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Life history context of reproductive aging in a wild primate model

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The pace of reproductive aging has been of considerable interest, especially in regard to the long postreproductive period in modern women. Here we use data for both sexes from a 37-year longitudinal study of a wild baboon population to place reproductive aging within a life history context for this species, a primate relative of humans that evolved in the same savannah habitat as humans did. We examine the patterns and pace of reproductive aging, including birth rates and reproductive hormones for both sexes, and compare reproductive aging to age-related changes in several other traits. Reproductive senescence occurs later in baboon females than males. Delayed senescence in females relative to males is also found in several other traits, such as dominance status and body condition, but not in molar wear or glucocorticoid profiles. Survival, health, and well-being are the product of risk factors in morphological, physiological, and behavioral traits that differ in rate of senescence and in dependence on social or ecological conditions; some will be very sensitive to differences in circumstances and others less so.

Keywords: reproductive aging; baboons; toothwear; body condition; steroid hormones; senescence

Over 30 years ago, Sarah Hrdy introduced what arguably stands as the first published lifespan perspective on female reproductive strategies in wild nonhuman primates.[1–3] Prevailing wisdom at the time was that senescence did not occur in wild populations. In contrast, Hrdy posited that female nonhuman primates experience age-related reproductive decline and a postreproductive stage that presages the long postreproductive period of modern women (see Hawkes and Smith[3a]). Moreover, she suggested that within natural societies of nonhuman primates, such as those of the langur monkeys she studied in Asia, reproductive senescence is associated with fitness benefits.[1–3]

Thus, our study of reproductive aging in wild baboons has roots in Hrdy's perspective on langur reproductive strategies, but relevant data for aging in natural populations were largely unavailable at that time. In fact, patterns of aging in wild animals, not just wild primates, still remain largely undescribed despite their importance to understanding fundamental aspects of life-history evolution, and despite early speculation on their importance in the evolutionary and behavioral ecology of humans and other species.

Using almost four decades of data from the Amboseli Baboon Research Project (ABRP), we are now in a position to evaluate reproductive aging in wild female primates and compare females' reproductive time-course with that of males. In addition, we examine reproductive aging of both sexes in the context of aging patterns in several other traits, addressing the question of whether reproductive aging resembles or stands out from that of other traits. We begin with a general introduction to baboons and their relationships to humans, and then describe the Amboseli baboon population, the ABRP longitudinal life-history research program, and a brief overview of relevant methods.

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Wild baboons as a model for understanding human aging

Baboons (genus *Papio*) are among the best studied of the cercopithecine primates.[4] They are large, diurnal, semi-terrestrial monkeys that are highly selective and flexible foragers. Baboons have a close evolutionary relationship with humans (~94% sequence similarity genome-wide)[5] and striking behavioral and ecological similarities as well.[6] They have achieved a nearly continental distribution in Africa, occupying habitats ranging from moist evergreen forests to deserts, and from equatorial to temperate regions. Among primates, this positions baboons as second only to humans in geographical and environmental range. Their ability to cope with environmental extremes and with high levels of predictable and unpredictable environmental variability, even during demanding life stages, such as parental care and aging, is similarly shared with humans. Furthermore, baboons show little or no seasonality of reproduction in most habitats. In other words, baboons have both adapted to diverse habitats and, in major aspects of their life histories, including those associated with reproduction, have largely escaped from the seasonal constraints of these diverse habitats. This is a combination of traits that they share with humans but with few other primates. Like many human hunter-gatherer societies, most baboon (sub)species live in stable social groups of 20–100 members, including multiple adults and juveniles of both sexes. Baboons also possess highly differentiated social relationships, and a flexible mating and social system. These traits position baboons as a widespread "generalist" species, like humans.

In the wild, female baboons usually reach menarche early in their fifth year; during adulthood they have highly visible and regular sexual swellings that indicate ovarian cycle phase,[7] and they exhibit skin-color changes on their hindquarters that indicate pregnancy, beginning by the end of the first trimester of their 6-month gestation. Infants are completely dependent on their mothers for almost a year, followed by a second year of increasing independence during which time their mothers usually conceive again. Males experience testicular enlargement and associated onset of sperm production in their sixth or seventh year, but do not become fully adult until they are about 8–10 years old, when they achieve an adult body mass nearly twice that of adult females. Males usually disperse from their group of birth as older subadults or young adults. Females and males do not form permanent mating bonds with each other. Instead, mating takes place in the context of mate-guarding episodes, typically called consortships. Demographic senescence in Amboseli is evident by about 15 years of age.[8] In Amboseli and two other wild populations, the oldest reported individuals were 27-year-old females.[8a] Baboons and humans spend a similar proportion of their lifetime in the several major life stages (infancy, the juvenile period, adolescence, and adulthood), with each stage in baboons—and the total lifespan—lasting about one-third as many years as in humans.

The Amboseli ecosystem, baboon population, and baboon research project

Located at the northwestern base of Mt. Kilimanjaro, the Amboseli-Longido ecosystem is a semi-arid, short-grass savanna in a Pleistocene lakebed. This ecosystem exhibits both seasonal and long-term patterns of environmental change, ones that are typical, in type and magnitude, of the changes that characterized the East African environments in which both humans and baboons evolved.[9,10]

The ABRP, ongoing since 1971, includes detailed longitudinal data on demography, ontogeny, ecology, behavior, parentage, and steroid hormone profiles on known individuals that are part of the robust undisturbed Amboseli baboon population (see www.princeton.edu/~baboon and publications therein). At any given time, the ABRP monitors approximately 300 individually known animals of all ages. The data reported here were obtained solely on animals that move freely through their environment and subsist entirely on natural food sources found in the wild. We visually recognize all individuals in our five study groups; like humans, baboons have highly distinctive facial and morphological features that make them easily recognizable to experienced observers. All animals in study groups are well habituated to the presence of neutral observers.

Our various methods are described in the next section.

Methods

We employ several distinct research methodologies in collecting individual-based data,

including the following for the results presented herein: (1) observational monitoring of demographic and behavioral events for all individuals in the study population, (2) genetic paternity analysis, (3) steroid hormone analysis, and (4) occasional darting to immobilize animals in order to take morphometric measurements and perform other procedures. Data are subsequently stored and accessed through our long-term database, BABASE (www.papio.biology.edu).

Field methods for data collection

Our long-term analyses of data from ABRP depend on continuity and consistency in the quality and intensity of data collection over the years. We achieve this consistency through a number of key resources and strategies, including the presence of long-term observers and a comprehensive set of written protocols for field, lab, and data management, which are publicly available online at the ABRP website (www.princeton.edu/~baboon). Some types of data have been obtained since 1971, e.g., demographic events for some individuals. Other types of data collection began at various times since then. In particular, fecal samples for genetic analysis of paternity are available since 1993 (these samples represent individuals born as early as 1968), fecal samples for hormone metabolite extraction since 2000, and morphological data from 1989–1991 and 2006–2008.

Our observational methods are well documented, and we outline them briefly here. Six days per week, we follow 1–2 social groups of baboons each day for six observation hours per day. Throughout the day, we collect a diverse range of observational data including those of particular relevance for evaluating aging in the traits reported here. We begin each day with a systematic group census to record births, deaths, immigrations, and emigrations. We also record the color of each female's paracallosal skin, and the size and status (turgescent or deturgescent) of her sex skin.[7,11,12] This information allows us to retrospectively determine, for each female on each day of the study, her reproductive condition (pregnant, cycling, lactating) and, if cycling, the day of her cycle relative to ovulation. Throughout the day, while collecting systematic behavioral samples, we collect freshly deposited fecal samples from all individuals; these provide our primary window into the physiology of aging and our primary source of DNA for paternity determination (used for measuring male birth rates).

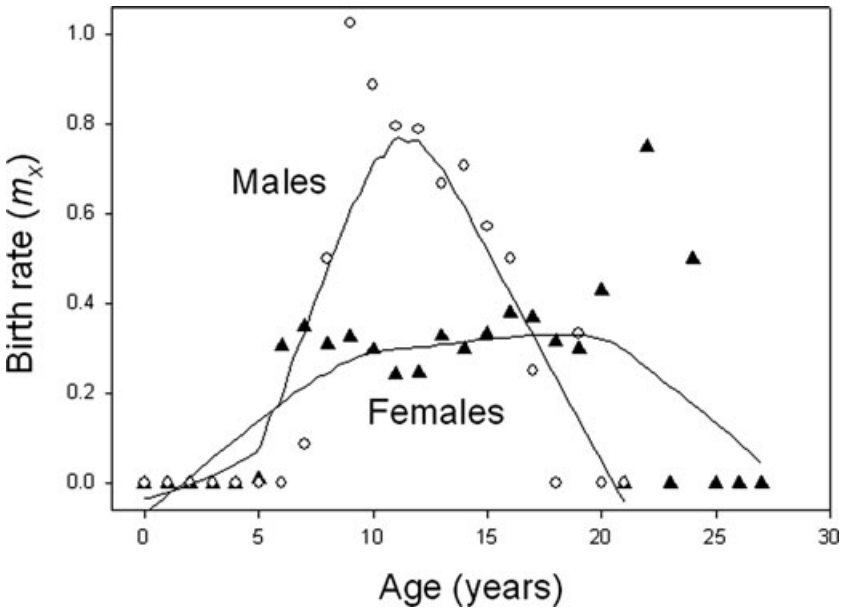

Figure 1. **Age-related patterns of birth rates for Amboseli baboons. Female birth rates (filled triangles) are stable until late adulthood. In contrast, male birth rates (open circles; based on genetic analysis) exhibit a strongly age-related pattern, following a similar pattern to dominance rank,[24] with a sharp peak early in adulthood followed by a relatively steep decline. Plotted with lowest curve, window = 0.5.**

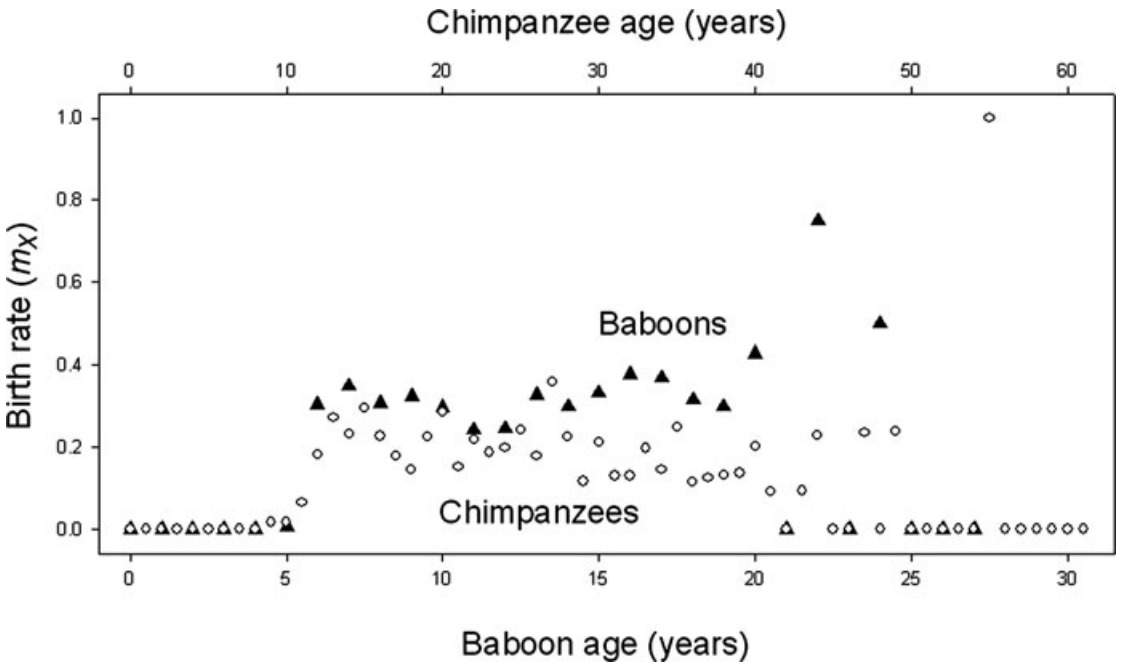

Figure 2. **Age-related patterns of birth rates for female Amboseli baboons and for chimpanzees—filled triangles for baboons, open circles for chimpanzees. Baboon data are as in Figure 1. Chimpanzee data are from Ref. 22; note that data for ages 53–61 years in the chimpanzee plot are from a single female. Data are plotted on a scale of two chimpanzee years to one for baboons.**

Genetic paternity analysis

Fecal DNA occurs in low quantity and is often degraded. However, extensive work by a number of groups, including ours, has clearly shown that with careful controls the results of fecal DNA analysis are reliable and repeatable.[13–17] We assign paternity based on exclusion and also through the use of the likelihood-based paternity assignment program CERVUS 2.0.[18] With these methods we have unambiguously assigned paternity to approximately 300 individuals born in Amboseli (Alberts *et al.*[17] and unpublished). Paternity assignments, which are comparable to the known maternities for females, provide the data for evaluating age-related patterns of male birth rates by associating each birth with the age of the infant's father.

Fecal steroid analysis (glucocorticoids and reproductive steroid hormones)

Freshly deposited fecal samples from known individuals are collected in vials prefilled with 95% ethanol to approximate a volumetric ratio of 2:5 feces to ethanol. Samples are stored in Amboseli for less than 2 weeks in a charcoal refrigerator, then are transported first to the University of Nairobi for initial processing and then to Princeton University for hormone extraction and purification followed by assay using an ^{125}I radioimmunoassay.[19–21]

Results and discussion

Age-related changes in reproduction: birth rates and steroid hormones

Baboon reproductive output declines with age, and the patterns of change differ from humans in potentially informative ways. In Amboseli, females continue to produce offspring in their early to mid-20s—equivalent to women in their 60s. In addition, birth rates start to decline only at approximately 18 years of age[8] (Fig. 1, also Ref. 12), an age that is equivalent to the 50s in humans (relying again on the general observation that the various baboon life stages are about one-third as long as the equivalent in humans). The age-related pattern of birth rates in baboon females is essentially the same as that recently reported for wild populations of chimpanzees.[22] Like the baboons, the chimpanzees exhibited declining birth rates only at relatively old ages and complete cessation of births occurred among only the very oldest individuals (Fig. 2).

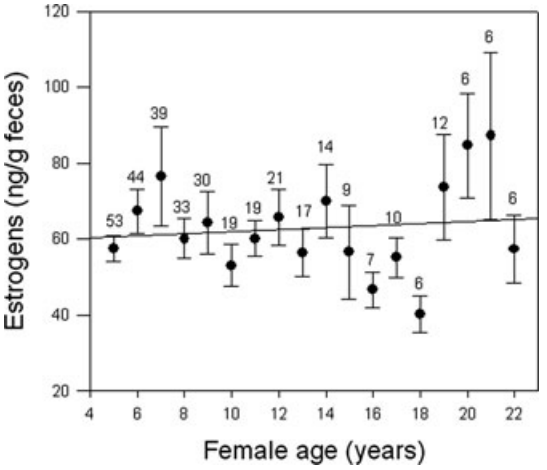

Figure 3. **Estrogen concentrations for baboon females are stable into relatively old age, following a similar pattern to that for female birth rates. The plotted value and bars for each year represent the mean and SE across all cycling individuals (pregnant and lactating individuals were excluded). Within any year, each female is represented by only a single data point, which is calculated as the mean of all values obtained for that female during that year of age. The number of individuals contributing to the data for each age appears just above the error bar for that age.**

As expected from the stable birth rates across most of adulthood for baboon females, female baboons also maintain relatively high estrogen concentrations into late adulthood (Fig. 3), although high variance characterizes the later age classes, consistent with findings of greater variance in reproductive measures among older women.[23] Sample sizes for individual fecal estrogen (fE) profiles for baboon females do not yet provide adequate statistical power to evaluate longitudinal patterns across adulthood, but the available data indicate individual patterns very similar to the populational one. In addition, we are initiating studies to evaluate age changes in progesterone; a small preliminary populational data set revealed no age-related change in progesterone (fP) concentration or in the fE/fP ratio ($P = 0.909$ and 0.577, respectively).

Male baboons in Amboseli, in contrast to females, experience peak paternity in early adulthood (around 9 years of age), and a steady age-related decline in reproductive output begins immediately thereafter (Fig. 1).[17] The decline in male birthrates occurs as male dominance rank declines because male reproductive output is highly influenced by competition with other males; high-ranking males generally obtain greater access to reproductive females than do low-ranking males.[24]

Adult male baboons also exhibit clear age-related decline in testosterone[21,25] (fT) (Fig. 4A), although testosterone decreases a few years later and the decline proceeds more gradually than the changes in male birth rates. This decline in testosterone occurs when estrogens in cycling females remain high. This population-level pattern could result from a situation in which males with initially high testosterone experience high mortality risk, so that surviving males are disproportionately those with consistently low T, having exhibited little or no decrease in T concentrations during aging. However, initial examination of individual trajectories of T for Amboseli males (Fig. 4B), reveals that declining T concentrations with age are characteristic of 17 of the 19 individual males that we have observed. Declines in T with age are widely documented in men and are often associated with health risks.[26,27] Interestingly, Feldman *et al.*[26] found steeper declines in their longitudinal study than suggested by cross-sectional trends, perhaps suggesting that men with more steep declines are at higher mortality risk. Future investigations will evaluate predictors and sequelae of individual variability in both peak levels and rate of decline in baboon males.

Preliminary analyses of a small data set (not graphed) indicate that estrogen (fE) concentrations in our population of male baboons increased ($R^2 = 0.396$, $P = 0.016$) and fT to fE ratios decreased with age ($R^2 = 0.558$, $P = 0.002$). High fE in males as in females may be protective against bone loss[28] and cardiovascular disease.[29] However, declines in T-to-E ratio are suggested by some studies of men[30–33] and are thought to have adverse consequences for male longevity.

In summary, in both offspring production and fecal estrogen profiles, female reproductive patterns are age-related only during relatively old ages, and the pattern in offspring production is strikingly similar to that reported for wild chimpanzees. In contrast, male reproductive patterns are highly age-related in both offspring production and fecal testosterone. They exhibit a pattern of rapid rise in early adulthood followed shortly thereafter by steady decline.[21] This decline parallels the well-known pattern of age-related dominance rank in male baboons.

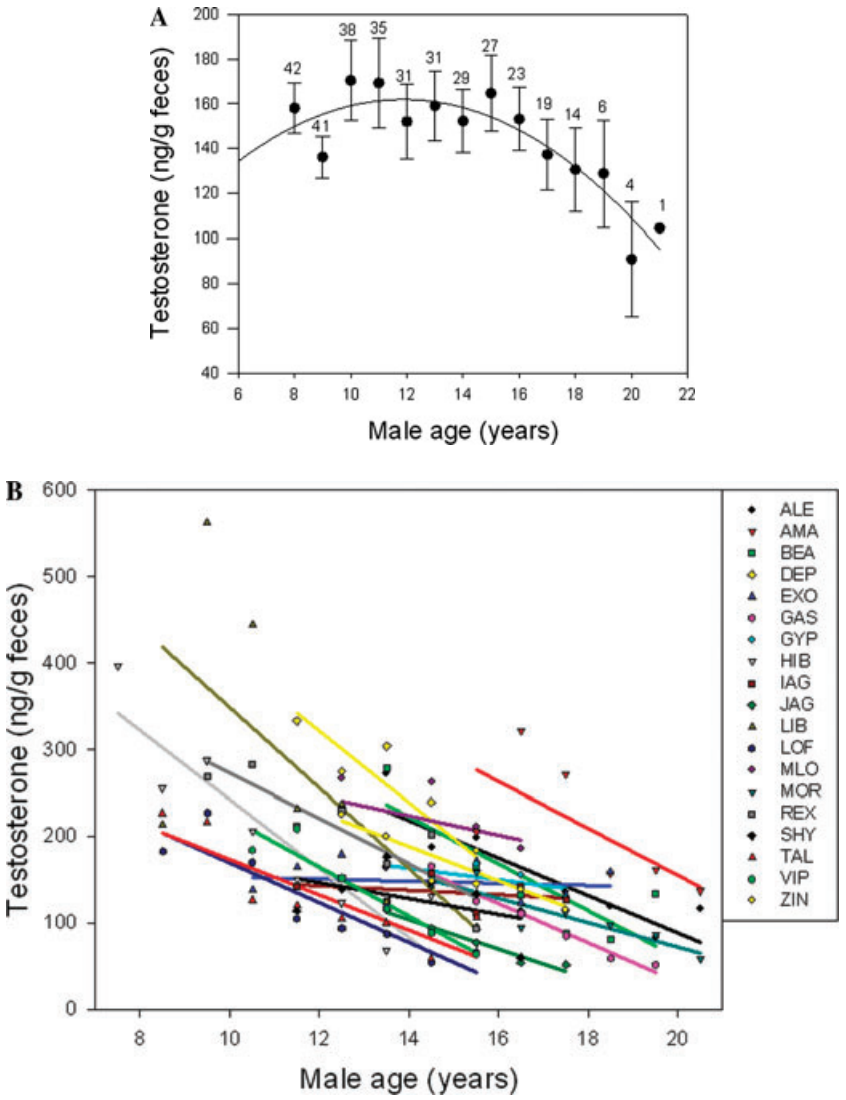

Figure 4. (A) Testosterone concentrations decline with age for baboon males in our sample, starting by mid-adulthood (see Fig. 3 for the contrasting pattern in females). Calculations and symbols as in Figure 3. (B) The population-level decline with age in testosterone concentrations can be explained by decline with age for individual adult male baboons across adulthood (at least 5 years of data for each male). Only 2 of 19 males did not exhibit a pattern of decline.

Age-related patterns of senescence in other morphological and physiological traits

Age-related changes in body mass index (BMI). In humans, having a low BMI is a known risk factor for mortality, particularly among the elderly,[34] so that the relationship between BMI and mortality risk is U-shaped, with mortality risk increasing at both extremes.[35,36] Studies of western humans have often focused on potential adverse effects of a high BMI (of being overweight or obese) because obesity is so prevalent in these societies. However, the adverse effects of obesity appear to be attenuated in old age, while the adverse effects of being underweight are exacerbated.[36–38]

In Amboseli, healthy baboons that subsist entirely on natural foods exhibit an extraordinarily low level of body fat, 1.9%, and they never approach obesity (although obesity does occur in baboons that visit refuse sites associated with tourist facilities, not the

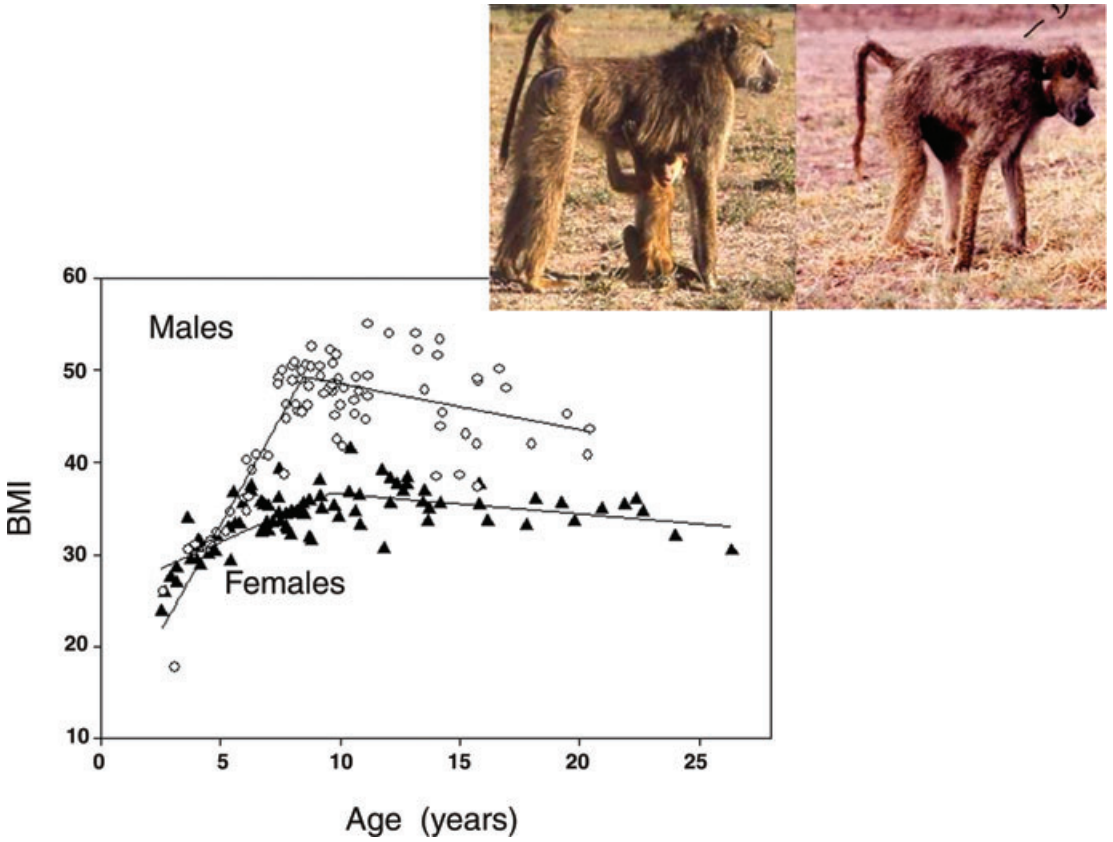

Figure 5. **BMI increases for females (filled triangles) during early years of adulthood (until about 10 years of age, approximately 4 years after their first birth) and then declines very gradually during aging. Male (open circles) BMI increases more dramatically until attainment of adulthood (age 8 years) and then begins a more rapid decline than that of female BMI. Plotted lines are for best-fit piecewise regression model, providing a somewhat better fit for males (adj $R^2 = 0.76$) and an equally good fit (adj $R^2 = 0.51$) for females than a quadratic model. Pictured is a female during early adulthood and the same female at age 27, the oldest age yet recorded for wild baboons.**

subjects of this study).[39] Not only is obesity absent, we have frequently observed animals that appear to be exceptionally thin, particularly old animals (Fig. 5) or females that are lactating during dry seasons or droughts.

We measured BMI in a subset of the Amboseli baboons that we briefly immobilized through darting. BMI exhibits clear age-related patterns and sex differences during adulthood (Fig. 5). The two sexes do not differ in BMI until the sixth year of life, when females experience their first conception and males enter into the subadult period that is characterized by an adolescent growth spurt not seen in females.[40] This male growth spurt occurs more in weight than in long bones and results in BMI in young adult males that is almost 50% greater, and body mass approximately 100% greater, than that of same-aged females. Male BMI peaks at about the onset of adulthood (8 years of age) and declines steadily throughout adulthood. Females, in contrast, continue to experience gradual increase in BMI during the early years of adulthood, peaking at approximately 10 years of age (4 years after the average age at first birth). Female BMI then declines steadily but at a slower rate than in males, narrowing the sex difference. Very few males live into their 20s,[8] and the limited data for males in the late teens suggest high variability and perhaps differential mortality for those of low BMI. Tooth wear is likely to be a major contributor to changes in BMI and is described below.

Age-related changes in tooth wear. Tooth wear increases with age in many species (including several

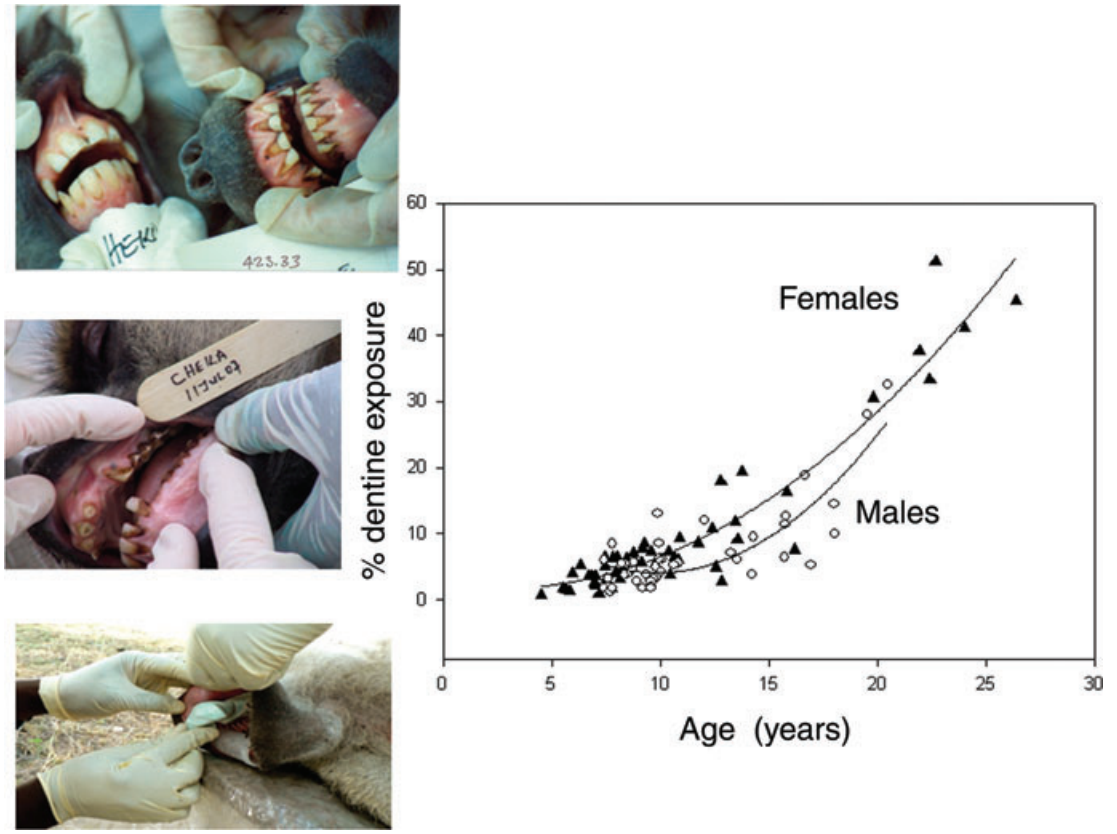

Figure 6. **Molar wear (measured as proportion of dentine exposure, PDE) is age-related in both sexes, as seen here for M1—the first molar. M1 wear tends to be as great in females (filled triangles) as in males (open circles) during aging. Quadratic models: adj $R^2 = 0.90$ for females, adj $R^2 = 0.69$ for males. Pictured is a comparison of a young adult female (7 years old) with her elderly mother (21 years old), also a 24-year-old female. Also shown is the molding technique used to obtain casts for measuring PDE.**

primates[41–44]). A landmark study in wild lemurs found that increased tooth wear in older mothers was associated with decreased survival of their infants,[43] indicating a strong link between tooth wear and food processing ability. In Amboseli, we have previously documented that periodontal health decreases with age.[45] Further, we have observed dramatic changes in tooth wear with age, using photographs taken during brief immobilizations (Fig. 6).

We recently collected high quality tooth impressions on a subset of baboons that were briefly immobilized through darting. We measured tooth wear as the percentage of dentine exposure on the occlusal surface. Our analysis of tooth wear shows a strong signal of age in both sexes (Fig. 6 for the M1—the first molar).[46,47,47a] Unlike age-related patterns of change in BMI and reproduction, the age-related pattern in molar wear does not exhibit a male-biased aging pattern (Fig. 6). However, qualitative observations suggest that females experience similar aging patterns on their molars as on their other teeth, whereas males experience more major breaks and total loss of these other teeth; this will be the subject of forthcoming evaluation.

Age-related changes in glucocorticoids. Aging-associated hypercortisolism, manifested either in basal levels or in a stress response that is resistant to feedback mechanisms, has been documented in humans and in several studies of nonhuman primates.[48,49] Chronically elevated glucocorticoid levels can jeopardize health and survival[50,51] by decreasing reproductive hormones,

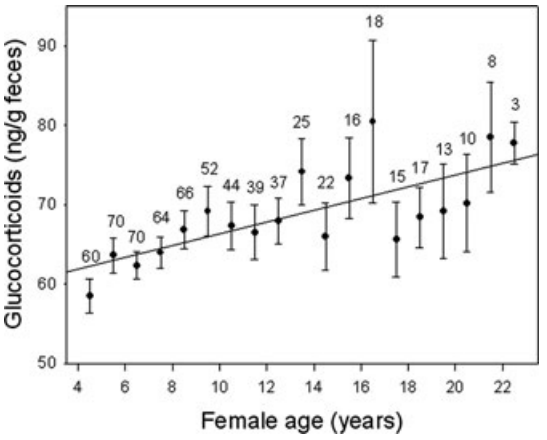

Figure 7. **Glucocorticoid concentrations increase gradually with age for females. Calculations and symbols as in Figure 3.**

suppressing immunity, promoting atherosclerosis and ulcers, decreasing muscle mass, and impairing growth and tissue repair.[52–54] Although the incidence of cardiovascular diseases and ulcers is unknown for wild baboons, an increased risk of infectious diseases, a decrease in cutaneous wound healing, and loss of muscle mass are all likely to increase mortality risk as well as morbidity in natural populations.[54]

We documented a striking age-related change in adrenocortical axis function in Amboseli baboons, using a rare opportunity in which we collected blood from over 100 animals in 1989 and 1990.[48] Males and females in our oldest age classes experienced both higher basal cortisol levels and increased resistance to downregulation. The single, cross-sectional measurements in that study provided the foundation for our recent ongoing studies of excreted glucocorticoids (fGC). Our initial analyses support our prior finding of an increase throughout adulthood in glucocorticoid concentrations for females (Fig. 7). Males, however, show no simple change with age in fGC in these longer-term analyses, and instead evidence more complex patterns, which are currently under investigation. Thus, glucocorticoids, like molar wear, exhibit age-related changes but not the strong male-biased sex differences in senescence that were evident in BMI, reproductive rates, and reproductive hormones.

Reproductive senescence in the wild: a comparison with other somatic systems and between the sexes

The signature of senescence in wild baboons is clear across diverse morphological, physiological, and behavioral systems, including reproduction of both females and males. However, the timing and pace of senescence differs across systems, in some cases between the sexes, and between baboons and humans, in multiple, informative ways. For example, reproductive senescence for female baboons is evident in birth rates and in estrogen levels only relatively late in life. Moreover, complete cessation of offspring production is experienced only by the very oldest females, those who reach their mid-20s, an age at which body condition as measured by BMI is very low and tooth wear is extensive. The age-related pattern of female baboon birth rates is the same as that in chimpanzee females. It stands in contrast to that observed in women, in which the timing of reproductive senescence far exceeds that of other organ systems, resulting in a long postreproductive period in humans (e.g., in Ref. 55 and sequala).

For baboon males, reproductive decline in both birth rates and testosterone concentrations parallel the early and rapid decline in male dominance status and in body condition (BMI). Thus, a potentially intertwined complex of traits—social, physiological, morphological, and offspring production—exhibit earlier and more rapid decline in males than in females. Recent comparisons of age-related patterns of androgens in men[33] and in several closely related monkey taxa[21] including Amboseli baboons, exhibit interesting predictability across taxa or subsets of human populations that can be related to levels of parental care or mating patterns. These findings suggest important directions for insights into plasticity of senescence patterns in men and nonhuman primate males across a range of taxa, as well as across ecological and social contexts.

Survival, overall health, and well-being reflect senescence and risk factors in many morphological, physiological, and behavioral traits. Each trait follows its own patterns of aging, either independently or in some cases with causative interrelationships. Age-related variability in these traits, in their causative relationships, and in their joint impact, will also exhibit varying degrees of dependence on social or ecological conditions; some will be very sensitive to differences in circumstances and others

perhaps less so. The age-related pattern in androgen concentrations among men and among nonhuman primates is one example of a trait that is highly contingent upon social context.[21,33] Another example of condition-dependent aging involves female reproduction in nonhuman primates. Some traits, such as age of menarche and fertility rates, exhibit strong response to differences in food availability; such responses are particularly evident where primates are provisioned by humans, either in captivity or in cases where the nonhuman populations live in close commensalism with humans and their foods. These situations provided most of the examples of postreproductive females first identified by Hrdy,[2] and they constitute the majority of those reported recently across a broad range of primates.[56] In addition, in these situations, we would expect that age-related senescence in body condition and tooth wear will be attenuated, as will demographic senescence. This may result in a greater prevalence of females experiencing a postreproductive period and perhaps, though not necessarily, an extended duration of the postreproductive phase if survival is enhanced more than fertility is (see Hawkes and Smith[3a]).

Understanding the evolutionary history, current diversity, and future potential of aging in humans and our closest relatives will require understanding the plasticities of various age-related traits and the contingencies among them. Nonhuman primate models from a range of ecological conditions will be essential for attaining this understanding, and critical for achieving a breadth of insights into aging.

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Conflicts of interest

The authors declare no conflicts of interest.

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