same period. In conclusion, uTT3 measurements inform on the effect of food intake and its associated metabolic response to variation in energetic status. Since uTT3 is reasonably robust to many issues associated with collection and storage of urine samples under field conditions, it is a promising biomarker for studies of energetic condition and basal metabolic rate in wild macaques.

Keywords

Chapter 7

General Discussion

The aim of this thesis was to investigate the manifestations of aging in natural animal populations by studying adult females from a population of wild Assamese macaques. The present work contributes to the emerging integration of social behavior into aging research (Chapter 2) and, by building on the established links between sociality and health in primates (Chapter 3), to investigations anchoring human-specific physiological aging within a broader comparative framework (Chapter 4 and 5). In the first study (Chapter 2), I combined a mixed-longitudinal and a within-individual centered statistical analytic approach to investigate age-related changes in social behavior and found that females experienced active social disengagement with advancing age (table 1). This social disengagement was concomitant with, rather than explained by, the expression of social selectivity towards preferred partners, and findings pointed towards increasing constraints limiting social relationships with age. The comparison of mixed-longitudinal and within-individual centered results further highlighted demographic processes, consistent with the selective disappearance of poorly socially connected individuals, contributing to dynamics of social aging at the population level. In the second study (Chapter 4), I focused on one hormonal system, the HPA axis, and found no evidence of age-related changes in activity of the HPA axis assessed from the measurement of fecal glucocorticoid concentrations (fGCs). In Chapter 5, I found that gut bacterial communities are equally diversified, less stable, and increasingly individualized with increasing age. Having established the patterns of age-related changes in those different traits independently, I attempted to draw connections between them by assessing the interdependence between social behavior and physiological aging (Chapter 4 and 5). However, I found no evidence suggesting that social behavior mediates age-related changes in physiological traits. In this final chapter, I will integrate these findings into a broader frame and discuss their implications.

Table 1. Summary table recapitulating age-related changes in female Assamese macaques and across chapters in female-female social behavior, fecal glucocorticoids concentrations (fGCs), and gut bacterial communities, measured mixed-longitudinally, within-individuals or between-individuals. Patterns can indicate an increase ($\uparrow$), a decrease ($\downarrow$), or no evidence for a change ($\rightarrow$) with age. Mixed-longitudinal patterns result from a combination of within- and between-individual effects. Between-individual age effects solely driven by within-individual age effects were denoted 0, while between-individual effects differing from within-individual effects (in either direction or magnitude) were denoted with the corresponding arrow.

		Age		
		Mixed-longitudinal	Within-individual	Between-individual
Chapter 2 – female-female social interactions	Grooming engagement	$\downarrow$ Active $\rightarrow$ Passive	$\downarrow$ Active $\rightarrow$ Passive	$\downarrow$ Active 0 Passive
	Grooming network size	$\downarrow$ Active $\rightarrow$ Passive	$\downarrow$ Active $\downarrow$ Passive	$\downarrow$ Active $\uparrow$ Passive
	Spatial segregation	$\uparrow$	$\rightarrow$	$\uparrow$
	Initiation of interactions	$\downarrow$ Active $\uparrow$ Passive	$\downarrow$ Active $\uparrow$ Passive	$\downarrow$ Active $\downarrow$ Passive
Chapter 4 – fGCs	Concentrations		$\rightarrow$	$\rightarrow$
Chapter 5 – Gut bacterial communities	Diversity	$\rightarrow$		
	Stability	$\downarrow$		
	Similarity	$\rightarrow$		
	Personalization	$\uparrow$		

7.1 Social behavior in old age: compensation or decline?

Female Assamese macaques decreased their active engagement in social interactions with advancing age, associated with a reduction in the number of partners they groomed. The reduction of grooming network size on a few selected partners has been associated with benefits such as reduced HPA axis activity and faster return to baseline following an instable social period in female chacma baboons (*Papio hamadryas ursinus*) (Crockford et al., 2008; Wittig et al., 2008). However, in the chacma baboons, reduction in network size occurred without females reducing their rate of grooming interactions. On the contrary, the results presented in Chapter 2 suggest that for aging female Assamese macaques, reduction in network size is likely driven, at least partly, by the reduction in grooming activity.

The central question, then, is why do aging individuals decrease their engagement in social interactions? Evidence in non-human primates converges on the maintenance of interest in social interactions well into old age (Almeling et al., 2017; Rathke and Fischer, 2021; Schino and Pinzaglia, 2018; van Noordwijk and van Schaik, 1987). For instance, old Barbary macaques (*Macaca sylvanus*) maintain interest in social cues (Almeling et al., 2016; Rathke and Fischer, 2021; Rosati and Santos, 2017) and regularly vocalize when witnessing interactions (Almeling et al., 2016; Rathke and Fischer, 2021), but this does not lead to interactions (Rathke et al., 2022). Lack of motivation to interact is often interpreted as resulting from some form of cognitive impairment (Röhr et al., 2020; Siracusa et al., 2022a). However, some evidence in humans has shown that a healthy brain can also drive a reduction in motivation into old age (Soutschek et al., 2021). During an experiment conducted on one group of young and one group of old healthy subjects, researchers stimulated the participants' frontopolar cortex, a brain region promoting reward obtainment and management of competing goals (Mansouri et al., 2017), and assessed the participants willingness to perform a task. Frontopolar cortex activity increased motivation to perform the task in young subjects but decreased motivation among elders. This suggested that a healthy aging brain may contribute to the shift from gain maximization to effort minimization with age, possibly as a response to a change in an individual psychological or physiological internal state (Cardini and Freund, 2020; Depping and Freund, 2011). The contribution of energetic deficit and frailty to social disengagement remains unclear given that both social decline and maintained social engagement with age are observed in provisioned and non-provisioned groups (Almeling et al., 2016; Archie et al., 2014; Corr, 2003; Nakamichi and Shizawa, 2003; Rathke and Fischer, 2021; Rosati et al., 2020; Schino and Pinzaglia, 2018; Siracusa et al., 2022b; Thompson González et al., 2021; van Noordwijk and van Schaik, 1987; Veenema et al., 1997). The non-invasive measurement of triiodothyronine, validated for application to field research in Chapter 6, could contribute to test whether decreasing triiodothyronine levels correlate with decreasing social activity, and thereby offer an opportunity to test directional causality from physiology to sociality.

It is important to keep an open mind, as age-related changes in behavior may not necessarily mean social aging, at least not in the sense of *deterioration* commonly associated with aging. Behavior offers great flexibility to individuals in managing external and internal pressures (Touitou et al., 2021a), so that modifications of behavior with age may represent the best strategy to compensate other age-related declines. In female Assamese macaques, I investigated age-related changes in fGCs and the gut microbiome to cover some physiological traits impacted by differences in social strategies (Chapter 3, 4 and 5). However, I found no evidence for age-related changes in fGCs, and no correlation between sociality (measured as bond strength to the top partners) and fGCs (controlled for age). Therefore, decreasing social engagement is unlikely to be an adaptation to HPA axis functional aging. Similarly,

female dyads that groomed longer did not have a more similar gut bacterial composition, suggesting no protective effect of reduced social contact with age. Overall, the joint examinations suggest decline as a likely cause of age-related social changes in female Assamese macaques.

7.2 Social and physiological aging: mediation or modulation?

I found no evidence for social interactions to act as a mediator (Chapter 4 and 5) of physiological aging. Concentrations of fGCs were neither correlated to the strength of the grooming bonds to the top partners nor age. When investigating the gut microbiome, group identity explained a small but non-negligible variance in similarity, consistent with previous findings (reviewed in Sarkar et al., 2020). Therefore, future investigations should also account for group membership when assessing the contribution of individual traits (e.g., age) to gut bacterial communities, otherwise unaccounted group effects will inflate the importance of individual traits (Risely et al., 2022). However, this influence of group membership only provides indirect evidence for social effects on the gut microbiome. Group members may exhibit higher composition similarity because they share a territory, interact frequently, or both. In one yellow baboon population (*Papio cynocephalus*) (Björk et al., 2022), similarity among group members arose in majority from roaming over a shared territory, which echoes the known infectious risk associated with shared-patch occupancy (Müller-Klein et al., 2019). On the contrary, neither in baboons nor in Assamese macaques did grooming interactions influence similarity (Björk et al., 2022; Chapter 5 of this thesis). In yellow baboons and Verreaux's sifakas (*Propithecus verreauxi*), genetic relatedness explained similarity better than matriline, suggesting stronger effects of genotype than social interactions (Björk et al., 2022; Rudolph et al., 2022).

Could this suggest that evidence for social transmission through grooming interactions arises from confounding effects of genetic relatedness (in a kin-structured network) and shared-patch occupancy? This is likely not the case. Previous research in both baboons and sifakas have found a correlation of grooming bond strength and similarity, while controlling for relatedness and spatial proximity (Perofsky et al., 2017; Tung et al., 2015). These overall conflicting results are better understood by considering time scales. Grooming bond strength influences similarity when samples are collected over short periods of time, such as a few weeks (Perofsky et al., 2017; Tung et al., 2015), but not over months or years in primates (Björk et al., 2022; Rudolph et al., 2022; Chapter 5 of this thesis). This also suggests that influence of social interactions on the aging gut microbiome are probably short-term, possibly attenuating age-related changes occurring in older individuals as long as close contact is maintained, without influencing patterns in the long run.

Another reason, which may explain why including social interactions did not alter the relationship between age and physiological traits, could be that sociality does not act as a mediator, but rather as

a modulator of physiological aging. There is repeated evidence that the effect of social bonds and integration on physiology and health is modulated by third variables, either individual traits, such as dominance status (Brent et al., 2011), reproductive state (Crockford et al., 2008; Emery Thompson et al., 2010), social partner' sex or dominance status (Fürtbauer et al., 2014; Sapolsky, 1992b), or context-dependences, such as timing to mating season or group-level social stability (Bergman et al., 2005; Sapolsky, 2005). For example, the benefits of female-female relationships in lowering injury risk and fGC concentrations are more pronounced in, or limited to, the non-mating season in female macaques (Fürtbauer et al., 2014; Pavez-Fox et al., 2022). Some of the modulation effects on HPA axis activity are thought to reflect differences in the degree of control over social relationships (Thompson, 1981). For example, in female chacma baboons (*Papio hamadryas ursinus*) having a more focused grooming network is associated with lower fGCs (Crockford et al., 2008), and buffers the rise in fGCs levels during a period of high instability (Wittig et al., 2008). In one population of rhesus macaques (*Macaca mulatta*), high-ranking females displayed lower fGC concentrations only when their social network narrowed, suggesting that a form of control over a more focused network modulates the relationship between dominance status and physiology (Brent et al., 2011). Consistent with this interpretation, social integration did not benefit survival in yellow-belied marmots (*Marmota flaviventer*), probably because increased social connectedness results from increasing population density rather than active social engagement in this facultatively social species (Blumstein et al., 2018). These findings demonstrate that the relationship between sociality and physiology is multidimensional, with a variety of optimal strategies.

This is important for our understanding of the benefits and consequences of sociality into old age. In Chapter 4, I found no evidence for correlations between fGCs and either age or bond strength to top partners. This could arise if the value of social bonds is different across ages, resulting in several age-specific social optima. The possibility that the added value of social bonds to survival and health changes over the lifespan has only rarely been directly addressed, and results are inconclusive (Brent et al., 2017; Holt-Lunstad et al., 2015; Yang et al., 2016). Describing how social bond strength, social status, and broader social level integration varies for specific age-classes will be a necessary first step requiring large enough cohort at different ages. It is further important to formulate hypotheses regarding which social system or environmental conditions should favor increasing, or conversely decreasing, benefits of sociality with age. In females from despotic macaque species, rank acquisition in adult individuals is constrained by inter-matriline dominance hierarchy (Chapais, 1988; Chapais et al., 1991; Silk, 2009). Support from young and prime-aged mothers may be critical to the rank achievement of their first daughters, and the engagement of these prime-aged females may further contribute to stabilize inter-matriline dynamics. With advancing age, females may be able to rely on

the engagement of their adult daughters, lowering the need for their own active involvement in social interactions, while retaining the value of social relationships. Consequently, we may observe decreasing active social engagement (Chapter 2) in the absence of negative consequences for physiology (e.g., GCs in Chapter 4) or health.

To test such hypotheses, it will be imperative to match measures of sociality to the underlying mechanism investigated. For example, when sociality was approximated by the number of available kin in the group, greater number of kin was associated with lower risk of injury (Pavez-Fox et al., 2022). At the same time, the positive influence of the number of kin on survival decreased from prime-age to old age (Brent et al., 2017). Although this may seem in agreement with the suggestion formulated above that sociality is less critical to aging females in despotic societies, the patterns are not actually consistent. Active disengagement from social interactions would not be costly if females can, anyway, rely on the direct and indirect support from their kin. Findings in rhesus macaques on the contrary suggest that kin support is not driving inter-individual differences in survival into old age. There is no definitive answer to this issue, and there is a possibility that decreasing added benefits of sociality into old age arises from a survivor bias in cross-sectional studies, a risk highlighted in Chapter 2.

One practical statistical way to investigate age-specific optima would be to include interactions between age and sociality metrics. Throughout the present thesis, I mainly investigated the influence of age without interaction as I think it necessary to first assess which patterns are consistent at the population level throughout adulthood. For those traits that exhibit no significant change with age, it will be interesting to assess interaction effects. Taking the relationship between age, sociality, and fGCs as an example (Chapter 4), one practical application would be to introduce an interaction between social bond strength, within-individual, and between-individual age, investigating the possibility that social bond strength has varying influence on fGCs as individuals age (within-individual effect), and that this variation may not be linear across adulthood (between-individual effect). The inclusion of non-linear effects can constitute a statistical challenge, but it will be an important next step towards a more complete understanding of differences in the pace of aging between individuals, and within individuals across traits, in natural animal populations.

7.3 The aging gut microbiome

The aging gut microbiome has become a central topic of research in human and veterinary medicine as the involvement of the gut bacterial composition has been demonstrated for a rapidly growing list of diseases (Agirman et al., 2021; Amato et al., 2021; Levy et al., 2017; Sencio et al., 2022). Given the diversity of taxa making up the gut microbial ecosystem and the multitude of external and internal factors influencing its dynamics, a central question is whether disease- and age-related changes are

mostly individualized or shared by many. This question had only been addressed in natural animal populations with cross-sectional or mixed-longitudinal short-term studies investigating the influence of host identity and age on the gut bacterial communities with a limited number of metrics. Recently, four studies (table 2) have contributed new perspectives to these issues, which I will now discuss. Although each study covers several topics, I will focus on individualization and age, and measures of bacterial inter-sample similarity (i.e., beta-diversity), intra-individual compositional stability, and composition dynamics, and briefly evoke at the end age-related changes in intra-sample diversity (i.e., alpha-diversity) and diurnal cyclicity in the gut bacterial composition.

Table 2. Summary table of studies investigating individualized gut bacterial composition over time and the correlates of host aging on gut bacterial communities, in spotted hyenas (Rojas et al., 2022), Assamese macaques (Chapter 5 of this thesis), yellow baboons (Björk et al., 2022; Grieneisen et al., 2021), and meerkats (Risely et al., 2022, 2021). Studies are arranged by alphabetical order of species' Latin name.

Species	Study years	N° subjects	N° samples	Samples per subject
Spotted hyenas (*Crocuta crocuta*)	23	12	301	Mean = 25 (range = 13–48)
Assamese macaques (*Macaca assamensis*)	1.5	51	543	Mean = 11 (range = 3–13)
Yellow baboons (*Papio cynocephalus*)	14	600	17,265	Median = 19
Meerkats (*Suricata suricatta*)	22	157	965	Mean = 7.5 (range = 4–14)

A first key finding is that the gut bacterial composition is strongly individualized over short time scales. In macaques, baboons, and meerkats, intra-individual similarity was highest for samples collected close in time (about 10 days apart in primates, less than two months in meerkats). Over longer periods of time, all studies found individual identity (ID) to explain the largest portion of variance in similarity (19.6, 8.6, 11.3, and 19 percent in macaques, baboons, hyenas, and meerkats, respectively). This means that, when considering the entire population of samples, ID is important to understand how samples are organized in the compositional space. However, how much individuals differ from each other is not as clear. In meerkats, intra-individual repeatability (another way to express individual signature) decreased to become undistinguishable from inter-individual repeatability for samples collected a year apart. In macaques, I found a small average difference between intra- and inter-individual similarity when analyzing all samples collected over one and a half years. In baboons, the

difference between intra-individual and inter-individual similarity appeared to be larger and for longer, although the use of a different similarity metric precludes direct comparison between studies.

Across studies, the high intra-individual similarity over very short time scales appears to result from the additive effect of environmental effects and host specificities. The individualized gut bacterial composition in baboons arises mostly from subtle interindividual differences in the relative abundance of taxa present, on average, at low relative abundance. In macaques, personalization was also the result of small interindividual differences in relative abundance, rather than in the presence/absence of taxa. In baboons, taxa contributing the most to interindividual differences also exhibit the highest heritability, which suggests that interindividual differences in host's genetics drive, at least partly, this phenomenon. As opposed to these differences in the relative abundance of low abundance taxa, environmental factors are responsible for high turn-over in the bacteria present in the gut and for inducing major variations in relative abundances. In meerkats, rapid changes in the presence/absence of taxa explained the lack of intra-individual consistency over time, and in my study, the seasons had a major role in explaining overall composition.

Following this argument, what could explain the persistence, over a year or longer, of individualized composition in some cases (here baboons) and not others (here meerkats)? Seasonality exerted a strong influence on composition and interannual composition dynamics in the primates, but not in meerkats. In the latter, the year of sample collection had the largest influence on composition, yet year did not account for similarity in baboons or hyenas. Long-term individualized composition could rely, partly, on the long-term stabilizing effect of seasonality on gut bacterial composition. Seasonality may contribute to cyclic colonization, or preferential growth, of the same taxa across years, which in interaction with host 'baseline bacterial signature', drives peaks of increasing intra-individual similarity over time. Although seasonality was not assessed in hyenas, the population ranges in south Kenya in a similar environment to the baboons and experience seasonality due to variation in abundance of migratory prey species. Interestingly, all hyenas experienced a major shift in bacterial communities over two years, without composition ever returning to the anterior state. Despite this shift, ID was still the strongest predictor of variance explained over the entire study, whereas the year of collection was not important. If as suggested by Mallott (2022), this pattern arises from combined individualized composition and individualized dynamics, hyenas would exhibit individualization patterns very similar to those seen in the sympatric baboons. I could not test the interannual effect of seasonality in macaques because each season was included only once. Despite marked seasonality, the environment at PKWS is rather unpredictable (Heesen et al., 2015, 2013), with some of the tree species constituting a significant part of the macaques' diet displaying irregular fruiting across years. This would be an

interesting opportunity to test whether intra-individual similarity increases across years for which seasons are comparable, and not when seasons are less consistent.

Are all individuals equally individualized? In macaques and meerkats, gut bacterial composition was increasingly individualized with advancing age. In macaques, I found that sample minimum dissimilarity (expressing the distance to the closest bacterial neighbor) linearly increased with age. In meerkats, intra-individual repeatability increased from young age to prime adulthood, and again from adulthood to old age. The consistency between studies is especially interesting as only females were sampled for my thesis, leaving a possibility that, with age, females would exhibit compositions closer to males, rather than being increasingly individualized. Both sexes were sampled in meerkats, yet age-related personalization remained. Together, these studies provide the first evidence for increasing personalization of gut bacterial composition with host age in non-humans (Figure 1).

Although the mechanism driving this personalization is not demonstrated in either study (see also Chapter 5 for a discussion focused on macaques), both investigated age-related changes in compositional stability as a potential driver. Surprisingly, older meerkats exhibited higher stability, whereas older female macaques displayed lower stability, and in both cases, age-related changes in stability were interpreted as promoting personalization. This could reveals important differences between the phenomenon observed. In meerkats, old individuals exhibited a more stable repartition in the relative abundance across taxa, possibly enhanced by a decrease in the acquisition of taxa from the environment. In macaques, older females exhibited faster changes in relative abundance across taxa than younger females, which, combined with seasonal effects which tend to homogenize compositions across individuals, could have resulted in a decreasing similarity to other females (i.e., personalization). To summarize, results from other study species bring a new perspective on my results and tend to strengthen the interpretation that increasing personalization with age results from dysbiosis rather than greater individual consistency with advancing age.
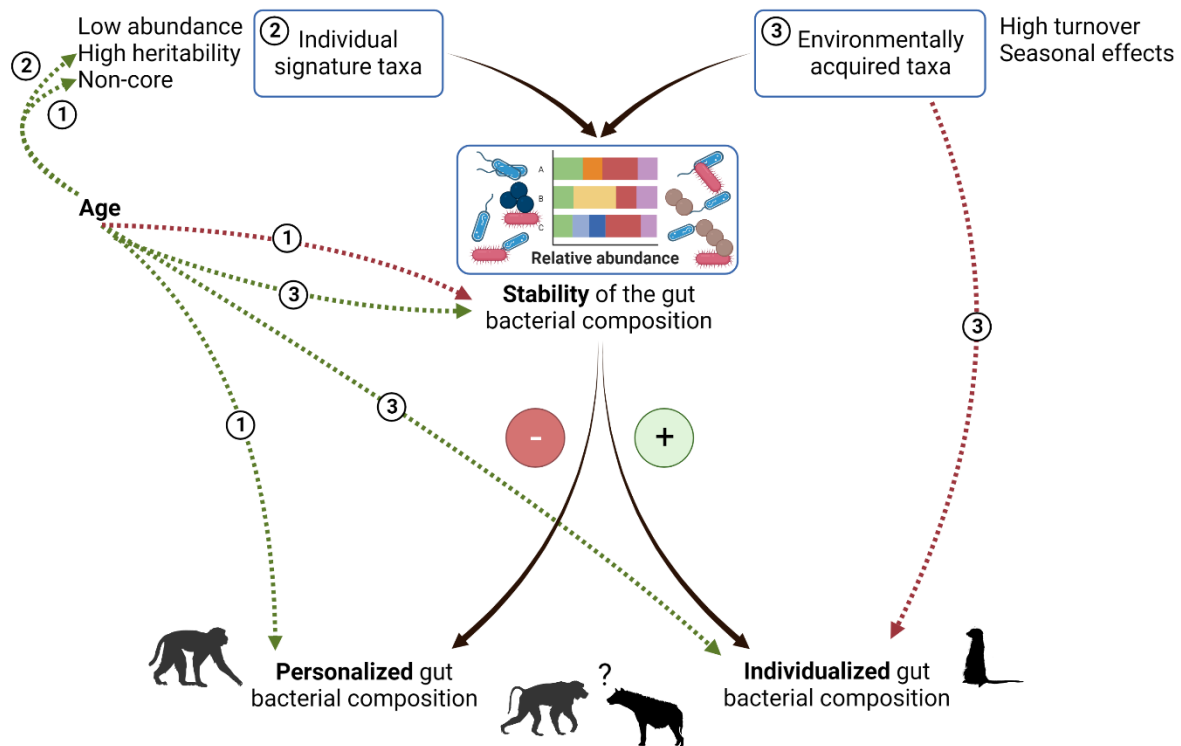
Figure 1. Age-related increase in non-core and highly heritable taxa and decrease in environmentally acquired taxa contribute to individualized age-related changes in the gut bacterial composition, which result in unstable *personalized* gut bacterial composition, or stable *individualized* gut bacterial composition. Suggested links are depicted with black arrows. Demonstrated associations are depicted with dashed arrows in green for positive, and red for negative effects. Circled numbers refer to (1) Chapter 5 of this thesis, (2) (Björk et al., 2022; Grieneisen et al., 2021) and (3) (Risely et al., 2022, 2021). Definitions for personalized and individualized are as introduced in Chapter 5 of this thesis and (Risely et al., 2022), respectively. Silhouette images are by Oscar Sanisidro (*Crocuta crocuta*) and T. Michael Keesey (*Suricata suricatta*) on PhyloPic.com. Image created with Biorender.

Aside from changes in similarity and stability, age correlated with slightly decreasing diversity in hyenas and baboons, although the significance of the very small effect in the latter probably results from the large sample size. In hyenas, age also explained a small portion of variance in similarity, about ten times the variance explained in macaques, and 1,000 times the effect in meerkats. It is unclear how the very low number of individuals, and possible changes in reproductive state which were not accounted for, may contribute to this result. In the meerkats, most bacterial taxa exhibited cyclic variation in relative abundance throughout the day, which were not influenced by age.

Overall, age does not consistently influence the gut bacterial diversity, the compositional similarity across individuals, the relative abundance of most taxa, or the diurnal cyclicity in their relative

abundance. However, evidence suggests that age could be associated with changes in stability. Whether these changes are the cause for increasingly individualized composition with advancing age needs further testing. As none of the studies discussed here differentiated changes arising within- from between-individuals, some results may also be due to selective disappearance effects. For example, six out of 12 hyenas died during the study conducted by Rojas and colleagues (2022). In meerkats, intra-individual consistency may increase with age if chances to succumb to other pathogens (e.g., tuberculosis (Müller-Klein et al., 2022)) are increased for those with unstable gut bacterial composition, creating an apparent increase in gut bacterial stability among the older individuals. Differentiating between within- and between-individual aging is not yet in practice in longitudinal analysis of microbiome data but could allow testing, in addition to aging, the survival benefits of individualized gut compositions into old age.

7.4 Conclusion and future research perspectives

"[…] though I feel a professional obligation to say something about the natural history of senescence, there is no time to do so, and even if there were, there would not be much to say. […] Whether animals can, or cannot, reveal an innate deterioration with age is almost literally a domestic problem; the fact is that under the exactions of natural life they do not do so. They simply do not live that long." Medawar, 1952, p.11-13.

At the time of Medawar inaugural lecture, evidence for aging in natural animal populations was indeed scant. Since then, our knowledge on the natural history of senescence has grown, and the emerging picture reveals a complexity and diversity across the tree of life, on which much is still to be said. In this thesis, I set out to investigate the manifestations of aging in the social behavior and physiology of adult female Assamese macaques living in their natural habitat, while using the sociality-health nexus as a framework to address the complex interdependences between aging traits. I found that, with age, females reduce their active engagement in social interactions with others, even though they do not experience decreasing opportunities to do so. I went on to test different scenarios compatible with the socio-emotional selectivity theory of aging, to find that the one supported was compatible with maintained selectivity into old age. As maintained selectivity cannot explain decreasing engagement, my findings emphasize that selectivity and engagement are independent social dimensions in the study population, which follow different trajectories into old age. To link social and physiological aging, I reviewed established benefits and risks for health associated with sociality in primates, and highlighted gaps and promising avenues of research. Starting my investigation of physiological aging with one of the best documented traits, I investigated aging in the activity of the HPA axis assessed from the concentrations of glucocorticoid metabolites in fecal samples and found no evidence of age-related

changes. Moving to less explored biomarkers of aging in natural populations, I found age to correlate with changes in the gut microbiome. Although age has seldom been found to influence the gut microbiome in free-living animals, combining several metrics offered insights on some rarely explored components of this multidimensional ecosystem. Overall gut bacterial composition was not associated with host age but became increasingly personalized, less stable, and enriched in pro-inflammatory bacteria with advancing age. This reveals some degree of host specificity in aging trajectories of the gut microbiome, which I suggested could arise from age-associated dysbiosis in this population.

Contrary to my predictions, I found no evidence that social aging contributes to age-related changes in physiological traits. This does not undermine the value of social relationships as some evidence could indicate the selective disappearance of poorly socially connected individuals in the population. However, it suggests that social aging is unlikely to contribute to age-related mortality via its influence on physiological functions. Although I found no evidence for the effects of sociality on physiology, I contributed to open new opportunities to test effects from physiology to sociality by validating the measurement of urinary triiodothyronine hormones as a biomarker of the metabolic response to energy shortage. As predicted, urinary triiodothyronine decreased when energy intake decreased, and variation in urinary hormone concentrations reflected fluctuations in body mass, offering an interesting opportunity to assess metabolic responses and body condition non-invasively. With this work, I have contributed to our understanding of age-specific changes in traits much less investigated than the better-known actuarial senescence patterns, and I would now suggest some further research directions.

The pattern of social aging revealed in this thesis is intriguing for several reasons. With age females decreased their active engagement in grooming, and lost several partners grooming them, despite receiving grooming at a constant frequency. This suggests that remaining old females' partners compensate for network's size reduction. This leaves a first important question unanswered: How closely related to the aging females are these partners? As female Assamese macaques bias their affiliative relationships to both maternal and paternal kin (De Moor et al., 2020), complete relatedness pedigree are necessary to answer. If, as I suspect, relationships with older females are increasingly one-sided due to decreasing engagement from aging females, we should ask: Is the investment of those partners dependent on their own age and the presence of immature offspring? How stable are the relationships with aging females? And are there any costs (e.g., reproductive, energetic) to maintaining relationships with aging females? This would allow investigating the consequences of aging, not only from the side of the aging individuals, but also for the collective. As more behavioral and physiological data are collected for the long-term project at the PKWS, estimating social bonds reciprocity, stability, and possible costs of bonds will be possible for more female dyads.

Social aging is intriguing for a second reason, namely the inter-individual variability in the slope of social engagement with age. Although inter-individual differences in the slope of disengagement with age was not addressed here because of the limited sample size, some individual trajectories suggest such differences. The question is what underlies these differences: Is the slope of disengagement with age associated with the number of close kin in the group? Are more distant kin also important? For those females with little available female support, could a solution be to capitalize on long-lasting male-female relationships (Ostner et al., 2013)?

Despite a growing understanding of the environmental and individual factors shaping the composition of the gut microbiome in natural populations, evidence is still lacking showing how these variations influence host health and fitness, especially in mammals. Because the gut microbiome is functionally redundant (Tian et al., 2020), some of the taxonomic changes may bear little consequences to the host. Functional annotations of metagenomes will help determine how fluctuations in taxonomic composition translate into differential functional capacities. Our understanding of the gut microbiome would benefit greatly for synergies between moderately invasive, and non-invasive wildlife studies. When deemed feasible, weighting and sampling blood in free-ranging populations will provide a more complete picture of the consequences of gut microbiome composition on host's physiological state via the measurement of serum fatty acid levels and inflammation markers. While this will strengthen the link between gut microbiome and host physiological state, long-term studies with detailed behavioral data will be in a privileged position to investigate how much changes in the gut microbiome can be compensated by the host at minimal cost (Touitou et al., 2021a).

The completion of more life-history trajectories in the Assamese macaque population will offer new perspective on the study of aging. Complete life-histories including age at death are the missing piece to explore how age-dependent and age-independent declines interact to shape age-distributions at the population-level. Information on age at death combined with advanced statistical analyses will allow investigating further the value of social bonds for survival and provide more decisive answers. If as many times stated, the hallmark of human aging is its heterogeneity (Badal et al., 2020; Müller and Ellwardt, 2022), then future investigations should take up the challenge of assessing inter-individual differences in aging trajectories in the wild. Although the small sample sizes of natural populations are less suited to model individualized aging, the inclusion of individual life-history parameters could be an easily applicable first step. Specifically, investigating how accumulated reproductive effort in combination with age at death may influence the onset of social, physiological, and actuarial senescence would allow integrating trade-offs to the sociality-health-aging nexus. Long-term animal studies collecting detailed behavioral data are also in a privileged position to investigate the late-life consequences of early life. While recent evidence in this macaque population suggests that the

influence of early-life on physiological functions persists into adulthood (Anzà, 2022), it is unclear whether such modifications benefit or harm individual fitness, and whether the pace of aging may be altered.

Because interdependencies between social and physiological systems are bidirectional, future research should aim to explore feedback loops. These loops are critical because they may accelerate decline in non-linear fashions, creating transitions between multiple discrete health states, some of which may significantly increase the probability of death. Thus, age may be associated with a gradual linear decline in some traits, and in other traits, with an increasing probability to enter a pathological transitory state (e.g., sickness). The combined used of linear models and multistate analyses could reveal how multifaceted aging processes leads to death.

At a broader level, these data will contribute to ongoing investigations on the link between sociality, aging, and lifespan across species. It remains unknown whether differences in age-distribution and lifespan arise from differences in baseline mortality or in the rate of aging, even across populations of closely phylogenetically related species. Finally, the recent emphasis on the loss of diversity in the gut microbiome with age in the new Copenhagen synthesis of human aging (Schmauck-Medina et al., 2022), shows the value of comparative research in reminding us to distinguish species-specific age-related changes from truly universal patterns.

References

Aartsen, M.J., van Tilburg, T., Smits, C.H.M., Knipscheer, K.C.P.M., 2004. A Longitudinal Study of the Impact of Physical and Cognitive Decline on the Personal Network in Old Age. J. Soc. Pers. Relatsh. 21, 249–266. https://doi.org/10.1177/0265407504041386

Abbott, D.H., Keverne, E.B., Bercovitch, F.B., Shively, C.A., Mendoza, S.P., Saltzman, W., Snowdon, C.T., Ziegler, T.E., Banjevic, M., Garland, T., Sapolsky, R.M., 2003. Are subordinates always stressed? a comparative analysis of rank differences in cortisol levels among primates. Horm. Behav. 43, 67–82. https://doi.org/10.1016/S0018-506X(02)00037-5

Abrams, P.A., 1993. Does Increased Mortality Favor the Evolution of More Rapid Senescence? Evolution 47, 877–887. https://doi.org/10.2307/2410191

Adams, M.R., Kaplan, J.R., Clarkson, T.B., Koritnik, D.R., 1985. Ovariectomy, social status, and atherosclerosis in cynomolgus monkeys. Arterioscler. Dallas Tex 5, 192–200.

Adriansjach, J., Baum, S.T., Lefkowitz, E.J., Van Der Pol, W.J., Buford, T.W., Colman, R.J., 2020. Age-related differences in the gut microbiome of rhesus macaques. J. Gerontol. Ser. A 75, 1293–1298. https://doi.org/10.1093/gerona/glaa048

Agirman, G., Yu, K.B., Hsiao, E.Y., 2021. Signaling inflammation across the gut-brain axis. Science 374, 1087–1092. https://doi.org/10.1126/science.abi6087

Agnihothri, R.V., Courville, A.B., Linderman, J.D., Smith, S., Brychta, R., Remaley, A., Chen, K.Y., Simchowitz, L., Celi, F.S., 2013. Moderate Weight Loss Is Sufficient to Affect Thyroid Hormone Homeostasis and Inhibit Its Peripheral Conversion. Thyroid 24, 19–26. https://doi.org/10.1089/thy.2013.0055

Alberts, S.C., Altmann, J., Brockman, D.K., Cords, M., Fedigan, L.M., Pusey, A., Stoinski, T.S., Strier, K.B., Morris, W.F., Bronikowski, A.M., 2013. Reproductive aging patterns in primates reveal that humans are distinct. Proc. Natl. Acad. Sci. U. S. A. 110, 13440–13445. https://doi.org/10.1073/pnas.1311857110

Albery, G.F., Clutton-Brock, T.H., Morris, A., Morris, S., Pemberton, J.M., Nussey, D.H., Firth, J.A., 2022. Ageing red deer alter their spatial behaviour and become less social. Nat. Ecol. Evol. 6, 1231–1238. https://doi.org/10.1038/s41559-022-01817-9

Ale, E.C., Binetti, A.G., 2021. Role of probiotics, prebiotics, and synbiotics in the elderly: insights into their applications. Front. Microbiol. 12, 19. https://doi.org/10.3389/fmicb.2021.631254

Alexander, R.D., 1974. The Evolution of Social Behavior. Annu. Rev. Ecol. Syst. 5, 325–383. https://doi.org/10.1146/annurev.es.05.110174.001545

Alleman, R.J., Bloomer, R.J., 2011. Hormonal response to lipid and carbohydrate meals during the acute postprandial period. J. Int. Soc. Sports Nutr. 8, 19. https://doi.org/10.1186/1550-2783-8-19

Almeling, L., Hammerschmidt, K., Sennhenn-Reulen, H., Freund, A.M., Fischer, J., 2016. Motivational Shifts in Aging Monkeys and the Origins of Social Selectivity. Curr. Biol. 26, 1744–1749. https://doi.org/10.1016/j.cub.2016.04.066

Almeling, L., Sennhenn-Reulen, H., Hammerschmidt, K., Freund, A.M., Fischer, J., 2017. Social interactions and activity patterns of old Barbary macaques: Further insights into the foundations of social selectivity. Am. J. Primatol. 79, e22711. https://doi.org/10.1002/ajp.22711

Alpert, A., Pickman, Y., Leipold, M., Rosenberg-Hasson, Y., Ji, X., Gaujoux, R., Rabani, H., Starosvetsky, E., Kveler, K., Schaffert, S., Furman, D., Caspi, O., Rosenschein, U., Khatri, P., Dekker, C.L., Maecker, H.T., Davis, M.M., Shen-Orr, S.S., 2019. A clinically meaningful metric of immune age derived from high-dimensional longitudinal monitoring. Nat. Med. 25, 487–495. https://doi.org/10.1038/s41591-019-0381-y

Altizer, S., Nunn, C.L., Thrall, P.H., Gittleman, J.L., Antonovics, J., Cunningham, A.A., Dobson, A.P., Ezenwa, V., Jones, K.E., Pedersen, A.B., Poss, M., Pulliam, J.R.C., 2003. Social Organization

and Parasite Risk in Mammals: Integrating Theory and Empirical Studies. Annu. Rev. Ecol. Evol. Syst. 34, 517–547. https://doi.org/10.1146/annurev.ecolsys.34.030102.151725

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour 49, 227–266.

Altmann, J., Gesquiere, L., Galbany, J., Onyango, P.O., Alberts, S.C., 2010. Life history context of reproductive aging in a wild primate model. Ann. N. Y. Acad. Sci. 1204, 127–138. https://doi.org/10.1111/j.1749-6632.2010.05531.x

Amato, K.R., Arrieta, M.-C., Azad, M.B., Bailey, M.T., Broussard, J.L., Bruggeling, C.E., Claud, E.C., Costello, E.K., Davenport, E.R., Dutilh, B.E., Ewald, H.A.S., Ewald, P., Hanlon, E.C., Julion, W., Keshavarzian, A., Maurice, C.F., Miller, G.E., Preidis, G.A., Segurel, L., Singer, B., Subramanian, S., Zhao, L., Kuzawa, C.W., 2021. The human gut microbiome and health inequities. Proc. Natl. Acad. Sci. 118. https://doi.org/10.1073/pnas.2017947118

Amato, K.R., Metcalf, J.L., Song, S.J., Hale, V.L., Clayton, J., Ackermann, G., Humphrey, G., Niu, K., Cui, D., Zhao, H., Schrenzel, M.D., Tan, C.L., Knight, R., Braun, J., 2016. Using the gut microbiota as a novel tool for examining colobine primate GI health. Glob. Ecol. Conserv. 7, 225–237. https://doi.org/10.1016/j.gecco.2016.06.004

An, R., Wilms, E., Masclee, A.A.M., Smidt, H., Zoetendal, E.G., Jonkers, D., 2018. Age-dependent changes in GI physiology and microbiota: time to reconsider? Gut 67, 2213–2222. https://doi.org/10.1136/gutjnl-2017-315542

Anestis, S.F., Breakey, A.A., Beuerlein, M.M., Bribiescas, R.G., 2009. Specific gravity as an alternative to creatinine for estimating urine concentration in captive and wild chimpanzee (Pan troglodytes) Samples. Am. J. Primatol. 71, 130–135. https://doi.org/10.1002/ajp.20631

Angelier, F., Moe, B., Weimerskirch, H., Chastel, O., 2007. Age-specific reproductive success in a long-lived bird: do older parents resist stress better? J. Anim. Ecol. 76, 1181–1191. https://doi.org/10.1111/j.1365-2656.2007.01295.x

Antonucci, T.C., Ajrouch, K.J., Birditt, K.S., 2014. The Convoy Model: Explaining Social Relations From a Multidisciplinary Perspective. The Gerontologist 54, 82–92. https://doi.org/10.1093/geront/gnt118

Anzà, S., 2022. Prenatal maternal stress effects in wild Assamese macaques (Macaca assamensis) (doctoral Thesis). https://doi.org/10.53846/goediss-9510

Anzà, S., Berghänel, A., Ostner, J., Schülke, O., 2022. Growth trajectories of wild Assamese macaques (Macaca assamensis) determined from parallel laser photogrammetry. Mamm. Biol. https://doi.org/10.1007/s42991-022-00262-2

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 R Soc B 281, 20141261. https://doi.org/10.1098/rspb.2014.1261

Arneson, A., Haghani, A., Thompson, M.J., Pellegrini, M., Kwon, S.B., Vu, H., Maciejewski, E., Yao, M., Li, C.Z., Lu, A.T., Morselli, M., Rubbi, L., Barnes, B., Hansen, K.D., Zhou, W., Breeze, C.E., Ernst, J., Horvath, S., 2022. A mammalian methylation array for profiling methylation levels at conserved sequences. Nat. Commun. 13, 783. https://doi.org/10.1038/s41467-022-28355-z

Askarova, S., Umbayev, B., Masoud, A.-R., Kaiyrlykyzy, A., Safarova, Y., Tsoy, A., Olzhayev, F., Kushugulova, A., 2020. The Links Between the Gut Microbiome, Aging, Modern Lifestyle and Alzheimer's Disease. Front. Cell. Infect. Microbiol. 10. https://doi.org/10.3389/fcimb.2020.00104

Aubry, L.M., Koons, D.N., Monnat, J.-Y., Cam, E., 2009. Consequences of recruitment decisions and heterogeneity on age-specific breeding success in a long-lived seabird. Ecology 90, 2491–2502. https://doi.org/10.1890/08-1475.1

Auer, S.K., Bassar, R.D., Salin, K., Metcalfe, N.B., 2016. Repeatability of metabolic rate is lower for animals living under field versus laboratory conditions. J. Exp. Biol. 219, 631–634. https://doi.org/10.1242/jeb.133678

Austad, S.N., 2006. Why women live longer than men: Sex differences in longevity. Gend. Med. 3, 79–92. https://doi.org/10.1016/S1550-8579(06)80198-1

Austad, S.N., Fischer, K.E., 2016. Sex Differences in Lifespan. Cell Metab. 23, 1022–1033. https://doi.org/10.1016/j.cmet.2016.05.019

Ayres, K.L., Booth, R.K., Hempelmann, J.A., Koski, K.L., Emmons, C.K., Baird, R.W., Balcomb-Bartok, K., Hanson, M.B., Ford, M.J., Wasser, S.K., 2012. Distinguishing the Impacts of Inadequate Prey and Vessel Traffic on an Endangered Killer Whale (Orcinus orca) Population. PLOS ONE 7, e36842. https://doi.org/10.1371/journal.pone.0036842

Azizi, F., 1978. Effect of dietary composition on fasting-induced changes in serum thyroid hormones and thyrotropin. Metab. - Clin. Exp. 27, 935–942. https://doi.org/10.1016/0026-0495(78)90137-3

Baayen, R.H., Davidson, D.J., Bates, D.M., 2008. Mixed-effects modeling with crossed random effects for subjects and items. J. Mem. Lang. 59, 390–412. https://doi.org/10.1016/j.jml.2007.12.005

Badal, V.D., Vaccariello, E.D., Murray, E.R., Yu, K.E., Knight, R., Jeste, D.V., Nguyen, T.T., 2020. The gut microbiome, aging, and longevity: a systematic review. Nutrients 12, 3759. https://doi.org/10.3390/nu12123759

Bahr, N.I., Palme, R., Möhle, U., Hodges, J.K., Heistermann, M., 2000. Comparative Aspects of the Metabolism and Excretion of Cortisol in Three Individual Nonhuman Primates. Gen. Comp. Endocrinol. 117, 427–438. https://doi.org/10.1006/gcen.1999.7431

Balasubramaniam, K., Beisner, B., Vandeleest, J., Atwill, E., McCowan, B., 2016. Social buffering and contact transmission: network connections have beneficial and detrimental effects on *Shigella* infection risk among captive rhesus macaques. PeerJ 4, e2630. https://doi.org/10.7717/peerj.2630

Bales, K.L., French, J.A., McWilliams, J., Lake, R.A., Dietz, J.M., 2006. Effects of social status, age, and season on androgen and cortisol levels in wild male golden lion tamarins (Leontopithecus rosalia). Horm. Behav. 49, 88–95. https://doi.org/10.1016/j.yhbeh.2005.05.006

Bana, B., Cabreiro, F., 2019. The microbiome and aging. Annu. Rev. Genet. 53, 239–261. https://doi.org/10.1146/annurev-genet-112618-043650

Baniel, A., Amato, K.R., Beehner, J.C., Bergman, T.J., Mercer, A., Perlman, R.F., Petrullo, L., Reitsema, L., Sams, S., Lu, A., Snyder-Mackler, N., 2021. Seasonal shifts in the gut microbiome indicate plastic responses to diet in wild geladas. Microbiome 9, 26. https://doi.org/10.1186/s40168-020-00977-9

Baniel, A., Petrullo, L., Mercer, A., Reitsema, L., Sams, S., Beehner, J.C., Bergman, T.J., Snyder-Mackler, N., Lu, A., 2022. Maternal effects on early-life gut microbiota maturation in a wild nonhuman primate. Curr. Biol. 32, 4508-4520.e6. https://doi.org/10.1016/j.cub.2022.08.037

Barr, D.J., Levy, R., Scheepers, C., Tily, H.J., 2013. Random effects structure for confirmatory hypothesis testing: keep it maximal. J. Mem. Lang. 68, 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Basolo, A., Begaye, B., Hollstein, T., Vinales, K.L., Walter, M., Santini, F., Krakoff, J., Piaggi, P., 2019. Effects of Short-term Fasting and Different Overfeeding Diets on Thyroid Hormones in Healthy Humans. Thyroid. https://doi.org/10.1089/thy.2019.0237

Basu, R., Singh, R., Basu, A., Johnson, C.M., Rizza, R.A., 2006. Effect of Nutrient Ingestion on Total-Body and Splanchnic Cortisol Production in Humans. Diabetes 55, 667–674. https://doi.org/10.2337/diabetes.55.03.06.db05-1335

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Beehner, J.C., Bergman, T.J., 2017. The next step for stress research in primates: To identify relationships between glucocorticoid secretion and fitness. Horm. Behav., Field endocrinology of nonhuman primates and humans 91, 68–83. https://doi.org/10.1016/j.yhbeh.2017.03.003

Behie, A.M., Pavelka, M.S.M., 2013. Interacting Roles of Diet, Cortisol Levels, and Parasites in Determining Population Density of Belizean Howler Monkeys in a Hurricane Damaged Forest Fragment, in: Marsh, L.K., Chapman, C.A. (Eds.), Primates in Fragments: Complexity and

Resilience, Developments in Primatology: Progress and Prospects. Springer, New York, NY, pp. 447–456. https://doi.org/10.1007/978-1-4614-8839-2_30

Behringer, V., Deimel, C., Hohmann, G., Negrey, J., Schaebs, F.S., Deschner, T., 2018. Applications for non-invasive thyroid hormone measurements in mammalian ecology, growth, and maintenance. Horm. Behav. 105, 66–85. https://doi.org/10.1016/j.yhbeh.2018.07.011

Behringer, V., Deschner, T., Murtagh, R., Stevens, J.M.G., Hohmann, G., 2014. Age-related changes in Thyroid hormone levels of bonobos and chimpanzees indicate heterochrony in development. J. Hum. Evol. 66, 83–88. https://doi.org/10.1016/j.jhevol.2013.09.008

Behringer, V., Stevens, J.M.G., Leendertz, F.H., Hohmann, G., Deschner, T., 2017. Validation of a Method for the Assessment of Urinary Neopterin Levels to Monitor Health Status in Non-human-primate Species. Front. Physiol. 8, 51. https://doi.org/10.3389/fphys.2017.00051

Behringer, V., Stevens, J.M.G., Wittig, R.M., Crockford, C., Zuberbühler, K., Leendertz, F.H., Deschner, T., 2019. Elevated neopterin levels in wild, healthy chimpanzees indicate constant investment in unspecific immune system. BMC Zool. 4, 2. https://doi.org/10.1186/s40850-019-0041-1

Belkaid, Y., Hand, T.W., 2014. Role of the microbiota in immunity and inflammation. Cell 157, 121–141. https://doi.org/10.1016/j.cell.2014.03.011

Bennett, G., Malone, M., Sauther, M.L., Cuozzo, F.P., White, B., Nelson, K.E., Stumpf, R.M., Knight, R., Leigh, S.R., Amato, K.R., 2016. Host age, social group, and habitat type influence the gut microbiota of wild ring-tailed lemurs (Lemur catta). Am. J. Primatol. 78, 883–892. https://doi.org/10.1002/ajp.22555

Berg, G., Rybakova, D., Fischer, D., Cernava, T., Vergès, M.-C.C., Charles, T., Chen, X., Cocolin, L., Eversole, K., Corral, G.H., Kazou, M., Kinkel, L., Lange, L., Lima, N., Loy, A., Macklin, J.A., Maguin, E., Mauchline, T., McClure, R., Mitter, B., Ryan, M., Sarand, I., Smidt, H., Schelkle, B., Roume, H., Kiran, G.S., Selvin, J., Souza, R.S.C. de, van Overbeek, L., Singh, B.K., Wagner, M., Walsh, A., Sessitsch, A., Schloter, M., 2020. Microbiome definition re-visited: old concepts and new challenges. Microbiome 8, 103. https://doi.org/10.1186/s40168-020-00875-0

Berghänel, A., Ostner, J., Schülke, O., 2011. Coalitions destabilize dyadic dominance relationships in male Barbary macaques (Macaca sylvanus). Behaviour 148, 1257–1275.

Bergman, T.J., Beehner, J.C., Cheney, D.L., Seyfarth, R.M., Whitten, P.L., 2005. Correlates of stress in free-ranging male chacma baboons, Papio hamadryas ursinus. Anim. Behav. 70, 703–713. https://doi.org/10.1016/j.anbehav.2004.12.017

Bergmann, N., Gyntelberg, F., Faber, J., 2014. The appraisal of chronic stress and the development of the metabolic syndrome: a systematic review of prospective cohort studies. Endocr. Connect. 3, R55–R80. https://doi.org/10.1530/EC-14-0031

Bergouignan, A., Habold, C., Rudwill, F., Gauquelin-Koch, G., Normand, S., Simon, C., Blanc, S., 2012. Urinary C-peptide Is Not an Accurate Bioindicator of Energy Balance in Humans. Obesity 20, 683–688. https://doi.org/10.1038/oby.2011.116

Biagi, E., Franceschi, C., Rampelli, S., Severgnini, M., Ostan, R., Turroni, S., Consolandi, C., Quercia, S., Scurti, M., Monti, D., Capri, M., Brigidi, P., Candela, M., 2016. Gut microbiota and extreme longevity. Curr. Biol. 26, 1480–1485. https://doi.org/10.1016/j.cub.2016.04.016

Bichet, C., Moiron, M., Matson, K.D., Vedder, O., Bouwhuis, S., 2022. Immunosenescence in the wild? A longitudinal study in a long-lived seabird. J. Anim. Ecol. 91, 458–469. https://doi.org/10.1111/1365-2656.13642

Björk, J.R., Dasari, M., Grieneisen, L., Archie, E.A., 2019. Primate microbiomes over time: Longitudinal answers to standing questions in microbiome research. Am. J. Primatol. 81, e22970. https://doi.org/10.1002/ajp.22970

Björk, J.R., Dasari, M.R., Roche, K., Grieneisen, L., Gould, T.J., Grenier, J.-C., Yotova, V., Gottel, N., Jansen, D., Gesquiere, L.R., Gordon, J.B., Learn, N.H., Wango, T.L., Mututua, R.S., Kinyua Warutere, J., Siodi, L., Mukherjee, S., Barreiro, L.B., Alberts, S.C., Gilbert, J.A., Tung, J., Blekhman, R., Archie, E.A., 2022. Synchrony and idiosyncrasy in the gut microbiome of wild baboons. Nat. Ecol. Evol. 6, 955–964. https://doi.org/10.1038/s41559-022-01773-4

Blacher, E., Tsai, C., Litichevskiy, L., Shipony, Z., Iweka, C.A., Schneider, K.M., Chuluun, B., Heller, H.C., Menon, V., Thaiss, C.A., Andreasson, K.I., 2022. Aging disrupts circadian gene regulation and function in macrophages. Nat. Immunol. 23, 229–236. https://doi.org/10.1038/s41590-021-01083-0

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. R. Soc. B Biol. Sci. 285, 20171934. https://doi.org/10.1098/rspb.2017.1934

Bolker, B.M., 2008. Ecological Models and Data in R. Princeton University Press. https://doi.org/10.2307/j.ctvcm4g37

Bonier, F., Martin, P.R., Moore, I.T., Wingfield, J.C., 2009a. Do baseline glucocorticoids predict fitness? Trends Ecol. Evol. 24, 634–642. https://doi.org/10.1016/j.tree.2009.04.013

Bonier, F., Moore, I.T., Martin, P.R., Robertson, R.J., 2009b. The relationship between fitness and baseline glucocorticoids in a passerine bird. Gen. Comp. Endocrinol., 9th International Symposium on Avian Endocrinology 163, 208–213. https://doi.org/10.1016/j.ygcen.2008.12.013

Born, J., Ditschuneit, I., Schreiber, M., Dodt, C., Fehm, H.L., 1995. Effects of age and gender on pituitary–adrenocortical responsiveness in humans. Eur. J. Endocrinol. 132, 705–711. https://doi.org/10.1530/eje.0.1320705

Borries, C., Koenig, A., 2008. Reproductive and Behavioral Characteristics of Aging in Female Asian Colobines. Primate Reprod. Aging 36, 80–102. https://doi.org/10.1159/000137686

Borries, C., Lu, A., Ossi-Lupo, K., Larney, E., Koenig, A., 2011. Primate life histories and dietary adaptations: a comparison of asian colobines and macaques. Am. J. Phys. Anthropol. 144, 286–299. https://doi.org/10.1002/ajpa.21403

Bosco, N., Noti, M., 2021. The aging gut microbiome and its impact on host immunity. Genes Immun. 22, 289–303. https://doi.org/10.1038/s41435-021-00126-8

Boswell, T., Woods, S.C., Kenagy, G.J., 1994. Seasonal Changes in Body Mass, Insulin, and Glucocorticoids of Free-Living Golden-Mantled Ground Squirrels. Gen. Comp. Endocrinol. 96, 339–346. https://doi.org/10.1006/gcen.1994.1189

Bouwhuis, S., Sheldon, B. c., Verhulst, S., Charmantier, A., 2009. Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. Proc. R. Soc. B Biol. Sci. 276, 2769–2777. https://doi.org/10.1098/rspb.2009.0457

Bowerman, K.L., Knowles, S.C.L., Bradley, J.E., Baltrūnaitė, L., Lynch, M.D.J., Jones, K.M., Hugenholtz, P., 2021. Effects of laboratory domestication on the rodent gut microbiome. ISME Commun. 1, 1–14. https://doi.org/10.1038/s43705-021-00053-9

Brent, L.J.N., Ruiz-Lambides, A., Platt, M.L., 2017. Family network size and survival across the lifespan of female macaques. Proc. R. Soc. B Biol. Sci. 284, 20170515. https://doi.org/10.1098/rspb.2017.0515

Brent, L.J.N., Semple, S., Dubuc, C., Heistermann, M., MacLarnon, A., 2011. Social capital and physiological stress levels in free-ranging adult female rhesus macaques. Physiol. Behav. 102, 76–83. https://doi.org/10.1016/j.physbeh.2010.09.022

Briard, L., Ezenwa, V.O., 2021. Parasitism and host social behaviour: a meta-analysis of insights derived from social network analysis. Anim. Behav. 172, 171–182. https://doi.org/10.1016/j.anbehav.2020.11.010

Bronikowski, A.M., Meisel, R.P., Biga, P.R., Walters, J.R., Mank, J.E., Larschan, E., Wilkinson, G.S., Valenzuela, N., Conard, A.M., de Magalhães, J.P., Duan, J. (Ellie), Elias, A.E., Gamble, T., Graze, R.M., Gribble, K.E., Kreiling, J.A., Riddle, N.C., 2022. Sex-specific aging in animals: Perspective and future directions. Aging Cell 21, e13542. https://doi.org/10.1111/acel.13542

Brooks, M., E., Kristensen, K., Benthem, K., J. ,van, Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M., Bolker, B., M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J. 9, 378. https://doi.org/10.32614/RJ-2017-066

Brown, J.L., Kersey, D.C., Freeman, E.W., Wagener, T., 2010. Assessment of diurnal urinary cortisol excretion in Asian and African elephants using different endocrine methods. Zoo Biol. 29, 274–283. https://doi.org/10.1002/zoo.20268

Brown, J.L., Wemmer, C.M., Lehnhardt, J., 1995. Urinary cortisol analysis for monitoring adrenal activity in elephants. Zoo Biol. 14, 533–542. https://doi.org/10.1002/zoo.1430140606

Buck, J.C., Lutterschmidt, W.I., 2017. Parasite abundance decreases with host density: evidence of the encounter-dilution effect for a parasite with a complex life cycle. Hydrobiologia 784, 201–210. https://doi.org/10.1007/s10750-016-2874-8

Bulterijs, S., Hull, R.S., Björk, V.C.E., Roy, A.G., 2015. It is time to classify biological aging as a disease. Front. Genet. 6.

Burke, C.W., Eastman, C.J., 1974. Thyroid hormones. Br. Med. Bull. 30, 93–99. https://doi.org/10.1093/oxfordjournals.bmb.a071175

Burke, C.W., Shakespear, R.A., 1976. Triiodothyronine and Thyroxine in Urine. II. Renal Handling, and Effect of Urinary Protein. J. Clin. Endocrinol. Metab. 42, 504–513. https://doi.org/10.1210/jcem-42-3-504

Burke, C.W., Shakespear, R.A., Russell Fraser, T., 1972. Measurement of thyroxine and triiodothyronine in human urine. The Lancet, Originally published as Volume 2, Issue 7788 300, 1177–1179. https://doi.org/10.1016/S0140-6736(72)92597-4

Burton, T., Killen, S.S., Armstrong, J.D., Metcalfe, N.B., 2011. What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? Proc. R. Soc. B Biol. Sci. 278, 3465–3473. https://doi.org/10.1098/rspb.2011.1778

Butler, M.J., IV, Behringer, D.C., 2021. Behavioral Immunity and Social Distancing in the Wild: The Same as in Humans? BioScience. https://doi.org/10.1093/biosci/biaa176

Buyken, A.E., Kellerhoff, Y., Hahn, S., Kroke, A., Remer, T., 2006. Urinary C-Peptide Excretion in Free-Living Healthy Children Is Related to Dietary Carbohydrate Intake but Not to the Dietary Glycemic Index. J. Nutr. 136, 1828–1833. https://doi.org/10.1093/jn/136.7.1828

Cammarota, G., Ianiro, G., Gasbarrini, A., 2014. Fecal microbiota transplantation for the treatment of Clostridium difficile infection: a systematic review. J. Clin. Gastroenterol. 48, 693–702. https://doi.org/10.1097/MCG.0000000000000046

Campos, F.A., Altmann, J., Cords, M., Fedigan, L.M., Lawler, R., Lonsdorf, E.V., Stoinski, T.S., Strier, K.B., Bronikowski, A.M., Pusey, A.E., Alberts, S.C., 2022. Female reproductive aging in seven primate species: Patterns and consequences. Proc. Natl. Acad. Sci. 119, e2117669119. https://doi.org/10.1073/pnas.2117669119

Campos, F.A., Archie, E.A., Gesquiere, L.R., Tung, J., Altmann, J., Alberts, S.C., 2021. Glucocorticoid exposure predicts survival in female baboons. Sci. Adv. 7, eabf6759. https://doi.org/10.1126/sciadv.abf6759

Capitanio, J.P., Cole, S.W., 2015. Social instability and immunity in rhesus monkeys: the role of the sympathetic nervous system. Philos. Trans. R. Soc. B Biol. Sci. 370. https://doi.org/10.1098/rstb.2014.0104

Capitanio, J.P., Mendoza, S.P., Lerche, N.W., Mason, W.A., 1998. Social stress results in altered glucocorticoid regulation and shorter survival in simian acquired immune deficiency syndrome. Proc. Natl. Acad. Sci. 95, 4714–4719. https://doi.org/10.1073/pnas.95.8.4714

Cardini, B.B., Freund, A.M., 2020. More or less energy with age? A motivational life-span perspective on subjective energy, exhaustion, and opportunity costs. Psychol. Aging 35, 369–384. https://doi.org/10.1037/pag0000445

Carlson, H.E., Drenick, E.J., Chopra, I.J., Hershman, J.M., 1977. Alterations in Basal and TRH-Stimulated Serum Levels of Thyrotropin, Prolactin, and Thyroid Hormones in Starved Obese Men. J. Clin. Endocrinol. Metab. 45, 707–713. https://doi.org/10.1210/jcem-45-4-707

Carstensen, L.L., 2019. Integrating cognitive and emotion paradigms to address the paradox of aging. Cogn. Emot. 33, 119–125. https://doi.org/10.1080/02699931.2018.1543181

Catry Paulo, Phillips Richard A, Phalan Ben, Croxall John P, 2006. Senescence effects in an extremely long-lived bird: the grey-headed albatross Thalassarche chrysostoma. Proc. R. Soc. B Biol. Sci. 273, 1625–1630. https://doi.org/10.1098/rspb.2006.3482

Cauter, E.V., Shapiro, E.T., Tillil, H., Polonsky, K.S., 1992. Circadian modulation of glucose and insulin responses to meals: relationship to cortisol rhythm. Am. J. Physiol.-Endocrinol. Metab. https://doi.org/10.1152/ajpendo.1992.262.4.E467

Cerroni, A.M., Tomlinson, G.A., Turnquist, J.E., Grynpas, M.D., 2000. Bone mineral density, osteopenia, and osteoporosis in the rhesus macaques of Cayo Santiago. Am. J. Phys. Anthropol. 113, 389–410. https://doi.org/10.1002/1096-8644(200011)113:3<389::AID-AJPA9>3.0.CO;2-I

Chapais, B., 1988. Experimental matrilineal inheritance of rank in female Japanese macaques. Anim. Behav. 36, 1025–1037. https://doi.org/10.1016/S0003-3472(88)80062-9

Chapais, B., Girard, M., Primi, G., 1991. Non-kin alliances, and the stability of matrilineal dominance relations in Japanese macaques. Anim. Behav. 41, 481–491. https://doi.org/10.1016/S0003-3472(05)80851-6

Charles, S.T., Carstensen, L.L., 2010. Social and emotional aging. Annu. Rev. Psychol. 61, 383–409. https://doi.org/10.1146/annurev.psych.093008.100448

Charmandari, E., Tsigos, C., Chrousos, G., 2005. Endocrinology of the Stress Response. Annu. Rev. Physiol. 67, 259–284. https://doi.org/10.1146/annurev.physiol.67.040403.120816

Charpentier, M.J.E., Givalois, L., Faurie, C., Soghessa, O., Simon, F., Kappeler, P.M., 2018. Seasonal glucocorticoid production correlates with a suite of small-magnitude environmental, demographic, and physiological effects in mandrills. Am. J. Phys. Anthropol. 165, 20–33. https://doi.org/10.1002/ajpa.23329

Chatzitomaris, A., Hoermann, R., Midgley, J.E., Hering, S., Urban, A., Dietrich, B., Abood, A., Klein, H.H., Dietrich, J.W., 2017. Thyroid Allostasis–Adaptive Responses of Thyrotropic Feedback Control to Conditions of Strain, Stress, and Developmental Programming. Front. Endocrinol. 8. https://doi.org/10.3389/fendo.2017.00163

Chen, S., Zhou, Y., Chen, Y., Gu, J., 2018. fastp: an ultra-fast all-in-one FASTQ preprocessor. Bioinformatics 34, i884–i890. https://doi.org/10.1093/bioinformatics/bty560

Cheynel, L., Lemaître, J.-F., Gaillard, J.-M., Rey, B., Bourgoin, G., Ferté, H., Jégo, M., Débias, F., Pellerin, M., Jacob, L., Gilot-Fromont, E., 2017. Immunosenescence patterns differ between populations but not between sexes in a long-lived mammal. Sci. Rep. 7, 13700. https://doi.org/10.1038/s41598-017-13686-5

Chiou, K.L., Montague, M.J., Goldman, E.A., Watowich, M.M., Sams, S.N., Song, J., Horvath, J.E., Sterner, K.N., Ruiz-Lambides, A.V., Martínez, M.I., Higham, J.P., Brent, L.J.N., Platt, M.L., Snyder-Mackler, N., 2020. Rhesus macaques as a tractable physiological model of human ageing. Philos. Trans. R. Soc. B Biol. Sci. 375, 20190612. https://doi.org/10.1098/rstb.2019.0612

Claesson, M.J., Cusack, S., O'Sullivan, O., Greene-Diniz, R., Weerd, H. de, Flannery, E., Marchesi, J.R., Falush, D., Dinan, T., Fitzgerald, G., Stanton, C., Sinderen, D. van, O'Connor, M., Harnedy, N., O'Connor, K., Henry, C., O'Mahony, D., Fitzgerald, A.P., Shanahan, F., Twomey, C., Hill, C., Ross, R.P., O'Toole, P.W., 2011. Composition, variability, and temporal stability of the intestinal microbiota of the elderly. Proc. Natl. Acad. Sci. 108, 4586–4591. https://doi.org/10.1073/pnas.1000097107

Claesson, M.J., Jeffery, I.B., Conde, S., Power, S.E., O'Connor, E.M., Cusack, S., Harris, H.M.B., Coakley, M., Lakshminarayanan, B., O'Sullivan, O., Fitzgerald, G.F., Deane, J., O'Connor, M., Harnedy, N., O'Connor, K., O'Mahony, D., van Sinderen, D., Wallace, M., Brennan, L., Stanton, C., Marchesi, J.R., Fitzgerald, A.P., Shanahan, F., Hill, C., Ross, R.P., O'Toole, P.W., 2012. Gut microbiota composition correlates with diet and health in the elderly. Nature 488, 178–184. https://doi.org/10.1038/nature11319

Clayton, J.B., Gomez, A., Amato, K., Knights, D., Travis, D.A., Blekhman, R., Knight, R., Leigh, S., Stumpf, R., Wolf, T., Glander, K.E., Cabana, F., Johnson, T.J., 2018. The gut microbiome of

nonhuman primates: lessons in ecology and evolution. Am. J. Primatol. 80, e22867. https://doi.org/10.1002/ajp.22867

Clegg, A., Young, J., Iliffe, S., Rikkert, M.O., Rockwood, K., 2013. Frailty in elderly people. The Lancet 381, 752–762. https://doi.org/10.1016/S0140-6736(12)62167-9

Clutton-Brock, T., Sheldon, B.C., 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends Ecol. Evol. 25, 562–573. https://doi.org/10.1016/j.tree.2010.08.002

Clutton-Brock, T.H., Isvaran, K., 2007. Sex differences in ageing in natural populations of vertebrates. Proc. R. Soc. B Biol. Sci. 274, 3097–3104. https://doi.org/10.1098/rspb.2007.1138

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 BBA - Mol. Basis Dis., Model Systems of Aging 1864, 2680–2689. https://doi.org/10.1016/j.bbadis.2017.05.028

Cohen, A.A., Coste, C.F.D., Li, X.-Y., Bourg, S., Pavard, S., 2020. Are trade-offs really the key drivers of ageing and life span? Funct. Ecol. 34, 153–166. https://doi.org/10.1111/1365-2435.13444

Cohen, A.A., Milot, E., Yong, J., Seplaki, C.L., Fülöp, T., Bandeen-Roche, K., Fried, L.P., 2013. A novel statistical approach shows evidence for multi-system physiological dysregulation during aging. Mech. Ageing Dev. 134, 110–117. https://doi.org/10.1016/j.mad.2013.01.004

Cohen, S., Janicki-Deverts, D., Doyle, W.J., Miller, G.E., Frank, E., Rabin, B.S., Turner, R.B., 2012. Chronic stress, glucocorticoid receptor resistance, inflammation, and disease risk. Proc. Natl. Acad. Sci. 109, 5995–5999. https://doi.org/10.1073/pnas.1118355109

Cohen, S., Janicki-Deverts, D., Turner, R.B., Doyle, W.J., 2015. Does Hugging Provide Stress-Buffering Social Support? A Study of Susceptibility to Upper Respiratory Infection and Illness. Psychol. Sci. 26, 135–147. https://doi.org/10.1177/0956797614559284

Cohen, S., Kaplan, J.R., Cunnick, J.E., Manuck, S.B., Rabin, B.S., 1992. Chronic Social Stress, Affiliation, and Cellular Immune Response in Nonhuman Primates. Psychol. Sci. 3, 301–305. https://doi.org/10.1111/j.1467-9280.1992.tb00677.x

Cohen, S., Line, S., Manuck, S.B., Rabin, B.S., Heise, E.R., Kaplan, J.R., 1997. Chronic Social Stress, Social Status, and Susceptibility to Upper Respiratory Infections in Nonhuman Primates. Psychosom. Med. 59, 213.

Cohen, S., Wills, T.A., 1985. Stress, social support, and the buffering hypothesis. Psychol. Bull. 98, 310–357. https://doi.org/10.1037/0033-2909.98.2.310

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. 201612191. https://doi.org/10.1073/pnas.1612191113

Cole, S.W., Hawkley, L.C., Arevalo, J.M., Sung, C.Y., Rose, R.M., Cacioppo, J.T., 2007. Social regulation of gene expression in human leukocytes. Genome Biol. 8, R189. https://doi.org/10.1186/gb-2007-8-9-r189

Colman, R.J., McKiernan, S.H., Aiken, J.M., Weindruch, R., 2005. Muscle mass loss in Rhesus monkeys: Age of onset. Exp. Gerontol. 40, 573–581. https://doi.org/10.1016/j.exger.2005.05.001

Cooper, E.B., Watowich, M.M., Beeby, N., Whalen, C., Cayo Biobank Research Unit, Montague, M.J., Brent, L.J.N., Snyder-Mackler, N., Higham, J.P., 2022. Concentrations of urinary neopterin, but not suPAR, positively correlate with age in rhesus macaques. Front. Ecol. Evol. 10.

Cornwell, B., 2009. Good health and the bridging of structural holes. Soc. Netw. 31, 92–103. https://doi.org/10.1016/j.socnet.2008.10.005

Cornwell, B., Goldman, A., Laumann, E.O., 2021. Homeostasis Revisited: Patterns of Stability and Rebalancing in Older Adults' Social Lives. J. Gerontol. Ser. B 76, 778–789. https://doi.org/10.1093/geronb/gbaa026

Corr, J., 2003. Social behavior in aged rhesus macaques. Coll. Antropol. 27, 87–94.

Côté, I.M., Poulin, R., 1995. Parasitism and group size in social animals: a meta-analysis. Behav. Ecol. 6, 159–165. https://doi.org/10.1093/beheco/6.2.159

Coyte, K.Z., Schluter, J., Foster, K.R., 2015. The ecology of the microbiome: Networks, competition, and stability. Science 350, 663–666. https://doi.org/10.1126/science.aad2602

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

Creel, S., 2001. Social dominance and stress hormones. Trends Ecol. Evol. 16, 491–497.

Creel, S., MarushaCreel, N., Monfort, S.L., 1996. Social stress and dominance. Nature 379, 212. https://doi.org/10.1038/379212a0

Crespi, E.J., Williams, T.D., Jessop, T.S., Delehanty, B., 2013. Life history and the ecology of stress: how do glucocorticoid hormones influence life-history variation in animals? Funct. Ecol. 27, 93–106. https://doi.org/10.1111/1365-2435.12009

Cristóbal-Azkarate, J., Maréchal, L., Semple, S., Majolo, B., MacLarnon, A., 2016. Metabolic strategies in wild male Barbary macaques: evidence from faecal measurement of thyroid hormone. Biol. Lett. https://doi.org/10.1098/rsbl.2016.0168

Crockford, C., Wittig, R.M., Whitten, P.L., Seyfarth, R.M., Cheney, D.L., 2008. Social stressors and coping mechanisms in wild female baboons (Papio hamadryas ursinus). Horm. Behav. 53, 254–265. https://doi.org/10.1016/j.yhbeh.2007.10.007

Croft, D.P., Brent, L.J.N., Franks, D.W., Cant, M.A., 2015. The evolution of prolonged life after reproduction. Trends Ecol. Evol. 30, 407–416. https://doi.org/10.1016/j.tree.2015.04.011

Cumming, E., Henry, W.E., 1961. Growing Old, the Process of Disengagement. Basic Books.

da Silva, R., Conde, D.A., Baudisch, A., Colchero, F., 2022. Slow and negligible senescence among testudines challenges evolutionary theories of senescence. Science 376, 1466–1470. https://doi.org/10.1126/science.abl7811

Danforth, E., Burger, A.G., 1989. The Impact of Nutrition on Thyroid Hormone Physiology and Action. Annu. Rev. Nutr. 9, 201–227. https://doi.org/10.1146/annurev.nu.09.070189.001221

Dansereau, G., Wey, T.W., Legault, V., Brunet, M.A., Kemnitz, J.W., Ferrucci, L., Cohen, A.A., 2019. Conservation of physiological dysregulation signatures of aging across primates. Aging Cell 18, e12925. https://doi.org/10.1111/acel.12925

Dauncey, M.J., 1990. Thyroid hormones and thermogenesis. Proc. Nutr. Soc. 49, 203–215. https://doi.org/10.1079/PNS19900024

Dauncey, M.J., Ramsden, D.B., Kapadi, A.L., Macari, M., Ingram, D.L., 1983. Increase in plasma concentrations of 3,5,3'-triiodothyronine and thyroxine after a meal, and its dependence on energy intake. Horm. Metab. Res. Horm. Stoffwechselforschung Horm. Métab. 15, 499–502. https://doi.org/10.1055/s-2007-1018768

de la Cuesta-Zuluaga, J., Kelley, S.T., Chen, Y., Escobar, J.S., Mueller, N.T., Ley, R.E., McDonald, D., Huang, S., Swafford, A.D., Knight, R., Thackray, V.G., 2019. Age- and Sex-Dependent Patterns of Gut Microbial Diversity in Human Adults. mSystems 4, e00261-19. https://doi.org/10.1128/mSystems.00261-19

De Magalhães, J.P., Costa, J., 2009. A database of vertebrate longevity records and their relation to other life-history traits. J. Evol. Biol. 22, 1770–1774. https://doi.org/10.1111/j.1420-9101.2009.01783.x

De Moor, D., Roos, C., Ostner, J., Schülke, O., 2020. Female Assamese macaques bias their affiliation to paternal and maternal kin. Behav. Ecol. 31, 493–507. https://doi.org/10.1093/beheco/arz213

De Nys, H.M., Löhrich, T., Wu, D., Calvignac-Spencer, S., Leendertz, F.H., 2017. Wild African great apes as natural hosts of malaria parasites: current knowledge and research perspectives. Primate Biol. 4, 47–59. https://doi.org/10.5194/pb-4-47-2017

Defolie, C., Merkling, T., Fichtel, C., 2020. Patterns and variation in the mammal parasite–glucocorticoid relationship. Biol. Rev. 95, 74–93. https://doi.org/10.1111/brv.12555

Degnan, P.H., Pusey, A.E., Lonsdorf, E.V., Goodall, J., Wroblewski, E.E., Wilson, M.L., Rudicell, R.S., Hahn, B.H., Ochman, H., 2012. Factors associated with the diversification of the gut microbial

communities within chimpanzees from Gombe National Park. Proc. Natl. Acad. Sci. 109, 13034–13039. https://doi.org/10.1073/pnas.1110994109

Denryter, K., Conner, M.M., Stephenson, T.R., German, D.W., Monteith, K.L., 2022. Survival of the fattest: How body fat and migration influence survival in highly seasonal environments. Funct. Ecol. 36, 2569–2579. https://doi.org/10.1111/1365-2435.14151

Depping, M.K., Freund, A.M., 2011. Normal Aging and Decision Making: The Role of Motivation. Hum. Dev. 54, 349–367.

Deschner, T., Hohmann, G., Ortmann, S., Schaebs, F.S., Behringer, V., 2020. Urinary total T3 levels as a method to monitor metabolic changes in relation to variation in caloric intake in captive bonobos (Pan paniscus). Gen. Comp. Endocrinol. 285, 113290. https://doi.org/10.1016/j.ygcen.2019.113290

Deschner, T., Kratzsch, J., Hohmann, G., 2008. Urinary C-peptide as a method for monitoring body mass changes in captive bonobos (Pan paniscus). Horm. Behav. 54, 620–626. https://doi.org/10.1016/j.yhbeh.2008.06.005

Devaux, C.A., Mediannikov, O., Medkour, H., Raoult, D., 2019. Infectious Disease Risk Across the Growing Human-Non Human Primate Interface: A Review of the Evidence. Front. Public Health 7, 305. https://doi.org/10.3389/fpubh.2019.00305

Diamond, P., LeBlanc, J., 1987. Hormonal control of postprandial thermogenesis in dogs. Am. J. Physiol.-Endocrinol. Metab. 253, E521–E529. https://doi.org/10.1152/ajpendo.1987.253.5.E521

Dias, P.A.D., Coyohua-Fuentes, A., Canales-Espinosa, D., Chavira-Ramírez, R., Rangel-Negrín, A., 2017. Hormonal correlates of energetic condition in mantled howler monkeys. Horm. Behav. 94, 13–20. https://doi.org/10.1016/j.yhbeh.2017.06.003

Dibakou, S.E., Souza, A., Boundenga, L., Givalois, L., Mercier-Delarue, S., Simon, F., Prugnolle, F., Huchard, E., Charpentier, M.JE., 2020. Ecological, parasitological and individual determinants of plasma neopterin levels in a natural mandrill population. Int. J. Parasitol. Parasites Wildl. 11, 198–206. https://doi.org/10.1016/j.ijppaw.2020.02.009

Dickens, M.J., Romero, L.M., 2013. A consensus endocrine profile for chronically stressed wild animals does not exist. Gen. Comp. Endocrinol. 191, 177–189. https://doi.org/10.1016/j.ygcen.2013.06.014

Dobson, A.J., Barnett, A., 2008. An Introduction to Generalized Linear Models. CRC Press.

Dodt, C., Dittmann, J., Hruby, J., Späth-Schwalbe, E., Born, J., Schüttler, R., Fehm, H.L., 1991. Different regulation of adrenocorticotropin and cortisol secretion in young, mentally healthy elderly and patients with senile dementia of Alzheimer's type. J. Clin. Endocrinol. Metab. 72, 272–276. https://doi.org/10.1210/jcem-72-2-272

Donovan, M., Liu, Y., Wang, Z., 2018. Anxiety-like behavior and neuropeptide receptor expression in male and female prairie voles: The effects of stress and social buffering. Behav. Brain Res. 342, 70–78. https://doi.org/10.1016/j.bbr.2018.01.015

Douyon, L., Schteingart, D.E., 2002. Effect of obesity and starvation on thyroid hormone, growth hormone, and cortisol secretion. Endocrinol. Metab. Clin. North Am. 31, 173–189. https://doi.org/10.1016/S0889-8529(01)00023-8

Duan, J., Yin, B., Li, W., Chai, T., Liang, W., Huang, Y., Tan, X., Zheng, P., Wu, J., Li, Yifan, Li, Yan, Zhou, W., Xie, P., 2019. Age-related changes in microbial composition and function in cynomolgus macaques. Aging 11, 12080–12096. https://doi.org/10.18632/aging.102541

Duboscq, J., Romano, V., Sueur, C., MacIntosh, A.J.J., 2016. Network centrality and seasonality interact to predict lice load in a social primate. Sci. Rep. 6, 22095. https://doi.org/10.1038/srep22095

Duffield, K.R., Bowers, E.K., Sakaluk, S.K., Sadd, B.M., 2017. A dynamic threshold model for terminal investment. Behav. Ecol. Sociobiol. 71, 185. https://doi.org/10.1007/s00265-017-2416-z

Eales, J.G., 1988. The Influence of Nutritional State on Thyroid Function in Various Vertebrates. Integr. Comp. Biol. 28, 351–362. https://doi.org/10.1093/icb/28.2.351

Edgar, R.C., 2016. UNOISE2: improved error-correction for Illumina 16S and ITS amplicon sequencing. https://doi.org/10.1101/081257

Elliott, K.H., O'Reilly, K.M., Hatch, S.A., Gaston, A.J., Hare, J.F., Anderson, W.G., 2014. The prudent parent meets old age: A high stress response in very old seabirds supports the terminal restraint hypothesis. Horm. Behav. 66, 828–837. https://doi.org/10.1016/j.yhbeh.2014.11.001

Ellis, S., Johnstone, R.A., Cant, M.A., Franks, D.W., Weiss, M.N., Alberts, S.C., Balcomb, K.C., Benton, C.H., Brent, L.J.N., Crockford, C., Davidian, E., Delahay, R.J., Ellifrit, D.K., Höner, O.P., Meniri, M., McDonald, R.A., Nichols, H.J., Thompson, F.J., Vigilant, L., Wittig, R.M., Croft, D.P., 2022. Patterns and consequences of age-linked change in local relatedness in animal societies. Nat. Ecol. Evol. 6, 1766–1776. https://doi.org/10.1038/s41559-022-01872-2

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. R. Soc. B Biol. Sci. 286, 20191991. https://doi.org/10.1098/rspb.2019.1991

Emery Thompson, M., 2017. Energetics of feeding, social behavior, and life history in non-human primates. Horm. Behav., Field endocrinology of nonhuman primates and humans 91, 84–96. https://doi.org/10.1016/j.yhbeh.2016.08.009

Emery Thompson, M., Fox, S.A., Berghänel, A., Sabbi, K.H., Phillips-Garcia, S., Enigk, D.K., Otali, E., Machanda, Z.P., Wrangham, R.W., Muller, M.N., 2020a. Wild chimpanzees exhibit humanlike aging of glucocorticoid regulation. Proc. Natl. Acad. Sci. 117, 8424–8430. https://doi.org/10.1073/pnas.1920593117

Emery Thompson, M., Machanda, Z.P., Fox, S.A., Sabbi, K.H., Otali, E., Thompson González, N., Muller, M.N., Wrangham, R.W., 2020b. Evaluating the impact of physical frailty during ageing in wild chimpanzees (Pan troglodytes schweinfurthii). Philos. Trans. R. Soc. B Biol. Sci. 375, 20190607. https://doi.org/10.1098/rstb.2019.0607

Emery Thompson, M., Muller, M.N., Kahlenberg, S.M., Wrangham, R.W., 2010. Dynamics of social and energetic stress in wild female chimpanzees. Horm. Behav. 58, 440–449. https://doi.org/10.1016/j.yhbeh.2010.05.009

Estrada, A., Garber, P.A., Rylands, A.B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekaris, K.A.-I., Nijman, V., Heymann, E.W., Lambert, J.E., Rovero, F., Barelli, C., Setchell, J.M., Gillespie, T.R., Mittermeier, R.A., Arregoitia, L.V., de Guinea, M., Gouveia, S., Dobrovolski, R., Shanee, S., Shanee, N., Boyle, S.A., Fuentes, A., MacKinnon, K.C., Amato, K.R., Meyer, A.L.S., Wich, S., Sussman, R.W., Pan, R., Kone, I., Li, B., 2017. Impending extinction crisis of the world's primates: Why primates matter. Sci. Adv. 3, e1600946. https://doi.org/10.1126/sciadv.1600946

Evans, I.E.M., Martyr, A., Collins, R., Brayne, C., Clare, L., 2019. Social Isolation and Cognitive Function in Later Life: A Systematic Review and Meta-Analysis. J. Alzheimers Dis. JAD 70, S119–S144. https://doi.org/10.3233/JAD-180501

Ezenwa, V., 2004. Host social behavior and parasitic infection: a multifactorial approach. Behav. Ecol. 15, 446–454. https://doi.org/10.1093/beheco/arh028

Ezenwa, V., Archie, E.A., Craft, M.E., Hawley, D.M., Martin, L.B., Moore, J., White, L., 2016a. Host behaviour–parasite feedback: an essential link between animal behaviour and disease ecology. Proc. R. Soc. B Biol. Sci. 283, 20153078. https://doi.org/10.1098/rspb.2015.3078

Ezenwa, V., Gerardo, N.M., Inouye, D.W., Medina, M., Xavier, J.B., 2012. Animal Behavior and the Microbiome. Science 338, 198–199. https://doi.org/10.1126/science.1227412

Ezenwa, V., Ghai, R.R., McKay, A.F., Williams, A.E., 2016b. Group living and pathogen infection revisited. Curr. Opin. Behav. Sci., Behavioral ecology 12, 66–72. https://doi.org/10.1016/j.cobeha.2016.09.006

Ezenwa, V., Worsley-Tonks, K.E.L., 2018. Social living simultaneously increases infection risk and decreases the cost of infection. Proc. R. Soc. B Biol. Sci. 285, 20182142. https://doi.org/10.1098/rspb.2018.2142

Faith, J.J., Guruge, J.L., Charbonneau, M., Subramanian, S., Seedorf, H., Goodman, A.L., Clemente, J.C., Knight, R., Heath, A.C., Leibel, R.L., Rosenbaum, M., Gordon, J.I., 2013. The long-term stability of the human gut microbiota. Science 341, 1237439. https://doi.org/10.1126/science.1237439

Fay, R., Martin, J., Plard, F., 2022. Distinguishing within- from between-individual effects: How to use the within-individual centring method for quadratic patterns. J. Anim. Ecol. 91, 8–19. https://doi.org/10.1111/1365-2656.13606

Fay, R., Ravussin, P.-A., Arrigo, D., von Rönn, J.A.C., Schaub, M., 2021. Age-specific reproduction in female pied flycatchers: evidence for asynchronous aging. Oecologia 196, 723–734. https://doi.org/10.1007/s00442-021-04963-2

Fedurek, P., McFarland, R., Majolo, B., Lehmann, J., 2022. Social responses to the natural loss of individuals in Barbary macaques. Mamm. Biol. https://doi.org/10.1007/s42991-022-00283-x

Ferrari, E., Cravello, L., Muzzoni, B., Casarotti, D., Paltro, M., Solerte, S.B., Fioravanti, M., Cuzzoni, G., Pontiggia, B., Magri, F., 2001. Age-related changes of the hypothalamic-pituitary-adrenal axis: pathophysiological correlates. Eur. J. Endocrinol. 144, 319–329. https://doi.org/10.1530/eje.0.1440319

Finn, K.R., Silk, M.J., Porter, M.A., Pinter-Wollman, N., 2019. The use of multilayer network analysis in animal behaviour. Anim. Behav. 149, 7–22. https://doi.org/10.1016/j.anbehav.2018.12.016

Fischer, J., Kitchen, D.M., Seyfarth, R.M., Cheney, D.L., 2004. Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. Behav. Ecol. Sociobiol. 56, 140–148. https://doi.org/10.1007/s00265-003-0739-4

Flores, G.E., Caporaso, J.G., Henley, J.B., Rideout, J.R., Domogala, D., Chase, J., Leff, J.W., Vázquez-Baeza, Y., Gonzalez, A., Knight, R., Dunn, R.R., Fierer, N., 2014. Temporal variability is a personalized feature of the human microbiome. Genome Biol. 15, 531. https://doi.org/10.1186/s13059-014-0531-y

Foerster, S., Cords, M., Monfort, S.L., 2012. Seasonal Energetic Stress in a Tropical Forest Primate: Proximate Causes and Evolutionary Implications. PLoS ONE 7. https://doi.org/10.1371/journal.pone.0050108

Fogel, A.S., Oduor, P.O., Nyongesa, A.W., Kimwele, C.N., Alberts, S.C., Archie, E.A., Tung, J., 2023. Ecology and age, but not genetic ancestry, predict fetal loss in a wild baboon hybrid zone. Am. J. Biol. Anthropol. 180, 618–632. https://doi.org/10.1002/ajpa.24686

Fontana, L., Partridge, L., 2015. Promoting Health and Longevity through Diet: From Model Organisms to Humans. Cell 161, 106–118. https://doi.org/10.1016/j.cell.2015.02.020

Fontenelle, L.C., Feitosa, M.M., Severo, J.S., Freitas, T.E.C., Morais, J.B.S., Torres-Leal, F.L., Henriques, G.S., Marreiro, D. do N., 2016. Thyroid Function in Human Obesity: Underlying Mechanisms. Horm. Metab. Res. 48, 787–794. https://doi.org/10.1055/s-0042-121421

Forstmeier, W., Schielzeth, H., 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. Behav. Ecol. Sociobiol. 65, 47–55. https://doi.org/10.1007/s00265-010-1038-5

Forsum, E., Hillman, P.E., Nesheim, M.C., 1981. Effect of Energy Restriction on Total Heat Production, Basal Metabolic Rate, and Specific Dynamic Action of Food in Rats. J. Nutr. 111, 1691–1697. https://doi.org/10.1093/jn/111.10.1691

Fox, J., Weisberg, S., 2018. An R Companion to Applied Regression. SAGE Publications.

Franceschi, C., Garagnani, P., Vitale, G., Capri, M., Salvioli, S., 2017. Inflammaging and 'Garb-aging.' Trends Endocrinol. Metab. 28, 199–212. https://doi.org/10.1016/j.tem.2016.09.005

Frankish, C.K., Manica, A., Phillips, R.A., 2020. Effects of age on foraging behavior in two closely related albatross species. Mov. Ecol. 8, 7. https://doi.org/10.1186/s40462-020-0194-0

Freeland, W.J., 1979. Primate Social Groups as Biological Islands. Ecology 60, 719–728. https://doi.org/10.2307/1936609

Freund, A.M., Hennecke, M., Brandstätter, V., Martin, M., Boker, S.M., Charles, S.T., Fishbach, A., Hess, T.M., Heckhausen, J., Gow, A.J., Isaacowitz, D.M., Klusmann, V., Lachman, M.E., Mayr, U., Oettingen, G., Robert, P., Röcke, C., Rothermund, K., Scholz, U., Tobler, P.N., Zacher, H.,

Zadeh, R.S., Participants of the Workshop "Motivation and Healthy Aging" in Zurich, S., December 2019, 2021. Motivation and Healthy Aging: A Heuristic Model. J. Gerontol. Ser. B 76, S97–S104. https://doi.org/10.1093/geronb/gbab128

Friant, S., Ziegler, T.E., Goldberg, T.L., 2016. Primate reinfection with gastrointestinal parasites: behavioural and physiological predictors of parasite acquisition. Anim. Behav. 117, 105–113. https://doi.org/10.1016/j.anbehav.2016.04.006

Frost, F., Kacprowski, T., Rühlemann, M., Pietzner, M., Bang, C., Franke, A., Nauck, M., Völker, U., Völzke, H., Dörr, M., Baumbach, J., Sendler, M., Schulz, C., Mayerle, J., Weiss, F.U., Homuth, G., Lerch, M.M., 2021. Long-term instability of the intestinal microbiome is associated with metabolic liver disease, low microbiota diversity, diabetes mellitus and impaired exocrine pancreatic function. Gut 70, 522–530. https://doi.org/10.1136/gutjnl-2020-322753

Froy, H., Börger, L., Regan, C.E., Morris, A., Morris, S., Pilkington, J.G., Crawley, M.J., Clutton-Brock, T.H., Pemberton, J.M., Nussey, D.H., 2018. Declining home range area predicts reduced late-life survival in two wild ungulate populations. Ecol. Lett. 21, 1001–1009. https://doi.org/10.1111/ele.12965

Froy, H., Sparks, A.M., Watt, K., Sinclair, R., Bach, F., Pilkington, J.G., Pemberton, J.M., McNeilly, T.N., Nussey, D.H., 2019. Senescence in immunity against helminth parasites predicts adult mortality in a wild mammal. Science 365, 1296–1298. https://doi.org/10.1126/science.aaw5822

Fuligni, A.J., Telzer, E.H., Bower, J., Cole, S.W., Kiang, L., Irwin, M.R., 2009. A Preliminary Study of Daily Interpersonal Stress and C-Reactive Protein Levels Among Adolescents From Latin American and European Backgrounds. Psychosom. Med. 71, 329–333. https://doi.org/10.1097/PSY.0b013e3181921b1f

Fulop, T., Dupuis, G., Baehl, S., Le Page, A., Bourgade, K., Frost, E., Witkowski, J.M., Pawelec, G., Larbi, A., Cunnane, S., 2016. From inflamm-aging to immune-paralysis: a slippery slope during aging for immune-adaptation. Biogerontology 17, 147–157. https://doi.org/10.1007/s10522-015-9615-7

Fürtbauer, I., Heistermann, M., Schülke, O., Ostner, J., 2014. Low female stress hormone levels are predicted by same- or opposite-sex sociality depending on season in wild Assamese macaques. Psychoneuroendocrinology 48, 19–28. https://doi.org/10.1016/j.psyneuen.2014.05.022

Fürtbauer, I., Schülke, O., Heistermann, M., Ostner, J., 2010. Reproductive and Life History Parameters of Wild Female Macaca assamensis. Int. J. Primatol. 31, 501–517. https://doi.org/10.1007/s10764-010-9409-3

Gaillard, J.-M., Festa-Bianchet, M., Delorme, D., Jorgenson, J., 2000. Body mass and individual fitness in female ungulates: bigger is not always better. Proc. R. Soc. Lond. B Biol. Sci. 267, 471–477. https://doi.org/10.1098/rspb.2000.1024

Gaillard, J.-M., Lemaître, J.-F., 2020. An integrative view of senescence in nature. Funct. Ecol. 34, 4–16. https://doi.org/10.1111/1365-2435.13506

Gaitan, J.E., Wahner, H.W., Gorman, C.A., Jiang, N.-S., 1975. Measurement of triiodothyronine in unextracted urine. J. Lab. Clin. Med. 86, 538–546. https://doi.org/10.5555/uri:pii:0022214375900633

Galbany, J., Altmann, J., Pérez-Pérez, A., Alberts, S.C., 2011. Age and individual foraging behavior predict tooth wear in Amboseli baboons. Am. J. Phys. Anthropol. 144, 51–59. https://doi.org/10.1002/ajpa.21368

Galton, V.A., Hernandez, A., St Germain, D.L., 2014. The 5'-deiodinases are not essential for the fasting-induced decrease in circulating thyroid hormone levels in male mice: possible roles for the type 3 deiodinase and tissue sequestration of hormone. Endocrinology 155, 3172–3181. https://doi.org/10.1210/en.2013-1884

Gao, X., Lin, H., Revanna, K., Dong, Q., 2017. A Bayesian taxonomic classification method for 16S rRNA gene sequences with improved species-level accuracy. BMC Bioinformatics 18, 247. https://doi.org/10.1186/s12859-017-1670-4

Garratt, M., Lemaître, J.-F., Douhard, M., Bonenfant, C., Capron, G., Warnant, C., Klein, F., Brooks, R.C., Gaillard, J.-M., 2015. High Juvenile Mortality Is Associated with Sex-Specific Adult Survival and Lifespan in Wild Roe Deer. Curr. Biol. 25, 759–763. https://doi.org/10.1016/j.cub.2014.11.071

Gelman, A., Hill, J., 2007. Data Analysis Using Regression and Multilevel/Hierarchical Models, 1st edition. ed. Cambridge University Press, Cambridge ; New York.

Georgiev, A., 2012. Energetic Costs of Reproductive Effort in Male Chimpanzees.

Gesquiere, L.R., Khan, M., Shek, L., Wango, T.L., Wango, E.O., Alberts, S.C., Altmann, J., 2008. Coping with a challenging environment: Effects of seasonal variability and reproductive status on glucocorticoid concentrations of female baboons (Papio cynocephalus). Horm. Behav. 54, 410–416. https://doi.org/10.1016/j.yhbeh.2008.04.007

Gesquiere, L.R., Onyango, P.O., Alberts, S.C., Altmann, J., 2011. Endocrinology of year-round reproduction in a highly seasonal habitat: Environmental variability in testosterone and glucocorticoids in baboon males. Am. J. Phys. Anthropol. 144, 169–176. https://doi.org/10.1002/ajpa.21374

Gesquiere, L.R., Pugh, M., Alberts, S.C., Markham, A.C., 2018. Estimation of energetic condition in wild baboons using fecal thyroid hormone determination. Gen. Comp. Endocrinol. 260, 9–17. https://doi.org/10.1016/j.ygcen.2018.02.004

Ghosh, T.S., Das, M., Jeffery, I.B., O'Toole, P.W., 2020. Adjusting for age improves identification of gut microbiome alterations in multiple diseases. eLife 9, e50240. https://doi.org/10.7554/eLife.50240

Ghosh, T.S., Shanahan, F., O'Toole, P.W., 2022. The gut microbiome as a modulator of healthy ageing. Nat. Rev. Gastroenterol. Hepatol. 1–20. https://doi.org/10.1038/s41575-022-00605-x

Girard-Buttoz, C., Heistermann, M., Rahmi, E., Agil, M., Ahmad Fauzan, P., Engelhardt, A., 2014. Costs of mate-guarding in wild male long-tailed macaques (Macaca fascicularis): Physiological stress and aggression. Horm. Behav. 66, 637–648. https://doi.org/10.1016/j.yhbeh.2014.09.003

Girard-Buttoz, C., Higham, J.P., Heistermann, M., Wedegärtner, S., Maestripieri, D., Engelhardt, A., 2011. Urinary C-Peptide Measurement as a Marker of Nutritional Status in Macaques. PLOS ONE 6, e18042. https://doi.org/10.1371/journal.pone.0018042

Gladyshev, V., N., 2014. The Free Radical Theory of Aging Is Dead. Long Live the Damage Theory! Antioxid. Redox Signal. https://doi.org/10.1089/ars.2013.5228

Gómez, J.M., Nunn, C.L., Verdú, M., 2013. Centrality in primate–parasite networks reveals the potential for the transmission of emerging infectious diseases to humans. Proc. Natl. Acad. Sci. 110, 7738–7741. https://doi.org/10.1073/pnas.1220716110

Goncharova, N., Chigarova, O., Rudenko, N., Oganyan, T., 2019. Glucocorticoid Negative Feedback in Regulation of the Hypothalamic-Pituitary-Adrenal Axis in Rhesus Monkeys With Various Types of Adaptive Behavior: Individual and Age-Related Differences. Front. Endocrinol. 10. https://doi.org/10.3389/fendo.2019.00024

Goncharova, N.D., Lapin, B.A., 2002. Effects of aging on hypothalamic–pituitary–adrenal system function in non-human primates. Mech. Ageing Dev. 123, 1191–1201. https://doi.org/10.1016/S0047-6374(02)00012-X

Goymann, W., 2005. Noninvasive Monitoring of Hormones in Bird Droppings: Physiological Validation, Sampling, Extraction, Sex Differences, and the Influence of Diet on Hormone Metabolite Levels. Ann. N. Y. Acad. Sci. 1046, 35–53. https://doi.org/10.1196/annals.1343.005

Grieneisen, L., Dasari, M., Gould, T.J., Björk, J.R., Grenier, J.-C., Yotova, V., Jansen, D., Gottel, N., Gordon, J.B., Learn, N.H., Gesquiere, L.R., Wango, T.L., Mututua, R.S., Warutere, J.K., Siodi, L., Gilbert, J.A., Barreiro, L.B., Alberts, S.C., Tung, J., Archie, E.A., Blekhman, R., 2021. Gut microbiome heritability is nearly universal but environmentally contingent. Science 373, 181–186. https://doi.org/10.1126/science.aba5483

Grieneisen, L., Muehlbauer, A.L., Blekhman, R., 2020. Microbial control of host gene regulation and the evolution of host–microbiome interactions in primates. Philos. Trans. R. Soc. B Biol. Sci. 375, 20190598. https://doi.org/10.1098/rstb.2019.0598

Grieneisen, L.E., Livermore, J., Alberts, S., Tung, J., Archie, E.A., 2017. Group living and male dispersal predict the core gut microbiome in wild baboons. Integr. Comp. Biol. 57, 770–785. https://doi.org/10.1093/icb/icx046

Griffin, R.H., Nunn, C.L., 2012. Community structure and the spread of infectious disease in primate social networks. Evol. Ecol. 26, 779–800. https://doi.org/10.1007/s10682-011-9526-2

Guarner, V., Rubio-Ruiz, M.E., 2015. Low-Grade Systemic Inflammation Connects Aging, Metabolic Syndrome and Cardiovascular Disease 40, 99–106. https://doi.org/10.1159/000364934

Gupta, V.K., Kim, M., Bakshi, U., Cunningham, K.Y., Davis, J.M., Lazaridis, K.N., Nelson, H., Chia, N., Sung, J., 2020. A predictive index for health status using species-level gut microbiome profiling. Nat. Commun. 11, 4635. https://doi.org/10.1038/s41467-020-18476-8

Gust, D.A., Wilson, M.E., Stocker, T., Conrad, S., Plotsky, P.M., Gordon, T.P., 2000. Activity of the Hypothalamic-Pituitary-Adrenal Axis Is Altered by Aging and Exposure to Social Stress in Female Rhesus Monkeys1. J. Clin. Endocrinol. Metab. 85, 2556–2563. https://doi.org/10.1210/jcem.85.7.6696

Haase, C.G., Long, A.K., Gillooly, J.F., 2016. Energetics of stress: linking plasma cortisol levels to metabolic rate in mammals. Biol. Lett. 12, 20150867. https://doi.org/10.1098/rsbl.2015.0867

Habig, B., Doellman, M.M., Woods, K., Olansen, J., Archie, E.A., 2018. Social status and parasitism in male and female vertebrates: a meta-analysis. Sci. Rep. 8, 3629. https://doi.org/10.1038/s41598-018-21994-7

Habig, B., Jansen, D.A.W.A.M., Akinyi, M.Y., Gesquiere, L.R., Alberts, S.C., Archie, E.A., 2019. Multi-scale predictors of parasite risk in wild male savanna baboons (*Papio cynocephalus*). Behav. Ecol. Sociobiol. 73, 134. https://doi.org/10.1007/s00265-019-2748-y

Haldane, J.B.S., 1941. New Paths in Genetics. Allen Unwin.

Hämäläinen, A., Dammhahn, M., Aujard, F., Eberle, M., Hardy, I., Kappeler, P.M., Perret, M., Schliehe-Diecks, S., Kraus, C., 2014. Senescence or selective disappearance? Age trajectories of body mass in wild and captive populations of a small-bodied primate. Proc R Soc B 281, 20140830. https://doi.org/10.1098/rspb.2014.0830

Hämäläinen, A., Dammhahn, M., Aujard, F., Kraus, C., 2015a. Losing grip: Senescent decline in physical strength in a small-bodied primate in captivity and in the wild. Exp. Gerontol. 61, 54–61. https://doi.org/10.1016/j.exger.2014.11.017

Hämäläinen, A., Heistermann, M., Kraus, C., 2015b. The stress of growing old: sex- and season-specific effects of age on allostatic load in wild grey mouse lemurs. Oecologia 178, 1063–1075. https://doi.org/10.1007/s00442-015-3297-3

Hamilton, W.D., 1966. The moulding of senescence by natural selection. J. Theor. Biol. 12, 12–45. https://doi.org/10.1016/0022-5193(66)90184-6

Hannum, G., Guinney, J., Zhao, L., Zhang, L., Hughes, G., Sadda, S., Klotzle, B., Bibikova, M., Fan, J.-B., Gao, Y., Deconde, R., Chen, M., Rajapakse, I., Friend, S., Ideker, T., Zhang, K., 2013. Genome-wide Methylation Profiles Reveal Quantitative Views of Human Aging Rates. Mol. Cell 49, 359–367. https://doi.org/10.1016/j.molcel.2012.10.016

Harris, B.N., Saltzman, W., 2013. Effects of aging on hypothalamic-pituitary-adrenal (HPA) axis activity and reactivity in virgin male and female California mice (Peromyscus californicus). Gen. Comp. Endocrinol. 186, 41–49. https://doi.org/10.1016/j.ygcen.2013.02.010

Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., Robinson, B.S., Hodgson, D.J., Inger, R., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6, e4794. https://doi.org/10.7717/peerj.4794

Hartig, F., 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Haunhorst, C.B., Fürtbauer, I., Schülke, O., Ostner, J., 2020. Female macaques compete for 'power' and 'commitment' in their male partners. Evol. Hum. Behav. 41, 117–125. https://doi.org/10.1016/j.evolhumbehav.2019.11.001

Haunhorst, C.B., Heesen, M., Ostner, J., Schülke, O., 2017. Social bonds with males lower the costs of competition for wild female Assamese macaques. Anim. Behav. 125, 51–60. https://doi.org/10.1016/j.anbehav.2017.01.008

Haunhorst, C.B., Schülke, O., Ostner, J., 2016. Opposite-sex social bonding in wild Assamese macaques. Am. J. Primatol. 78, 872–882. https://doi.org/10.1002/ajp.22554

Hawkley, L.C., Capitanio, J.P., 2015. Perceived social isolation, evolutionary fitness and health outcomes: a lifespan approach. Philos. Trans. R. Soc. B Biol. Sci. 370, 20140114. https://doi.org/10.1098/rstb.2014.0114

Hawley, D.M., Etienne, R.S., Ezenwa, V., Jolles, A.E., 2011. Does Animal Behavior Underlie Covariation Between Hosts' Exposure to Infectious Agents and Susceptibility to Infection? Implications for Disease Dynamics. Integr. Comp. Biol. 51, 528–539. https://doi.org/10.1093/icb/icr062

Hawley, D.M., Ezenwa, V.O., 2022. Parasites, host behavior and their feedbacks, in: Animal Behavior and Parasitism, Oxford University Press. Oxford University Press.

Hayward, A.D., Moorad, J., Regan, C.E., Berenos, C., Pilkington, J.G., Pemberton, J.M., Nussey, D.H., 2015. Asynchrony of senescence among phenotypic traits in a wild mammal population. Exp. Gerontol., Aging in the Wild: Insights from Free-Living and Non-Model organisms 71, 56–68. https://doi.org/10.1016/j.exger.2015.08.003

Healy, K., Ezard, T.H.G., Jones, O.R., Salguero-Gómez, R., Buckley, Y.M., 2019. Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. Nat. Ecol. Evol. 3, 1217–1224. https://doi.org/10.1038/s41559-019-0938-7

Heesen, M., Macdonald, S., Ostner, J., Schülke, O., 2015. Ecological and Social Determinants of Group Cohesiveness and Within-Group Spatial Position in Wild Assamese Macaques. Ethology 121, 270–283. https://doi.org/10.1111/eth.12336

Heesen, M., Rogahn, S., Macdonald, S., Ostner, J., Schülke, O., 2014. Predictors of food-related aggression in wild Assamese macaques and the role of conflict avoidance. Behav. Ecol. Sociobiol. 68, 1829–1841. https://doi.org/10.1007/s00265-014-1792-x

Heesen, M., Rogahn, S., Ostner, J., Schülke, O., 2013. Food abundance affects energy intake and reproduction in frugivorous female Assamese macaques. Behav. Ecol. Sociobiol. 67, 1053–1066. https://doi.org/10.1007/s00265-013-1530-9

Heidinger, B.J., Chastel, O., Nisbet, I.C.T., Ketterson, E.D., 2010. Mellowing with age: older parents are less responsive to a stressor in a long-lived seabird. Funct. Ecol. 24, 1037–1044. https://doi.org/10.1111/j.1365-2435.2010.01733.x

Heistermann, M., Ademmer, C., Kaumanns, W., 2004. Ovarian Cycle and Effect of Social Changes on Adrenal and Ovarian Function in Pygathrix nemaeus. Int. J. Primatol. 25, 689–708. https://doi.org/10.1023/B:IJOP.0000023581.17889.0f

Heistermann, M., Higham, J.P., 2015. Urinary neopterin, a non-invasive marker of mammalian cellular immune activation, is highly stable under field conditions. Sci. Rep. 5, 16308. https://doi.org/10.1038/srep16308

Heistermann, M., Palme, R., Ganswindt, A., 2006. Comparison of different enzymeimmunoassays for assessment of adrenocortical activity in primates based on fecal analysis. Am. J. Primatol. 68, 257–273. https://doi.org/10.1002/ajp.20222

Hennessy, M.B., Kaiser, S., Sachser, N., 2009. Social buffering of the stress response: Diversity, mechanisms, and functions. Front. Neuroendocrinol., Hormones & Social Behavior 30, 470–482. https://doi.org/10.1016/j.yfrne.2009.06.001

Herrera, J., Nunn, C.L., 2019. Behavioural ecology and infectious disease: implications for conservation of biodiversity. Philos. Trans. R. Soc. B Biol. Sci. 374, 20180054. https://doi.org/10.1098/rstb.2018.0054

Hicks, A.L., Lee, K.J., Couto-Rodriguez, M., Patel, J., Sinha, R., Guo, C., Olson, S.H., Seimon, A., Seimon, T.A., Ondzie, A.U., Karesh, W.B., Reed, P., Cameron, K.N., Lipkin, W.I., Williams, B.L., 2018.

Gut microbiomes of wild great apes fluctuate seasonally in response to diet. Nat. Commun. 9, 1786. https://doi.org/10.1038/s41467-018-04204-w

Higham, J.P., 2016. Field endocrinology of nonhuman primates: past, present, and future. Horm. Behav. 84, 145–155. https://doi.org/10.1016/j.yhbeh.2016.07.001

Higham, J.P., Girard-Buttoz, C., Engelhardt, A., Heistermann, M., 2011a. Urinary C-Peptide of Insulin as a Non-Invasive Marker of Nutritional Status: Some Practicalities. PLOS ONE 6, e22398. https://doi.org/10.1371/journal.pone.0022398

Higham, J.P., Heistermann, M., Maestripieri, D., 2011b. The energetics of male–male endurance rivalry in free-ranging rhesus macaques, Macaca mulatta. Anim. Behav. 81, 1001–1007. https://doi.org/10.1016/j.anbehav.2011.02.001

Higham, J.P., Kraus, C., Stahl-Hennig, C., Engelhardt, A., Fuchs, D., Heistermann, M., 2015. Evaluating noninvasive markers of nonhuman primate immune activation and inflammation. Am. J. Phys. Anthropol. 158, 673–684. https://doi.org/10.1002/ajpa.22821

Higham, J.P., Stahl-Hennig, C., Heistermann, M., 2020. Urinary suPAR: a non-invasive biomarker of infection and tissue inflammation for use in studies of large free-ranging mammals. R. Soc. Open Sci. 7, 191825. https://doi.org/10.1098/rsos.191825

Hinde, R.A., 1976. Interactions, Relationships and Social Structure. Man 11, 1–17. https://doi.org/10.2307/2800384

Hoffman, C.L., Higham, J.P., Mas-Rivera, A., Ayala, J.E., Maestripieri, D., 2010. Terminal investment and senescence in rhesus macaques (Macaca mulatta) on Cayo Santiago. Behav. Ecol. 21, 972–978. https://doi.org/10.1093/beheco/arq098

Hoffmann, C., Zimmermann, F., Biek, R., Kuehl, H., Nowak, K., Mundry, R., Agbor, A., Angedakin, S., Arandjelovic, M., Blankenburg, A., Brazolla, G., Corogenes, K., Couacy-Hymann, E., Deschner, T., Dieguez, P., Dierks, K., Düx, A., Dupke, S., Eshuis, H., Formenty, P., Yuh, Y.G., Goedmakers, A., Gogarten, J.F., Granjon, A.-C., McGraw, S., Grunow, R., Hart, J., Jones, S., Junker, J., Kiang, J., Langergraber, K., Lapuente, J., Lee, K., Leendertz, S.A., Léguillon, F., Leinert, V., Löhrich, T., Marrocoli, S., Mätz-Rensing, K., Meier, A., Merkel, K., Metzger, S., Murai, M., Niedorf, S., De Nys, H., Sachse, A., van Schijndel, J., Thiesen, U., Ton, E., Wu, D., Wieler, L.H., Boesch, C., Klee, S.R., Wittig, R.M., Calvignac-Spencer, S., Leendertz, F.H., 2017. Persistent anthrax as a major driver of wildlife mortality in a tropical rainforest. Nature 548, 82–86. https://doi.org/10.1038/nature23309

Holt-Lunstad, J., Smith, T.B., Baker, M., Harris, T., Stephenson, D., 2015. Loneliness and Social Isolation as Risk Factors for Mortality: A Meta-Analytic Review. Perspect. Psychol. Sci. 10, 227–237. https://doi.org/10.1177/1745691614568352

Hooks, K.B., O'Malley, M.A., 2017. Dysbiosis and its discontents. mBio 8, e01492-17. https://doi.org/10.1128/mBio.01492-17

Horvath, S., 2013. DNA methylation age of human tissues and cell types. Genome Biol. 14, 3156. https://doi.org/10.1186/gb-2013-14-10-r115

Hostinar, C.E., Sullivan, R.M., Gunnar, M.R., 2014. Psychobiological Mechanisms Underlying the Social Buffering of the HPA Axis: A Review of Animal Models and Human Studies across Development. Psychol. Bull. 140. https://doi.org/10.1037/a0032671

Hrdy, S.B., Hrdy, D.B., 1976. Hierarchical Relations Among Female Hanuman Langurs (Primates: Colobinae, Presbytis entellus). Science 193, 913–915. https://doi.org/10.1126/science.193.4256.913

Huang, G., Wang, L., Li, J., Hou, R., Wang, M., Wang, Z., Qu, Q., Zhou, W., Nie, Y., Hu, Y., Ma, Y., Yan, L., Wei, H., Wei, F., 2022. Seasonal shift of the gut microbiome synchronizes host peripheral circadian rhythm for physiological adaptation to a low-fat diet in the giant panda. Cell Rep. 38, 110203. https://doi.org/10.1016/j.celrep.2021.110203

Huffman, M.A., 2015. Chimpanzee self-medication: a historical perspective of the key findings, in: Hosaka, K., Zamma, K., Nakamura, M., Itoh, N. (Eds.), Mahale Chimpanzees: 50 Years of Research. Cambridge University Press, Cambridge, pp. 340–353.

Isbell, L.A., Young, T.P., 2002. Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. Behaviour 139, 177–202. https://doi.org/10.1163/156853902760102645

Jackson, M.A., Jeffery, I.B., Beaumont, M., Bell, J.T., Clark, A.G., Ley, R.E., O'Toole, P.W., Spector, T.D., Steves, C.J., 2016. Signatures of early frailty in the gut microbiota. Genome Med. 8, 8. https://doi.org/10.1186/s13073-016-0262-7

Janiak, M.C., Montague, M.J., Villamil, C.I., Stock, M.K., Trujillo, A.E., DePasquale, A.N., Orkin, J.D., Bauman Surratt, S.E., Gonzalez, O., Platt, M.L., Martínez, M.I., Antón, S.C., Dominguez-Bello, M.G., Melin, A.D., Higham, J.P., 2021. Age and sex-associated variation in the multi-site microbiome of an entire social group of free-ranging rhesus macaques. Microbiome 9, 68. https://doi.org/10.1186/s40168-021-01009-w

Jeffery, I.B., Lynch, D.B., O'Toole, P.W., 2016. Composition and temporal stability of the gut microbiota in older persons. ISME J. 10, 170–182. https://doi.org/10.1038/ismej.2015.88

Jesus, L.A. de, Carvalho, S.D., Ribeiro, M.O., Schneider, M., Kim, S.-W., Harney, J.W., Larsen, P.R., Bianco, A.C., 2001. The type 2 iodothyronine deiodinase is essential for adaptive thermogenesis in brown adipose tissue. J. Clin. Invest. 108, 1379–1385. https://doi.org/10.1172/JCI13803

Johnson, A.A., English, B.W., Shokhirev, M.N., Sinclair, D.A., Cuellar, T.L., 2022. Human age reversal: Fact or fiction? Aging Cell 21, e13664. https://doi.org/10.1111/acel.13664

Johnson, A.J., Vangay, P., Al-Ghalith, G.A., Hillmann, B.M., Ward, T.L., Shields-Cutler, R.R., Kim, A.D., Shmagel, A.K., Syed, A.N., Walter, J., Menon, R., Koecher, K., Knights, D., 2019. Daily sampling reveals personalized diet-microbiome associations in humans. Cell Host Microbe 25, 789-802.e5. https://doi.org/10.1016/j.chom.2019.05.005

Johnson, R.L., Kapsalis, E., 1995. Ageing, infecundity and reproductive senescence in free-ranging female rhesus monkeys. Reproduction 105, 271–278. https://doi.org/10.1530/jrf.0.1050271

Jones, O.R., Gaillard, J.-M., Tuljapurkar, S., Alho, J.S., Armitage, K.B., Becker, P.H., Bize, P., Brommer, J., Charmantier, A., Charpentier, M., Clutton-Brock, T., Dobson, F.S., Festa-Bianchet, M., Gustafsson, L., Jensen, H., Jones, C.G., Lillandt, B.-G., McCleery, R., Merilä, J., Neuhaus, P., Nicoll, M.A.C., Norris, K., Oli, M.K., Pemberton, J., Pietiäinen, H., Ringsby, T.H., Roulin, A., Saether, B.-E., Setchell, J.M., Sheldon, B.C., Thompson, P.M., Weimerskirch, H., Jean Wickings, E., Coulson, T., 2008. Senescence rates are determined by ranking on the fast–slow life-history continuum. Ecol. Lett. 11, 664–673. https://doi.org/10.1111/j.1461-0248.2008.01187.x

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

Kajokaite, K., Whalen, A., Koster, J., Perry, S., 2022. Social integration predicts survival in female white-faced capuchin monkeys. Behav. Ecol. 33, 807–815. https://doi.org/10.1093/beheco/arac043

Kalbitz, J., Ostner, J., Schülke, O., 2016. Strong, equitable and long-term social bonds in the dispersing sex in Assamese macaques. Anim. Behav. 113, 13–22. https://doi.org/10.1016/j.anbehav.2015.11.005

Kamat, V., Hecht, W.L., Rubin, R.T., 1995. Influence of meal composition on the postprandial response of the pituitary–thyroid axis. Eur. J. Endocrinol. 133, 75–79. https://doi.org/10.1530/eje.0.1330075

Kamis, A.B., 1982. Circadian variations in serum thyroid hormones in Macaca fascicularis. Primates 23, 596–597. https://doi.org/10.1007/BF02373974

Kappeler, P.M., Cremer, S., Nunn, C.L., 2015. Sociality and health: impacts of sociality on disease susceptibility and transmission in animal and human societies. Philos. Trans. R. Soc. B Biol. Sci. 370, 20140116. https://doi.org/10.1098/rstb.2014.0116

Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol. Biol. Evol. 30, 772–780. https://doi.org/10.1093/molbev/mst010

Kesner, J.S., Knecht, E.A., Krieg, E.F., 1995. Stability of urinary female reproductive hormones stored under various conditions. Reprod. Toxicol. 9, 239–244. https://doi.org/10.1016/0890-6238(95)00005-U

Kiecolt-Glaser, J.K., Gouin, J.-P., Hantsoo, L., 2010. Close relationships, inflammation, and health. Neurosci. Biobehav. Rev., Psychophysiological Biomarkers of Health 35, 33–38. https://doi.org/10.1016/j.neubiorev.2009.09.003

Kim, B., 2008. Thyroid Hormone as a Determinant of Energy Expenditure and the Basal Metabolic Rate. Thyroid 18, 141–144. https://doi.org/10.1089/thy.2007.0266

Kirkwood, T.B.L., 1977. Evolution of ageing. Nature 270, 301–304. https://doi.org/10.1038/270301a0

Kirkwood, T.B.L., Austad, S.N., 2000. Why do we age? Nature 408, 233–238. https://doi.org/10.1038/35041682

Klandorf, H., Harvey, S., 1985. Food intake regulation of circulating thyroid hormones in domestic fowl. Gen. Comp. Endocrinol. 60, 162–170. https://doi.org/10.1016/0016-6480(85)90310-7

Klein, A., Zimmermann, E., Radespiel, U., Schaarschmidt, F., Springer, A., Strube, C., 2018. Ectoparasite communities of small-bodied Malagasy primates: seasonal and socioecological influences on tick, mite and lice infestation of *Microcebus murinus* and *M. ravelobensis* in northwestern Madagascar. Parasit. Vectors 11, 459. https://doi.org/10.1186/s13071-018-3034-y

Klieverik, L.P., Coomans, C.P., Endert, E., Sauerwein, H.P., Havekes, L.M., Voshol, P.J., Rensen, P.C.N., Romijn, J.A., Kalsbeek, A., Fliers, E., 2009. Thyroid hormone effects on whole-body energy homeostasis and tissue-specific fatty acid uptake in vivo. Endocrinology 150, 5639–5648. https://doi.org/10.1210/en.2009-0297

Klindworth, A., Pruesse, E., Schweer, T., Peplies, J., Quast, C., Horn, M., Glöckner, F.O., 2013. Evaluation of general 16S ribosomal RNA gene PCR primers for classical and next-generation sequencing-based diversity studies. Nucleic Acids Res. 41, e1. https://doi.org/10.1093/nar/gks808

Knott, C.D., 1998. Changes in Orangutan Caloric Intake, Energy Balance, and Ketones in Response to Fluctuating Fruit Availability. Int. J. Primatol. 19, 1061–1079. https://doi.org/10.1023/A:1020330404983

Knutie, S.A., Wilkinson, C.L., Kohl, K.D., Rohr, J.R., 2017. Early-life disruption of amphibian microbiota decreases later-life resistance to parasites. Nat. Commun. 8, 86. https://doi.org/10.1038/s41467-017-00119-0

Konrad, M., Vyleta, M.L., Theis, F.J., Stock, M., Tragust, S., Klatt, M., Drescher, V., Marr, C., Ugelvig, L.V., Cremer, S., 2012. Social Transfer of Pathogenic Fungus Promotes Active Immunisation in Ant Colonies. PLOS Biol. 10, e1001300. https://doi.org/10.1371/journal.pbio.1001300

Kozłowska, L., Rosołowska-Huszcz, D., 2004. Leptin, thyrotropin, and thyroid hormones in obese/overweight women before and after two levels of energy deficit. Endocrine 24, 147–153. https://doi.org/10.1385/ENDO:24:2:147

Kraft, T.S., Stieglitz, J., Trumble, B.C., Garcia, A.R., Kaplan, H., Gurven, M., 2020. Multi-system physiological dysregulation and ageing in a subsistence population. Philos. Trans. R. Soc. B Biol. Sci. 375, 20190610. https://doi.org/10.1098/rstb.2019.0610

Krause, J., Ruxton, G.D., 2002. Living in Groups, Oxford Series in Ecology and Evolution. Oxford University Press, Oxford, New York.

Kroeger, S.B., Blumstein, D.T., Armitage, K.B., Reid, J.M., Martin, J.G.A., 2018. Age, state, environment, and season dependence of senescence in body mass. Ecol. Evol. 8, 2050–2061. https://doi.org/10.1002/ece3.3787

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. B Biol. Sci. 376, 20190745. https://doi.org/10.1098/rstb.2019.0745

Kröger, H., Pakpahan, E., Hoffmann, R., 2015. What causes health inequality? A systematic review on the relative importance of social causation and health selection. Eur. J. Public Health 25, 951–960. https://doi.org/10.1093/eurpub/ckv111

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in Linear Mixed Effects Models. J. Stat. Softw. 82, 1–26. https://doi.org/10.18637/jss.v082.i13

Laich, A., Neurauter, G., Wirleitner, B., Fuchs, D., 2002. Degradation of serum neopterin during daylight exposure. Clin. Chim. Acta Int. J. Clin. Chem. 322, 175–178. https://doi.org/10.1016/s0009-8981(02)00076-1

Landys, M.M., Ramenofsky, M., Wingfield, J.C., 2006. Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. Gen. Comp. Endocrinol. 148, 132–149. https://doi.org/10.1016/j.ygcen.2006.02.013

Lang, F.R., Carstensen, L.L., 1994. Close emotional relationships in late life: Further support for proactive aging in the social domain. Psychol. Aging 9, 315–324. https://doi.org/10.1037/0882-7974.9.2.315

Lang, F.R., Staudinger, U.M., Carstensen, L.L., 1998. Perspectives on Socioemotional Selectivity in Late Life: How Personality and Social Context Do (and Do Not) Make a Difference. J. Gerontol. Ser. B 53B, P21–P30. https://doi.org/10.1093/geronb/53B.1.P21

Lans, A.A.J.J. van der, Hoeks, J., Brans, B., Vijgen, G.H.E.J., Visser, M.G.W., Vosselman, M.J., Hansen, J., Jörgensen, J.A., Wu, J., Mottaghy, F.M., Schrauwen, P., Lichtenbelt, W.D. van M., 2013. Cold acclimation recruits human brown fat and increases nonshivering thermogenesis. J. Clin. Invest. 123, 3395–3403. https://doi.org/10.1172/JCI68993

Lecomte, V.J., Sorci, G., Cornet, S., Jaeger, A., Faivre, B., Arnoux, E., Gaillard, M., Trouvé, C., Besson, D., Chastel, O., Weimerskirch, H., 2010. Patterns of aging in the long-lived wandering albatross. Proc. Natl. Acad. Sci. 107, 6370–6375. https://doi.org/10.1073/pnas.0911181107

Lee, D.S., Kang, Y.H.R., Ruiz-Lambides, A.V., Higham, J.P., 2021. The observed pattern and hidden process of female reproductive trajectories across the life span in a non-human primate. J. Anim. Ecol. 90, 2901–2914. https://doi.org/10.1111/1365-2656.13590

Legler, M., Brandenberger, G., Hietter, B., Siméoni, M., Reinhardt, B., 1982. Diurnal Cortisol Peaks and Their Relationships to Meals. J. Clin. Endocrinol. Metab. 55, 757–761. https://doi.org/10.1210/jcem-55-4-757

Leite, G., Pimentel, M., Barlow, G.M., Chang, C., Hosseini, A., Wang, J., Parodi, G., Sedighi, R., Rezaie, A., Mathur, R., 2021. Age and the aging process significantly alter the small bowel microbiome. Cell Rep. 36, 109765. https://doi.org/10.1016/j.celrep.2021.109765

Lemaître, J.-F., Pavard, S., Giraudeau, M., Vincze, O., Jennings, G., Hamede, R., Ujvari, B., Thomas, F., 2020a. Eco-evolutionary perspectives of the dynamic relationships linking senescence and cancer. Funct. Ecol. 34, 141–152. https://doi.org/10.1111/1365-2435.13394

Lemaître, J.-F., Ronget, V., Tidière, M., Allainé, D., Berger, V., Cohas, A., Colchero, F., Conde, D.A., Garratt, M., Liker, A., Marais, G.A.B., Scheuerlein, A., Székely, T., Gaillard, J.-M., 2020b. Sex differences in adult lifespan and aging rates of mortality across wild mammals. Proc. Natl. Acad. Sci. 117, 8546–8553. https://doi.org/10.1073/pnas.1911999117

Lendvai, Á.Z., Giraudeau, M., Bókony, V., Angelier, F., Chastel, O., 2015. Within-individual plasticity explains age-related decrease in stress response in a short-lived bird. Biol. Lett. 11, 20150272. https://doi.org/10.1098/rsbl.2015.0272

Lenth, R., 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Leroy, E.M., Rouquet, P., Formenty, P., Souquière, S., Kilbourne, A., Froment, J.-M., Bermejo, M., Smit, S., Karesh, W., Swanepoel, R., Zaki, S.R., Rollin, P.E., 2004. Multiple Ebola Virus Transmission Events and Rapid Decline of Central African Wildlife. Science 303, 387–390. https://doi.org/10.1126/science.1092528

Levine, J.A., 2005. Measurement of energy expenditure. Public Health Nutr. 8, 1123–1132. https://doi.org/10.1079/PHN2005800

Levy, M., Kolodziejczyk, A.A., Thaiss, C.A., Elinav, E., 2017. Dysbiosis and the immune system. Nat. Rev. Immunol. 17, 219–232. https://doi.org/10.1038/nri.2017.7

Li, T., Zhang, Y., 2015. Social network types and the health of older adults: Exploring reciprocal associations. Soc. Sci. Med. 130, 59–68. https://doi.org/10.1016/j.socscimed.2015.02.007

Linehan, E., Fitzgerald, D.C., 2015. Ageing and the immune system: focus on macrophages. Eur. J. Microbiol. Immunol. 5, 14–24. https://doi.org/10.1556/EUJMI-D-14-00035

Liu, W., Li, Y., Learn, G.H., Rudicell, R.S., Robertson, J.D., Keele, B.F., Ndjango, J.-B.N., Sanz, C.M., Morgan, D.B., Locatelli, S., Gonder, M.K., Kranzusch, P.J., Walsh, P.D., Delaporte, E., Mpoudi-Ngole, E., Georgiev, A.V., Muller, M.N., Shaw, G.M., Peeters, M., Sharp, P.M., Rayner, J.C., Hahn, B.H., 2010. Origin of the human malaria parasite Plasmodium falciparum in gorillas. Nature 467, 420–425. https://doi.org/10.1038/nature09442

Lloyd-Price, J., Abu-Ali, G., Huttenhower, C., 2016. The healthy human microbiome. Genome Med. 8, 51. https://doi.org/10.1186/s13073-016-0307-y

Lloyd-Price, J., Mahurkar, A., Rahnavard, G., Crabtree, J., Orvis, J., Hall, A.B., Brady, A., Creasy, H.H., McCracken, C., Giglio, M.G., McDonald, D., Franzosa, E.A., Knight, R., White, O., Huttenhower, C., 2017. Strains, functions and dynamics in the expanded Human Microbiome Project. Nature 550, 61–66. https://doi.org/10.1038/nature23889

Lodge, E., Ross, C., Ortmann, S., MacLarnon, A.M., 2013. Influence of diet and stress on reproductive hormones in Nigerian olive baboons. Gen. Comp. Endocrinol. 191, 146–154. https://doi.org/10.1016/j.ygcen.2013.06.016

Logan, M., Sanson, G.D., 2002. The effects of tooth wear on the activity patterns of free-ranging koalas (Phascolarctos cinereus Goldfuss). Aust. J. Zool. 50, 281–292. https://doi.org/10.1071/zo01022

Löhrich, T., Behringer, V., Wittig, R.M., Deschner, T., Leendertz, F.H., 2018. The Use of Neopterin as a Noninvasive Marker in Monitoring Diseases in Wild Chimpanzees. EcoHealth 15, 792–803. https://doi.org/10.1007/s10393-018-1357-y

López-Otín, C., Blasco, M.A., Partridge, L., Serrano, M., Kroemer, G., 2023. Hallmarks of aging: An expanding universe. Cell 186, 243–278. https://doi.org/10.1016/j.cell.2022.11.001

López-Otín, C., Blasco, M.A., Partridge, L., Serrano, M., Kroemer, G., 2013. The hallmarks of aging. Cell 153, 1194–1217. https://doi.org/10.1016/j.cell.2013.05.039

Louca, S., Polz, M.F., Mazel, F., Albright, M.B.N., Huber, J.A., O'Connor, M.I., Ackermann, M., Hahn, A.S., Srivastava, D.S., Crowe, S.A., Doebeli, M., Parfrey, L.W., 2018. Function and functional redundancy in microbial systems. Nat. Ecol. Evol. 2, 936–943. https://doi.org/10.1038/s41559-018-0519-1

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

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. J. Open Source Softw. 6, 3139. https://doi.org/10.21105/joss.03139

Lukas, D., Clutton-Brock, T.H., 2013. The Evolution of Social Monogamy in Mammals. Science 341, 526–530. https://doi.org/10.1126/science.1238677

Luke, S.G., 2017. Evaluating significance in linear mixed-effects models in R. Behav. Res. Methods 49, 1494–1502. https://doi.org/10.3758/s13428-016-0809-y

Macdonald, S., 2014. Female social relationships among wild Assemese macaques (Macaca assamensis) (doctoralThesis). https://doi.org/10.53846/goediss-4599

Macdonald, S., Schülke, O., Ostner, J., 2013. The Absence of Grooming for Rank-Related Benefits in Female Assamese Macaques (Macaca assamensis). Int. J. Primatol. 34, 571–584. https://doi.org/10.1007/s10764-013-9680-1

MacDougall-Shackleton, S.A., Bonier, F., Romero, L.M., Moore, I.T., 2019. Glucocorticoids and "Stress" are Not Synonymous. Integr. Org. Biol. https://doi.org/10.1093/iob/obz017

Machanda, Z.P., Rosati, A.G., 2020. Shifting sociality during primate ageing. Philos. Trans. R. Soc. B Biol. Sci. 375, 20190620. https://doi.org/10.1098/rstb.2019.0620

MacIntosh, A.J.J., Jacobs, A., Garcia, C., Shimizu, K., Mouri, K., Huffman, M.A., Hernandez, A.D., 2012. Monkeys in the Middle: Parasite Transmission through the Social Network of a Wild Primate. PLOS ONE 7, e51144. https://doi.org/10.1371/journal.pone.0051144

MacNulty, D.R., Smith, D.W., Vucetich, J.A., Mech, L.D., Stahler, D.R., Packer, C., 2009. Predatory senescence in ageing wolves. Ecol. Lett. 12, 1347–1356. https://doi.org/10.1111/j.1461-0248.2009.01385.x

Maestripieri, D., Georgiev, A.V., 2016. What cortisol can tell us about the costs of sociality and reproduction among free-ranging rhesus macaque females on Cayo Santiago. Am. J. Primatol. 78, 92–105. https://doi.org/10.1002/ajp.22368

Maffei, V.J., Kim, S., Blanchard, E., IV, Luo, M., Jazwinski, S.M., Taylor, C.M., Welsh, D.A., 2017. Biological aging and the human gut microbiota. J. Gerontol. Ser. A 72, 1474–1482. https://doi.org/10.1093/gerona/glx042

Magdub, A., Johnson, H.D., Belyea, R.L., 1982. Effect of Environmental Heat and Dietary Fiber on Thyroid Physiology of Lactating Cows1. J. Dairy Sci. 65, 2323–2331. https://doi.org/10.3168/jds.S0022-0302(82)82504-6

Maklakov, A.A., Chapman, T., 2019. Evolution of ageing as a tangle of trade-offs: energy versus function. Proc. R. Soc. B Biol. Sci. 286, 20191604. https://doi.org/10.1098/rspb.2019.1604

Maklakov, A.A., Rowe, L., Friberg, U., 2015. Why organisms age: Evolution of senescence under positive pleiotropy? BioEssays 37, 802–807. https://doi.org/10.1002/bies.201500025

Mallott, E.K., 2022. Individualized composition or community dynamics? A new statistical approach to assess the individuality of host-associated microbiomes. Proc. R. Soc. B Biol. Sci. 289, 20221794. https://doi.org/10.1098/rspb.2022.1794

Mangiafico, S., 2020. rcompanion: Functions to Support Extension Education Program Evaluation.

Mansouri, F.A., Koechlin, E., Rosa, M.G.P., Buckley, M.J., 2017. Managing competing goals — a key role for the frontopolar cortex. Nat. Rev. Neurosci. 18, 645–657. https://doi.org/10.1038/nrn.2017.111

Marescot, L., Benhaiem, S., Gimenez, O., Hofer, H., Lebreton, J.-D., Olarte-Castillo, X.A., Kramer-Schadt, S., East, M.L., 2018. Social status mediates the fitness costs of infection with canine distemper virus in Serengeti spotted hyenas. Funct. Ecol. 32, 1237–1250. https://doi.org/10.1111/1365-2435.13059

Marmot, M.G., Sapolsky, R.M., 2014. Of Baboons and Men: Social Circumstances, Biology, and the Social Gradient in Health. National Academies Press (US).

Martin, J.G.A., Festa-Bianchet, M., 2011. Age-independent and age-dependent decreases in reproduction of females. Ecol. Lett. 14, 576–581. https://doi.org/10.1111/j.1461-0248.2011.01621.x

Martin, J.S., Koski, S.E., Bugnyar, T., Jaeggi, A.V., Massen, J.J.M., 2021. Prosociality, social tolerance and partner choice facilitate mutually beneficial cooperation in common marmosets, *Callithrix jacchus*. Anim. Behav. 173, 115–136. https://doi.org/10.1016/j.anbehav.2020.12.016

Martin, M., 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet.journal 17, 10–12. https://doi.org/10.14806/ej.17.1.200

Masi, S., Gustafsson, E., Saint Jalme, M., Narat, V., Todd, A., Bomsel, M.-C., Krief, S., 2012. Unusual feeding behavior in wild great apes, a window to understand origins of self-medication in humans: Role of sociality and physiology on learning process. Physiol. Behav. 105, 337–349. https://doi.org/10.1016/j.physbeh.2011.08.012

Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., Bates, D., 2017. Balancing Type I error and power in linear mixed models. J. Mem. Lang. 94, 305–315. https://doi.org/10.1016/j.jml.2017.01.001

McCallister, J.M., Smith, T.E., Elwood, R.W., 2004. Validation of urinary cortisol as an indicator of hypothalamic-pituitary-adrenal function in the bearded emperor tamarin (Saguinus imperator subgrisescens). Am. J. Primatol. 63, 17–23. https://doi.org/10.1002/ajp.20033

McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models, 2nd ed. Chapman and Hall, London. https://doi.org/10.1201/9780203753736

McDonald, R.A., Delahay, R.J., Carter, S.P., Smith, G.C., Cheeseman, C.L., 2008. Perturbing implications of wildlife ecology for disease control. Trends Ecol. Evol. 23, 53–56. https://doi.org/10.1016/j.tree.2007.10.011

McEwen, B.S., Wingfield, J.C., 2003. The concept of allostasis in biology and biomedicine. Horm. Behav. 43, 2–15.

Medawar, P.B., 1952. An Unsolved Problem of Biology, in: The Uniqueness of the Individual. Routledge.

Metcalf, C.J.E., Roth, O., Graham, A.L., 2020. Why leveraging sex differences in immune trade-offs may illuminate the evolution of senescence. Funct. Ecol. 34, 129–140. https://doi.org/10.1111/1365-2435.13458

Mikuła-Pietrasik, J., Pakuła, M., Markowska, M., Uruski, P., Szczepaniak-Chicheł, L., Tykarski, A., Książek, K., 2021. Nontraditional systems in aging research: an update. Cell. Mol. Life Sci. 78, 1275–1304. https://doi.org/10.1007/s00018-020-03658-w

Miller, E.T., Svanbäck, R., Bohannan, B.J.M., 2018. Microbiomes as Metacommunities: Understanding Host-Associated Microbes through Metacommunity Ecology. Trends Ecol. Evol. 33, 926–935. https://doi.org/10.1016/j.tree.2018.09.002

Miller, G.E., Chen, E., Parker, K.J., 2011. Psychological Stress in Childhood and Susceptibility to the Chronic Diseases of Aging: Moving Towards a Model of Behavioral and Biological Mechanisms. Psychol. Bull. 137, 959–997. https://doi.org/10.1037/a0024768

Mistrick, J., Gilbertson, M., White, L., Craft, M., 2022. Constructing animal networks for parasite transmission inference, in: Animal Behavior and Parasitism, Oxford University Press. Oxford University Press.

Mitchell, E.L., Davis, A.T., Brass, K., Dendinger, M., Barner, R., Gharaibeh, R., Fodor, A.A., Kavanagh, K., 2017. Reduced intestinal motility, mucosal barrier function, and inflammation in aged monkeys. J. Nutr. Health Aging 21, 354–361. https://doi.org/10.1007/s12603-016-0725-y

Mizoguchi, K., Ishige, A., Aburada, M., Tabira, T., 2003. Chronic stress attenuates glucocorticoid negative feedback: involvement of the prefrontal cortex and hippocampus. Neuroscience 119, 887–897. https://doi.org/10.1016/S0306-4522(03)00105-2

Moeller, A.H., Foerster, S., Wilson, M.L., Pusey, A.E., Hahn, B.H., Ochman, H., 2016. Social behavior shapes the chimpanzee pan-microbiome. Sci. Adv. 2, e1500997. https://doi.org/10.1126/sciadv.1500997

Monaghan, P., Charmantier, A., Nussey, D.H., Ricklefs, R.E., 2008. The evolutionary ecology of senescence. Funct. Ecol. 22, 371–378. https://doi.org/10.1111/j.1365-2435.2008.01418.x

Moorad, J., Promislow, D., Silvertown, J., 2019. Evolutionary Ecology of Senescence and a Reassessment of Williams' 'Extrinsic Mortality' Hypothesis. Trends Ecol. Evol. 34, 519–530. https://doi.org/10.1016/j.tree.2019.02.006

Moorad, J.A., Ravindran, S., 2022. Natural Selection and the Evolution of Asynchronous Aging. Am. Nat. 199, 551–563. https://doi.org/10.1086/718589

Mor-Barak, M.E., Miller, L.S., 1991. A Longitudinal Study of the Causal Relationship Between Social Networks and Health of the Poor Frail Elderly. J. Appl. Gerontol. 10, 293–310. https://doi.org/10.1177/073346489101000305

Most, J., Redman, L.M., 2020. Impact of calorie restriction on energy metabolism in humans. Exp. Gerontol. 133, 110875. https://doi.org/10.1016/j.exger.2020.110875

Müller, B., Ellwardt, L., 2022. Social Networks and Health Inequalities in Old Age, in: Klärner, A., Gamper, M., Keim-Klärner, S., Moor, I., von der Lippe, H., Vonneilich, N. (Eds.), Social Networks and Health Inequalities: A New Perspective for Research. Springer International Publishing, Cham, pp. 181–202. https://doi.org/10.1007/978-3-030-97722-1_10

Muller, M.N., Wrangham, R.W., 2004. Dominance, cortisol and stress in wild chimpanzees (Pan troglodytes schweinfurthii). Behav. Ecol. Sociobiol. 55, 332–340. https://doi.org/10.1007/s00265-003-0713-1

Müller, N., Heistermann, M., Strube, C., Schülke, O., Ostner, J., 2017. Age, but not anthelmintic treatment, is associated with urinary neopterin levels in semi-free ranging Barbary macaques. Sci. Rep. 7, 41973. https://doi.org/10.1038/srep41973

Müller-Klein, N., Heistermann, M., Strube, C., Franz, M., Schülke, O., Ostner, J., 2019. Exposure and susceptibility drive reinfection with gastrointestinal parasites in a social primate. Funct. Ecol. 33, 1088–1098. https://doi.org/10.1111/1365-2435.13313

Müller-Klein, N., Heistermann, M., Strube, C., Morbach, Z.M., Lilie, N., Franz, M., Schülke, O., Ostner, J., 2019. Physiological and social consequences of gastrointestinal nematode infection in a nonhuman primate. Behav. Ecol. 30, 322–335. https://doi.org/10.1093/beheco/ary168

Müller-Klein, N., Risely, A., Schmid, D.W., Manser, M., Clutton-Brock, T., Sommer, S., 2022. Two decades of tuberculosis surveillance reveal disease spread, high levels of exposure and mortality and marked variation in disease progression in wild meerkats. Transbound. Emerg. Dis. 69, 3274–3284. https://doi.org/10.1111/tbed.14679

Munro, C., Stabenfeldt, G., 1985. Development of a cortisol enzyme immunoassay in plasma. Clin. Chem. 956.

Murillo, T., Schneider, D., Fichtel, C., Daniel, R., 2022a. Dietary shifts and social interactions drive temporal fluctuations of the gut microbiome from wild redfronted lemurs. ISME Commun. 2, 1–11. https://doi.org/10.1038/s43705-021-00086-0

Murillo, T., Schneider, D., Heistermann, M., Daniel, R., Fichtel, C., 2022b. Assessing the drivers of gut microbiome composition in wild redfronted lemurs via longitudinal metacommunity analysis. Sci. Rep. 12, 21462. https://doi.org/10.1038/s41598-022-25733-x

Nair, R., Mahadevan, S., Muralidharan, R.S., Madhavan, S., 2014. Does fasting or postprandial state affect thyroid function testing? Indian J. Endocrinol. Metab. 18, 705–707. https://doi.org/10.4103/2230-8210.139237

Nakamichi, M., 2003. Age-related differences in social grooming among adult female Japanese monkeys (Macaca fuscata). Primates 44, 239–246. https://doi.org/10.1007/s10329-003-0036-x

Nakamichi, M., 1991. Behavior of old females: comparisons of Japanese monkeys in the Arashiyama East and West groups, in: The Monkeys of Arashiyama: Thirty-Five Years of Research in Japan and the West. State University of New York Press, pp. 175–193.

Nakamichi, M., 1984. Behavioral characteristics of old female Japanese monkeys in a free-ranging group. Primates 25, 192–203. https://doi.org/10.1007/BF02382391

Nakamichi, M., Shizawa, Y., 2003. Distribution of Grooming Among Adult Females in a Large, Free-Ranging Group of Japanese Macaques. Int. J. Primatol. 24, 607–625. https://doi.org/10.1023/A:1023744515134

Nakamura, Y., Walker, B.R., Ikuta, T., 2016. Systematic review and meta-analysis reveals acutely elevated plasma cortisol following fasting but not less severe calorie restriction. Stress 19, 151–157. https://doi.org/10.3109/10253890.2015.1121984

Narat, V., Amato, K.R., Ranger, N., Salmona, M., Mercier-Delarue, S., Rupp, S., Ambata, P., Njouom, R., Simon, F., Giles-Vernick, T., LeGoff, J., 2020. A multi-disciplinary comparison of great ape gut microbiota in a central African forest and European zoo. Sci. Rep. 10, 19107. https://doi.org/10.1038/s41598-020-75847-3

Narayan, E.J., Webster, K., Nicolson, V., Mucci, A., Hero, J.-M., 2013. Non-invasive evaluation of physiological stress in an iconic Australian marsupial: The Koala (Phascolarctos cinereus). Gen. Comp. Endocrinol. 187, 39–47. https://doi.org/10.1016/j.ygcen.2013.03.021

Nathanielsz, P.W., Huber, H.F., Li, C., Clarke, G.D., Kuo, A.H., Zambrano, E., 2020. The nonhuman primate hypothalamo-pituitary-adrenal axis is an orchestrator of programming-aging interactions: role of nutrition. Nutr. Rev. 78, 48–61. https://doi.org/10.1093/nutrit/nuaa018

Nearing, J.T., Douglas, G.M., Comeau, A.M., Langille, M.G.I., 2018. Denoising the Denoisers: an independent evaluation of microbiome sequence error-correction approaches. PeerJ 6, e5364. https://doi.org/10.7717/peerj.5364

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A.M., Agil, M., Widdig, A., Engelhardt, A., 2011. Assessing dominance hierarchies: Validation and advantages of progressive evaluation with Elo-rating. Anim. Behav. 82, 911–921. https://doi.org/10.1016/j.anbehav.2011.07.016

Nieminen, P., Saarela, S., Pyykönen, T., Asikainen, J., Mononen, J., Mustonen, A.-M., 2004. Endocrine response to fasting in the overwintering captive raccoon dog (Nyctereutes procyonoides). J. Exp. Zoolog. A Comp. Exp. Biol. 301A, 919–929. https://doi.org/10.1002/jez.a.126

Nugraha, T.P., Heistermann, M., Agil, M., Purwantara, B., Supriatna, I., Gholib, G., van Schaik, C.P., Weingrill, T., 2017. Validation of a field-friendly extraction and storage method to monitor fecal steroid metabolites in wild orangutans. Primates 58, 285–294. https://doi.org/10.1007/s10329-016-0583-6

Nunn, C.L., Altizer, S., Jones, K.E., Sechrest, W., 2003. Comparative Tests of Parasite Species Richness in Primates. Am. Nat. 162, 597–614. https://doi.org/10.1086/378721

Nunn, C.L., Jordán, F., McCabe, C.M., Verdolin, J.L., Fewell, J.H., 2015. Infectious disease and group size: more than just a numbers game. Philos. Trans. R. Soc. B Biol. Sci. 370, 20140111. https://doi.org/10.1098/rstb.2014.0111

Nunn, C.L., Scully, E.J., Kutsukake, N., Ostner, J., Schülke, O., Thrall, P.H., 2014. Mating Competition, Promiscuity, and Life History Traits as Predictors of Sexually Transmitted Disease Risk in Primates. Int. J. Primatol. 35, 764–786. https://doi.org/10.1007/s10764-014-9781-5

Nunn, C.L., Thrall, P.H., Leendertz, F.H., Boesch, C., 2011. The Spread of Fecally Transmitted Parasites in Socially-Structured Populations. PLOS ONE 6, e21677. https://doi.org/10.1371/journal.pone.0021677

Nurmi, N.O., Hohmann, G., Goldstone, L.G., Deschner, T., Schülke, O., 2018. The "tolerant chimpanzee"—towards the costs and benefits of sociality in female bonobos. Behav. Ecol. 29, 1325–1339. https://doi.org/10.1093/beheco/ary118

Nussey, D.H., Coulson, T., Delorme, D., Clutton-Brock, T.H., Pemberton, J.M., Festa-Bianchet, M., Gaillard, J.-M., 2011. Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. Ecology 92, 1936–1947. https://doi.org/10.1890/11-0308.1

Nussey, D.H., Coulson, T., Festa-Bianchet, M., Gaillard, J.-M., 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. Funct. Ecol. 22, 393–406. https://doi.org/10.1111/j.1365-2435.2008.01408.x

Nussey, D.H., Froy, H., Lemaitre, J.-F., Gaillard, J.-M., Austad, S.N., 2013. Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. Ageing Res. Rev., Special Issue: Invertebrate Models of Aging 12, 214–225. https://doi.org/10.1016/j.arr.2012.07.004

Nussey, D.H., Watt, K., Pilkington, J.G., Zamoyska, R., McNeilly, T.N., 2012. Age-related variation in immunity in a wild mammal population. Aging Cell 11, 178–180. https://doi.org/10.1111/j.1474-9726.2011.00771.x

O'Dwyer, K., Dargent, F., Forbes, M.R., Koprivnikar, J., 2020. Parasite infection leads to widespread glucocorticoid hormone increases in vertebrate hosts: A meta-analysis. J. Anim. Ecol. 89, 519–529. https://doi.org/10.1111/1365-2656.13123

Oppert, J.M., Dussault, J.H., Tremblay, A., Després, J.P., Thériault, G., Bouchard, C., 1994. Thyroid hormones and thyrotropin variations during long term overfeeding in identical twins. J. Clin. Endocrinol. Metab. 79, 547–553. https://doi.org/10.1210/jcem.79.2.8045975

Ostner, J., Heistermann, M., Schülke, O., 2008. Dominance, aggression and physiological stress in wild male Assamese macaques (Macaca assamensis). Horm. Behav. 54, 613–619. https://doi.org/10.1016/j.yhbeh.2008.05.020

Ostner, J., Schülke, O., 2018. Chapter Four - Linking Sociality to Fitness in Primates: A Call for Mechanisms, in: Naguib, M., Barrett, L., Healy, S.D., Podos, J., Simmons, L.W., Zuk, M. (Eds.), Advances in the Study of Behavior. Academic Press, pp. 127–175. https://doi.org/10.1016/bs.asb.2017.12.001

Ostner, J., Vigilant, L., Bhagavatula, J., Franz, M., Schülke, O., 2013. Stable heterosexual associations in a promiscuous primate. Anim. Behav. 86, 623–631. https://doi.org/10.1016/j.anbehav.2013.07.004

O'Toole, P.W., Jeffery, I.B., 2015. Gut microbiota and aging. Science 350, 1214–1215. https://doi.org/10.1126/science.aac8469

Otte, C., Hart, S., Neylan, T.C., Marmar, C.R., Yaffe, K., Mohr, D.C., 2005. A meta-analysis of cortisol response to challenge in human aging: importance of gender. Psychoneuroendocrinology 30, 80–91. https://doi.org/10.1016/j.psyneuen.2004.06.002

Paciência, F.M.D., Rushmore, J., Chuma, I.S., Lipende, I.F., Caillaud, D., Knauf, S., Zinner, D., 2019. Mating avoidance in female olive baboons (*Papio anubis*) infected by Treponema pallidum. Sci. Adv. 5, eaaw9724. https://doi.org/10.1126/sciadv.aaw9724

Parker, B.J., Wearsch, P.A., Veloo, A.C.M., Rodriguez-Palacios, A., 2020. The genus Alistipes: gut bacteria with emerging implications to inflammation, cancer, and mental health. Front. Immunol. 11, 906. https://doi.org/10.3389/fimmu.2020.00906

Partridge, L., Deelen, J., Slagboom, P.E., 2018. Facing up to the global challenges of ageing. Nature 561, 45–56. https://doi.org/10.1038/s41586-018-0457-8

Pastor-Satorras, R., Castellano, C., Van Mieghem, P., Vespignani, A., 2015. Epidemic processes in complex networks. Rev. Mod. Phys. 87, 925–979. https://doi.org/10.1103/RevModPhys.87.925

Patel, V.I., Akshay, B.K., 2019. A comparative study on outcomes of preprandial versus postprandial thyroid function test. Int. J. Otorhinolaryngol. Head Neck Surg. 5, 1662–1664. https://doi.org/10.18203/issn.2454-5929.ijohns20194945

Patrono, L.V., Pléh, K., Samuni, L., Ulrich, M., Röthemeier, C., Sachse, A., Muschter, S., Nitsche, A., Couacy-Hymann, E., Boesch, C., Wittig, R.M., Calvignac-Spencer, S., Leendertz, F.H., 2020. Monkeypox virus emergence in wild chimpanzees reveals distinct clinical outcomes and viral diversity. Nat. Microbiol. 5, 955–965. https://doi.org/10.1038/s41564-020-0706-0

Patterson, J.E.H., Ruckstuhl, K.E., 2013. Parasite infection and host group size: a meta-analytical review. Parasitology 140, 803–813. https://doi.org/10.1017/S0031182012002259

Pavelka, M.S.M., 1990. Do old female monkeys have a specific social role? Primates 31, 363–373. https://doi.org/10.1007/BF02381107

Pavez-Fox, M.A., Kimock, C.M., Rivera-Barreto, N., Negron-Del Valle, J.E., Phillips, D., Ruiz-Lambides, A., Snyder-Mackler, N., Higham, J.P., Siracusa, E.R., Brent, L.J.N., 2022. Reduced injury risk links sociality to survival in a group-living primate. iScience 25, 105454. https://doi.org/10.1016/j.isci.2022.105454

Pavitt, A.T., Pemberton, J.M., Kruuk, L.E.B., Walling, C.A., 2016. Testosterone and cortisol concentrations vary with reproductive status in wild female red deer. Ecol. Evol. 6, 1163–1172. https://doi.org/10.1002/ece3.1945

Pavitt, A.T., Walling, C.A., Möstl, E., Pemberton, J.M., Kruuk, L.E.B., 2015. Cortisol but not testosterone is repeatable and varies with reproductive effort in wild red deer stags. Gen. Comp. Endocrinol. 222, 62–68. https://doi.org/10.1016/j.ygcen.2015.07.009

Pearce, E., 2012. Thyroid hormone and obesity. Curr. Opin. Endocrinol. Diabetes Obes. 19, 408–413. https://doi.org/10.1097/MED.0b013e328355cd6c

Peckre, L.R., Defolie, C., Kappeler, P.M., Fichtel, C., 2018. Potential self-medication using millipede secretions in red-fronted lemurs: combining anointment and ingestion for a joint action against gastrointestinal parasites? Primates J. Primatol. 59, 483–494. https://doi.org/10.1007/s10329-018-0674-7

Pedersen, A.B., Altizer, S., Poss, M., Cunningham, A.A., Nunn, C.L., 2005. Patterns of host specificity and transmission among parasites of wild primates. Int. J. Parasitol. 35, 647–657. https://doi.org/10.1016/j.ijpara.2005.01.005

Pelletier, F., Festa-Bianchet, M., 2004. Effects of body mass, age, dominance and parasite load on foraging time of bighorn rams, Ovis canadensis. Behav. Ecol. Sociobiol. 56, 546–551. https://doi.org/10.1007/s00265-004-0820-7

Perofsky, A.C., Ancel Meyers, L., Abondano, L.A., Di Fiore, A., Lewis, R.J., 2021. Social groups constrain the spatiotemporal dynamics of wild sifaka gut microbiomes. Mol. Ecol. 30, 6759–6775. https://doi.org/10.1111/mec.16193

Perofsky, A.C., Lewis, R.J., Abondano, L.A., Di Fiore, A., Meyers, L.A., 2017. Hierarchical social networks shape gut microbial composition in wild Verreaux's sifaka. Proc. R. Soc. B Biol. Sci. 284, 20172274. https://doi.org/10.1098/rspb.2017.2274

Peters, A., Delhey, K., Nakagawa, S., Aulsebrook, A., Verhulst, S., 2019. Immunosenescence in wild animals: meta-analysis and outlook. Ecol. Lett. 22, 1709–1722. https://doi.org/10.1111/ele.13343

Petrullo, L., Baniel, A., Jorgensen, M.J., Sams, S., Snyder-Mackler, N., Lu, A., 2021. Early life gut microbiome dynamics mediate maternal effects on infant growth in vervet monkeys (preprint). Physiology. https://doi.org/10.1101/2021.05.11.443657

Petrullo, L., Delaney, D., Boutin, S., McAdam, A.G., Lane, J.E., Boonstra, R., Palme, R., Dantzer, B., 2022a. The glucocorticoid response to environmental change is not specific to agents of natural selection in wild red squirrels. Horm. Behav. 146, 105262. https://doi.org/10.1016/j.yhbeh.2022.105262

Petrullo, L., Ren, T., Wu, M., Boonstra, R., Palme, R., Boutin, S., McAdam, A.G., Dantzer, B., 2022b. Glucocorticoids coordinate changes in gut microbiome composition in wild North American red squirrels. Sci. Rep. 12, 2605. https://doi.org/10.1038/s41598-022-06359-5

Picq, J.-L., 1992. Aging and Social Behaviour in Captivity in Microcebus murinus. Folia Primatol. (Basel) 59, 217–220. https://doi.org/10.1159/000156664

Poirotte, C., Charpentier, M.J.E., 2022. Inter-individual variation in parasite avoidance behaviors and its epidemiological, ecological, and evolutionary consequences, in: Animal Behavior and Parasitism, Oxford University Press. Oxford University Press.

Poirotte, C., Charpentier, M.J.E., 2020. Unconditional care from close maternal kin in the face of parasites. Biol. Lett. 16, 20190869. https://doi.org/10.1098/rsbl.2019.0869

Poirotte, C., Massol, F., Herbert, A., Willaume, E., Bomo, P.M., Kappeler, P.M., Charpentier, M.J.E., 2017. Mandrills use olfaction to socially avoid parasitized conspecifics. Sci. Adv. 3, e1601721. https://doi.org/10.1126/sciadv.1601721

Pontzer, H., 2015. Energy Expenditure in Humans and Other Primates: A New Synthesis. Annu. Rev. Anthropol. 44, 169–187. https://doi.org/10.1146/annurev-anthro-102214-013925

Popkes, M., Valenzano, D.R., 2020. Microbiota–host interactions shape ageing dynamics. Philos. Trans. R. Soc. B Biol. Sci. 375, 20190596. https://doi.org/10.1098/rstb.2019.0596

Pradeep, T.V.S., Varma, S.H., Tirupati, S., Sarathi, V., Kumar, K.D., 2018. Postprandial decline in thyroid-stimulating hormone is significant but not its correlation with postprandial change in plasma glucose. Thyroid Res. Pract. 15, 113. https://doi.org/10.4103/trp.trp_36_18

Price, M.N., Dehal, P.S., Arkin, A.P., 2010. FastTree 2 – approximately maximum-likelihood trees for large alignments. PLOS ONE 5, e9490. https://doi.org/10.1371/journal.pone.0009490

Pujo, J., Petitfils, C., Faouder, P.L., Eeckhaut, V., Payros, G., Maurel, S., Perez-Berezo, T., Hul, M.V., Barreau, F., Blanpied, C., Chavanas, S., Immerseel, F.V., Bertrand-Michel, J., Oswald, E., Knauf, C., Dietrich, G., Cani, P.D., Cenac, N., 2021. Bacteria-derived long chain fatty acid exhibits anti-inflammatory properties in colitis. Gut 70, 1088–1097. https://doi.org/10.1136/gutjnl-2020-321173

Qaid, M.M., Abdelrahman, M.M., 2016. Role of insulin and other related hormones in energy metabolism—A review. Cogent Food Agric. 2, 1267691. https://doi.org/10.1080/23311932.2016.1267691

Qiu, X., Zhao, X., Cui, X., Mao, X., Tang, N., Jiao, C., Wang, D., Zhang, Y., Ye, Z., Zhang, H., 2020. Characterization of fungal and bacterial dysbiosis in young adult Chinese patients with Crohn's disease. Ther. Adv. Gastroenterol. 13, 1756284820971202. https://doi.org/10.1177/1756284820971202

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glöckner, F.O., 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Res. 41, D590–D596. https://doi.org/10.1093/nar/gks1219

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rabast, U., Hahn, A., Reiners, C., Ehl, M., 1981. Thyroid hormone changes in obese subjects during fasting and a very-low-calorie diet. Int. J. Obes. 5, 305–311.

Ragonnaud, E., Biragyn, A., 2021. Gut microbiota as the key controllers of "healthy" aging of elderly people. Immun. Ageing 18, 2. https://doi.org/10.1186/s12979-020-00213-w

Rapp-Santos, K.J., Altamura, L.A., Norris, S.L., Lugo-Roman, L.A., Rico, P.J., Hofer, C.C., 2017. Comparison of Saliva Collection Methods for the Determination of Salivary Cortisol Levels in Rhesus Macaques (Macaca mulatta), Cynomolgus Macaques (Macaca fascicularis), and African Green Monkeys (Chlorocebus aethiops). J. Am. Assoc. Lab. Anim. Sci. JAALAS 56, 181–189.

Rathke, E.-M., Berghänel, A., Bissonnette, A., Ostner, J., Schülke, O., 2017. Age-dependent change of coalitionary strategy in male Barbary macaques. Primate Biol. 4, 1–7. https://doi.org/10.5194/pb-4-1-2017

Rathke, E.-M., Fischer, J., 2021. Social aging in male and female Barbary macaques. Am. J. Primatol. 83, e23272. https://doi.org/10.1002/ajp.23272

Rathke, E.-M., Fischer, J., 2020. Differential ageing trajectories in motivation, inhibitory control and cognitive flexibility in Barbary macaques (Macaca sylvanus). Philos. Trans. R. Soc. B Biol. Sci. 375, 20190617. https://doi.org/10.1098/rstb.2019.0617

Rathke, E.-M., Mundry, R., Fischer, J., 2022. Older Barbary macaques show limited capacity for self-regulation to avoid hazardous social interactions. Commun. Biol. 5, 1–8. https://doi.org/10.1038/s42003-022-04012-5

Ratiner, K., Abdeen, S.K., Goldenberg, K., Elinav, E., 2022. Utilization of Host and Microbiome Features in Determination of Biological Aging. Microorganisms 10, 668. https://doi.org/10.3390/microorganisms10030668

Raulo, A., Allen, B.E., Troitsky, T., Husby, A., Firth, J.A., Coulson, T., Knowles, S.C.L., 2021. Social networks strongly predict the gut microbiota of wild mice. ISME J. 15, 2601–2613. https://doi.org/10.1038/s41396-021-00949-3

Raulo, A., Dantzer, B., 2018. Associations between glucocorticoids and sociality across a continuum of vertebrate social behavior. Ecol. Evol. 8, 7697–7716. https://doi.org/10.1002/ece3.4059

Raulo, A., Ruokolainen, L., Lane, A., Amato, K., Knight, R., Leigh, S., Stumpf, R., White, B., Nelson, K.E., Baden, A.L., Tecot, S.R., 2018. Social behaviour and gut microbiota in red-bellied lemurs (*Eulemur rubriventer*): in search of the role of immunity in the evolution of sociality. J. Anim. Ecol. 87, 388–399. https://doi.org/10.1111/1365-2656.12781

Reed, T.E., Kruuk, L.E.B., Wanless, S., Frederiksen, M., Cunningham, E.J.A., Harris, M.P., 2008. Reproductive Senescence in a Long-Lived Seabird: Rates of Decline in Late-Life Performance Are Associated with Varying Costs of Early Reproduction. Am. Nat. 171, E89–E101. https://doi.org/10.1086/524957

Reese, A.T., Phillips, S.R., Owens, L.A., Venable, E.M., Langergraber, K.E., Machanda, Z.P., Mitani, J.C., Muller, M.N., Watts, D.P., Wrangham, R.W., Goldberg, T.L., Emery Thompson, M., Carmody, R.N., 2021. Age Patterning in Wild Chimpanzee Gut Microbiota Diversity Reveals Differences from Humans in Early Life. Curr. Biol. 31, 613-620.e3. https://doi.org/10.1016/j.cub.2020.10.075

Reimers, T.J., McGarrity, M.S., Strickland, D., 1986. Effect of fasting on thyroxine, 3,5,3'-triiodothyronine, and cortisol concentrations in serum of dogs. Am. J. Vet. Res. 47, 2485–2490.

Reinke, B.A., Cayuela, H., Janzen, F.J., Lemaître, J.-F., Gaillard, J.-M., Lawing, A.M., Iverson, J.B., Christiansen, D.G., Martínez-Solano, I., Sánchez-Montes, G., Gutiérrez-Rodríguez, J., Rose, F.L., Nelson, N., Keall, S., Crivelli, A.J., Nazirides, T., Grimm-Seyfarth, A., Henle, K., Mori, E., Guiller, G., Homan, R., Olivier, A., Muths, E., Hossack, B.R., Bonnet, X., Pilliod, D.S., Lettink, M., Whitaker, T., Schmidt, B.R., Gardner, M.G., Cheylan, M., Poitevin, F., Golubović, A., Tomović, L., Arsovski, D., Griffiths, R.A., Arntzen, J.W., Baron, J.-P., Le Galliard, J.-F., Tully, T., Luiselli, L., Capula, M., Rugiero, L., McCaffery, R., Eby, L.A., Briggs-Gonzalez, V., Mazzotti, F., Pearson, D., Lambert, B.A., Green, D.M., Jreidini, N., Angelini, C., Pyke, G., Thirion, J.-M., Joly, P., Léna, J.-P., Tucker, A.D., Limpus, C., Priol, P., Besnard, A., Bernard, P., Stanford, K., King, R., Garwood, J., Bosch, J., Souza, F.L., Bertoluci, J., Famelli, S., Grossenbacher, K., Lenzi, O., Matthews, K., Boitaud, S., Olson, D.H., Jessop, T.S., Gillespie, G.R., Clobert, J., Richard, M., Valenzuela-Sánchez, A., Fellers, G.M., Kleeman, P.M., Halstead, B.J., Grant, E.H.C., Byrne, P.G., Frétey, T., Le Garff, B., Levionnois, P., Maerz, J.C., Pichenot, J., Olgun, K., Üzüm, N., Avcı, A., Miaud, C., Elmberg, J., Brown, G.P., Shine, R., Bendik, N.F., O'Donnell, L., Davis, C.L., Lannoo, M.J., Stiles, R.M., Cox, R.M., Reedy, A.M., Warner, D.A., Bonnaire, E., Grayson, K., Ramos-Targarona, R., Baskale, E., Muñoz, D., Measey, J., de Villiers, F.A., Selman, W., Ronget, V., Bronikowski, A.M., Miller, D.A.W., 2022. Diverse aging rates in ectothermic tetrapods provide insights for the evolution of aging and longevity. Science 376, 1459–1466. https://doi.org/10.1126/science.abm0151

Reitmeier, S., Hitch, T.C.A., Treichel, N., Fikas, N., Hausmann, B., Ramer-Tait, A.E., Neuhaus, K., Berry, D., Haller, D., Lagkouvardos, I., Clavel, T., 2021. Handling of spurious sequences affects the outcome of high-throughput 16S rRNA gene amplicon profiling. ISME Commun. 1, 1–12. https://doi.org/10.1038/s43705-021-00033-z

Ren, T., Grieneisen, L.E., Alberts, S.C., Archie, E.A., Wu, M., 2016. Development, diet, and dynamism: longitudinal and cross-sectional predictors of gut microbial communities in wild baboons. Environ. Microbiol. 18, 1312–1325. https://doi.org/10.1111/1462-2920.12852

Renson, A., Mullan Harris, K., Dowd, J.B., Gaydosh, L., McQueen, M.B., Krauter, K.S., Shannahan, M., Aiello, A.E., 2020. Early Signs of Gut Microbiome Aging: Biomarkers of Inflammation, Metabolism, and Macromolecular Damage in Young Adulthood. J. Gerontol. Ser. A 75, 1258–1266. https://doi.org/10.1093/gerona/glaa122

Reul, J.M.H.M., Rothuizen, J., de Kloet, E.R., 1991. Age-related changes in the dog hypothalamic-pituitary-adrenocortical system: Neuroendocrine activity and corticosteroid receptors. J. Steroid Biochem. Mol. Biol. 40, 63–69. https://doi.org/10.1016/0960-0760(91)90168-5

Richter, C., Heesen, M., Nenadić, O., Ostner, J., Schülke, O., 2016. Males matter: increased home range size is associated with the number of resident males after controlling for ecological factors in wild Assamese macaques. Am. J. Phys. Anthropol. 159, 52–62. https://doi.org/10.1002/ajpa.22834

Ricklefs, R.E., 2010. Insights from comparative analyses of aging in birds and mammals. Aging Cell 9, 273–284. https://doi.org/10.1111/j.1474-9726.2009.00542.x

Rifkin, J.L., Nunn, C.L., Garamszegi, L.Z., 2012. Do Animals Living in Larger Groups Experience Greater Parasitism? A Meta-Analysis. Am. Nat. 180, 70–82. https://doi.org/10.1086/666081

Rimbach, R., Bisanzio, D., Galvis, N., Link, A., Di Fiore, A., Gillespie, T.R., 2015. Brown spider monkeys (*Ateles hybridus*): a model for differentiating the role of social networks and physical contact on parasite transmission dynamics. Philos. Trans. R. Soc. B Biol. Sci. 370, 20140110. https://doi.org/10.1098/rstb.2014.0110

Rincon, A.V., Ostner, J., Heistermann, M., Deschner, T., 2019. Measuring urinary cortisol and testosterone levels in male Barbary macaques: A comparison of EIA and LC–MS. Gen. Comp. Endocrinol. 281, 117–125. https://doi.org/10.1016/j.ygcen.2019.05.017

Risely, A., 2020. Applying the core microbiome to understand host–microbe systems. J. Anim. Ecol. 89, 1549–1558. https://doi.org/10.1111/1365-2656.13229

Risely, A., Schmid, D.W., Müller-Klein, N., Wilhelm, K., Clutton-Brock, T.H., Manser, M.B., Sommer, S., 2022. Gut microbiota individuality is contingent on temporal scale and age in wild meerkats. Proc. R. Soc. B Biol. Sci. 289, 20220609. https://doi.org/10.1098/rspb.2022.0609

Risely, A., Wilhelm, K., Clutton-Brock, T., Manser, M.B., Sommer, S., 2021. Diurnal oscillations in gut bacterial load and composition eclipse seasonal and lifetime dynamics in wild meerkats. Nat. Commun. 12, 6017. https://doi.org/10.1038/s41467-021-26298-5

Roach, D.A., Carey, J.R., 2014. Population Biology of Aging in the Wild. Annu. Rev. Ecol. Evol. Syst. 45, 421–443. https://doi.org/10.1146/annurev-ecolsys-120213-091730

Roff, D.A., Fairbairn, D.J., 2007. The evolution of trade-offs: where are we? J. Evol. Biol. 20, 433–447. https://doi.org/10.1111/j.1420-9101.2006.01255.x

Rognes, T., Flouri, T., Nichols, B., Quince, C., Mahé, F., 2016. VSEARCH: a versatile open source tool for metagenomics. PeerJ 4, e2584. https://doi.org/10.7717/peerj.2584

Rohleder, N., 2014. Stimulation of systemic low-grade inflammation by psychosocial stress. Psychosom. Med. 76, 181–189. https://doi.org/10.1097/PSY.0000000000000049

Röhr, S., Löbner, M., Gühne, U., Heser, K., Kleineidam, L., Pentzek, M., Fuchs, A., Eisele, M., Kaduszkiewicz, H., König, H.-H., Brettschneider, C., Wiese, B., Mamone, S., Weyerer, S., Werle, J., Bickel, H., Weeg, D., Maier, W., Scherer, M., Wagner, M., Riedel-Heller, S.G., 2020. Changes in Social Network Size Are Associated With Cognitive Changes in the Oldest-Old. Front. Psychiatry 11.

Rohrer, J.M., Murayama, K., 2023. These Are Not the Effects You Are Looking for: Causality and the Within-/Between-Persons Distinction in Longitudinal Data Analysis. Adv. Methods Pract. Psychol. Sci. 6, 25152459221140842. https://doi.org/10.1177/25152459221140842

Rojas, C.A., Holekamp, K.E., Viladomat Jasso, M., Souza, V., Eisen, J.A., Theis, K.R., 2022. Taxonomic, Genomic, and Functional Variation in the Gut Microbiomes of Wild Spotted Hyenas Across 2 Decades of Study. mSystems 8, e00965-22. https://doi.org/10.1128/msystems.00965-22

Romaní-Pérez, M., López-Almela, I., Bullich-Vilarrubias, C., Rueda-Ruzafa, L., Gómez Del Pulgar, E.M., Benítez-Páez, A., Liebisch, G., Lamas, J.A., Sanz, Y., 2021. Holdemanella biformis improves glucose tolerance and regulates GLP-1 signaling in obese mice. FASEB J. 35, e21734. https://doi.org/10.1096/fj.202100126R

Romano, V., Shen, M., Pansanel, J., MacIntosh, A.J.J., Sueur, C., 2018. Social transmission in networks: global efficiency peaks with intermediate levels of modularity. Behav. Ecol. Sociobiol. 72, 154. https://doi.org/10.1007/s00265-018-2564-9

Romero, L.M., Dickens, M.J., Cyr, N.E., 2009. The reactive scope model — A new model integrating homeostasis, allostasis, and stress. Horm. Behav. 55, 375–389. https://doi.org/10.1016/j.yhbeh.2008.12.009

Roney, J.R., Higham, J.P., 2017. Synthesizing research on field endocrinology of nonhuman primates and humans. Horm. Behav., Field endocrinology of nonhuman primates and humans 91, 1–2. https://doi.org/10.1016/j.yhbeh.2017.03.011

Ronget, V., Gaillard, J.-M., 2020. Assessing ageing patterns for comparative analyses of mortality curves: Going beyond the use of maximum longevity. Funct. Ecol. 34, 65–75. https://doi.org/10.1111/1365-2435.13474

Ronget, V., Garratt, M., Lemaître, J.-F., Gaillard, J.-M., 2017. The 'Evo-Demo' Implications of Condition-Dependent Mortality. Trends Ecol. Evol. 32, 909–921. https://doi.org/10.1016/j.tree.2017.09.003

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. R. Soc. B Biol. Sci. 283, 20160376. https://doi.org/10.1098/rspb.2016.0376

Rosati, A.G., Hagberg, L., Enigk, D.K., Otali, E., Thompson, M.E., Muller, M.N., Wrangham, R.W., Machanda, Z.P., 2020. Social selectivity in aging wild chimpanzees. Science 370, 473–476. https://doi.org/10.1126/science.aaz9129

Rosati, A.G., Santos, L.R., 2017. Tolerant Barbary macaques maintain juvenile levels of social attention in old age, but despotic rhesus macaques do not. Anim. Behav. 130, 199–207. https://doi.org/10.1016/j.anbehav.2017.06.019

Rosenbaum, M., Hirsch, J., Murphy, E., Leibel, R.L., 2000. Effects of changes in body weight on carbohydrate metabolism, catecholamine excretion, and thyroid function. Am. J. Clin. Nutr. 71, 1421–1432. https://doi.org/10.1093/ajcn/71.6.1421

Roth, G.S., Handy, A.M., Mattison, J.A., Tilmont, E.M., Ingram, D.K., Lane, M.A., 2002. Effects of Dietary Caloric Restriction and Aging on Thyroid Hormones of Rhesus Monkeys. Horm. Metab. Res. 34, 378–382. https://doi.org/10.1055/s-2002-33469

Rowe, J.W., Kahn, R.L., 1997. Successful Aging. The Gerontologist 37, 433–440. https://doi.org/10.1093/geront/37.4.433

Rowe, J.W., Kahn, R.L., 1987. Human Aging: Usual and Successful. Science 237, 143–149. https://doi.org/10.1126/science.3299702

RStudio Team, 2022. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA.

Rudolph, K., Schneider, D., Fichtel, C., Daniel, R., Heistermann, M., Kappeler, P.M., 2022. Drivers of gut microbiome variation within and between groups of a wild Malagasy primate. Microbiome 10, 28. https://doi.org/10.1186/s40168-021-01223-6

Rupp, S., Ambata, P., Narat, V., Giles-Vernick, T., 2016. Beyond the Cut Hunter: A Historical Epidemiology of HIV Beginnings in Central Africa. EcoHealth 13, 661–671. https://doi.org/10.1007/s10393-016-1189-6

Rushmore, J., Bisanzio, D., Gillespie, T.R., 2017. Making New Connections: Insights from Primate–Parasite Networks. Trends Parasitol. 33, 547–560. https://doi.org/10.1016/j.pt.2017.01.013

Rushmore, J., Caillaud, D., Hall, R.J., Stumpf, R.M., Meyers, L.A., Altizer, S., 2014. Network-based vaccination improves prospects for disease control in wild chimpanzees. J. R. Soc. Interface 11. https://doi.org/10.1098/rsif.2014.0349

Sadoughi, B., Anzà, S., Defolie, C., Manin, V., Müller-Klein, N., Murillo, T., Ulrich, M., Wu, D., 2022a. Parasites in a social world: Lessons from primates, in: Ezenwa, V., Altizer, S.M., Hall, R. (Eds.), Animal Behavior and Parasitism. Oxford University Press, p. 0. https://doi.org/10.1093/oso/9780192895561.003.0003

Sadoughi, B., Girard-Buttoz, C., Engelhardt, A., Heistermann, M., Ostner, J., 2021a. Non-invasive assessment of metabolic responses to food restriction using urinary triiodothyronine and cortisol measurement in macaques. Gen. Comp. Endocrinol. 306, 113736. https://doi.org/10.1016/j.ygcen.2021.113736

Sadoughi, B., Lacroix, L., Berbesque, C., Meunier, H., Lehmann, J., 2021b. Effects of social tolerance on stress: hair cortisol concentrations in the tolerant Tonkean macaques (Macaca tonkeana) and the despotic long-tailed macaques (Macaca fascicularis). Stress 24, 1033–1041. https://doi.org/10.1080/10253890.2021.1998443

Sadoughi, B., Schneider, D., Daniel, R., Schülke, O., Ostner, J., 2022b. Aging gut microbiota of wild macaques are equally diverse, less stable, but progressively personalized. Microbiome 10, 95. https://doi.org/10.1186/s40168-022-01283-2

Sah, P., Leu, S.T., Cross, P.C., Hudson, P.J., Bansal, S., 2017. Unraveling the disease consequences and mechanisms of modular structure in animal social networks. Proc. Natl. Acad. Sci. 114, 4165–4170. https://doi.org/10.1073/pnas.1613616114

Samson, D.R., Louden, L.A., Gerstner, K., Wylie, S., Lake, B., White, B.J., Nunn, C.L., Hunt, K.D., 2019. Chimpanzee (*Pan troglodytes schweinfurthii*) Group Sleep and Pathogen-Vector Avoidance: Experimental Support for the Encounter-Dilution Effect. Int. J. Primatol. 40, 647–659. https://doi.org/10.1007/s10764-019-00111-z

Sapolsky, R.M., 2021. Glucocorticoids, the evolution of the stress-response, and the primate predicament. Neurobiol. Stress 14, 100320. https://doi.org/10.1016/j.ynstr.2021.100320

References

Sapolsky, R.M., 2005. The Influence of Social Hierarchy on Primate Health. Science 308, 648–652. https://doi.org/10.1126/science.1106477

Sapolsky, R.M., 2004. Why Zebras Don't Get Ulcers: The Acclaimed Guide to Stress, Stress-Related Diseases, and Coping (Third Edition). Henry Holt and Company.

Sapolsky, R.M., 1993. Endocrinology alfresco: psychoendocrine studies of wild baboons. Recent Prog. Horm. Res. 48, 437–468. https://doi.org/10.1016/b978-0-12-571148-7.50020-8

Sapolsky, R.M., 1992a. Do glucocorticoid concentrations rise with age in the rat? Neurobiol. Aging 13, 171–174. https://doi.org/10.1016/0197-4580(92)90025-S

Sapolsky, R.M., 1992b. Cortisol Concentrations and the Social Significance of Rank Instability Among Wild Baboons. Psychoneuroendocrinology 17, 701–709. https://doi.org/10.1016/0306-4530(92)90029-7

Sapolsky, R.M., Altmann, J., 1991. Incidence of hypercortisolism and dexamethasone resistance increases with age among wild baboons. Biol. Psychiatry 30, 1008–1016. https://doi.org/10.1016/0006-3223(91)90121-2

Sapolsky, R.M., Krey, L.C., McEwen, B.S., 2002. The Neuroendocrinology of Stress and Aging: The Glucocorticoid Cascade Hypothesis. Sci. Aging Knowl. Environ. 2002, cp21–cp21. https://doi.org/10.1126/sageke.2002.38.cp21

Sapolsky, R.M., Romero, L.M., Munck, A.U., 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocr. Rev. 21, 55–89. https://doi.org/10.1210/edrv.21.1.0389

Sarkar, A., Harty, S., Johnson, K.V.-A., Moeller, A.H., Archie, E.A., Schell, L.D., Carmody, R.N., Clutton-Brock, T.H., Dunbar, R.I.M., Burnet, P.W.J., 2020. Microbial transmission in animal social networks and the social microbiome. Nat. Ecol. Evol. 4, 1020–1035. https://doi.org/10.1038/s41559-020-1220-8

Sato, Y., Atarashi, K., Plichta, D.R., Arai, Y., Sasajima, S., Kearney, S.M., Suda, W., Takeshita, K., Sasaki, T., Okamoto, S., Skelly, A.N., Okamura, Y., Vlamakis, H., Li, Y., Tanoue, T., Takei, H., Nittono, H., Narushima, S., Irie, J., Itoh, H., Moriya, K., Sugiura, Y., Suematsu, M., Moritoki, N., Shibata, S., Littman, D.R., Fischbach, M.A., Uwamino, Y., Inoue, T., Honda, A., Hattori, M., Murai, T., Xavier, R.J., Hirose, N., Honda, K., 2021. Novel bile acid biosynthetic pathways are enriched in the microbiome of centenarians. Nature 599, 458–464. https://doi.org/10.1038/s41586-021-03832-5

Savtchenko, A., Greenbelt, M., 2016. Goddard Earth Sciences Data and Information Services Center TRMM (TMPA-RT) Near Real-Time Precipitation L3 1 day 0.25 degree x 0.25 degree V7, Accessed: 01 June 2021.

Schaebs, F.S., Wolf, T.E., Behringer, V., Deschner, T., 2016. Fecal thyroid hormones allow for the noninvasive monitoring of energy intake in capuchin monkeys. J. Endocrinol. 231, 1–10. https://doi.org/10.1530/JOE-16-0152

Schino, G., Pinzaglia, M., 2018. Age-related changes in the social behavior of tufted capuchin monkeys. Am. J. Primatol. 80, e22746. https://doi.org/10.1002/ajp.22746

Schloissnig, S., Arumugam, M., Sunagawa, S., Mitreva, M., Tap, J., Zhu, A., Waller, A., Mende, D.R., Kultima, J.R., Martin, J., Kota, K., Sunyaev, S.R., Weinstock, G.M., Bork, P., 2013. Genomic variation landscape of the human gut microbiome. Nature 493, 45–50. https://doi.org/10.1038/nature11711

Schmauck-Medina, T., Molière, A., Lautrup, S., Zhang, J., Chlopicki, S., Madsen, H.B., Cao, S., Soendenbroe, C., Mansell, E., Vestergaard, M.B., Li, Z., Shiloh, Y., Opresko, P.L., Egly, J.-M., Kirkwood, T., Verdin, E., Bohr, V.A., Cox, L.S., Stevnsner, T., Rasmussen, L.J., Fang, E.F., 2022. New hallmarks of ageing: a 2022 Copenhagen ageing meeting summary. Aging 14, 6829–6839. https://doi.org/10.18632/aging.204248

Schoenle, L.A., Zimmer, C., Miller, E.T., Vitousek, M.N., 2021. Does variation in glucocorticoid concentrations predict fitness? A phylogenetic meta-analysis. Gen. Comp. Endocrinol. 300, 113611. https://doi.org/10.1016/j.ygcen.2020.113611

Schoenle, L.A., Zimmer, C., Vitousek, M.N., 2018. Understanding Context Dependence in Glucocorticoid–Fitness Relationships: The Role of the Nature of the Challenge, the Intensity and Frequency of Stressors, and Life History. Integr. Comp. Biol. 58, 777–789. https://doi.org/10.1093/icb/icy046

Schülke, O., Anzà, S., Crockford, C., De Moor, D., Deschner, T., Fichtel, C., Gogarten, J.F., Kappeler, P.M., Manin, V., Müller-Klein, N., Prox, L., Sadoughi, B., Touitou, S., Wittig, R.M., Ostner, J., 2022. Quantifying within-group variation in sociality—covariation among metrics and patterns across primate groups and species. Behav. Ecol. Sociobiol. 76, 50. https://doi.org/10.1007/s00265-022-03133-5

Schülke, O., Bhagavatula, J., Vigilant, L., Ostner, J., 2010. Social Bonds Enhance Reproductive Success in Male Macaques. Curr. Biol. 20, 2207–2210. https://doi.org/10.1016/j.cub.2010.10.058

Schülke, O., Pesek, D., Whitman, B., J., Ostner, J., 2011. Ecology of Assamese macaques (Macaca assamensis) at Phu Phieo Wildlife Sanctuary, Thailand. J. Wildl. Thail. 1–15.

Scott, C., Dantzer, B., Goymann, W., Rubenstein, D.R., Boonstra, R., 2012. The ecology of stress: effects of the social environment. Funct. Ecol. 27, 66–80. https://doi.org/10.1111/j.1365-2435.2012.02029.x

Selman, C., Blount, J.D., Nussey, D.H., Speakman, J.R., 2012. Oxidative damage, ageing, and life-history evolution: where now? Trends Ecol. Evol. 27, 570–577. https://doi.org/10.1016/j.tree.2012.06.006

Sencio, V., Machelart, A., Robil, C., Benech, N., Hoffmann, E., Galbert, C., Deryuter, L., Heumel, S., Hantute-Ghesquier, A., Flourens, A., Brodin, P., Infanti, F., Richard, V., Dubuisson, J., Grangette, C., Sulpice, T., Wolowczuk, I., Pinet, F., Prévot, V., Belouzard, S., Briand, F., Duterque-Coquillaud, M., Sokol, H., Trottein, F., 2022. Alteration of the gut microbiota following SARS-CoV-2 infection correlates with disease severity in hamsters. Gut Microbes 14, 2018900. https://doi.org/10.1080/19490976.2021.2018900

Setchell, J.M., Smith, T., Wickings, E.J., Knapp, L.A., 2010. Stress, social behaviour, and secondary sexual traits in a male primate. Horm. Behav. 58, 720–728. https://doi.org/10.1016/j.yhbeh.2010.07.004

Sharp, P.M., Rayner, J.C., Hahn, B.H., 2013. Great Apes and Zoonoses. Science 340, 284–286. https://doi.org/10.1126/science.1236958

Sharp, S.P., Clutton-Brock, T.H., 2010. Reproductive senescence in a cooperatively breeding mammal. J. Anim. Ecol. 79, 176–183. https://doi.org/10.1111/j.1365-2656.2009.01616.x

Sherry, D.S., Ellison, P.T., 2007. Potential applications of urinary C-peptide of insulin for comparative energetics research. Am. J. Phys. Anthropol. 133, 771–778. https://doi.org/10.1002/ajpa.20562

Sherwin, E., Bordenstein, S.R., Quinn, J.L., Dinan, T.G., Cryan, J.F., 2019. Microbiota and the social brain. Science 366, eaar2016. https://doi.org/10.1126/science.aar2016

Shively, C.A., Laber-Laird, K., Anton, R.F., 1997. Behavior and physiology of social stress and depression in female cynomolgus monkeys. Biol. Psychiatry 41, 871–882. https://doi.org/10.1016/S0006-3223(96)00185-0

Shively, C.A., Musselman, D.L., Willard, S.L., 2009. Stress, depression, and coronary artery disease: Modeling comorbidity in female primates. Neurosci. Biobehav. Rev., The Inevitable Link between Heart and Behavior: New Insights from Biomedical Research and Implications for Clinical Practice 33, 133–144. https://doi.org/10.1016/j.neubiorev.2008.06.006

Shutt, K., MacLarnon, A., Heistermann, M., Semple, S., 2007. Grooming in Barbary macaques: Better to give than to receive? Biol. Lett. 3, 231–3. https://doi.org/10.1098/rsbl.2007.0052

Shutt, K., Setchell, J.M., Heistermann, M., 2012. Non-invasive monitoring of physiological stress in the Western lowland gorilla (Gorilla gorilla gorilla): Validation of a fecal glucocorticoid assay and methods for practical application in the field. Gen. Comp. Endocrinol. 179, 167–177. https://doi.org/10.1016/j.ygcen.2012.08.008

Silk, J., Cheney, D., Seyfarth, R., 2013. A practical guide to the study of social relationships. Evol. Anthropol. Issues News Rev. 22, 213–225. https://doi.org/10.1002/evan.21367

Silk, J.B., 2009. Nepotistic cooperation in non-human primate groups. Philos. Trans. R. Soc. B Biol. Sci. 364, 3243–3254. https://doi.org/10.1098/rstb.2009.0118

Silk, J.B., 1994. Social Relationships of Male Bonnet Macaques: Male Bonding in a Matrilineal Society. Behaviour 130, 271–291.

Silk, J.B., Altmann, J., Alberts, S.C., 2006. Social relationships among adult female baboons (papio cynocephalus) I. Variation in the strength of social bonds. Behav. Ecol. Sociobiol. 61, 183–195. https://doi.org/10.1007/s00265-006-0249-2

Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., Cheney, D.L., 2010. Strong and Consistent Social Bonds Enhance the Longevity of Female Baboons. Curr. Biol. 20, 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067

Silk, J.B., Kappeler, P.M., 2017. Sociality in Primates, in: Rubenstein, D.R., Abbot, P. (Eds.), Comparative Social Evolution. Cambridge University Press, pp. 253–283.

Silk, J.B., Seyfarth, R.M., Cheney, D.L., 2018. Quality versus quantity: do weak bonds enhance the fitness of female baboons? Anim. Behav. 140, 207–211. https://doi.org/10.1016/j.anbehav.2018.04.013

Silk, J.B., Städele, V., Roberts, E.K., Vigilant, L., Strum, S.C., 2020. Shifts in Male Reproductive Tactics over the Life Course in a Polygynandrous Mammal. Curr. Biol. 30, 1716-1720.e3. https://doi.org/10.1016/j.cub.2020.02.013

Silva, J.E., 2006. Thermogenic Mechanisms and Their Hormonal Regulation. Physiol. Rev. 86, 435–464. https://doi.org/10.1152/physrev.00009.2005

Silva, J.E., 1995. Thyroid Hormone Control of Thermogenesis and Energy Balance. Thyroid 5, 481–492. https://doi.org/10.1089/thy.1995.5.481

Simmons, H.A., 2016. Age-Associated Pathology in Rhesus Macaques (Macaca mulatta). Vet. Pathol. 53, 399–416. https://doi.org/10.1177/0300985815620628

Siracusa, E.R., Higham, J.P., Snyder-Mackler, N., Brent, L.J.N., 2022a. Social ageing: exploring the drivers of late-life changes in social behaviour in mammals. Biol. Lett. 18, 20210643. https://doi.org/10.1098/rsbl.2021.0643

Siracusa, E.R., Negron-Del Valle, J.E., Phillips, D., Platt, M.L., Higham, J.P., Snyder-Mackler, N., Brent, L.J.N., 2022b. Within-individual changes reveal increasing social selectivity with age in rhesus macaques. Proc. Natl. Acad. Sci. 119, e2209180119. https://doi.org/10.1073/pnas.2209180119

Smith, J.E., Lacey, E.A., Hayes, L.D., 2017. Sociality in non-primate mammals, in: Rubenstein, D.R., Abbot, P. (Eds.), Comparative Social Evolution. Cambridge University Press, Cambridge, pp. 284–319.

Smith, P., Willemsen, D., Popkes, M., Metge, F., Gandiwa, E., Reichard, M., Valenzano, D.R., 2017. Regulation of life span by the gut microbiota in the short-lived African turquoise killifish. eLife 6, e27014. https://doi.org/10.7554/eLife.27014

Smithson, M., Verkuilen, J., 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychol. Methods 11, 54–71. https://doi.org/10.1037/1082-989X.11.1.54

Snaith, T.V., Chapman, C.A., Rothman, J.M., Wasserman, M.D., 2008. Bigger groups have fewer parasites and similar cortisol levels: a multi-group analysis in red colobus monkeys. Am. J. Primatol. 70, 1072–1080. https://doi.org/10.1002/ajp.20601

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., 2019. Social status alters chromatin accessibility and the gene regulatory response to glucocorticoid stimulation in rhesus macaques. Proc. Natl. Acad. Sci. 116, 1219–1228. https://doi.org/10.1073/pnas.1811758115

Sosa, S., Sueur, C., Puga-Gonzalez, I., 2021. Network measures in animal social network analysis: Their strengths, limits, interpretations and uses. Methods Ecol. Evol. 12, 10–21. https://doi.org/10.1111/2041-210X.13366

Soutschek, A., Bagaïni, A., Hare, T.A., Tobler, P.N., 2021. Reconciling psychological and neuroscientific accounts of reduced motivation in aging. Soc. Cogn. Affect. Neurosci. nsab101. https://doi.org/10.1093/scan/nsab101

Speakman, J.R., 1999. The Cost of Living: Field Metabolic Rates of Small Mammals, in: Fitter, A.H., Raffaelli, D.G. (Eds.), Advances in Ecological Research. Academic Press, pp. 177–297. https://doi.org/10.1016/S0065-2504(08)60019-7

Speakman, J.R., Blount, J.D., Bronikowski, A.M., Buffenstein, R., Isaksson, C., Kirkwood, T.B.L., Monaghan, P., Ozanne, S.E., Beaulieu, M., Briga, M., Carr, S.K., Christensen, L.L., Cochemé, H.M., Cram, D.L., Dantzer, B., Harper, J.M., Jurk, D., King, A., Noguera, J.C., Salin, K., Sild, E., Simons, M.J.P., Smith, S., Stier, A., Tobler, M., Vitikainen, E., Peaker, M., Selman, C., 2015. Oxidative stress and life histories: unresolved issues and current needs. Ecol. Evol. 5, 5745–5757. https://doi.org/10.1002/ece3.1790

Spencer, C.A., Lum, S.M., Wilber, J.F., Kaptein, E.M., Nicoloff, J.T., 1983. Dynamics of serum thyrotropin and thyroid hormone changes in fasting. J. Clin. Endocrinol. Metab. 56, 883–888. https://doi.org/10.1210/jcem-56-5-883

Springer, A., Kappeler, P.M., Nunn, C.L., 2017. Dynamic vs. static social networks in models of parasite transmission: predicting *Cryptosporidium* spread in wild lemurs. J. Anim. Ecol. 86, 419–433. https://doi.org/10.1111/1365-2656.12617

St. Lawrence, S., Dumas, M.N., Petelle, M., Blumstein, D.T., Martin, J.G.A., 2022. Sex-specific reproductive strategies in wild yellow-bellied marmots (Marmota flaviventer): senescence and genetic variance in annual reproductive success differ between the sexes. Behav. Ecol. Sociobiol. 76, 84. https://doi.org/10.1007/s00265-022-03191-9

Stowe, J.D., Cooney, T.M., 2015. Examining Rowe and Kahn's Concept of Successful Aging: Importance of Taking a Life Course Perspective. The Gerontologist 55, 43–50. https://doi.org/10.1093/geront/gnu055

Stull, C.L., Rodiek, A.V., 1988. Responses of Blood Glucose, Insulin and Cortisol Concentrations to Common Equine Diets. J. Nutr. 118, 206–213. https://doi.org/10.1093/jn/118.2.206

Suda, A.K., Pittman, C.S., Shimizu, T., Chambers, J.B., 1978. The Production and Metabolism of 3,5,3'-Triiodothyronine and 3,3',5'-Triiodothyronine in Normal and Fasting Subjects. J. Clin. Endocrinol. Metab. 47, 1311–1319. https://doi.org/10.1210/jcem-47-6-1311

Sukmak, M., Wajjwalku, W., Ostner, J., Schülke, O., 2014. Dominance rank, female reproductive synchrony, and male reproductive skew in wild Assamese macaques. Behav. Ecol. Sociobiol. 68, 1097–1108. https://doi.org/10.1007/s00265-014-1721-z

Suvorov, A., Karaseva, A., Kotyleva, M., Kondratenko, Y., Lavrenova, N., Korobeynikov, A., Kozyrev, P., Kramskaya, T., Leontieva, G., Kudryavtsev, I., Guo, D., Lapidus, A., Ermolenko, E., 2018. Autoprobiotics as an approach for restoration of personalised microbiota. Front. Microbiol. 9, 1869. https://doi.org/10.3389/fmicb.2018.01869

Takeshita, K., Mizuno, S., Mikami, Y., Sujino, T., Saigusa, K., Matsuoka, K., Naganuma, M., Sato, T., Takada, T., Tsuji, H., Kushiro, A., Nomoto, K., Kanai, T., 2016. A single species of Clostridium subcluster XIVa decreased in ulcerative colitis patients. Inflamm. Bowel Dis. 22, 2802–2810. https://doi.org/10.1097/MIB.0000000000000972

Tamanai-Shacoori, Z., Smida, I., Bousarghin, L., Loreal, O., Meuric, V., Fong, S.B., Bonnaure-Mallet, M., Jolivet-Gougeon, A., 2017. Roseburia spp.: a marker of health? Future Microbiol. 12, 157–170. https://doi.org/10.2217/fmb-2016-0130

References

Tamashiro, K.L., Sakai, R.R., Shively, C.A., Karatsoreos, I.N., Reagan, L.P., 2011. Chronic stress, metabolism, and metabolic syndrome. Stress 14, 468–474. https://doi.org/10.3109/10253890.2011.606341

Tap, J., Furet, J.-P., Bensaada, M., Philippe, C., Roth, H., Rabot, S., Lakhdari, O., Lombard, V., Henrissat, B., Corthier, G., Fontaine, E., Doré, J., Leclerc, M., 2015. Gut microbiota richness promotes its stability upon increased dietary fibre intake in healthy adults. Environ. Microbiol. 17, 4954–4964. https://doi.org/10.1111/1462-2920.13006

Thevaranjan, N., Puchta, A., Schulz, C., Naidoo, A., Szamosi, J.C., Verschoor, C.P., Loukov, D., Schenck, L.P., Jury, J., Foley, K.P., Schertzer, J.D., Larché, M.J., Davidson, D.J., Verdú, E.F., Surette, M.G., Bowdish, D.M.E., 2017. Age-associated microbial dysbiosis promotes intestinal permeability, systemic inflammation, and macrophage dysfunction. Cell Host Microbe 21, 455-466.e4. https://doi.org/10.1016/j.chom.2017.03.002

Thierry, B., 2007. Unity in diversity: Lessons from macaque societies. Evol. Anthropol. Issues News Rev. 16, 224–238. https://doi.org/10.1002/evan.20147

Thompson, C.L., Powell, B.L., Williams, S.H., Hanya, G., Glander, K.E., Vinyard, C.J., 2017. Thyroid hormone fluctuations indicate a thermoregulatory function in both a tropical (Alouatta palliata) and seasonally cold-habitat (Macaca fuscata) primate. Am. J. Primatol. 79, e22714. https://doi.org/10.1002/ajp.22714

Thompson González, N., Machanda, Z., Otali, E., Muller, M.N., Enigk, D.K., Wrangham, R., Emery Thompson, M., 2021. Age-related change in adult chimpanzee social network integration. Evol. Med. Public Health 9, 448–459. https://doi.org/10.1093/emph/eoab040

Thompson, N.A., 2019. Understanding the links between social ties and fitness over the life cycle in primates. Behaviour 156, 859–908. https://doi.org/10.1163/1568539X-00003552

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

Thompson, S.C., 1981. Will it hurt less if I can control it? A complex answer to a simple question. Psychol. Bull. 90, 89–101. https://doi.org/10.1037/0033-2909.90.1.89

Tian, L., Wang, X.-W., Wu, A.-K., Fan, Y., Friedman, J., Dahlin, A., Waldor, M.K., Weinstock, G.M., Weiss, S.T., Liu, Y.-Y., 2020. Deciphering functional redundancy in the human microbiome. Nat. Commun. 11, 6217. https://doi.org/10.1038/s41467-020-19940-1

Tidière, M., Gaillard, J., Müller, D.W.H., Lackey, L.B., Gimenez, O., Clauss, M., Lemaître, J., 2015. Does sexual selection shape sex differences in longevity and senescence patterns across vertebrates? A review and new insights from captive ruminants. Evolution 69, 3123–3140. https://doi.org/10.1111/evo.12801

Tidière, M., Thevenot, X., Deligiannopoulou, A., Douay, G., Whipple, M., Siberchicot, A., Gaillard, J.-M., Lemaître, J.-F., 2018. Maternal reproductive senescence shapes the fitness consequences of the parental age difference in ruffed lemurs. Proc. R. Soc. B Biol. Sci. 285, 20181479. https://doi.org/10.1098/rspb.2018.1479

Tomiyama, A.J., Mann, T., Vinas, D., Hunger, J.M., DeJager, J., Taylor, S.E., 2010. Low Calorie Dieting Increases Cortisol. Psychosom. Med. 72, 357–364. https://doi.org/10.1097/PSY.0b013e3181d9523c

Touitou, S., Heistermann, M., Schülke, O., Ostner, J., 2021a. The effect of reproductive state on activity budget, feeding behavior, and urinary C-peptide levels in wild female Assamese macaques. Behav. Ecol. Sociobiol. 75, 128. https://doi.org/10.1007/s00265-021-03058-5

Touitou, S., Heistermann, M., Schülke, O., Ostner, J., 2021b. Triiodothyronine and cortisol levels in the face of energetic challenges from reproduction, thermoregulation and food intake in female macaques. Horm. Behav. 131, 104968. https://doi.org/10.1016/j.yhbeh.2021.104968

Touitou, Y., Sulon, J., Bogdan, A., Reinberg, A., Sodoyez, J.-C., Demey-Ponsart, E., 1983. Adrenocortical hormones, ageing and mental condition: seasonal and circadian rhythms of plasma 18-hydroxy-11-deoxycorticosterone, total and free cortisol and urinary corticosteroids. J. Endocrinol. 96, 53–64. https://doi.org/10.1677/joe.0.0960053

Trosvik, P., de Muinck, E.J., Rueness, E.K., Fashing, P.J., Beierschmitt, E.C., Callingham, K.R., Kraus, J.B., Trew, T.H., Moges, A., Mekonnen, A., Venkataraman, V.V., Nguyen, N., 2018. Multilevel social structure and diet shape the gut microbiota of the gelada monkey, the only grazing primate. Microbiome 6, 84. https://doi.org/10.1186/s40168-018-0468-6

Tsuji, Y., Kazahari, N., Kitahara, M., Takatsuki, S., 2008. A more detailed seasonal division of the energy balance and the protein balance of Japanese macaques (Macaca fuscata) on Kinkazan Island, northern Japan. Primates 49, 157–160. https://doi.org/10.1007/s10329-007-0070-1

Tung, J., Barreiro, L.B., Burns, M.B., Grenier, J.-C., Lynch, J., Grieneisen, L.E., Altmann, J., Alberts, S.C., Blekhman, R., Archie, E.A., 2015. Social networks predict gut microbiome composition in wild baboons. eLife 4, e05224. https://doi.org/10.7554/eLife.05224

United Nations, D. of E. and S.A., Population Division, 2017. World Population Ageing 2017 - Highlights (ST/ESA/SER.A/397).

Uno, H., 1997. Age-related pathology and biosenescent markers in captive rhesus macaques. AGE 20, 1–13. https://doi.org/10.1007/s11357-997-0001-5

Uren Webster, T.M., Rodriguez-Barreto, D., Consuegra, S., Garcia de Leaniz, C., 2020. Cortisol-Related Signatures of Stress in the Fish Microbiome. Front. Microbiol. 11, 1621.

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. B Biol. Sci. 376, 20190744. https://doi.org/10.1098/rstb.2019.0744

Valderrama, X., Robinson, J.G., Attygalle, A.B., Eisner, T., 2000. Seasonal Anointment with Millipedes in a Wild Primate: A Chemical Defense Against Insects? J. Chem. Ecol. 26, 2781–2790. https://doi.org/10.1023/A:1026489826714

Van Cauter, E., Leproult, R., Kupfer, D.J., 1996. Effects of gender and age on the levels and circadian rhythmicity of plasma cortisol. J. Clin. Endocrinol. Metab. 81, 2468–2473. https://doi.org/10.1210/jcem.81.7.8675562

van de Pol, M., Verhulst, S., 2006. Age-Dependent Traits: A New Statistical Model to Separate Within- and Between-Individual Effects. Am. Nat. 167, 766–773. https://doi.org/10.1086/503331

van de Pol, M., Wright, J., 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. Anim. Behav. 77, 753–758. https://doi.org/10.1016/j.anbehav.2008.11.006

van den Beld, A.W., Kaufman, J.-M., Zillikens, M.C., Lamberts, S.W.J., Egan, J.M., van der Lely, A.J., 2018. The physiology of endocrine systems with ageing. Lancet Diabetes Endocrinol. 6, 647–658. https://doi.org/10.1016/S2213-8587(18)30026-3

van Noordwijk, M.A., van Schaik, C.P., 1987. Competition among female long-tailed macaques, Macaca fascicularis. Anim. Behav. 35, 577–589. https://doi.org/10.1016/S0003-3472(87)80284-1

van Schaik, C.P., van Noordwijk, M.A., van Bragt, T., Blankenstein, M.A., 1991. A pilot study of the social correlates of levels of urinary cortisol, prolactin, and testosterone in wild long-tailed macaques (Macaca fascicularis). Primates 32, 345–356. https://doi.org/10.1007/BF02382675

Veenema, H.C., Spruijt, B.M., Gispen, W.H., van Hooff, J.A.R.A.M., 1997. Aging, Dominance History, and Social Behavior in Java-Monkeys (Macaca fascicularis). Neurobiol. Aging 18, 509–515. https://doi.org/10.1016/S0197-4580(97)00107-3

Venkataraman, V.V., Glowacka, H., Fritz, J., Clauss, M., Seyoum, C., Nguyen, N., Fashing, P.J., 2014. Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (Theropithecus gelada). Am. J. Phys. Anthropol. 155, 17–32. https://doi.org/10.1002/ajpa.22571

Vicari, T., van den Borne, J.J.G.C., Gerrits, W.J.J., Zbinden, Y., Blum, J.W., 2008. Postprandial blood hormone and metabolite concentrations influenced by feeding frequency and feeding level in veal calves. Domest. Anim. Endocrinol. 34, 74–88. https://doi.org/10.1016/j.domaniend.2006.11.002

Vitousek, M.N., Johnson, M.A., Downs, C.J., Miller, E.T., Martin, L.B., Francis, C.D., Donald, J.W., Fuxjager, M.J., Goymann, W., Hau, M., Husak, J.F., Kircher, B.K., Knapp, R., Schoenle, L.A.,

Williams, T.D., 2019a. Macroevolutionary Patterning in Glucocorticoids Suggests Different Selective Pressures Shape Baseline and Stress-Induced Levels. Am. Nat. https://doi.org/10.1086/703112

Vitousek, M.N., Taff, C.C., Ryan, T.A., Zimmer, C., 2019b. Stress Resilience and the Dynamic Regulation of Glucocorticoids. Integr. Comp. Biol. 59, 251–263. https://doi.org/10.1093/icb/icz087

Wang, J., Chen, W.-D., Wang, Y.-D., 2020. The relationship between gut microbiota and inflammatory diseases: the role of macrophages. Front. Microbiol. 11, 1065. https://doi.org/10.3389/fmicb.2020.01065

Wasser, S.K., Azkarate, J.C., Booth, R.K., Hayward, L., Hunt, K., Ayres, K., Vynne, C., Gobush, K., Canales-Espinosa, D., Rodríguez-Luna, E., 2010. Non-invasive measurement of thyroid hormone in feces of a diverse array of avian and mammalian species. Gen. Comp. Endocrinol. 168, 1–7. https://doi.org/10.1016/j.ygcen.2010.04.004

Watowich, M.M., Chiou, K.L., Montague, M.J., Null, N., Simons, N.D., Horvath, J.E., Ruiz-Lambides, A.V., Martínez, M.I., Higham, J.P., Brent, L.J.N., Platt, M.L., Snyder-Mackler, N., Brent, L.J.N., Higham, J.P., Martínez, M.I., Montague, M.J., Platt, M.L., Snyder-Mackler, N., 2022. Natural disaster and immunological aging in a nonhuman primate. Proc. Natl. Acad. Sci. 119, e2121663119. https://doi.org/10.1073/pnas.2121663119

Wei, Z.-Y., Rao, J.-H., Tang, M.-T., Zhao, G.-A., Li, Q.-C., Wu, L.-M., Liu, S.-Q., Li, B.-H., Xiao, B.-Q., Liu, X.-Y., Chen, J.-H., 2021. Characterization of Changes and Driver Microbes in Gut Microbiota During Healthy Aging Using a Captive Monkey Model. Genomics Proteomics Bioinformatics. https://doi.org/10.1016/j.gpb.2021.09.009

Welcker, J., Chastel, O., Gabrielsen, G.W., Guillaumin, J., Kitaysky, A.S., Speakman, J.R., Tremblay, Y., Bech, C., 2013. Thyroid Hormones Correlate with Basal Metabolic Rate but Not Field Metabolic Rate in a Wild Bird Species. PLOS ONE 8, e56229. https://doi.org/10.1371/journal.pone.0056229

Wensink, M.J., Caswell, H., Baudisch, A., 2017. The Rarity of Survival to Old Age Does Not Drive the Evolution of Senescence. Evol. Biol. 44, 5–10. https://doi.org/10.1007/s11692-016-9385-4

Westneat, D.F., Araya-Ajoy, Y.G., Allegue, H., Class, B., Dingemanse, N., Dochtermann, N.A., Garamszegi, L.Z., Martin, J.G.A., Nakagawa, S., Réale, D., Schielzeth, H., 2020. Collision between biological process and statistical analysis revealed by mean centring. J. Anim. Ecol. 89, 2813–2824. https://doi.org/10.1111/1365-2656.13360

Williams, G.C., 1957. Pleiotropy, Natural Selection, and the Evolution of Senescence. Evolution 11, 398–411. https://doi.org/10.2307/2406060

Williams, P.D., Day, T., 2003. Antagonistic pleiotropy, mortality source interactions, and the evolutionary theory of senescence. Evol. Int. J. Org. Evol. 57, 1478–1488. https://doi.org/10.1111/j.0014-3820.2003.tb00356.x

Williams, P.D., Day, T., Fletcher, Q., Rowe, L., 2006. The shaping of senescence in the wild. Trends Ecol. Evol. 21, 458–463. https://doi.org/10.1016/j.tree.2006.05.008

Wilmanski, T., Diener, C., Rappaport, N., Patwardhan, S., Wiedrick, J., Lapidus, J., Earls, J.C., Zimmer, A., Glusman, G., Robinson, M., Yurkovich, J.T., Kado, D.M., Cauley, J.A., Zmuda, J., Lane, N.E., Magis, A.T., Lovejoy, J.C., Hood, L., Gibbons, S.M., Orwoll, E.S., Price, N.D., 2021. Gut microbiome pattern reflects healthy ageing and predicts survival in humans. Nat. Metab. 3, 274–286. https://doi.org/10.1038/s42255-021-00348-0

Wilson, Q.N., Wells, M., Davis, A.T., Sherrill, C., Tsilimigras, M.C.B., Jones, R.B., Fodor, A.A., Kavanagh, K., 2018. Greater microbial translocation and vulnerability to metabolic disease in healthy aged female monkeys. Sci. Rep. 8, 11373. https://doi.org/10.1038/s41598-018-29473-9

Wilson, S.N., Sindi, S.S., Brooks, H.Z., Hohn, M.E., Price, C.R., Radunskaya, A.E., Williams, N.D., Fefferman, N.H., 2020. How Emergent Social Patterns in Allogrooming Combat Parasitic Infections. Front. Ecol. Evol. 8. https://doi.org/10.3389/fevo.2020.00054

Wittig, R.M., Crockford, C., Lehmann, J., Whitten, P.L., Seyfarth, R.M., Cheney, D.L., 2008. Focused grooming networks and stress alleviation in wild female baboons. Horm. Behav. 54, 170–177. https://doi.org/10.1016/j.yhbeh.2008.02.009

Wittig, R.M., Crockford, C., Weltring, A., Langergraber, K.E., Deschner, T., Zuberbühler, K., 2016. Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. Nat. Commun. 7, 13361. https://doi.org/10.1038/ncomms13361

Wolden-Hanson, T., Davis, G.A., Baum, S.T., Kemnitz, J.W., 1993. Insulin levels, physical activity, and urinary catecholamine excretion of obese and non-obese rhesus monkeys. Obes. Res. 1, 5–17.

Worsley, S.F., Davies, C.S., Mannarelli, M.-E., Hutchings, M.I., Komdeur, J., Burke, T., Dugdale, H.L., Richardson, D.S., 2021. Gut microbiome composition, not alpha diversity, is associated with survival in a natural vertebrate population. Anim. Microbiome 3, 84. https://doi.org/10.1186/s42523-021-00149-6

Wrzus, C., Hänel, M., Wagner, J., Neyer, F.J., 2013. Social network changes and life events across the life span: a meta-analysis. Psychol. Bull. 139, 53–80. https://doi.org/10.1037/a0028601

Yang, S., Gerow, K.G., Huber, H.F., Considine, M.M., Li, C., Mattern, V., Comuzzie, A.G., Ford, S.P., Nathanielsz, P.W., 2017. A decline in female baboon hypothalamo-pituitary-adrenal axis activity anticipates aging. Aging 9, 1375–1385. https://doi.org/10.18632/aging.101235

Yang, Y.C., Boen, C., Gerken, K., Li, T., Schorpp, K., Harris, K.M., 2016. Social relationships and physiological determinants of longevity across the human life span. Proc. Natl. Acad. Sci. 113, 578–583. https://doi.org/10.1073/pnas.1511085112

Yatsunenko, T., Rey, F.E., Manary, M.J., Trehan, I., Dominguez-Bello, M.G., Contreras, M., Magris, M., Hidalgo, G., Baldassano, R.N., Anokhin, A.P., Heath, A.C., Warner, B., Reeder, J., Kuczynski, J., Caporaso, J.G., Lozupone, C.A., Lauber, C., Clemente, J.C., Knights, D., Knight, R., Gordon, J.I., 2012. Human gut microbiome viewed across age and geography. Nature 486, 222–227. https://doi.org/10.1038/nature11053

Yoshida, K., Sakurada, T., Kaise, N., Yamamoto, M., Kaise, K., Saito, S., Yoshinaga, K., 1980. Measurement of triiodothyronine in urine. Tohoku J. Exp. Med. 132, 389–395. https://doi.org/10.1620/tjem.132.389

Young, C., Majolo, B., Heistermann, M., Schülke, O., Ostner, J., 2014. Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. Proc. Natl. Acad. Sci. 111, 18195–18200. https://doi.org/10.1073/pnas.1411450111

Zambrano, E., Reyes-Castro, L.A., Nathanielsz, P.W., 2015. Aging, glucocorticoids and developmental programming. AGE 37, 52. https://doi.org/10.1007/s11357-015-9774-0

Zane, L., Ensminger, D.C., Vázquez-Medina, J.P., 2021. Short-term elevations in glucocorticoids do not alter telomere lengths: A systematic review and meta-analysis of non-primate vertebrate studies. PLOS ONE 16, e0257370. https://doi.org/10.1371/journal.pone.0257370

Zhang, J., Kobert, K., Flouri, T., Stamatakis, A., 2014. PEAR: a fast and accurate Illumina Paired-End reAd mergeR. Bioinformatics 30, 614–620. https://doi.org/10.1093/bioinformatics/btt593

Zheng, Z., Chen, H., 2020. Age sequences of the elderly' social network and its efficacies on well-being: an urban-rural comparison in China. BMC Geriatr. 20, 372. https://doi.org/10.1186/s12877-020-01773-8

Zhu, P., Liu, W., Zhang, X., Li, Meng, Liu, G., Yu, Y., Li, Z., Li, X., Du, J., Wang, X., Grueter, C.C., Li, Ming, Zhou, X., 2023. Correlated evolution of social organization and lifespan in mammals. Nat. Commun. 14, 372. https://doi.org/10.1038/s41467-023-35869-7

Ziegler, T.E., Scheffler, G., Snowdon, C.T., 1995. The Relationship of Cortisol Levels to Social Environment and Reproductive Functioning in Female Cotton-Top Tamarins, Saguinus oedipus. Horm. Behav. 29, 407–424. https://doi.org/10.1006/hbeh.1995.1028

Zmora, N., Zeevi, D., Korem, T., Segal, E., Elinav, E., 2016. Taking it personally: personalized utilization of the human microbiome in health and disease. Cell Host Microbe 19, 12–20. https://doi.org/10.1016/j.chom.2015.12.016

Acknowledgements

Curriculum Vitae

Baptiste Sadoughi

Graduate researcher

Doctor of Veterinary Medicine

Jüdenstrasse 10

37073 Göttingen – Germany

Mobil: +33(0) 6 67 84 73 99

Mail: baptistesadoughi@gmail.com

Date of birth: 27 February 1992

Place of birth: Paris – France

Nationality: French

Research Experience

Graduate Researcher

Since May 2019 *Georg-August-Universität Göttingen, Dept. Behavioral Ecology*

German Primate Center, Research Group Social Evolution of Primates

- Managed research camp, observed wild animals, collected and processed biological samples under remote tropical field condition in Thailand. Work required long day of physical activity in the forest, managing a team with culturally varied background and representing the lab in exchanges with local officials.
- Led a project bringing together PhD students from 3 institutions resulting in the publication of a chapter for an academic book, co-organized 3 conferences both online and in presence gathering over 300 cumulated international participants.
- Developed learning agility, statistical skills, and scientific writing skills by publishing 7 peer-reviewed articles in the field of behavioral ecology, endocrinology, and automated data processing.
- Expanded the laboratory database by implementing a new procedure for data preparation and storage on servers. Handling data in Excel and R, co-coordinating the work of a team of seven people.
- Supervised undergraduate students in designing, conducting, analyses and writing of their pilot research projects.

Undergraduate research program

Jan – July 2018 *Centre de Primatologie, Strasbourg, Unistra*

- Capture, handling, anesthesia and sampling of blood and hair on captive macaques for a veterinary dissertation research project. Behavioral observation, selection, and analysis of hematological and biochemical blood tests. Performed all analytical steps from the sampling of hair to the measurement of cortisol and testosterone with immunoassays.

Jul & Aug 2014 & **Eco-physiology and behavior**

National Museum of Natural History, Naturelle, France, République Démocratique du Congo, Ouganda

Jul 2016

- Sampling of urine and saliva to validate a cortisol immunoassay for urine samples of wild-living bonobos, assess salivary cortisol responses to a behavioral enrichment in captive orangutans,

and measure urinary triiodothyronine to investigate thyroid axis functions following exposure to pesticides in wild-living chimpanzees.

Education

Since May 2019 **Doctoral Studies**
Georg-August Universität Göttingen, Germany – Department of Behavioral Ecology

- Thesis: "Effects of progressing age on energy, sociality and health in wild female Assamese macaques"
- Supervisors: Prof. Julia Ostner and Dr. Oliver Schülke

2017 – 2018 **Masters of Research Primate Biology Behavior and Conservation**
Roehampton University, London, UK – Department of Life Sciences

- Master of Research, Grade: *Distinction*
- Thesis: "A comparison of the Impact of Rank and Rank Stability on Stress Physiology, Inflammation and Allostatic load in semi-free ranging egalitarian *Macaca tonkeana* and despotic *Macaca fascicularis*"
- Supervisors: Dr. Julia Lehmann, Prof. Stuart Semple and Dr. Colette Berbesque
- Behavioral observations and biological sampling on captive non-human primates Performed all steps from the processing of hair samples and use of hormonal immune assay for the measurement of cortisol and testosterone
- Learnt coding in R and linear mixed modelling for the research project conducted

2013 – 2018 **Studies of Veterinary Medicine**
ONIRIS – Nantes-Atlantic National College of Veterinary Medicine, Food Science and Engineering, France

- Doctor of Veterinary Medicine, Grade: *Distinction and Mention for Thesis Prize* (in French "*Mention très honorable avec proposition pour Prix de Thèse*")
- Medicine and surgery of small and large animals
- Animal welfare, epidemiology, and concept OneHealth
- Production and Biosafety of food production

2009 – 2013 **Undergraduate Studies of Biology**
Sorbonne Université Campus Pierre & Marie Curie Paris, France
University of Edinburgh, United-Kingdom. Erasmus exchange 3rd year

- Bachelor of Science in Biology Grade
- Admission into the excellence training program to prepare the admission to veterinary studies

Research skills

Technical skills

Data analysis   Data tidying and analysis with R (RStudio interface) and Excel.
Generalized mixed models analyses, parametric and non-parametric statistics.

Laboratory   Microbiome genetics DNA 16S extraction, amplification (PCR) and post-sequencing analysis.

Hormone assay (ELISA) in-house design, validation and use for various biological samples.

Animal Biology   Detailed systematic observation of animal behavior and interactions often under harsh climatic conditions and physical load.

Soft skills

Management Planification, task attribution and processing of long-term data from the lab team. Involves R procedure, coordinating with a colleague PhD student on the supervision of the process and lab assistants involved in the process.

Language English (professional proficiency) and French (native speaker). German (A2 level).

Courses Attended

Jan 2023 **How to find your postdoctoral position** by Dr. Dagmar Sigurdardottir. Hosted by the GAUSS Career Service Georg-August Universität Göttingen.

Sep 2022 **Leadership Skills for Scientists** by Dr. Alexander Britz. Advancing as a scientist, both out- as well as inside academia, comes with increased leadership responsibilities. In this interactive workshop, the participants learn the essential leadership skills which are necessary to be successful as a PhD student or Postdoc and to later facilitate a successful transition to a senior position at a research institution or the dream job outside academia. Hosted by the GAUSS Career Service Georg-August Universität Göttingen.

Feb 2022 **Analyzing dyadic data with Bayesian methods** by Dr. Aura Raulo, University of Oxford. Understanding the challenges associated to the modelization of dyadic data and the solutions to their analyzing provided by Bayesian statistics. Hosted by the Research Training Group 2070.

Jun 2021 **Linear Models and their application in R** by Dr. Roger Mundry. The course treated linear models from simple regressions to General and Generalized Linear Mixed Models (GLMM) modelling the impact of multiple predictors, categorical predictors and interactions, logistic, Poisson, zero-inflated, and negative binomial regression, the inclusion of grouping variables or 'random effects', formulating scientifically meaningful models. Host by the Leibniz Science Campus Primate Cognition.

Nov 2020 **Time and career management** by Peter Kronenberg from NaturalScience.careers. Hosted by SoHaPi Research Unit.

Sep 2020 **An introduction to Bayesian multilevel modeling in R** by Jordan Scott Martin, University of Zurich. Modeling of complex behavioral processes, specification of model priors, plotting and analysis of outcomes.

Teaching and Supervision Experience

Feb 2022 Course in Wildlife Monitoring Techniques Spring Semester 2022, "Macaques in the forest: Observing monkeys in the wild" invited talk by Dr. Sostra Chakrabarti, MacAlester College, United-States. Online lecture co-hosted with Dr. Delphine De Moor and James Stranks.

Since 2020 Georg-August Universität Göttingen, Dept. Behavioral Ecology
Co-supervised undergraduate students in designing, conducting, analyzing, and writing their pilot research projects and bachelor's thesis.

- Master's laboratory research rotation. Winter Semester 2022. Supervision of Master's thesis and Endocrinological analyses with Durée Ajam.
- Master's laboratory research rotation. Winter Semester 2022. Supervision of Pearl Amber Lee Väth.
- "Does allogrooming promote access to huddles in female Barbary macaques (Macaca sylvanus) at "Affenberg Salem?". Winter Semester 2021.
- "How does age influence the physical and social life of semi-free living Barbary macaques (Macaca sylvanus) at "Affenberg Salem?". Winter Semester 2021.

- "Non-invasive Biomarkers for Measuring Energetics in Primates: A Review". Summer Semester 2021.
- "The link between social relationships, physiological stress and aging in primates and other mammals". Summer Semester 2021.
- "Primate behaviour and the gut microbiome". Summer Semester 2021.

Research Funding, Honors and Awards

2022   LiebnizScience Campus conference visit grant (600€)

2022   Acquired funding from the Research Training Group 2070 for the organization of a workshop for PhD students and post-docs on Bayesian statistics by Dr Aura Raulo (University of Oxford) (700€).

2018   Best Masters overall performance in the Life Sciences, University of Roehampton

2014   Laureate of Merial Student Award 2014 (1000€)

2014   Laureate of France Vétérinaire International Award 2014 (100€)

Conference Attendance and Contribution

2022   **Baptiste Sadoughi**, Dominik Schneider, Rolf Daniel, Oliver Schülke, Julia Ostner. Aging manifests across the physical, physiological and social domains in wild female Assamese macaques (*Macaca assamensis*). *Joint conference of the European Federation of Primatology and the Gesellschaft für Primatologie*. Arnhem, Netherlands. Oral presentation.

2021   **Baptiste Sadoughi**, Dominik Schneider, Rolf Daniel, Oliver Schülke, Julia Ostner. The aging gut microbiota of wild female Assamese macaques. *33^{rdh} congress of the French Speaking Society of Primatology (SFDP)*. St Etienne, France. Oral presentation.

2020   **Baptiste Sadoughi**, Dominik Schneider, Rolf Daniel, Oliver Schülke, Julia Ostner. Aging bacterial gut microbiota of wild female Assamese macaques. *International Primatological Society – Latin American Society of Primatology Virtual Symposium: Sociality and Health in Primates*. Online presentation.

2020   **Baptiste Sadoughi**, Cédric Girard-Buttoz, Antje Engelhardt, Michael Heistermann & Julia Ostner. Non-invasive monitoring of metabolic responses to food restriction with immunoreactive urinary triiodothyronine and cortisol in captive macaques. *19th Summer Conference of the Association for the Study of Animal Behaviour*. Online pre-recorded presentation.

2019   **Baptiste Sadoughi.** Effects of progressing age on energy balance sociality and health in wild female Assamese macaques (Macaca assamensis). 40th *Thai Wildlife Symposium.* Bangkok, Thailand. Poster with title.

2018   **Baptiste Sadoughi**, Colette Berbesque, Hélène Meunier, Julia Lehmann. The impact of dominance rank on health: Study of hair cortisol and allostasis in tolerant Tonkean macaques. *31st congress of the French Speaking Society of Primatology (SFDP)*. Paris, France. Oral presentation.

2016   **Baptiste Sadoughi**, Manon Dirheimer, Pierrick Regnard, Fanélie Wanert. A case of strangulated inguinal hernia in a *Macaca fascicularis*. *29th congress of the French Speaking Society of Primatology (SFDP)*. Rennes, France. Oral presentation.

2014   M. Debuigne, V. Narat, **B. Sadoughi**, M. Saint-Jalmes, S. Krief. Do Orang-utans like to paint? Preliminary study on stress variations in captivity by salivary cortisol dosage and behavioural observations. *27th congress of the French Speaking Society of Primatology (SFDP)*. Poitiers, France. Oral presentation.

Invited Talks

2022   Invited talk with Marie Hirel by the French Ambassy in Germany for the 6th *Café des Sciences* "At the origins of life in society: mechanisms and consequences of social ties in primates" (in French "Aux origines de la vie en société: des mécanismes aux conséquences des liens sociaux chez nos cousins primates"). Berlin, Germany. Online conference https://www.youtube.com/watch?v=GtbjFakBJ5s&t=1516s

2019   Radio interview *Le labo des savoirs* Radio Prun', Nantes, France "Bonobo, chimpanzés: comprendre notre heritage primate". Broadcasted on Prun' on the 13/02/19, on France Culture on the 18/02/19 (cycle conférence), and on RCF le 20/02/2019. https://www.radiofrance.fr/franceculture/bonobos-chimpanzes-comprendre-notre-heritage-primate-3572122

Publications

2022   **Sadoughi, B.**, Anzà, S., Defolie, C., Manin, V., Müller-Klein, N., Murillo, T., Ulrich, M., Wu, D., 2022. Parasites in a social world: Lessons from primates, in: Ezenwa, V., Altizer, S.M., Hall, R. (Eds.), Animal Behavior and Parasitism. Oxford University Press, p. 0. https://doi.org/10.1093/oso/9780192895561.003.0003

2022   **Sadoughi, B.**, Schneider, D., Daniel, R., Schülke, O., Ostner, J., 2022. Aging gut microbiota of wild macaques are equally diverse, less stable, but progressively personalized. Microbiome 10, 95. https://doi.org/10.1186/s40168-022-01283-2

2022   Miss, F.M., **Sadoughi, B.**, Meunier, H., Burkart, J.M., 2022. Individual differences in co-representation in three monkey species (Callithrix jacchus, Sapajus apella and Macaca tonkeana) in the joint Simon task: the role of social factors and inhibitory control. Anim. Cogn. https://doi.org/10.1007/s10071-022-01622-8

2022   Schülke, O., Anzà, S., Crockford, C., De Moor, D., Deschner, T., Fichtel, C., Gogarten, J.F., Kappeler, P.M., Manin, V., Müller-Klein, N., Prox, L., **Sadoughi, B.**, Touitou, S., Wittig, R.M., Ostner, J., 2022. Quantifying within-group variation in sociality—covariation among metrics and patterns across primate groups and species. Behav. Ecol. Sociobiol. 76, 50. https://doi.org/10.1007/s00265-022-03133-5

2021   **Sadoughi, B.,** Lacroix, L., Berbesque, C., Meunier, H. & Lehmann, J. Effects of social tolerance on stress: hair cortisol concentrations in the tolerant Tonkean macaques (Macaca tonkeana) and the despotic long-tailed macaques (Macaca fascicularis). Stress 0, 1–9 (2021).

2021   Ballesta, S., **Sadoughi, B.**, Miss, F., Whitehouse, J., Aguenounon, G., Meunier, H., 2021. Assessing the reliability of an automated method for measuring dominance hierarchy in non-human primates. Primates. https://doi.org/10.1007/s10329-021-00909-7

2021   **Sadoughi, B.,** Girard-Buttoz, C., Engelhardt, A., Heistermann, M. & Ostner, J. Non-invasive assessment of metabolic responses to food restriction using urinary triiodothyronine and cortisol measurement in macaques. Gen. Comp. Endocrinol. 306, 113736 (2021).

2018   **Sadoughi, B.,** Dirheimer, M., Regnard, P. & Wanert, F. Surgical management of a strangulated inguinal hernia in a Cynomolgus Monkey (Macaca fascicularis): a case report with discussion of diagnosis, and review of literature. Rev. Primatol. (2018) doi:10.4000/primatologie.3372.

Further Professional Experience

Veterinarian Practitioner
Jun – Jul 2017   *Clinique Vétérinaire des Pommiers, Countances – France*
Jan – Apr 2018   *Clinique Vétérinaire des Trois Valets, Mussidan – France*

- Short-term contracts to support teams in times of high workload
- Performed companion and farm animal medicine
- Applied diagnostic and surgical skills, scientific and interpersonal communications abilities with other health professionals and clients.
- Conducted public health screening missions on cattle which allowed to get familiarized with the farming industry and welfare regulations. Required scheduling visits and constant communication.

Veterinarian Apprentice

Aug 2016   *Simian Laboratory Europe (Silabe)*

- Veterinary care, surgery and epidemiology of pathogens in primate
- Assisted the emergency surgery of an inguinal hernia in a macaque and published the case report in peer-reviewed scientific journal

Service & Outreach

Since 2019   **Member of the Ethics Committee for clinical and epidemiological veterinary research** at Oniris (Cervo in French) for the reviewing and approval of research involving animals (main reviewer for 8 research proposals, voting member on more than 30).

2018 – 2021   **Board member for the French Speaking Society of Primatology**

- Communication and social media coordinator for Twitter and Facebook. Launch a weekly post on primates directed to a general audience of followers. Interviewed scientists, video edited, and shared on Facebook and Youtube.
- Organized one online conference (Nov 2020) and one in presence conference (Nov 2021). Prior to conference, I contacted sponsors, planned the logistic and sanitary COVID-19 regulations, and relayed information between the board and the organization team on-site. During the conference, I co-chaired the Physiology & Health session.
- Piloted the estimation of conferences' carbon footprint.

2020-2021   **Peer-reviewing** for international peer-reviewed journals (e.g., Scientific Reports, Hormones & Behavior) and selection of conference abstracts for the French Speaking Society of Primatology (conference editions 2019, 2020 and 2021)

Feb 2022   Invited Dr Aura Raulo (University of Oxford) to give a statistical workshop on Bayesian statistics for the Research Training Group 2070.

Nov 2021   Invited Prof. Alexandra Freund (University of Zurich) to give a talk entitled "Exhaustion and Recovery: What's motivation got to do with it?" at the Leibniz Science Campus Primate Cognition (online).

2014-2017   Elected Student Representative in the Board for Teaching and Student affairs at Oniris (Conseil de l'Enseignement et de la Vie Etudiante in French).

Membership in professional societies

Animal Behavioral Research Societies
- Animal Behavior Society (ABS) – *former*
- French Speaking Society of Primatology (SFDP) – *active*
- International Primatological Society (IPS) – *former*
- Primate Society of Great Britain (PSGB) – *former*

Animal Welfare and Veterinary Medicine
- National France Order of Veterinarian (Ordre National des Vétérinaires)
- Compassion in World Farming (CIWF) France

Declaration

I hereby declare that all parts of my thesis titled 'The manifestations and interdependence of social and physiological aging in wild female Assamese macaques (*Macaca assamensis*)' were written by myself. Assistance of third parties was only accepted if scientifically justifiable and acceptable in regards to the examination regulations. Assistance or contributions to the individual chapters are indicated and all sources have been quoted.

Göttingen, 10th of April 2023

Baptiste Sadoughi