The Challenges of Senescence for Adult Male Chimpanzees

by

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Dedication

To Caitlin and growing old together.

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Abstract

All animals eventually die. For many, death comes early from external sources of mortality, such as predation, whereas for others, there is a chance to grow old. These aging organisms experience senescence, the declines in vitality and function with age. While senescence reduces survival and reproduction, many individuals persist and even successfully reproduce in their advanced age. How have evolutionary forces shaped senescence, and what does growing old look like in natural settings? How do animals compensate for senescence and continue to reproduce? Addressing these questions is key to understanding how natural selection shapes variation in longevity and other life history traits across species. Such forces may have been particularly important in the evolution of primates as especially long-lived mammals, and humans even more so. One of our closest living relatives, chimpanzees (*Pan troglodytes*), are especially long-lived and exhibit senescence across multiple dimensions. Aging male chimpanzees decline in rank, lose weight, reproduce less, and show shifts in social behavior. Yet in other ways, these males appear to “age gracefully” as they maintain certain measures of body condition, activity, and continue to sire offspring. What are the signs of growing old for male chimpanzees from a behavioral, ecological, and energetic perspective? What tradeoffs shape the continued reproductive effort of old males? To address these

questions and contribute to our understanding of the evolution of longevity, I studied a particularly long-lived cohort of 20 adult male chimpanzees (21-53 years old) over one year at Ngogo in Kibale National Park, Uganda. I found that old chimpanzees ate more slowly and processed less of their ingested food, which indicates that foraging senescence may shape the energetic profiles of old chimpanzees as a functional decline. To understand life history tradeoffs with age, I examined a suite of physiological and behavioral measures. During a food abundant period, old male chimpanzees showed no declines in energetic status or testosterone, and they climbed trees just as often as did younger adult males. But old males spent less time moving and more time resting than did younger individuals. When controlling for important factors such as rank, the social displays of old males were less frequent and covered shorter distances. And in times of food abundance, old males copulated less often than their younger counterparts. These results suggest that old male chimpanzees may strategically restrict activity to maintain reproductive condition, while engaging less in reproductive behaviors overall. Such findings provide a proximate explanation for why despite seemingly maintaining body condition, old male chimpanzees reproduce less. I also investigated social aging and found that various affiliative behaviors increased with age. Proximity to other adult males and grooming time increased with age, but only during high-quality diet periods, which could suggest that resource constraints shape the sociality of old chimpanzees. I also discuss preliminary evidence that old male chimpanzees adopt alternative reproductive tactics in the face of changing payoffs. As male chimpanzees age, foraging senescence and other deteriorations may generate new tradeoffs, yet males appear able to compensate by shifting their behaviors. These

results help us understand the evolution of aging and longevity in humans and other long-lived primates.

Chapter 1.

Introduction

This dissertation investigates the effects of senescence on the lives of adult male chimpanzees who are particularly long-lived primates (Hill et al. 2001, Gurven & Gomes 2017, Wood et al. 2017). Despite increasing observations of senescence in wild animals, little is known about the mechanisms through which aging impacts survival and reproduction. Descriptions of functional declines with age can help clarify how senescence shapes the lives of late life animals and their reproduction, providing insight into the evolution of longevity. I place special emphasis on identifying the challenges that senescence may pose for the everyday activities of adult male chimpanzees such as foraging, traveling, and socializing. Old adult males exhibit declines in traits including fecundity and dominance with associated behavioral changes like, in some cases, social withdrawal, but it is not clear how these patterns relate to the deteriorations of senescence. Such observations are at odds with the fact that chimpanzee males often appear to maintain body condition until late in life and in some ways, exhibit increased sociality. Whether aging chimpanzees alter their behavior to compensate for challenges

of senescence is unknown. To address these issues, I studied the behavior and physiology of 20 prime and old age adult male chimpanzees at Ngogo in Kibale National Park, Uganda.

Background

Longevity is a hallmark of human evolution. We live particularly long lives even without modern medicine. Our extended life histories shaped and continue to play important evolutionary and biocultural roles in human demography, reproduction, and culture (Kaplan et al. 2000, Crews 2003). Works that established the evolutionary theories of aging took particular note of human's exceptional longevity (Cole 1954, Medawar 1952, Williams 1957, Hamilton 1966). In these early writings and beyond, our lifespan has prompted important questions: Is our longevity an evolved adaptation? Why should we and other organisms favor future reproduction at the expense of current reproduction? Why do we have post-reproductive lifespans? Is our longevity unique? While biological research has made substantial progress in addressing these questions, they remain at the core of the study of aging, life history, and human evolution.

Explanations for the evolution for human longevity frequently address other derived or exaggerated traits. Compared to our closest relatives, humans not only have long lives, but also large brains and bodies that grow and develop slowly (Isler & van Schaik 2009). Consequently, explanations for human longevity often bundle life history traits in a co-evolutionary package (Gurven & Gomes 2017). For instance, hypotheses such as the embodied capital model (Kaplan & Robinson 2002) and grandmother hypothesis (Hawkes 2003) rely on mechanisms from our species' unique social systems

of multigenerational caregiving and/or resource transfer to the young, among others (Hrdy 1992, Hill & Hurtado 1996, Kaplan & Robinson 2002). As a result, such explanations have little power to explain the particular longevity of other primates. Despite frequent observations that humans are unique for our extended life-histories (Kaplan et al, 2000), our longer-life trend was already established for apes (family Hominidae*)* – who live twice as long as monkeys and strepsirrhines (Finch 2010). Indeed, as a clade, primates live longer than expected among mammals for their body size (Austad & Fisher 1992, Charnov & Berrigan 1993). While at the extreme for longevity, recent work has highlighted that human senescence falls on a continuum of primate aging (Bronikowski et al. 2011). In other words, human aging may be quantitatively rather than qualitatively distinct from aging in other apes. This claim is supported by studies of demographic variation among chimpanzees (*Pan troglodytes*), which have revealed that lifespans of our closest relatives can approach that of human hunter gatherers under certain ecological conditions (Wood et al. 2017). Consequently, attention to senescence in chimpanzees and other primates can inform explanations for how extreme longevity evolved in apes. Testing hypotheses of aging on other long-lived species, particularly those in the wild, is critical to understand the evolutionary forces that select for increased lifespans. Despite this, research on senescence and longevity has focused rarely on aging in long-lived wild animals (Finch 2010).

Chimpanzees (*Pan troglodytes*) are particularly relevant to human evolution as our lineages diverged between 6 and 9 million years ago (Pilbeam & Lieberman 2017). While there is debate about what chimpanzees can tell us about human evolution, there is substantial evidence that our last common ancestor closely resembled a modern

chimpanzee (Pilbeam & Lieberman 2017, cf. Sayers & Lovejoy 2008). Far more is known about chimpanzee aging than that of the other non-human great apes (Hill et al. 2001, Muller & Wrangham 2014, Wood et al. 2017). Of relevance here, chimpanzees are especially long-lived primates, with a maximum lifespan of over 60 years in the wild (Emery Thompson et al., 2007). Life expectancy at birth for both sexes ranges considerably across research sites: from 13 to 32.8 years (Wood et al. 2017). Overall, chimpanzees differ from human hunter-gatherers, exhibiting a life course that features higher mortality and lower age specific survival, especially during adulthood (Gurven & Gomes 2017).

Across the primate order, females live longer than males (Bronikowski et al 2011). Evolutionary explanations for this phenomenon attribute sex differences in life expectancy to differential vulnerability to environmental hazards, the intensity of sexual selection, and distinct patterns of parental care (Austad & Fisher 2016). Among the Ngogo chimpanzees, female life expectancy is 35.8 years compared to 29.6 years for males (Wood et al. 2017). Such differences, among other observations, have led some to propose that the selection for increased lifespan in primates occurs on females (Hrdy 2011), a debate which extends into hypotheses for human longevity (e.g. Hawkes et al. 1998, Harlow 1999). While the role of sex in longevity and aging represents an important area of research, in this dissertation, I present a study of aging in male chimpanzees.

A focus on males allowed this dissertation to investigate subjects with more readily comparable reproductive and energetic profiles. Firstly, and importantly for a study regarding the evolution of senescence, all adult males were still reproductive and

thus still had potential residual reproductive value. While fecundity drops concurrent with rank in advancing age, old males continue to copulate and reproduce (Watts 2018). While some long-term data indicate that few female chimpanzees survive long enough to become post-reproductive and post-reproductive life expectancy is short (Emery Thompson et al. 2007, Alberts et al. 2013), recent findings have highlighted that approximately a fifth of female lifespans are spent in a post-reproductive state at Ngogo (Wood et al. 2023). Indeed, at the time of this study, the seven oldest adult females in the population were believed to be post-reproductive and no longer cycling. As a result, the focus on males here avoids the application of a specific age cut-off for female subjects to exclude non-reproductive individuals, which would bias the chronological range of senescence under examination. Secondly, female chimpanzees have several significant sources of energetic variation that are not shared with males. Adult females have a greater differential degree of reproductive investment in accordance with dependent offspring (e.g. reproductive cycling, pregnancy, and/or nursing) (Murray et al. 2009, Emery Thompson et al. 2013), whereas males do not offer parental care. Additionally, owing to sex-differences in socio-spatial grouping, females often occupy more distinct core-areas, which represent dietary heterogeneity and vary in quality (Murray et al. 2006, Emery Thompson et al. 2007). For investigations of female chimpanzee foraging efficiency, energetics, and reproductive investment, it is critical to control for these important and potentially unquantified sources of variation. Therefore, a focus on males allowed this dissertation to examine late-life and reproductive individuals while controlling for covariates that were ostensibly more modest, more comparable, and more easily measured such as rank and party composition. It is worth

noting that some of the same aforementioned justifications undergird the extreme sex and gender bias in numerous scientific fields including biomedical research (Beery & Zucker 2011). This male subject dominance has resulted in poorer science and worse outcomes in women's health (Plevoka et al. 2020). I hope that future work continues to question assumptions such as those I have just made, and that my research here emphasizes rather than downplays the importance of studying senescence in female chimpanzees.

While many studies have described patterns of physiology and behavior across the lifespan, they have more commonly focused on life history stages of development or prime-adulthood rather than on the last third of life. Nonetheless, numerous patterns associated with aging are apparent from studies of wild chimpanzees. Broadly, these include declines in anatomical systems, demographic senescence, and social aging, which I will describe in more detail below. First, chimpanzees exhibit declines in anatomical systems such as tooth wear (Elgart 2010) and muscle loss (Emery Thompson et al. 2020a). Because feeding efficiency is both a determinant of individual fitness (Stephens et al. 2008) and a correlate of body condition (Jakob et al. 1996), studies of foraging behavior and, particularly, feeding efficiency may reveal important links between aging, physiology, and fitness. Second, aging male chimpanzees exhibit demographic senescence – declines in dominance (Watts 2018), fecundity, and potentially survival with age. Understanding how these patterns may relate to tradeoffs between resource acquisition, reproduction, and maintenance can inform our understanding of the life history of senescence. Third, like other elderly primates (Tarou et al. 2002), old male chimpanzees may exhibit social aging, or age-related shifts in

social relationships (Machanda & Rosati 2020, Rosati et al., 2020). However, it is unclear how such patterns may relate to physiological senescence.

In this dissertation, I address three main questions about the aging of male chimpanzees generated from the preceding observations. First, are old chimpanzees less effective at extracting resources from their environment, i.e., do they experience foraging senescence? Second, does aging generate life history tradeoffs for old male chimpanzees? And third, does physiological senescence shape male social aging? In summary, what are the challenges of senescence for wild male chimpanzees and how do they solve them?

The evolution of senescence

What is senescence?

Longevity is used here as synonymous with greater life expectancy. Life span is presumed to measure resistance to or the inverse of senescence. If longevity is one side of a coin, senescence is the other. Senescence is the set of age-related declines that adversely affect an organism's vitality and function (Rose 1991, Finch 2010). While often used interchangeably with aging – including in this dissertation – aging refers to the passage of chronological time, while senescing involves the declines that typically accompany it. "Aging per se is simply the fact of existence through time, the phenomenon of becoming older. Senescence is a progressive degeneration…" (Crews 2003). Senescence results in decreased reproduction and increased mortality (Partridge & Barton 1993). Nearly all multicellular organisms die, and nearly all death is preceded by declines in biological function. While senescence often presents itself as

synchronous deteriorators across an organism due to shared proximate mechanisms (Crews 2003), some systems senesce at different rates. In particular, the senescence of the ‘deteriorating’ soma and ‘indispensable’ germline can be uncoupled (Kirkwood 2017), as has occurred in a few species where females experience relatively early reproductive senescence.

Because the manifestations of senescence are the result of diverse environmental and biological factors, no one distinct mechanism of senescence has been found and likely never will be. Most sources of senescence are deteriorations – mechanistically speaking – from the inherent fragility of anatomical structures from DNA to organs (Crews 2003). While senescence often refers to the full suite of age-related deteriorations, all such declines are molecular in origin. Molecular aging includes the accumulation of damage through mechanisms like oxidative stress, which translates into declines in cell function (Finkel & Holbrook, 2000). Deteriorations impact numerous physiological systems, resulting in syndromes such as chronically high levels of proinflammatory measures in blood and tissue with increased age (Francheschi et al. 2006). Consequently, declining system integrity impairs interconnected physiological systems such as immune functioning (Hughes & Reynolds 2005) and musculoskeletal health (Habiballa et al. 2019). These system declines contribute to senescent phenotypes, ultimately manifesting as diminished performance across biological functions.

Evolutionary theories of aging

Aging's deleterious effect on fitness also presents an evolutionary puzzle: shouldn't Darwinian fitness select against these negative impacts? Medawar (1952) was the first to describe the evolutionary paradox of senescence. Genes that promote longevity would allow an organism to live longer and have more offspring. These "longevity genes" would lead to the evolution of a Darwinian demon – an animal that lives forever. Since no such demon exists, Medawar (1952) argued there must be fundamental physiological or genetic constraints that limit lifespan. Because bodies and cells contain a multitude of repair systems, ultimate explanations of aging must address why systems of growth and repair fail when there is no obvious biological mandate to do so (Williams 1957). While most of this dissertation will focus on proximate mechanisms, such as functional declines, it is important to provide an evolutionary foundation for examining those mechanisms.

Early explanations for the phenomenon of aging and death invoked group selection: to make way for future generations, or "eliminate the old and therefore worn-out members of a population" (Weissman 1891 as cited in Williams 1957). Modern theories had to reconcile selection on the individual level to conform with an adaptive view of senescence. The foundation of the evolutionary theory of aging is that the strength of natural selection declines with age (Fisher 1930). This concept was later formalized as the "selection shadow," wherein extrinsic mortality increases with age and therefore a trait will have a greater cumulative impact on fitness earlier rather than later in life (Haldane 1941, Medawar 1952). All organisms live with the threats of predation, disease, and other hazards, and thus have an increasingly lower probability of living to

each subsequent age. After an organism reaches sexual maturity, the chances of reproducing drop off precipitously because of this extrinsic mortality. A decline in the strength of selection stems from the reduction of the residual reproductive value with age (Hamilton 1966). As a result, selection pressures are inherently weaker for any traits restricted to late-life because the selection shadow has hidden them from evolutionary forces.

The selection shadow principle provides a basis for two hypotheses about the evolution of aging. First, the mutation accumulation hypothesis proposes that deleterious mutations confined to late life accumulate because selection is too weak to weed them out (Medawar 1952). Second, the antagonistic pleiotropy hypothesis posits that because genes have linked effects, mutations that have a positive effect early in life and negative effects late in life will still be under positive selection (Williams 1957). Most hypotheses for the evolution of aging are largely variations derived from these two main themes (Maklakov et al, 2015). Austad (1992) estimated that while over 300 proximate explanations for senescence have been proposed, there are only two theories that address ultimate causes. For instance, the antagonistic pleiotropy hypothesis adopts a population genetics lens, while the analogous disposable soma theory provides an account of early- and late-life tradeoffs the perspective of physiological ecology (Kirkwood & Rose 1991). The disposable soma hypothesis postulates that organisms allocate limited resources to current reproduction and somatic maintenance, while optimal allocation of resources will result in suboptimal somatic maintenance in the long run, which results in senescence (Kirkwood 2017).

There is compelling evidence from both laboratory and wild studies that reproduction generates costs associated with increases in mortality. For instance, in a pioneering set of experiments with fruit flies (*Drosophilia*) that restricted breeding to older adults – which is expected to reduce aging by pushing the selection shadow later in life – *Drosophila* lived longer and reproduced less (Rose et al. 2004). Similarly, reproduction at early ages in the wild can be associated with increased senescence later in life (Reznick 1985, Nussey et al. 2008). Understanding the proximate physiological mechanisms underlying aging provides insight into the evolutionary forces that may shape observed patterns in aging. Because most mechanisms that enhance survival (considered somatic maintenance) or reproduction require metabolic resources, and because these resources are finite, it is likely that tradeoffs in the allocation of energy drive the evolution of senescence (see also *allocation theory*, Stearns 1992).

Senescence in the wild

Despite the enduring misconception that wild animals rarely age, senescence is commonly detected in nature (Monaghan et al. 2008, Bronikowski et al. 2011, Nussey et al. 2013). While the study of senescence has received great attention, there is limited evidence regarding how physiological declines affect fitness, particularly in wild animals (Nussey 2008). Much of what we know comes from mechanistic studies of humans and short-lived laboratory animals (Monaghan et al. 2008, Finch 2010). Yet laboratory conditions are different from those experienced by wild animals, whose environments alter both the nature and magnitude of tradeoffs that result in senescence (Nussey et al. 2013). To understand the evolution and ecology of senescence, we need more

information on how senescence manifests in natural systems, where functional declines can translate directly to loss of fitness in the real world where natural selection operates (Peters 2019). In particular, Nussey et al. (2008) call for more studies that examine multiple traits simultaneously when examining senescence in wild animals. Similarly, Holmes & Martin (2009) point out that there are scant observations that connect the behavior of aging animals with their declining reproductive success.

In most animals, reproductive success and survival increase at the start and decrease at the end of life (Ricklefs 2008). Senescence and its timing are part of a related suite of life history traits that occur on the slow-fast continuum: animals with slower life histories (e.g., those with smaller clutch size/litters and later age at maturity) senesce more slowly than animals with faster life histories (Jones et al. 2008). Explanations for increased lifespan across this spectrum rely on either improved efficiency of energy acquisition or reallocation away from processes such as reproduction. Such connections have led to a particular focus on declines in foraging performance with age (Nussey et al. 2013). Lecomte et al. (2010) proposed that feeding performance may be one of the first phenotypic traits to reflect aging in natural conditions, referring to it as a potential “cornerstone” that shapes patterns of senescence in wild animals. Therefore, foraging behavior, the set of processes organisms use to acquire nutrients, merits special attention as it determines the amount of available energy for an organism to expend on fitness-related tasks like mating (Altmann 1998).

Primates are firmly on the slow end of the spectrum; we have long-life histories compared to other mammals of similar size and share exceptionally slow rates of

growth, reproduction, and aging. Energetic analyses have shown that primates use surprisingly little energy, expending half the energy expected for a placental mammal, which appears to be a systemic metabolic adaptation rather than a reflection of reduced physical activity (Pontzer et al. 2014). Such data draw parallels between the life history of primates and birds or bats, the “flying Methuselahs” that also have extended lifespans and lower than expected metabolisms (Munshi-South & Wilkinson 2009, Williams et al., 2010). Evolutionary theory predicts a coevolutionary relationship between the low-mortality rates that characterizes primates and evolved mechanisms that prevent age-related damages. Longer-lived species presumably have mechanisms to delay or reduce senescence (Elliot et al. 2014), which are likely to shape how their physiological tradeoffs manifest (Kirkwood 2002). These considerations lead to two conclusions concerning the study of aging in primates. First, old age may be a particularly evolutionary salient life history stage for long-lived primates. Second, the nature of resource acquisition and tradeoffs among primates and other long-lived wild animals are likely to be qualitatively different from those observed in short-lived laboratory organisms. Therefore, understanding why primates under resource limited natural conditions make trade-offs between somatic maintenance and reproduction can shed light on the evolution of aging and longevity.

Chimpanzee natural history and aging

Chimpanzees live in communities of 20 to 200 individuals and occupy relatively large territories that vary between 5–30 km^2, depending on habitat type and quality (Chapman 1993, Newton-Fisher 2003, Muller & Mitani 2005). Individuals within

communities fission and fuse forming temporary parties that change in size and composition (Nishida 1990, Pepper et al. 1999). While females typically emigrate at sexual maturity, males are philopatric and remain in their natal communities for life (Nishida and Kawanaka 1972). As a consequence, males are quite gregarious and form strong social bonds with each other, often sharing high degrees of relatedness (Nishida 1968, Goodall 1986, Goldberg & Wrangham 1997, Mitani 2009). Male kin live together throughout their lives and cooperate via coalitions, meat sharing, and territorial boundary patrols (Langergraber et al. 2007). Within communities, males compete for rank and form linear dominance hierarchies (Bygott 1979, Muller 2002). Competition among males over reproductive opportunities for estrous females is intense, especially for females who have already reproduced successfully (Sobolewski 2013). Between communities, male chimpanzees compete via their group territorial behavior (Watts & Mitani 2001, Wilson & Wrangham 2003).

Chimpanzees have been characterized as ripe fruit specialists; there is a positive association between feeding time on non-fig fruit and estimated fruit abundance at both Ngogo and Kanyawara (Conklin-Brittain et al. 1998, Watts et al. 2012). At Ngogo, a 15-year study (Watts et al. 2012) documented that their diet was composed of mesocarp from non-fig fruits (42.3% of feeding time) and figs (28.4%), leaves and leaf buds (19.6%), seeds (4.0%), flowers (2.5%), pith and stems (2.2%), cambium (0.6%), and roots (0.4%) with other food types each accounting for less than 0.1%**.** During the dissertation study period, the most common food items were non-fig fruits (51%), figs (30%), leaves (9%), and pith/stems (3%), which fell within the range of monthly-observed proportions of these items from prior study of Ngogo chimpanzee diet over

multiple years (Watts et al. 2012). However, this study's observed proportions slightly exceeded the same study's annual maximum proportions for fruit (51% to 49.6%) and pith/stems (3.0% to 2.4%), whereas the proportion of leaves fell well below the annual minimum (9% to 16.3%) (for a summary of popular diet items during the study period, see Table S2). These contrasts indicate that the study period was a high-quality food period and are consistent with long-term trends in increasing fruit abundance at Ngogo (Potts et al. 2020).

Senescence shapes a variety of characteristics in later life for humans, but the extent to which it determines physiological and behavioral outcomes in our closest ape relatives remains unclear (Finch 2010, Emery Thompson 2020a). In at least some ways, chimpanzees may appear to present phenotypes largely unaltered by the passage of several decades of adult life. Nonetheless, several anatomical declines are documented in wild chimpanzees (for a comparative summary of age-related pathologies in captive apes, see Lowenstein et al. 2016). Old chimpanzees, like humans, exhibit muscle wasting, known as sarcopenia (Pusey et al. 2005, Emery Thompson et al. 2012). Emery Thompson et al. (2020a) found that estimated lean body mass increased through the early 30s, and then sharply declined such that by age 40, males had lower lean body mass than at previous adult age. Concurrently, age-related bone loss is observed across non-human primates (Madimenos 2015) including wild chimpanzees (Morbeck et al. 2002) and is hypothesized to impede locomotor performance in wild chimpanzees (Sumner et al. 1989). One study described an old female with bone mineral density that was below human osteoporosis criteria (Gunji et al. 2003), but it is less clear if males may experience comparable levels of bone loss. Regarding teeth, periodontal disease

and tooth loss appear to be common among elderly apes in the wild (Kilgore 1989). Nearly toothless chimpanzees have survived in the wild for years (Miles & Grigson 2003). Nonetheless, two studies on a measure of chewing efficacy, fecal particle size, showed no decline with age (Weary et al. 2017, Schulz-Kornas et al. 2020). Regarding immune function, immunosenescence is well documented among primate models of human health (Haberthur et al. 2010) and wild animals (Peters et al. 2019). Old chimpanzees in the wild exhibit increased immune-burdens with greater immune-activation (Negrey et al. 2020) and viral richness (Negrey et al. 2021). Meanwhile, chimpanzees experience humanlike aging of glucocorticoid regulation as cortisol increases with age, which suggests increased stress, accompanied by a blunting of the diurnal rhythm (Emery Thompson et al. 2020b).

Male chimpanzees exhibit common features of demographic senescence: they reproduce less in late adult life and may experience greater mortality risks (Wood et al. 2017). Recently, a longitudinal study by Emery Thompson et al. (2020a) combined physiological and behavioral observations. The authors found that male chimpanzees experience declines in body mass with age but there was little evidence to link such to declines to negative health outcomes. For instance, even in chimpanzees where body mass declined with age, rates of travel or resting did not decrease, and individuals appeared to maintain good body condition until close to death (Emery Thompson et al. 2020a). The same study found that old chimpanzees spent less time foraging, ate less ripe fruit, and were more likely to forage terrestrially (Emery Thompson et al. 2020a), leading the authors to conclude that increased weakness or fatigue with age may limit climbing behavior. Nevertheless, there was only a weak association between these

declines with an index of body condition, lean muscle mass. A separate longitudinal study at Kanyawara showed that older individuals were more likely to be solitary, but were also more affiliative (Rosati et al. 2020).

The preceding considerations regarding the strength of old chimpanzees leads me to sometimes refer to chimpanzees as “aging gracefully,” a phrase used by Elliot et al. (2015) to describe how old thick-billed murres adjusted to physiological changes so that there was no net effect on their foraging behavior. Perhaps similarly, aging chimpanzees appear able to balance deteriorations of age with an observed capacity to maintain condition and survivorship until late in life (Emery Thompson et al. 2020a, Wood et al. 2017). Emily Otali summarized their ability well when she said, “[T]hey handle old age much better than we do” (Vernimmen 2021). A goal of this dissertation is to investigate how chimpanzees may succeed in meeting the challenges of aging as they achieve remarkable longevity for a wild animal.

What constitutes old age in male chimpanzees? The demarcations of this stage should correspond to the timing of aforementioned physiological declines. Because research has focused on prime-aged males, an exact age of onset for the senescing phenotype is uncertain. In addition, various functional traits senesce at different rates and have complex, non-linear relationships with life history traits like fertility and morbidity. Goodall (1986) described old age as 33 and up, a chronological age that approximately coincides with the start of declines in lean muscle mass in the Gombe and Kanyawara chimpanzee communities. At Ngogo, however, a decrease in lean muscle mass may not appear until later, by approximately 40 years of age (Negrey unpublished data). Male chimpanzee social rank displays a ∩-shape curve with age,

and Ngogo males attain their maximum rank later than in other chimpanzee communities at 28-30 years (Watts 2018). This decrease in dominance appears concomitant with declines in reproduction; the same males' fertility declines after 30 (Langergraber unpublished data). In a sample of 161 Ngogo infants of known paternity, the median age of fathers at conception was 23.6 years, and 75% of all infants are sired by males who are under 30.3 years old whereas 95% are sired by males under 38 years old. Consequently, certain deteriorations of senescence may manifest by the mid-thirties even in the Ngogo chimpanzees, but may not accumulate to affect traits like lean body mass until closer to age 40. Therefore, while age-specific deterioration rates may be variable across sites, and may be delayed at Ngogo, senescent phenotypes are likely to be apparent in the late thirties. Based on physical and social milestones in chimpanzee development, I categorized "young adults" as 16-21 years, "prime-aged" as 21-29, "middle-aged" as 30-37, and "old-aged" as 38 and above. However, this "old-aged" phenotype is still distinct from the marked decline that appears near death, when weight loss is pronounced (Emery Thompson et al. 2020a).

"Old age" may be a pragmatic signifier for the considerable accumulation of age-related deteriorations, but it both fails to consider the early and gradual nature of deterioration accumulation or the important uncoupling of biological and chronological age. First, in humans age-related changes to physiology are known to accumulate from early life (even infancy), affecting systems years before resulting diseases are diagnosed (Barker et al. 2002, Gavrilov & Gavrilova 2004). Therefore, studies seeking to identify onsets of senescent phenotypes should consider an early range of life-history stages rather than solely late-life individuals (Belsky et al. 2015). Second, because

there is considerable intraspecific variation in senescence, chronologic age may vary substantially from pacing markers of senescence, potentially even from young adulthood (Belsky et al. 2015). Such considerations weaken the utility of a defined old age cut-off. Reframing old age as “the last third of life” addresses some of these issues, providing instead a relative timeframe (although I do not adopt the term thoroughly in this dissertation). Hereafter, I treat age as a continuous variable. While I characterize results as contrasting “old” and “prime-aged” chimpanzees, this is solely for descriptive purposes to communicate results of age-specific relationships.

This study

The preceding discussion highlights two major gaps in our understanding of aging in wild adult male chimpanzees. First, how do the physiological deteriorations of senescence manifest as functional declines in behaviors such as foraging performance that may precede demographic senescence? Second, how does senescence constrain or shape adult male behavior in chimpanzees, particularly social aging? This dissertation also addresses the call for studies that examine multiple traits simultaneously when describing senescence in wild animals (Nussey et al. 2008). Specifically, I draw on insights into the evolution and ecology of senescence from studies outside of biological anthropology, especially ecology and evolutionary biology’s examination of non-primates, notably long-lived aquatic birds. With recent and increasing interest in senescence from biological anthropology scholars (Emery Thompson et al. 2020c), an interdisciplinary investigation that puts these typically

disparate fields in conversation will help build our understanding of senescence in primates.

This dissertation is based on fieldwork that I conducted from 2016 to 2019 at Ngogo in Kibale National Park, Uganda. The results presented here are from data that I collected from August 2018 through August 2019. The Ngogo study site is largely primary rainforest interspersed by regenerating forest and grasslands (Struhsaker 1997). The chimpanzee community at Ngogo is an ideal population for a cross-sectional study of aging and senescence. Ngogo is a large population of chimpanzees comprising roughly 200 individuals and for many years was the largest chimpanzee community described, nearly three times the size of most other groups (Wilson et al. 2014). The chimpanzees there have been studied continuously by John Mitani, David Watts, and others since 1995 (Watts 2012). In January 2018, the Ngogo community split into two groups from pre-existing sociospatial subgroups into the Ngogo Central and Ngogo West communities (Sandel & Watts 2021). Together, the communities occupy territories over an approximately 35 km^2 area. All subjects included in this study were well-habituated. Subjects were 20 adult males ranging from age 21 to 53 years old at the start of study (mean age = 32 years), which included the 10 oldest males in the population. Seven of these focal subjects belonged to the Ngogo West community, and 13 from the Ngogo Central community, which reflects the demographic differences between these two groups. Accordingly, subjects included ten “prime-aged” individuals, five “middle-” and five “old-aged” individuals. Detailed descriptions of the research methods and considerations of a cross-sectional approach are provided in the three chapters that address my central research questions.

The results of my research are presented in three chapters. Chapter 2 describes evidence for foraging senescence in male chimpanzees. I evaluate the relationships between age and various measures of foraging performance within a framework that subcategorizes various foraging behaviors and measures by their associated function: either food *access*, *consumption*, or *digestion*. Foraging behavioral outcomes include arboreality and climbing distance, ingestion rates, food selection, and fecal particle sizes, measures of chewing efficacy. Chapter 3 investigates whether patterns in physiological and behavioral investment may present tradeoffs with age, in particular between maintenance (represented by the "terminal restraint" hypothesis, McNamara et al. 2009) and reproduction (the "terminal investment" hypothesis, Williams 1966). I also consider an alternative life history framework focused on resource management – whether old chimpanzees strategically prioritize the acquisition of resources or restrict energy use all together. I consider how various measures change with age including urinary C-peptide insulin as proxy for energetic status), urinary testosterone as a proxy for reproductive investment, climbing distances, activity budget, social display rate and frequency, as well as copulation rates. Chapter 4 describes the patterns of affiliative behaviors as a function of age and evaluates hypotheses that address how senescence may constrain the behavior of old males. In the Conclusion, I synthesize my findings and their implications for senescence in chimpanzees and the evolution of longevity as a life history trait. I also discuss future directions of research that arise from this work.

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Chapter 2.

Evidence for Foraging Senescence in Wild Male Chimpanzees

Abstract

Observations of functional decline with age in wild animals are relatively rare, but help us understand how senescence can result in decreased reproduction and increased mortality. Declines in foraging performance may be especially relevant to senescence because body condition corresponds to feeding performance, which in turn determines energy available for fitness-related activities. I investigated whether chimpanzees experience foraging senescence in a cross-sectional study of adult males (n=20, 21-53 years) over 12 months (n=1288 observation hours) at Ngogo in Kibale National Park, Uganda. I found that neither climbing behaviors during foraging nor food item selection varied with age. Old chimpanzees, however, ingested non-fig fruit and leaf items more slowly and may have selected ripe over unripe figs. Two measures of fecal particle size, a proxy for chewing efficacy, increased with age, which indicates that old chimpanzees were worse at processing their food. These results provide the first direct evidence for foraging senescence in wild chimpanzees. Notably, these age-related changes appear long before death and late-life frailty. In addition to other

aspects of functional senescence, diminishing foraging returns could constrain chimpanzee behavior and precipitate declines in fitness.

Introduction

Age-related changes that adversely affect organisms' vitality and function (Finch 1994) are ubiquitous in wild vertebrates (reviewed in Nussey 2013 and Jones et al. 2014). This decline, known as senescence, encompasses both the proximate mechanisms of molecular deterioration (such as oxidative stress) and declines in survival and reproduction with age (Kirkwood 2005, Gaillard & Lemaître 2020). Despite great interest in studying senescence, there is limited evidence regarding how physiological declines translate into fitness consequences, particularly in wild animals (Nussey 2008). Such links would inform our understanding of how natural selection shapes variation in longevity and other life history traits. Much of what we know comes from mechanistic studies of humans and short-lived laboratory animals (Monaghan et al. 2008, Finch 2010). Yet laboratory conditions are different from those experienced by wild animals, whose environments alter both the nature and magnitude of tradeoffs that result in senescence (Nussey et al. 2013). To understand the evolution and ecology of senescence, we need more information on how senescence manifests in natural systems, where functional declines can translate directly to loss of fitness in the real world where natural selection operates (Peters 2019).

Foraging performance has recently received some attention as an arena of behavioral changes that may have particular importance in shaping the aging process (Nussey et al. 2013). Foraging, the act of extracting resources from the environment,

determines the amount of energy or nutrients that animals can allocate to maintenance or reproduction (Boggs 1992, Stearns 1992). Consequently, foraging ability can directly affect survival and reproduction (Altmann 1998). Researchers have observed age-related declines in foraging performance in several wild taxa: worker honey bees (*Apis mellifera*) (Dukas 2008, Higginson & Barnard 2004), albatross (*Thalassarche & Diomedea spp.)* (Catry et al. 2006, Lecomte et al. 2010, Clay et al. 2016, Frankish et al. 2020;), and mammals such as moose (*Alces alces*) (Montgomery et al. 2013), reindeer (*Rangifer tarandus*) (Skogland 1988, Veiberg et al. 2009), wolves (*Canis lupus*) (Macnulty et al. 2009), and humans (Kaplan et al. 2000). These studies examine a range of foraging behaviors, including age-related differences in activity budgets, diets, digesta particle size, and other foraging characteristics linked to physiological declines. Collectively, these reflect and represent foraging senescence, a term first used in the literature by Pardo et al. (2013). Lecomte et al. (2010) proposed that feeding efficacy may be one of the first phenotypic traits to reflect aging in natural conditions, referring to it as a potential “cornerstone” that shapes patterns of senescence in wild animals.

There are two challenges for studies that investigate foraging senescence. First, deteriorations with age may be compensated for and thus difficult to detect and declines in disparate systems such as social phenotypes may indirectly alter feeding behavior. Individuals can adjust for physiological aging by adopting behavioral strategies that are less affected by their physical decline. For instance, koalas (*Phascolarctos cinereus*) with worn teeth chew absolutely more (Logan 2003). Alternatively, concurrent physiological declines may offset one another. Elliot et al. (2015) showed that old thick-billed murres adjusted to physiological changes so that there was no net effect on

foraging behavior, which the authors referred to as “aging gracefully.” Second, disentangling effects of senescence remains challenging due to synchronous declines across systems, in which physiological and behavioral traits are inextricably linked (Crews 2003). In particular, behavioral changes may be due to social rather than foraging-based declines. Shifts in sociality with age are well documented and can affect foraging decisions (Siracusa et al. 2022). Importantly, dominance rank often declines with age due to decreased fighting condition (Perlman et al. 2016). Because dominance and social relationships are often predictors of foraging efficacy - particularly in primates (Wittig & Boesch 2003, Vogel 2005) - changes in foraging outcomes are not necessarily due to declines in feeding performance. For instance, in chimpanzees increased mating competition reduces foraging effort (Georgiev et al. 2014). Consequently, a study that only examines a single marker of aging or does not control for social confounds is susceptible to misidentifying or overlooking primary factors of aging (Lecomte et al. 2010).

Primates as an Order are characterized by long-lives (Washburn 1981, Finch et al. 1990, Jones 2011) and experience well-documented, age-specific changes in traits, including mortality (Bronikowski et al. 2011), reproduction (Caro et al. 1995, Alberts et al. 2013), immune-function (Haberthur et al. 2010), and sociality (Machanda & Rosati 2020). One facet that has received particular attention is the effect of tooth wear on the ability of wild primates to chew and ingest food. Primates have brachydont, or low-crowned teeth, which wear down considerably as individuals age (e.g. *Alouatta palliata,* Dennis et al. 2004; *Mandrillus sphinx,* Galbany et al. 2014). There is evidence that tooth wear impairs chewing ability, with associated declines observed in old sifakas

(*Propithecus edwardsi*) (King et al. 2005, 2012) and geladas (*Theropithicus gelada*) (Venkataraman et al. 2014). In contrast, initial studies in chimpanzees on fecal particle size (FPS), a proxy for ingesta particle size reduction, have not found a relationship between age and FPS (Weary et al. 2017, Schulz-Kornas et al. 2020). Similarly, an analysis of mountain gorilla (*Gorilla beringei*) molars suggested that observed lifetime wear was insufficient to decrease shearing forces (Glowacka et al. 2016), consistent with other findings that wear does not lead to mechanical senescence (Elgart 2010). Other age-related changes in foraging behavior have been described, but their effect on foraging efficacy remains unclear. For instance, a longitudinal study showed that old chimpanzees (*Pan troglodytes schweinfurthii*) spent less time foraging, ate less ripe fruit, and were more likely to forage terrestrially (Emery Thompson et al. 2020), leading the authors to conclude that increased weakness or fatigue with age may limit climbing behavior. Nevertheless, there was only a weak association between these declines with an index of body condition, lean muscle mass. A study in the same chimpanzee community showed that older individuals were more likely to be solitary, and thus forage alone (Rosati et al. 2020), but again this was not linked to feeding performance. To date, no study has simultaneously examined multiple measures of foraging performance in old primates. An investigation of the intrinsic attributes of elderly primates will provide crucial insights into the ecological forces that shape senescence.

Here I present results of a cross-sectional study investigating the links between age and foraging behaviors to determine whether chimpanzees experience foraging senescence. Chimpanzees are excellent models for studying aging. They are among the longest-lived vertebrates, reaching over 60 years of age in the wild (Wood et al.

2017), and age-related changes in their health and sociality are well described (Gurven & Gomes 2017). Chimpanzees have a fission-fusion social organization that allows the formation of temporary subgroups of varying sizes (Nishida 1968, Goodall 1986). One primary determinant of party size is food availability, as smaller parties allow individuals to avoid feeding competition (White & Wrangham 1988, Sakura 1994, Mitani et al. 2002). Fission-fusion dynamics allow for individuals to vary their social contexts while foraging, and thus permit me to examine of potentially confounding effects of party composition and age. I investigated several components of the foraging behavior and performance of adult male chimpanzees at Ngogo in Kibale National Park.

Foraging is a multifaceted system that engages nearly all parts of an organism's anatomy, meaning that description of changes in foraging performance requires simultaneous investigation of multiple dimensions. I divide foraging into three primary goals: to *access* nutrients via locomotion; to *consume* via selection and ingestion; and to *process* via mastication and digestion. While these actions are neither comprehensive nor independent from one another, they allow us to assess different arenas of foraging senescence and potentially link outcomes to their respective physiological underpinnings. Specifically, I seek to answer the following questions:

1. Do older chimpanzees climb less when foraging? (*access*)
2. Do older chimpanzees select different food items and consume them more slowly? (*consume*)
3. Does chewing efficacy decline with age? (*process*)

Regarding *access,* old chimpanzees, like humans, exhibit both muscle wasting and bone loss, which is hypothesized to hinder locomotion (Morbeck et al. 2002). After peaking at approximately 30 years of age, male chimpanzees lose muscle mass as measured by the ratio of urinary creatinine to specific gravity (Emery Thompson et al. 2012; Emery Thompson et al. 2020). This occurs at Ngogo (Negrey unpublished data), where males have a greater life expectancy (Wood et al. 2017). Concurrently, age-related bone loss is observed across non-human primates (Madimenos 2015) and is hypothesized to impede locomotor performance in wild chimpanzees (Sumner et al. 1989). Decreased mobility may be especially consequential for chimpanzees who have greater day ranges than any other non-human ape (Chapman & Chapman 2000). Due to the greater energetic costs of arboreal movement (Pontzer & Wrangham 2004), declines may affect climbing distances, which leads to the prediction of decreased arboreality in old chimpanzees (**Table 1**).

Food item selection is an observable foraging decision, and food items vary with respect to where they are found in relation to the forest floor and their mechanical properties. Shifts in dietary preferences may therefore reflect changes in access or processing capacity (Kinzey & Norconk 1990). This leads to the prediction that old chimpanzees select foods with relatively weak mechanical properties and are thus easier to process (Vogel et al. 2008). Additionally, senescence could diminish intake rates, a key determinant of an organism's foraging performance (Nakagawa 2009). I predict that feeding rates decline with age **(Table 1**), acting through several pathways such as decreased movement within feeding bouts (Emery Thompson et al. 2020,),

lower rates of chewing efficacy (Galbany et al. 2016,), and other declines such as diminished vision with increasing near-sightedness with age (Ryu et al. 2016).

Lastly, regarding processing, chewing reduces the size of food particles, which increases the speed with which food can be digested and fermented; this facilitates nutrient uptake in the gut (Bjorndal et al. 1990, Hummer et al. 2020). Chewing efficacy is the rate at which food is reduced to a certain particle size, and is influenced by factors such as oral anatomy, dental wear, and the direction and force of chewing movements (Pérez-Barbería & Gordon 1998). Fecal particle size (FPS) provides a physiologically salient measure of chewing performance in terrestrial mammals (Fritz et al. 2012). In contrast to the graminivorous herbivores for whom FPS measurements are well studied, chimpanzees are frugivorous. Fruit-dominated diets are characterized by weaker food mechanical properties (FMPs) (Vogel et al. 2008, c.f. Coiner-Collier et al. 2016), which may explain why nearly toothless chimpanzees have survived in the wild for years (Miles & Grigson 2003). While prior studies did not find a decrease in chimpanzee fecal particle size with age (Weary et al. 2017, Schulz-Kornas et al. 2020), these analyses included limited repeat sampling of old individuals. Fecal samples collected across dietary seasons from a sample including old chimpanzees will clarify whether, as I predict, feces will contain more large, undigested particles as well as greater fecal particle size with age in chimpanzees (**Table 1**).

foraging goal	outcome	description of measure and [data class]	correlation with age	
			prediction	result
access	arboreality	whether foraging took place in trees (≥3m) [binary]	↓	—
	climbing distance	|Δheight| between scans in foraging context [continuous, zero inflated]	↓	—
consume	food item selection	item identity of food: non-fig fruit, fig, leaf, pith [categorical]	↓ leaf/pith	—
	fruit ripeness selection	food item ripeness for non-fig fruit and figs [binary]	↑	(↑ fig)
	intake rate	number of items ingested over discrete sample [count]	↓	↓
process	large undigested particles	mass of large particles in fecal sample (>4 mm) [continuous]	↑	↑
	FPS (0.025-4 mm)	weighted dMEAN of fecal particle size (0.025-4 mm) [continuous]	↑	↑

Table 1. Description of foraging measure outcomes with their respective predictions and results. Symbols for correlations are as follows: "—" no correlation; "↓" negative correlation; "↑" positive correlation. Parentheses indicates weak support.

Materials & Methods

Study site and subjects

I observed chimpanzees at Ngogo in Kibale National Park, Uganda (between 0°13′–0°41′ N and 30°19′–30° 32′ E) from August 2018 to August 2019. The Ngogo study site is surrounded by other chimpanzee communities and covered by mature, mid-altitude rainforest interspersed with secondary growth, swamp forest, and grasslands (Struhsaker 1997, Lwanga 2003). Researchers have studied the Ngogo chimpanzee community since 1995, and all subjects were well habituated to human observation (Watts 2012). In January 2018, the Ngogo community split into the Ngogo Central and Ngogo West communities (Sandel & Watts 2021). Together, the communities occupy territories that cover an approximately 35 km^2 area. For the majority of the study period, Ngogo Central comprised 121 individuals, including 24 adult males and 40 adult females, and Ngogo West had 84 individuals including 7 adult males and 24 adult females.

Subjects were 20 adult males ranging from age 21 to 53 years old at the start of study (**Table S1**). While young adulthood includes individuals 16-20 years old, this period has been characterized as a distinct social life stage (Goodall 1983, Kawanaka 1989). I excluded young adults from analysis because their continued physical and social maturation might influence foraging performance. The ages of males born in 1995 or later are known with a precision of between one day and a few months. For males born earlier (17 of 20 subjects), this study uses ages provided by Wood et al. (2017). These estimates are based on comparison of the appearance of males when first observed to that of known-aged males; visual assessment of when males who were immature at the study's start attained full, adult body mass; and comparisons among those who were already adults with respect to visible traits associated with senescence (e.g., muscle mass). Genealogical information for most males born before 1995 is known from an ongoing, long-term genetic study of the Ngogo chimpanzees (Langergraber et al. 2007, 2013). These data furnish an additional, key source of information to estimate the age of males born before 1995 (see Wood et al. 2017).

Behavioral data collection

Sharifah Namaganda and I observed subjects via continuous focal animal sampling (Altmann 1974). Focal sessions typically lasted 2 hours, after which we switched to a new focal subject. When no other focal subject was present, we remained with the current subject. Some focal sessions terminated early when chimpanzees were lost. In these situations, we included observations if subjects were followed for at least 30 minutes. Because chimpanzees live in fission–fusion societies and form temporary

sub-groups known as parties, not all males were available for observation every day. We attempted to equalize the number of focal follows by rotating through subjects opportunistically, prioritizing males that had been observed less often than others during any given month. Namaganda and I conducted a total of 688 focal follows for 1288 hours of focal observations on subjects (mean 64.4 ± SD 10.3 hours per subject). I conducted an additional 132 hours of focal observation on non-focal adults, which were incorporated in the generation of the dietary indices that were predictors of foraging outcomes (see below). All observations were recorded digitally on a handheld device using *HanDbase IOS* software.

We collected behavioral data during scans every 15 minutes (n=5180 scans). This included food items consumed and whether subjects were arboreal, defined as ≥ 3m off of the ground. Adult male chimpanzees were classified as resting in 44% of scans, foraging in 27%, moving in 15%, and socializing in 13%. Of the scans where the subject was foraging (n=1367), they were considered arboreal in 80% (see results section). During scans, I collected additional data regarding subject height above the forest floor. I used a Haglöf clinometer to estimate the vertical angle of chimpanzees from my position and combined this with their visually assessed horizontal distance to calculate heights relative to the forest floor (Bezanson et al. 2012). I measured consecutive heights to calculate the |∆height| between scans. To assess locomotion in foraging contexts, I considered only consecutive scans where foraging had occurred anytime in the past 15 minutes. In this context, subjects traversed a mean absolute vertical distance of 7.7 m every 15 minutes (±SD 10.5 m, 0–47.2 m, n=1419).

In 1367 foraging scans (representing 342 hours), the most common food items were non-fig fruits (51%), figs (30%), leaves (9%), and pith/stems (3%), which fell within the range of monthly-observed proportions of these items from a prior study of Ngogo chimpanzee diet over a 15-year period (Watts et al. 2012). However, this study's observed proportions slightly exceeded the same study's annual maximum proportions for fruit (51% to 49.6%) and pith/stems (3.0% to 2.4%), whereas the proportion of leaves fell well below the annual minimum (9% to 16.3%). These differences indicate that the study period was a high-quality food period and are in line with long-term trends in increasing fruit abundance at Ngogo (Potts et al. 2020). For a summary of popular food items throughout the study see **Table S2.**

I also opportunistically recorded food intake rates over 2-minute segments during feeding bouts of focal males. During these, I counted units of food ingested (Rothman et al. 2012). Predefined units were characterized as the smallest consistently observable quantity of a given food, i.e. a single fruit or leaf. I analyzed intake rates from food items with at least 15 recorded segments and only those that were consistently consumed in their entirety. Consequently, I excluded wadged fig fruits (*Ficus mucuso*), wherein the chimpanzee maneuvers the fruit into a pulp to extract juices and later expels the remaining pulp and seeds (Lambert 1999), as well as one fruit for which inconsistent amounts of mesocarp were scraped from a single, large seed (*Warburgia ugandensis*). According to preliminary analyses, the oldest subject, Brownface (53 years), exhibited outlier ingestion rates. I frequently observed the nearly edentulous Brownface consuming particular food items whole (*Uvariopsis congensis*), with virtually no chewing effort, an observation confirmed through examining his fecal samples. Therefore, I

excluded ingestion rates of Brownface for *Uvariopsis* from analysis and for other food items, included a dummy variable for his identity to account for high leverage observations. In sum, the intake analysis included nine food items measured over 444 intake samples (n=13.5 hours, mean=1.5 hours/food item ±SD 1.4 hours).

Fecal collection and particle size analysis

Namaganda and I collected 188 fecal samples from the 20 subjects opportunistically, attempting to equalize sample collection over the study period (mean 9 samples/subject, ±1.8). Immediately after defecation, we placed fecal samples in water-tight plastic bags to prevent loss of moisture and weighed them at the end of the day. Large particles over 4 mm – including whole fruit, seeds, plant fibers, or bones – were separated and then weighed. Removal of these large "undigested" particles ensured that disproportionately large particles would not bias the final weight and moisture content of the fecal particles in subsequent laboratory analysis. Fecal samples consisted of 27.8% (±17.8% SD) large undigested particles (>4 mm). Next, 10–15 g of each sample was stored in 50 mL plastic test tubes and submerged in laboratory grade ethanol (70% solution) for preservation. An equivalent portion of each sample was also dried to constant weight in a solar oven (*Sunworks Solar Food Dryer*) at roughly 55 C° to determine dry matter concentration (Weary et al. 2017).

I transported samples to the Clinic for Zoo Animals, Exotic Pets and Wildlife at the University of Zurich, where Namaganda and I employed a standardized wet sieving method (Fritz et al. 2012). Fecal samples were left in beakers of water overnight with magnetic stirrers to disintegrate the sample without altering particle sizes, and then

poured onto the sieve cascade (linear dimension of holes: of 0.025, 0040, 0.063, 0.0125, 0.25, 0.5, 1.0, 2.0, 4.0, and 8.0 mm) on a vibrating sieving machine (Retsch AS 200 digit, Haan, Germany). The remains on each sieve were transferred to pre-weighed petri dishes and dried at 103 Cº overnight. After cooling to room temperature in a desiccator, they were weighed using an analysis balance with measuring accuracy of 1 mg, after which the petri dish weight was subtracted. Larger seeds passed intact were removed manually from the two largest sieves and weighed separately (**Figure 1**).

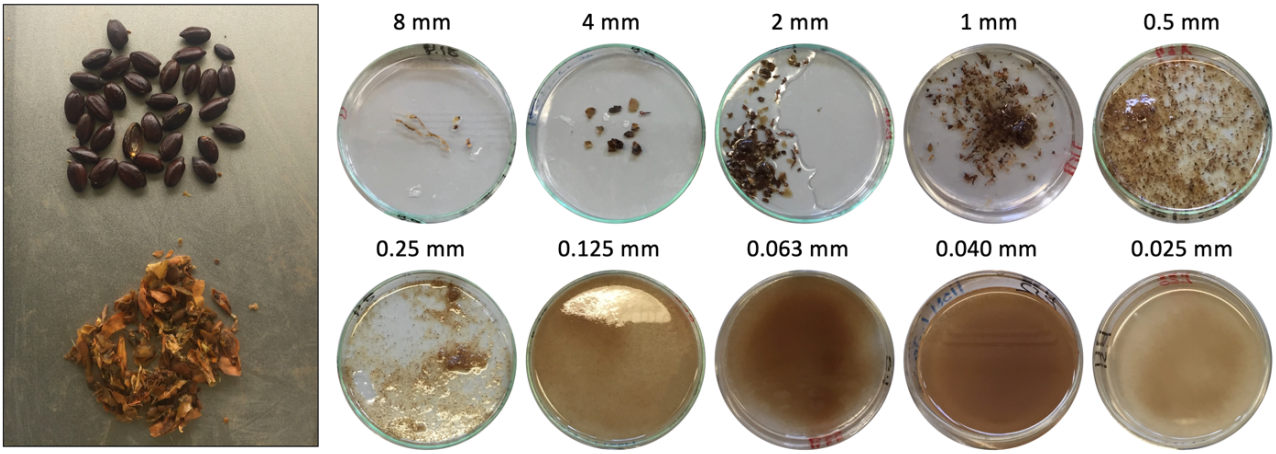

Figure 1. Material from a single chimpanzee fecal sample, Jackson (28 years old), on 04-May-19. The left image depicts the large particles (approximately > 4 mm) separated immediately after collection. These large, undigested particles were weighed and analyzed as a proportion of total fecal mass. 10–15g of remaining fecal material was later processed via the wet sieving method, with this product depicted on the right. Any remaining seeds were removed from the 4 mm and 8 mm dishes. After drying, we calculated the FPS dMEAN from sieves 0.025–4 mm.

I calculated fecal particle sizes (FPS) from dry-weights on each sieve as the proportion of total fecal material. The FPS was calculated according to the dMEAN procedure of Fritz et al. (2012) as

$$FPS = \sum_{i=1}^{n} p(i) * \frac{S(i+1) + S(i)}{2}$$

where *i* is the number of sieves in the respective cascade, *p(i)* is the proportion of dry matter on sieve *i*, and *S(i)* the pore size of the sieve. Maximum particle length (MPL mm) was also recorded. In this way, I calculated FPS for various sieve cascades and scenarios with and without excluding seeds, and whether or not MPL was included. Because large undigested particles such as seeds > 4mm were removed prior to the wet sieving method and analyzed separately, we used FPS values calculated from a non-overlapping subset of the cascade ($FPS_{0.025–4\ mm}$). In this way, our measurements of large, undigested particles and $FPS_{0.025–4\ mm}$ did not overlap particles of the same size. Preliminary analysis showed that the two measures were not correlated with one another. Although not included here, other FPS dMean values with and without seeds were also calculated, and results described here were consistent across multiple measures.

Covariates and predictors

I generated and employed the following covariates as predictors in my models (summarized in **Table 2**).

Table 2. Description of predictors for outcomes and their inclusion in for foraging outcome global models, which were then input into dredge() {MuMIn].

Description of predictors for foraging measures			included in models						
type	predictor	predictor description and [data class]	arboreality	|Δheight|	food item	fruit ripeness	intake rate	large particles	FPS
fixed	date	three date terms: nuermic date of sample, cos(pi * date), and sin (pi * date) [numeric, continuous]	▪	▪	▪	▪	▪	▪	▪
	time	three time terms: numeric time of sample, cos(pi * time), and sin (pi * time) [numeric, continuous]	▪	▪	▪	▪	▪		
	observer	observer identity: BJF or SN [categorical]	▪		▪	▪			
	community	identity of chimpanzee communinity: Ngogo Central or Ngogo West [categorical]	▪	▪	▪	▪	▪	▪	▪
	% high-quality fruit	daily population-wide index of the proportion of ripe non-fig fruit and *Ficus mucuso* fruit in the diet. Generated as predictions from GAM of time spent feeding on high-quality fruit per focal as a function of date [numeric, continuous]	▪	▪				▪	▪
	% time spent foraging	daily population-wide index of the proportion of time spent foraging. Generated as predictions from GAM of time spent within foraging bouts per focal as a function of date and community [numeric, continuous]	▪	▪				▪	▪
	age / age^2	subject age or age^2 at sample, selection from preliminary analysis of per-variable sum of model weights [numeric, continuous]	▪	▪	▪	▪	▪	▪	▪
	rank	daily dominance rank (Elo score) [numeric, continuous]	▪	▪	▪	▪	▪	▪	▪
	party size	the number of chimpanzees in association throughout the day, excluding dependents younger than age 8 [numeric, discrete]	▪	▪	▪	▪	▪	▪	▪
	number of estrus females	the number of sexually receptive parous female chimpanzees in association throughout the day [numeric, discrete]	▪	▪	▪	▪	▪	▪	▪
	foraging bout progress	starting time of intake sample as proportion of way through feeding bout time [numeric, continuous]					▪		
	food item	food item identity (non-fig fruit, fig, or leaf) [categorical]					▪		
	quality	food item status according to maturiation: low quality for unripe fruit or mature leaves [categorical]					▪		
	foraging context	a score [1,3] of how much foraging activity occurred in the 15-minute period of and between scans [ordinal]		▪					
	residual (age ~ birth year)	control for birth cohort						▪	▪
random	subject ID	male identity [categorical]	▪	▪	▪	▪	▪	▪	▪
	food ID	food item identity [categorical]					▪		
offset	intake sample duration	duration of intake sample [numeric, continuous]					▪		
	fecal sample mass	fecal sample mass (g) [numeric, continuous]						▪	

Dietary variation and quality: Chimpanzee diets often vary, even over short periods, and individual food items differ widely in their nutritional values (Watts et al 2012, Uwimbabazi 2021). Previous work has shown that various behavioral and physiological outcomes vary in response to seasonal dietary changes such as chimpanzee party size (Hashimoto et al. 2003), movement (Chapman et al. 1995),

physiology such as cortisol levels (Muller and Wrangham 2004), and energetic balance (Emery Thompson et al. 2009). Accordingly, controlling for diet quality and composition can help improve model capacity to estimate the effects (i.e., β coefficients) of other predictors of behavioral and physiological outcomes.

I calculated daily population-wide indices of: 1) the proportion of high-quality fruit in the diet and 2) the proportion of time spent foraging. First, I defined high-quality food items as ripe non-fig fruit and ripe *Ficus mucuso* figs. Chimpanzees have been characterized as ripe fruit specialists; there is a positive association between feeding time on non-fig fruit and estimated fruit abundance (Conklin-Brittain et al. 1998, Watts et al. 2012). In the nearby Kanyawara chimpanzee community, non-fig-fruits have a strong effect on female reproductive function (Emery Thompson & Wrangham 2008) and are positively correlated with energetic status (Emery Thompson et al. 2009). At Ngogo, the amount of non-fig-fruits in the diet correlate with standardized dietary diversity (Watts et al. 2012), suggesting they play an important role in the diet as well as in the frequency of energetically expensive behaviors, e.g. hunts and hunting patrols (Watts & Mitani 2001). In addition, *Ficus mucuso* figs are abundant at Ngogo and appear to play an important dietary role: they are the most frequently ingested, accounting for 25% of all feeding time (compared with 18% in Watt et al. 2012). Therefore, I included feeding time on ripe *Ficus mucuso* figs in the calculation of proportion of high-quality fruit in the diet. Second, I included the proportion of time spent foraging as a predictor that corresponds to the quality of the diet; during high-quality seasons, chimpanzees are able to meet their nutritional needs quickly (Wrangham et al. 1998).

Researchers frequently use monthly averages of ecological indices as predictors (e.g. Mitani & Watts 2005, Emery Thompson et al. 2009), often because measures of food availability come from periodic phenological surveys. However, such values condense dietary variation along a continuous variable (date) into a categorical series with artificial breaks (months). Because we calculated diet indices from behavioral data, we instead generated daily values via novel methods that employed generalized additive models to predict foraging behavior outcomes with date as a predictor. For this purpose, we used *ad libitum* data on foraging bout start time, stop time, and food item across the study period. The outcome variables were: 1) number of minutes spent foraging on high-quality fruit during a focal sample; and 2) number of minutes spent foraging. Both sets of models included fixed effects of date, community, observer, and sex; used focal duration as an offset (i.e., beta coefficients were set to 1); and fit random intercepts for focal ID and compared these models using Generalized Akaike Information Criteria. Because sex was not a reliable predictor of either foraging index, we included data from adult females and non-focal adult males in the calculation of indices when available because they improved model accuracy especially when sample sizes were small (n=1437 observation hours). I then used the respective top model to predict a daily value of each index with all other predictors set to their mean (**Figure S1**).

Rank: I assigned dominance ranks based on the direction of pant-grunts, a distinctive call that is a formal signal of subordinance, and decided agonistic encounters between dyads. To allow a burn in period and to coincide with the start of the community split at Ngogo, we modeled rank trajectories from January 2016 through

August 2019 using interactions between males ≥16 years old extracted from the focal and *ad libitum* observations collected by John Mitani and other long-term researchers at Ngogo (n=287 interactions for Ngogo West, mean 40/individual; n=2058 interactions for Ngogo Central, 76/individual). I used these interactions to calculate daily Elo scores, which estimate a subject's dominance strength while accounting for demographic changes and missing data (Albers & de Vries 2001), performing maximum-likelihood implementation of the Elo method using the {EloOptimized} package (Feldblum et al. 2016). While there is a documented correlation between age and rank – which in some primate species takes a concave or inverse-U shape (e.g. Nepal grey langurs, *Semnopithicus schitaceous*, Perlman et al. 2016; the Ngogo chimpanzees, Watts et al. 2018) – there was no correlation between rank and age among these subjects during the study period. Therefore, rank was included as a control variable in the same models as age (mean Elo ratings shown in **Table S1**).

Party size: Namaganda and I recorded the identities of individuals in daily association with focal subjects. Because of established relationships with both competition and ecological conditions such as patch size (White & Wrangham 1988, Sakura 1994), party size was an important predictor to include. Defining a party presents challenges due to chimpanzees' tendency to disperse over a wide area yet move together (Nishida 1990, Pepper et al. 1999). Therefore, we included party size as the number of chimpanzees in association during the day, excluding individuals younger than age eight as these include pre-adolescent, infants, and juveniles who are still dependent on their mother (Pusey 1990).

Number of parous estrous females: We recorded the swelling status of adult females in daily association with focal subjects. The presence of sexually receptive female chimpanzees, particularly parous females, has several effects on male behavior and physiology (Sobolewski et al. 2012). To control for this potential source of variation, I therefore included the ratio of sexually receptive parous estrous females to the number of adult males in association. Estrous females were identified as those with a full sexual swelling and mated males. Parous females are those who have had at least one offspring. I excluded females who were unlikely to conceive, defined as those that had a dependent offspring younger than 2.51 years. This is equivalent to the mean interbirth interval (5.49 years) minus 2SD of this interval (1.18 years) minus gestation length (0.62 years). Hereafter, parous estrous females excluding those unlikely to conceive are referred to simply as estrous females.

Temporal effects: Many behavioral and ecological time series exhibit periodic, seasonal, or cyclical effects of various kinds. To control for and describe these oscillations' effects on various outcomes which may generate temporal autocorrelations, we included predictors based on trigonometric sine and cosine functions of both date and time, referred to as harmonic regression models (Young et al. 1999). The standard sine and cosine functions are smooth and symmetric, and thus are appropriate for outcomes that have exhibited steady rise and fall over the course of the day or across seasons.

Foraging context: Not all climbing behaviors relate to foraging. To exclude instances in which climbing may not have been associated with foraging and to account for variation in foraging activity over the 15-minute duration when climbing was

measured, I incorporated an ordinal score of foraging context. A score of one was assigned to the following conditions: if the end-scan's behavioral state was recorded as foraging, if the start-scan's behavioral state was recorded as foraging, and if a feeding bout occurred in the period in-between the start- and end-scans. The foraging context score was then the sum of those values, which ranged from 0–3, wherein a higher score corresponds to a greater extent of foraging behavior associated with the vertical distance. All climbing distances associated with a foraging context score of 0 were excluded, as these were not considered to represent climbing in a foraging context.

Data analyses

I conducted preliminary data exploration, analysis, and visualization in R (version 4.2.2; R Core Team 2022) via RStudio version 2022.12.0 (RStudio Team, 2022). To determine the effects of age on various physiological and behavioral outcomes, I adopted an information theoretic approach using generalized linear mixed models (GLMMs) to model variation in each outcome. I fit models using {lme4} (Bates et al. 2004), {glmmTMB} (Brooks et al. 2017), {mclogit} (Elff 2022), and {gamlss} (Rigdy & Stasinopoulos 2005) to support a variety of distributions for outcome variables. For all analyses, we fit ecologically plausible models (including interactions when warranted) with alternative distributions appropriate to the outcome of interest (e.g., binomial for binary outcomes, ordered logit for categorical outcomes, gamma distributions for continuous outcomes). When available, I compared model performance in different packages to select the best fit. Following model fitting, we performed model selection using the dredge() function {MuMIn} package (Bartón 2009), which employs an

information theoretic multi-model selection approach based on Akaike's Information Criterion (AIC), or when n/K > 40, indicating a high number of terms relative to small sample size, AICc (Burnham & Anderson 2004). I then performed model averaging across models with cumulative weight of 0.95 using function model.avg() {MuMn}, which averaged predictions on their link scale to obtain weighted averaged estimates for each predictor. However, one exception is the categorical analysis of food item selection, as the results were derived from the top model with the majority of model weight rather than a weighted model average. This was due to the model object type being incompatible with function model.avg(). Because the fixed effect of age was absent from all top models, the selection of the top model in this case is appropriate for interpretation with respect to my predictions.

I considered predictors to be reliable when the 95% confidence intervals of their effect sizes did not overlap the null effect. To control for the non-independence of samples, I included random effects for subject ID and for intake rate analysis, and random effects for diet item. Prior to model fitting, I examined pair-wise correlation plots (see supplementary materials) to ensure highly correlated variables ($r \geq 0.7$) were not included in the same model to avoid issues with model convergence with the exception of date and time harmonic terms. Because of this, *percent high-quality fruit* and *percent time foraging* were not included together in any model. In preliminary analysis, I compared the performance of these dietary predictors and in the complete model included only the one with a greater performance according to AIC. Similarly, I conducted preliminary analyses to determine whether to include *age* or age^2 in model construction. Although both may be included to as a quadratic effect of age, to facilitate

transparent results I only included one. All continuous predictors were centered on the mean and standardized to permit direct comparison of effect size magnitude. Offsets were transformed according to their respective model's link function to place them on the same scale as the outcome. The outcome variables (**Table 1**) were: (1) whether foraging was arboreal; (2) absolute vertical displacement foraging contexts; (3) food item selection; (4) food item ripeness for non-fig fruit and figs; (5) counts of food units ingested; (6) mass of fecal "undigested" material; and (7) fecal particle size (dMean 0.025–0.04 mm).

Results

Old chimpanzees were not more terrestrial, nor did they climb less while foraging

Age did not have an effect on arboreality (β = 1.17±1.31) (**Figure 2A)**. The probability of arboreal foraging, however, increased by 1.81 (±1.34 SE) times for each SD increase in *percent high-quality fruit* (equal to a 19% increase) and varied reliably with time of day (**Table S3**). The correlations of age with both probability of climbing (|∆height| > 0) (*nu*) and absolute distance climbed (*mu*) were both unreliable with 95% and 50% confidence intervals overlapping null effect, respectively, but were directionally consistent with the prediction. For each 1SD increase in age, the model average predicted a 1.23 (±1.21) times increase in the probability of no vertical displacement when this displacement was greater than zero (**Figure 2C, Table S4**). Subsequently, this model average predicted that climbing distance per 15-minute interval would

decrease by 0.6±1.3 meters for each additional 10 years of life (compared to the mean distance of 7.7 m). The number of estrous females in association was negatively correlated with the probability of climbing; for each SD increase in the number of estrous females, the probability of climbing decreased by 1.49(±1.15) times. Time predictors had reliable effects on the probability of climbing, but not distance climbed, while climbing probability and distance increased in foraging contexts.

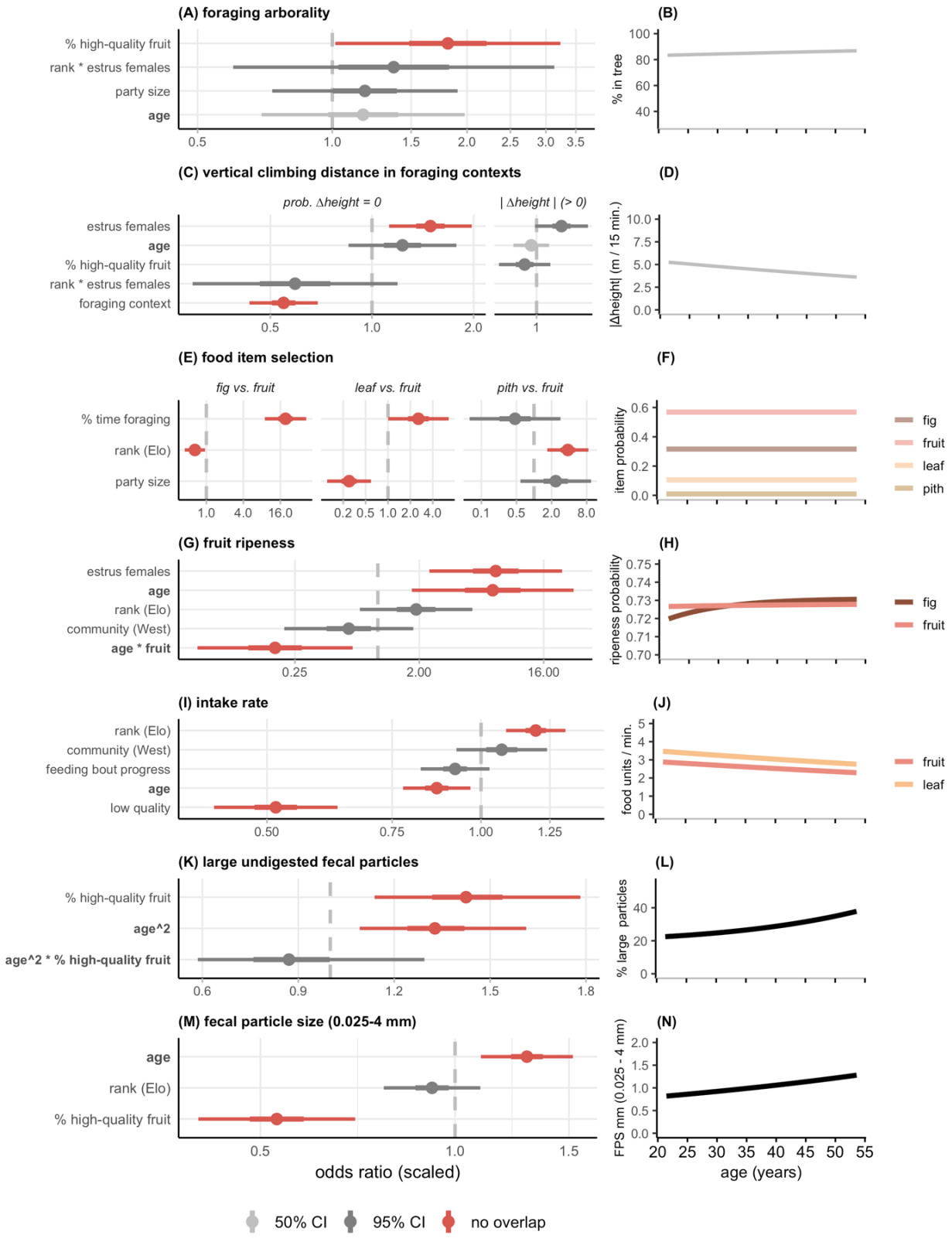
(A) foraging arborality
% high-quality fruit
rank * estrus females
party size
age
0.5
1.0
1.5
2.0
2.5
3.0
3.5
(B)
% in tree
100
80
60
40
(C) vertical climbing distance in foraging contexts
prob. Δheight = 0
| Δheight | (> 0)
estrus females
age
% high-quality fruit
rank * estrus females
foraging context
0.5
1.0
2.0
1
(D)
|Δheight| (m / 15 min.)
10.0
7.5
5.0
2.5
0.0
(E) food item selection
fig vs. fruit
leaf vs. fruit
pith vs. fruit
% time foraging
rank (Elo)
party size
1.0
4.0
16.0
0.2
0.5
1.0
2.0
4.0
0.1
0.5
2.0
8.0
(F)
item probability
0.6
0.4
0.2
0.0
fig
fruit
leaf
pith
(G) fruit ripeness
estrus females
age
rank (Elo)
community (West)
age * fruit
0.25
2.00
16.00
(H)
ripeness probability
0.75
0.74
0.73
0.72
0.71
0.70
fig
fruit
(I) intake rate
rank (Elo)
community (West)
feeding bout progress
age
low quality
0.50
0.75
1.00
1.25
(J)
food units / min.
5
4
3
2
1
0
fruit
leaf
(K) large undigested fecal particles
% high-quality fruit
age^2
age^2 * % high-quality fruit
0.6
0.9
1.2
1.5
1.8
(L)
% large particles
40
20
0
(M) fecal particle size (0.025-4 mm)
age
rank (Elo)
% high-quality fruit
0.5
1.0
1.5
odds ratio (scaled)
(N)
FPS mm (0.025 - 4 mm)
2.0
1.5
1.0
0.5
0.0
20
25
30
35
40
45
50
55
age (years)
50% CI
95% CI
no overlap

Figure 2. Compilation of coefficients and predictions from weighted model averages for foraging performance outcomes with respect to age. For each measure of foraging performance, the left column depicts coefficient plots and the right column depicts age effect predictions, both from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Predictors are centered and standardized so the magnitude of beta coefficients are directly comparable. Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect. Coefficient plots exclude control predictors (time of day predictors, date, and observer) and predictors with 50% CI overlap other than age for visual clarity. See corresponding supplementary figures for complete coefficient plots. Bolded terms indicate effects of age or age^2 and their interactions. The right column depicts predictions from age and its interaction effects, if present, with all other predictors held at their mean.

Older males did not consume different food items, but may have selected more ripe figs

Age was absent from top performing models of food selection; consequently, there was no reliable effect of age on food item selection. In contrast, rank had a negative correlation with the consumption of figs. With each SD increase in rank, the probability of consuming figs over non-fig fruit decreased by 0.65(±1.21), while the probability of consuming pith increased by 3.80(±1.51) times (**Table S5**). Party size was also correlated with diet items. The probability of consuming leaves decreased by 0.30(±1.41) times for each SD increase in party size; chimpanzees in larger parties ate more fruit and fewer leaves. Additionally, a control for diet seasonality, percent time spent foraging, was positively correlated with the selection of figs and leaves: for each SD increase in percent time spent foraging, the probability of fig over non-fig fruit consumption increased by 19.37(±1.49) times and leaf over fruit increased by 2.56(±1.61) times. These results confirm previous findings that non-fig fruit, not fig or leaf, is associated with higher quality diet at Ngogo. Time predictors also had reliable

effects on diet selection, indicating that different food items were more likely to be eaten at certain times of day.

This food item analyses included all stages of food maturation, so I modeled the outcome of ripeness for non-fig fruit and fig items separately. In contrast to item, ripeness varied with age: age was reliably and positively correlated with the selection of ripe items. However, the effect size was quite small. The probability of consuming ripe items increased by 6.83(±1.99) times for figs for each SD increase in age (**Table S6**). Due to an interaction effect between age and type fruit, the effective change in the overall amount of ripe items was lower: the weighted model average predicted that 25 year old chimpanzee was 72% likely to consume ripe figs whereas a 45 year old chimpanzee was 73% (**Figure 2H**). Diet ripeness was also positively correlated with the number of estrous females in association. Subjects were 7.18(±1.75) times more likely to consume ripe fig or non-fig fruit for each SD increase in the number of estrous females.

Older chimpanzees ingested food more slowly

Age was negatively correlated with ingestion rate among an array of leaf and non-fig fruit food items. Items were ingested 0.87(±1.06) times more slowly for each SD increase in age (**Table S7**). In addition, ingestion rates varied with food maturity and subject rank. Ingestion rate also varied consistently according to maturity/quality (low quality = unripe non-fig fruit, mature leaves; high quality = ripe non-fig fruit, young leaves). Low quality items were consumed 0.51(±1.11) times more slowly than high

quality items. Additionally, for each SD increase in rank, items were consumed 1.19(±1.05) times more quickly (**Figure 2I**).

Old chimpanzees excreted larger fecal particle sizes

Two reliable predictors of the proportion of large undigested fecal were the percentage of high-quality fruit in the diet and age^2 **(Figure 2K**). For each SD increase in high-quality fruit, the mass of large, undigested particles increased by 1.42 (±1.12) times (**Table S8**). For each SD increase in age^2, large, undigested particle mass increased by 1.33 (±1.11) times. In the same fecal samples, the mean-weighted particle size ($FPS_{0.025–4\ mm}$) was 0.80 mm (±0.75 SD). The two reliable predictors were a linear effect of date and age (**Figure 2M**). For each SD increase in age, FPS increased by 1.29 (±1.09 SE) times (**Table S9**). Because the oldest and nearly edentulous subject, Brownface, displayed distinct patterns of ingestion (see *Behavioral data collection*), I performed a sensitivity analysis to examine whether these correlations between age and fecal sample characteristics were due to Brownface's measurements being outliers. For both undigested matter and FPS, the effect of age remained after controlling for Brownface's leverage in the model.

Discussion

This study highlights the relationship between age and a suite of foraging measures in adult chimpanzees. I demonstrate that measures of food processing and ingestion were negatively correlated with age. In this field-based, cross-sectional study, I used detailed behavioral monitoring to characterize foraging outcomes across 20

individuals. In contrast to prior observations, old chimpanzees were not more terrestrial in foraging contexts (**Figure 2A, 2B**) and I found only weak evidence that old chimpanzees climbed shorter vertical distances while foraging (**Figure 2C, 2D**). Declining mobility, therefore, is unlikely to limit aging chimpanzees' access to foods via arboreal locomotion. Diet item did not vary with age (**Figure 2E, 2F**), but old chimpanzees appeared to be more likely to consume ripe figs (**Figure 2G, 2H**). Consequently, it does not appear likely that old chimpanzees adjust behavior to prioritize different foods, such those more accessible foods with weaker mechanical properties. However, ingestion rate of both leaves and non-fig fruits also declined with age (**Figure 2I, 2J).** Most notably, processing performance decreased with age across seasons and diets; both the amount of large undigested fecal material and the fecal particle size increased with age (**Figure 2K–N**). Both of these and declines in ingestion rate may be linked to decreased chewing efficacy, the predominant determinant of fecal particle size in terrestrial herbivores (McLeod & Minson 1988; Spalinger & Robbins 1992). If old chimpanzees take longer to chew and derive fewer resources from digesta, then senescence may limit energetic or nutritional yields. Taken together, these findings suggest that physiological deteriorations of age likely contribute to diminishing foraging performance, i.e., foraging senescence.

Old primates may become less social as they age (Almeling et al. 2016, Siracusa et al. 2022), and old chimpanzees are more likely to be in smaller parties or alone while also engaging in more grooming (Goodall 1986, Rosati et al. 2020). Because of chimpanzees' fission-fusion social organization, this aging social phenotype can lead to differing foraging decisions between prime and old age chimpanzees. Therefore, it is

possible that observed changes in foraging behavior with age may not be attributed to functional senescence, but rather as a byproduct of foraging in different social circumstances. However, because my analysis controlled for the effects of dominance rank and party composition, it is unlikely that shifting sociality alone explains these relationships between age and foraging performance.

Locomotion and mobility in aging chimpanzees

Contrary to my predictions, I did not find that old chimpanzees were more terrestrial nor did they climb shorter vertical distances in foraging contexts (**Figure 2C, 2D**). Conversely, a longitudinal study from the Kanyawara community just 10 km away from Ngogo revealed that terrestriality increased with age and suggested that together with decreased ripe fruit consumption, “climbing may have been the key limitation on feeding” (Emery Thompson et al. 2020). In fact, older primates may move more slowly (Shively et al. 2012), which has been attributed to decreased mobility. Elderly wild chimpanzees have exhibited limited evidence of arthritis, osteoporosis, and skeletal trauma all of which have been proposed to limit movement (Jurmain 1989, Sumner et al. 1989, Morbeck et al. 2002, Carter et al. 2008). Despite prior fundings and my predictions, I found no differences in either arboreality nor climbing distance during foraging been prime- and old age chimpanzees. Factors that may explain this discrepancy include differences in climbing behavior between these populations, methodological differences in data collection, and the limitations of cross-sectional data.

First, the Ngogo chimpanzees spend more time eating ripe fruit, less time resting, and have shorter and less variable patch residency times than their Kanyawara

counterparts (Potts et al. 2011). How these factors might influence overall climbing behavior is unclear, but it is likely that the Ngogo chimpanzees spend more time foraging arboreally given the increased consumption of ripe fruit over terrestrial foodstuffs. Perhaps absolutely greater rates of climbing could diminish differences between age-groups than cases where climbing is less frequent. Second, Emery Thompson et al. (2020) considered activity data across behavioral contexts and over a longer time span. Consequently, a key distinction is that this study specifically considered foraging contexts. Because foraging is a daily requirement for wild animals, differences in locomotion may be more apparent outside of foraging contexts. (N.B. in Chapter 3, I examine climbing behavior across all behavioral contexts and again there is no reliable effect of age). The Kanyawara study also collected data on full day, nest-to-nest follows, while I collected data during two-hour focals that infrequently saw subjects leaving or entering their evening nests. Therefore, the Kanyawara study may highlight differences in arboreality related to nesting. If old males either left their nests later in the morning or entered them earlier in the evening, this could result in overall increased rates of arboreality according to their measures. Third, while mobility may decline with age, perhaps those who senesce to the point of exhibiting declines in foraging locomotion do not live very long and thus the effects of age may be detectable in longitudinal studies, such Emery Thompson et al. (2020), but not cross-sectional studies as the one conducted here. Because I examined vertical travel distances and not simply a binary measure of arboreality, this study provides an additional measure of movement, both of which fail to document an effect of age on climbing effort. Because prior studies have found that travel speed declines with age (Shivley et al. 2012), future

studies should consider how additional mobility measures such as gait speed and terrestrial travel distances vary with age.

Dietary changes with age and ingestion rates

These analyses suggest that the ingestion of ripe fruit varied with age: older males were more likely to consume ripe figs although the magnitude of the change was quite small, equivalent to approximately 3% diet shift over the course of adulthood (**Figure 2G, 2H**). Nonetheless, because food broadly correspond with a food's nutritional and mechanical properties, this shift may reflect changes in diet preferences with age. Though I predicted that old chimpanzees compensated for reduced processing efficacy by selecting more easily processed foods, this is not evident in my results as item selection did not vary with age. This may be due to the fact that leaves at Ngogo do not have consistently different mechanical properties (toughness and elastic modulus) than either non-fig fruit or figs (van Casteren et al. 2018). Indeed, food item type is often a poor predictor of either mechanical or nutritional properties (Coiner-Collier et al. 2016). These findings indicate that future studies should generate more precise predictions based on known properties of specific foods.

Fruit ripeness on the other hand may be more reliably associated with weaker mechanical properties (Vogel et al. 2008). These findings contrast with those from Emery Thompson et al. (2020) who found a decline in ripe fruit consumption with age. However, dietary differences between the sites are well established, particularly involving the decreased reliance on figs and increased abundance of ripe non-fig fruit at Ngogo (Potts et al. 2011). Ultimately, it is not clear why old chimpanzees would

consume more ripe figs, but not more ripe non-fig fruit. While the analysis of ingestion rate revealed that ripe non-fig fruits and young leaves are eaten more quickly, the precise effects of fig mechanical properties on food processing are unclear. The differential impact of food mechanical properties on aging phenotypes may be worth further consideration. For instance: figs have small seeds while non-fig fruits typically have larger seeds, and seed size may impede processing and reduction, particularly for old chimpanzees. The finding that there are more large seeds in old chimpanzees' feces is consistent with this idea, as this could be an indicator that the ability to process large seeds particularly declines with age. While diet change with age is a developed area of research (Rapaport & Brown 2008), shifts in food preferences across primate adulthood have received less attention (but see Vogel et al. 2017 for changes across sex and season). To determine the causes and consequences of dietary shifts with age, additional research is required to investigate the mechanical properties of foods and their role in selection, including intra-species differences between ripe and unripe food items.

I found that intake rates were lower in old- compared to prime-aged chimpanzees (**Figure 2I**). I have been unable to identify any other findings of lower feeding rates attributable to senescence in primates, although several studies present indirect evidence of declining chewing ability (e.g. King et al 2005, 2012, Venkataraman et al. 2014). A possible explanation for a decline with age is that old chimpanzees may compensate for diminished chewing efficacy by slowing their intake rates to allow more time for mastication. This explanation is consistent with findings from gerontology wherein older humans with fewer teeth eat more slowly or chew more (Naka et al.

2014). However, in chimpanzees it is not possible to eliminate other potentially concurrent diminishing capacities as explanations for observed associations with age, such as digital dexterity and eyesight, which are known to senesce in wild great apes (Ryu et al. 2016).

An important limitation of this analysis of ingestion rate is that it included only the more frequently consumed food items, and solely non-fig fruits and leaves. Increasing the sample size and incorporating other items with more robust mechanical properties, such as pith or wood, can help clarify the nature of declines in ingestion rate with age. One exception, however, comes from the nearly edentulous Brownface, who was observed to consume particular food items whole, forgoing chewing almost entirely. While this might contradict the prediction of chewing more slowly, Brownface's behavior is consistent with investing less effort in chewing due to greatly diminished returns; in other words, increased chewing evidently cannot compensate for the complete or nearly complete loss of chewing functionality.

Fecal particle sizes increased with age, indicating reduced processing efficacy

Age was positively associated with two uncorrelated measures of fecal composition: the amount of large undigested matter in feces (> 4mm) and the mean fecal particle size (FPS 0.025–4 mm), a proxy for ingesta particle size reduction. Because the key determinant of fecal particle size in herbivores is chewing efficacy (McLeod & Minson 1988, Spalinger & Robbins 1992), these results suggest that processing efficacy decreased with age in male chimpanzees. Brownface (53 years old), had the highest proportion of large undigested components in his feces.

Brownface's diminished ability to chew likely led him to swallow many more items whole. These patterns are again consistent with changes in consumption for elderly humans, who select different items based on their mechanical qualities and swallow larger items in response to tooth loss (Ikebe et al. 2011, Naka et al. 2014).

Because the amount of large undigested particles and $FPS_{0.025–4\ mm}$ were uncorrelated with each other, it is unlikely that an increased amount of large, hard items like seeds impeded mastication by old chimpanzees. This is supported by the negative correlation between percent high-quality fruit and $FPS_{0.025–4\ mm}$. In other words, diets full of ripe non-fig fruit produced feces with well-processed, small particles, but also with more undigested material like seeds. While both measures make it clear that processing performance is lower in old chimpanzees, additional work can clarify whether certain diet items exacerbates this effect. To offset the effects of reduced chewing efficacy, organisms may either increase chewing effort per unit food processed or select food items that are more easily processed (Perez-Barberia & Gordon 1998). In sum, the preceding findings are consistent with increased chewing effort in old age chimpanzees.

Prior work on chimpanzees did not find a relationship between age and FPS (Weary et al. 2016, Schultz-Kornas et al. 2020), though this relationship was documented in a study of geladas (*Theropithicus gelada*). Weary et al. (2016) attributed the lack of relationship between age and FPS in chimpanzees to their frugivorous diets. This places fewer mechanical demands on masticatory function than do the graminivorous diets of geladas. The discrepancy between my findings and that of Weary et al. (2016) and Schultz-Kornaz et al. (2020) can be attributed to differences in sampling, diet, or processing method. First, I analyzed more samples collected from a

narrower demographic range of adults – 20 adult males from 21–53 years old (mean 9 samples/ID),) – whereas Schultz-Kornas et al. report from 4 mixed-sex adults ranging from 17–25 years (mean 7.5 samples/ID) in addition to non-adults, and Weary et al. from 21 mixed-sex adults ranging from 17–55 years (3.4 samples/ID) in addition to non-adults. As a result, this study provides a more focused evaluations of the effect of age, avoiding potential confounding effects arising from sex and life history stage variations. Second, prior studies took place at different sites and thus analyzed foods from distinct chimpanzee diets, a determinant of FPS that may interact with age (see Potts et al. 2011 for a review of Kanyawara and Ngogo dietary differences). Third, following recommendations from Weary et al. (2017), I removed seeds and other large particles prior to FPS analysis, which became our measure of large, undigested matter. Consequently, our FPS values may have been less biased by the inclusion of disproportionately large particles.

While associations between tooth wear and senescence have been documented in some primates (King et al. 2005 for *Propithecus edwardsi*, Cuozzo et al. 2005 for *Lemur catta),* declines in chewing efficacy have not yet been reported in great apes. These findings contrast with Glowacka et al. (2016), who concluded that molar wear in gorillas, assessed via topographic analyses, does not lead to a decrease in chewing efficacy. This is surprising because chimpanzees are more frugivorous than mountain gorillas. By contrast, it accords with findings that rates of tooth wear are greater in *Pan* than *Gorilla* (Elgart 2010). Wild chimpanzees live much longer than do gorillas (Bronikowski et al. 2011); because of this, dental wear may play a more important role in genus *Pan*. Although studies have documented age-related wear in chimpanzee

teeth (e.g. Klukkert et al. 2012), I am not aware of a systematic examination of wear rates across adulthood.

Limitations of this study

By collecting data from the same individuals at the same time, our study avoids confounding effects of inter-annual variability in resources. Nevertheless, the findings of cross-sectional studies such as the one performed here should be interpreted cautiously when applied to senescence. While cross-sectional methods have been employed in wild populations to assess demographic senescence (Nesse 1988, Mysterud et al. 2001) and functional senescence (Lecomte et al. 2012), conclusions derived from this research have been called into question (Nussey et al. 2008). Cross-sectional studies face three main challenges when it comes to identifying effects of senescence: cohort effects, survivorship bias, and mortality proximity.

First, between-individual comparisons do not distinguish from cohort exposure history. Studies may over- or under-estimate true senescence because older subjects experienced different early life conditions (Wood et al. 1992). Such cohort effects are likely more salient in short-lived organisms, for whom brief life history stages are encompassed by homogenous environmental conditions. In contrast, chimpanzees have a particularly prolonged development, and thus only secular trends are likely to generate cohort effects rather than intra-annual heterogeneity. While we know little about the social conditions of the Ngogo chimpanzees before long-term observation began in 1995, the Kibale National Park has had protected status since 1932 and the study area was never subjected to commercial logging (Struhsaker 1997). Phenological

data from 1998 to 2017 indicate that the productivity of consumed fruits has shifted, increasing from 1998 to 2008 and then moderately declining (Potts et al. 2020). Consequently, while conditions at Ngogo appear not to have shifted dramatically since the birth of our oldest study subject (est. 1966), I cannot rule out the possibility that variation in conditions like food availability may have generated moderate cohort effects. To test whether the correlations I found between age and fecal particles can be attributed to such cohort effects, I used the residual of age to birth-year as a control for variation in birth timing. I found no relationship between birth-year residual and fecal particles when controlling for age, which suggests that age explains variation in digestive performance better than birth year.

Second, cross-sectional studies are susceptible to confounding effects from phenotypic covariance between traits that favor reproduction and survival (Nussey et al. 2008). Consequently, mortality selection could mean that this study is one of exceptional survivors, chimpanzees who may have necessarily senesced more slowly than their peers. If this is the case, then our observed effects of age on trait senescence are underestimates because our pool of older subjects necessarily represents slower agers (Vaupel et al. 1979). For instance, if chimpanzees who invest less in reproduction are more likely to survive to old age, then a cross-sectional analysis could reveal apparent progressive senescence of reproductive investment due to the predominance of old age cohort chimpanzees. There is some evidence of tradeoffs between reproduction and lifespan in humans (Penn & Smith 2007), but evidence from captive primates is mixed (Tidiére et al. 2017). Notably at Ngogo, about 52% of male chimpanzees live past the age of 30, and 33% live past the age of 40 (Wood et al.

2017). Diseases for which age positively predicts morbidity could contribute to such an effect, as may have been the case in a 2016-2017 outbreak of a respiratory virus where individuals ≥30 years old were 3.86 times as likely to die than younger adults (Negrey et al. 2019). Nonetheless, a common source of mortality for adult males is extrinsic. Male chimpanzees make lethal coalitionary attacks on their neighbors (Mitani et al. 2010). Due to the stochastic nature of such deaths, this common mortality source likely has a weak selection signature against senescence; therefore, there is little *a priori* justification to believe that the surviving members of older cohorts present an especially biased sample with respect to senescing phenotypes.

Finally, prior studies have found that individuals show more pronounced senescent phenotypes immediately preceding death (Coulson & Fairweather 2001), including in chimpanzees for whom poor condition was acutely associated with illness and death (Emery Thompson et al. 2020). Therefore, the senescence documented here may not reflect steady, age-related decline but rather the greater likelihood that aged subjects were in immediate proximity to death. As data presented in this paper were collected in 2018–2019, I can now assess mortality proximity post-hoc. Of the 20 subjects, 13 were still alive as of November 2022. Of the deceased, four were killed by conspecifics (Hicks DOB 1997, Basie DOB 1983 killed in 2019; Porkpie DOB 1994 killed in 2001, and Jackson DOB 1991 killed in 2022) and three from unknown causes. Of the latter, Cash (1993) is suspected to have succumbed to disease in April 2021, as he displayed chronic signs of a skin infection, during the study period. The two remaining individuals, Bartok (1973) and Monk (1972) were considered old, and their bodies were not recovered after disappearing in May 2020 and July 2020. Thus, I

cannot rule out that their behavior during the study period was shaped by proximity to death, although they survived at least another 9 to 11 months from the end of the study period. Notably, my oldest subject, Brownface (born est. 1966), lived for almost another four years following the conclusion of this study. Brownface displayed an apparently senescent phenotype with, for instance, the largest mean fecal particle size and, according to photographic analysis, has been nearly toothless since at least 2012 (Finkel unpublished data). His perseverance suggests that individuals can survive prolonged periods with diminished foraging performance. Therefore, I conclude that while mortality proximity may putatively explain some of the foraging senescence documented here, it is unlikely to explain its extent or consistency across subjects.

Significance for aging in the wild

Lecomte et al. (2010) proposed that feeding efficacy may be one of the first phenotypic traits to reflect aging in natural conditions, referring to it as a potential "cornerstone" that shapes patterns of senescence in wild animals. While I did not examine the timing of onset of foraging senescence against that of traits like immunosenescence, my findings support the idea that organisms' ability to extract energy from their environments could play an important role in shaping late-life fitness. I demonstrate that foraging declines signal senescence, but it remains to be seen whether they represent a driver that precipitates further deteriorations under new time or resource limitations in old age.

The evolution of longevity for organisms such as chimpanzees has puzzled researchers because life history theory proposes that the increased somatic investment

necessary to reduce mortality is energetically costly and diverts energy away from early reproduction (Gavrilova & Gavrilova 2002). Explanations for increased lifespan, therefore, often rely on increased energy acquisition or reallocation away from processes such as current reproduction. While there is widespread evidence of demographic senescence (Nussey et al. 2013), as well as increases to mortality or declines in reproduction with age, this study provides important data on functional senescence in the wild where limited resources constrain and affect behavior (Finch 2010). Without direct observational studies of wild populations, it is unclear how aging physiologies translate into declines in fitness (Monaghan et al. 2008). If old male chimpanzees, and other animals, exhibit declines in foraging performance that decrease the resources available for allocation, than foraging senescence may represent a proximate mechanism for demographic senescence.

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Supporting Information

Table S1. Subjects in order of increasing age (n = 20). Age corresponds to age at study midpoint (February 2018) and ranks reflect the average Elo rating over the study period.

ID	age	birth year	community	Elo rating (mean)	ordinal rank
Wes	21.7	1997	West	-452.73	5
Django	22.1	1997	Central	-435.42	13
Hicks	22.1	1997	Central	-279.4	11
Evans	23.1	1996	Central	17.34	7
Wayne	23.1	1996	West	-674.24	6
Peterson	24.1	1995	Central	137.56	5
Hutcherson	25.1	1994	West	579.17	1
Porkpie	25.1	1994	Central	-130.61	9
Cash	26.1	1993	Central	-444.11	14
Jackson	28.1	1991	Central	696.64	1
Richmond	32.1	1987	West	197.56	2
Rollins	33.1	1986	West	-444.92	5
Dexter	34.1	1985	Central	-601.36	16
Morton	35.1	1984	Central	286.74	3
Basie	36.1	1983	Central	65.75	7
Miles	38.1	1981	Central	116.66	6
Garrison	42.1	1977	West	-304.48	4
Bartok	46.1	1973	Central	-17.73	8
Monk	47.1	1972	Central	-407.54	12
Brownface	53.1	1966	Central	-628.16	16

Table S2. Composition of the diet for popular food items (% feeding time ≥ 1) over the study period (August 2018 – August 2019). Items here constituted 82.5% of all foraging time.

species	part	% feeding time
Ficus mucuso	fig	25.2
Uvariopsis congensis	fruit	13.1
Mimusops bagshawei	fruit	5.8
Morus mesozygia	fruit	4.9
Chrysophyllum albidum	fruit	3.9
Cordia millenii	fruit	3.5
Monodora myristica	fruit	3.0
Pseudospondias microcarpa	fruit	3.0
Pterygota mildbraedii	leaf	2.6
Ficus exasperata	leaf	2.5
Aningeria altissima	fruit	2.3
Celtis afruiticana	fruit	2.2
Ficus natalensis	fig	2.1
Treculia afruiticana	fruit	1.7
Ficus dawei	fig	1.6
Morus mesozygia	flower	1.5
Cola gigantean	fruit	1.3
Warburgia ugandensis	fruit	1.3
Celtis durandii	fruit	1.0

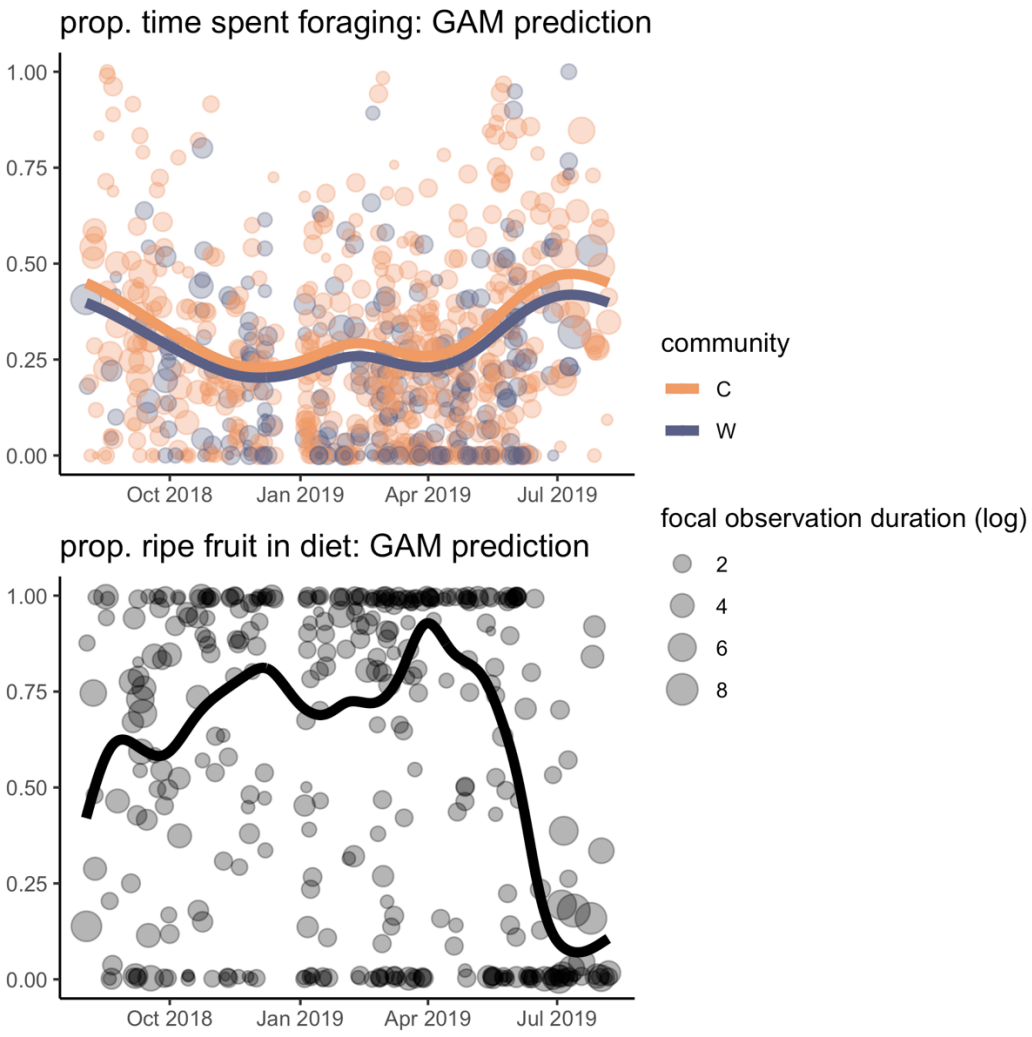

Figure S1. Diet quality indices and GAM predictions. Plots depicting the proxies of diet quality generated using generalized additive models from the underlying observational data: proportion of time spent foraging (top) and proportion of high-quality fruit in the diet (bottom). Each data point represents the proportion of a focal spent either foraging or the proportion of foraging time spent consuming high-quality fruits and their size corresponds to the focal follow duration. Lines depict predicted values from the top performing GAM (according to GAIC) for each date during the study period. Because community was included in the top model of proportion of time spent foraging, different values were predicted for each community on a given date.

Table S3. Arboreality model effects back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95) along with the SE and ranges for 50% and 95% confidence intervals.

variable	estimate	SE	CI.low	CI.high	overlap
% high quality fruit	1.81	1.34	1.02	3.23	no overlap
age	1.17	1.31	0.69	1.98	50% overlap
age * % high quality fruit	2.19	1.94	0.6	8.04	95% overlap
age * party size	0.38	2.08	0.09	1.59	95% overlap
community (West)	1.14	1.28	0.7	1.86	50% overlap
date (cos(pi*date))	1.71	1.27	1.06	2.74	no overlap
date (sin(pi*date))	1.95	1.23	1.3	2.94	no overlap
estrus females	1.13	1.21	0.78	1.64	50% overlap
intercept	5.48	1.2	3.85	7.79	no overlap
observer (SN)	0.71	1.28	0.44	1.15	95% overlap
party size	1.18	1.28	0.73	1.9	95% overlap
rank (Elo)	0.89	1.23	0.59	1.33	50% overlap
rank * estrus females	1.37	1.52	0.6	3.13	95% overlap
time	0.36	1.19	0.26	0.51	no overlap
time (cos(pi*time))	0.45	1.18	0.33	0.62	no overlap

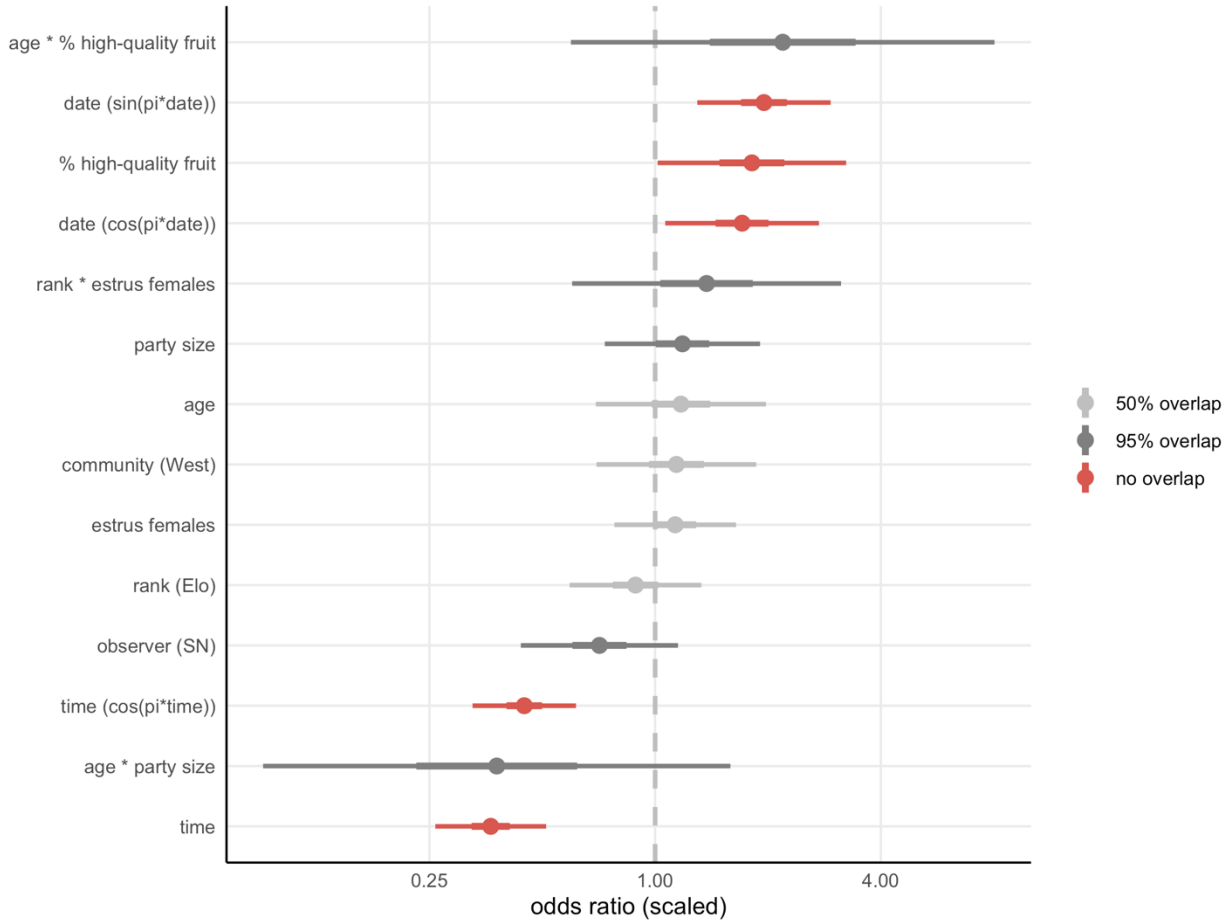

Figure S2. Arboreality coefficient plot from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S4. Climbing distance model effects, back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95) along with their SE and ranges for 50% and 95% confidence intervals.

variable	estimate	SE	CI.low	CI.high	overlap	parameter
% high quality fruit	0.92	1.09	0.77	1.1	95% overlap	| Δheight | (> 0)
age	0.96	1.06	0.85	1.09	50% overlap	| Δheight | (> 0)
age * estrus females	0.98	1.08	0.83	1.14	50% overlap	| Δheight | (> 0)
estrus females	1.19	1.1	0.99	1.42	95% overlap	| Δheight | (> 0)
foraging context	0.99	1.04	0.91	1.07	50% overlap	| Δheight | (> 0)
intercept	13.99	1.04	13.05	15	no overlap	| Δheight | (> 0)
% time foraging	5.89	1.43	2.9	11.94	no overlap	prob. Δheight = 0
age	1.23	1.21	0.85	1.78	95% overlap	prob. Δheight = 0
age * % time foraging	1.04	1.15	0.79	1.37	50% overlap	prob. Δheight = 0
date (cos(pi*date))	1.21	1.29	0.74	1.98	95% overlap	prob. Δheight = 0
date (sin(pi*date))	0.27	1.31	0.16	0.47	no overlap	prob. Δheight = 0
estrus females	1.49	1.15	1.12	1.98	no overlap	prob. Δheight = 0
foraging context	0.55	1.13	0.43	0.69	no overlap	prob. Δheight = 0
intercept	0.78	1.08	0.66	0.91	no overlap	prob. Δheight = 0
rank (Elo)	0.98	1.16	0.74	1.3	50% overlap	prob. Δheight = 0
rank * estrus females	0.59	1.43	0.29	1.19	95% overlap	prob. Δheight = 0
time	1.57	1.13	1.24	1.98	no overlap	prob. Δheight = 0
time (cos(pi*time))	1.76	1.13	1.38	2.23	no overlap	prob. Δheight = 0

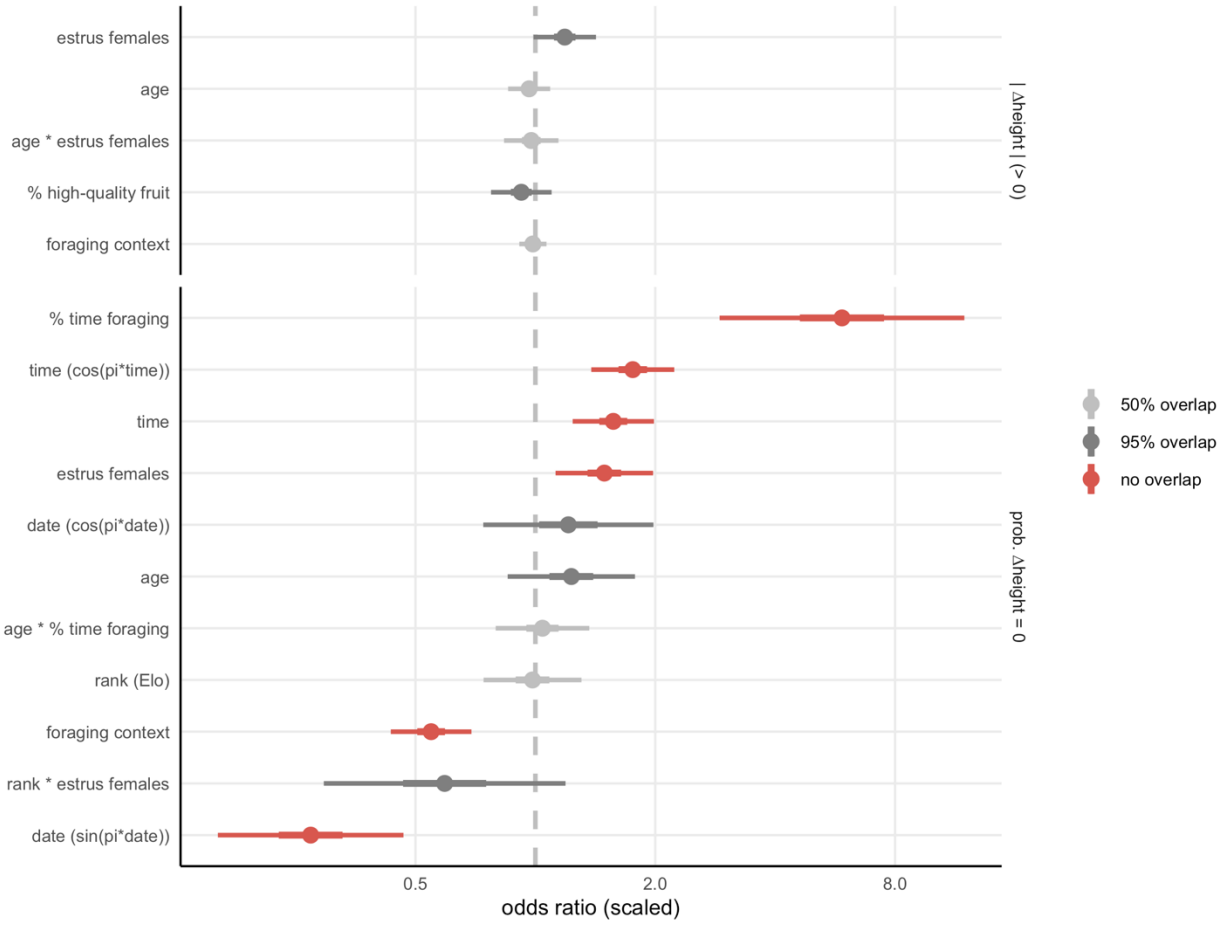

Figure S3. Climbing distance coefficient plot from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S5. Food item selection model effects. Back-transformed (exponentiated) beta-coefficients from the top model (cumulative weight >0.5) along with the SE and ranges for 50% and 95% confidence intervals.

variable	estimate	SE	CI.low	CI.high	overlap	parameter
% time foraging	19.37	1.49	8.92	42.08	no overlap	fig vs. fruit
date	0.33	1.39	0.17	0.62	no overlap	fig vs. fruit
date (cos(pi*date))	6.25	1.38	3.32	11.75	no overlap	fig vs. fruit
intercept	0.49	1.14	0.38	0.63	no overlap	fig vs. fruit
observer (SN)	1.21	1.17	0.88	1.65	95% overlap	fig vs. fruit
party size	1.03	1.21	0.71	1.49	50% overlap	fig vs. fruit
rank (Elo)	0.65	1.21	0.44	0.95	no overlap	fig vs. fruit
time	0.36	1.36	0.2	0.66	no overlap	fig vs. fruit
time (cos(pi*time))	1.3	1.16	0.98	1.73	95% overlap	fig vs. fruit
time (sin(pi*time))	2.7	1.35	1.49	4.88	no overlap	fig vs. fruit
% time foraging	2.56	1.61	1	6.53	no overlap	leaf vs. fruit
date	1.23	1.52	0.54	2.8	50% overlap	leaf vs. fruit
date (cos(pi*date))	0.78	1.53	0.34	1.79	50% overlap	leaf vs. fruit
intercept	0.15	1.19	0.11	0.21	no overlap	leaf vs. fruit
observer (SN)	0.44	1.39	0.23	0.84	no overlap	leaf vs. fruit
party size	0.3	1.41	0.15	0.59	no overlap	leaf vs. fruit
rank (Elo)	0.88	1.29	0.53	1.47	50% overlap	leaf vs. fruit
time	6.06	1.72	2.09	17.61	no overlap	leaf vs. fruit
time (cos(pi*time))	2.17	1.29	1.33	3.55	no overlap	leaf vs. fruit
time (sin(pi*time))	0.41	1.63	0.16	1.08	95% overlap	leaf vs. fruit
% time foraging	0.47	2.5	0.08	2.84	95% overlap	pith vs. fruit
date	36.53	2.56	5.81	229.88	no overlap	pith vs. fruit
date (cos(pi*date))	0.05	2.4	0.01	0.28	no overlap	pith vs. fruit
intercept	0.02	1.46	0.01	0.04	no overlap	pith vs. fruit
observer (SN)	0.78	1.81	0.24	2.48	50% overlap	pith vs. fruit
party size	2.36	2.04	0.58	9.52	95% overlap	pith vs. fruit
rank (Elo)	3.8	1.51	1.69	8.58	no overlap	pith vs. fruit
time	0.2	3.84	0.01	2.83	95% overlap	pith vs. fruit
time (cos(pi*time))	5.96	1.59	2.41	14.74	no overlap	pith vs. fruit
time (sin(pi*time))	14.92	3.12	1.61	138.59	no overlap	pith vs. fruit

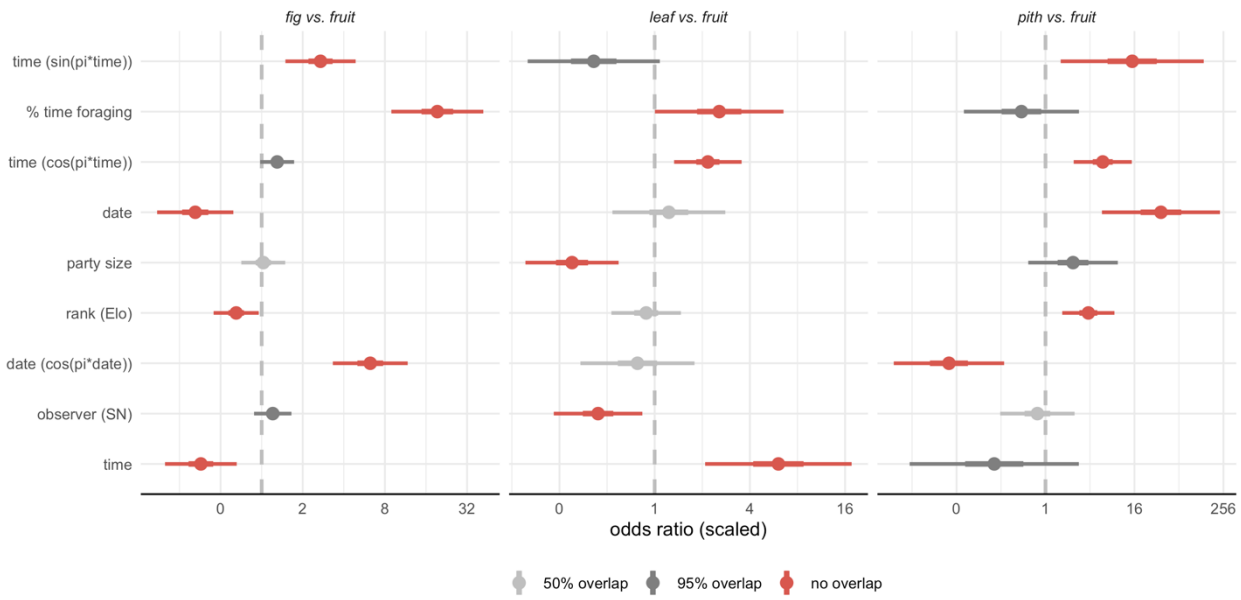

Figure S4. Food selection coefficient plot from back-transformed (exponentiated) beta-coefficients from top performing model (AIC weight ≥0 5). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S6. Fruit ripeness effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95) along with the SE and ranges for 50% and 95% confidence intervals.

variable	estimate	SE	CI.low	CI.high	overlap
% time foraging	0	2.05	0	0.02	no overlap
age	6.83	1.99	1.77	26.4	no overlap
age * % time foraging	0.27	2.71	0.04	1.89	95% overlap
age * fruit	0.18	1.94	0.05	0.66	no overlap
community (West)	0.62	1.73	0.21	1.81	95% overlap
date (cos(pi*date))	0.06	2.13	0.01	0.25	no overlap
estrus females	7.18	1.76	2.37	21.77	no overlap
intercept	51.27	1.6	20.53	128.04	no overlap
item = fruit	0.99	1.37	0.54	1.83	50% overlap
observer (SN)	2.6	1.41	1.32	5.11	no overlap
party size	1.03	1.28	0.64	1.66	50% overlap
rank (Elo)	1.9	1.62	0.74	4.86	95% overlap
time	4.64	2.3	0.91	23.81	95% overlap
time (sin(pi*time))	0.22	2.28	0.04	1.1	95% overlap

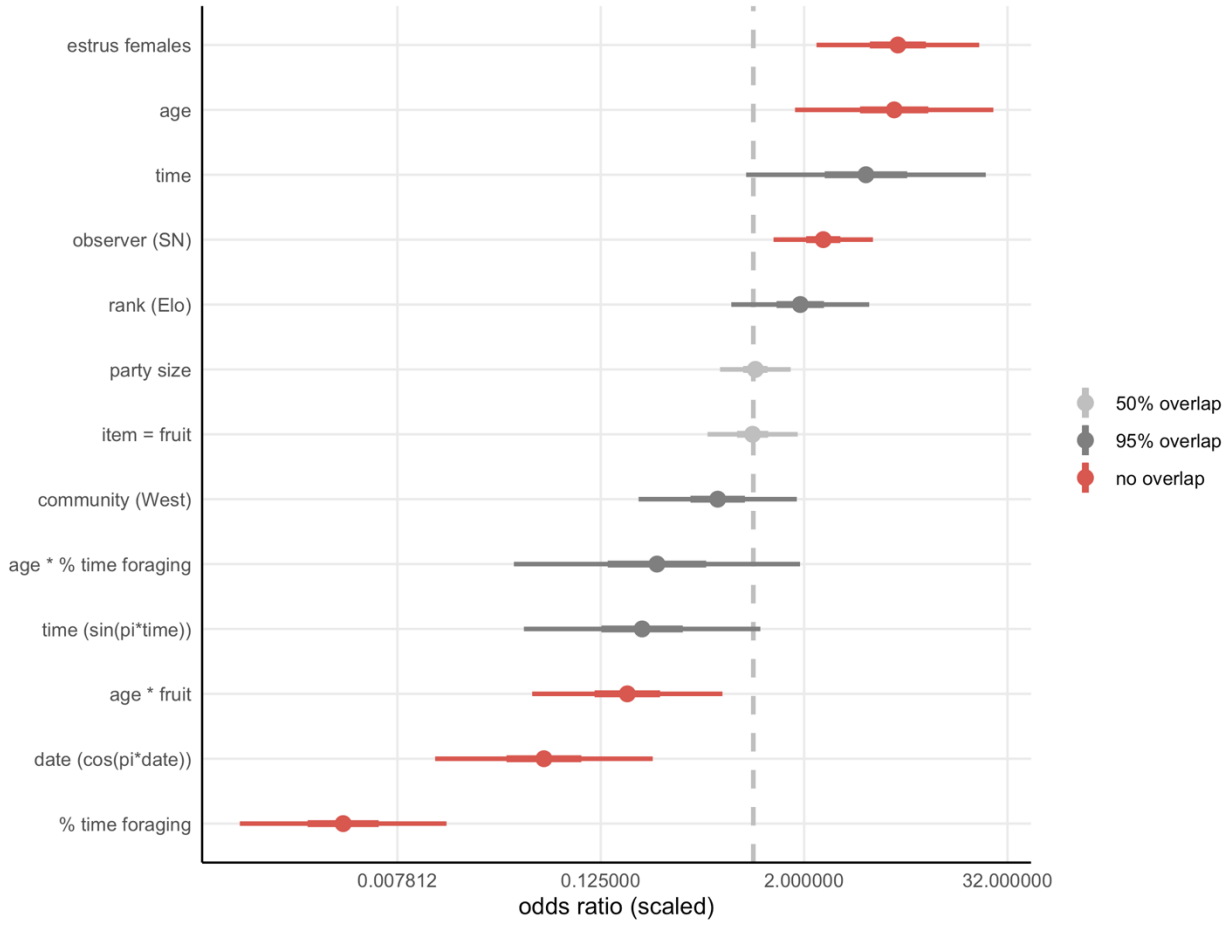

Figure S5. Fruit ripeness coefficient plot from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S7. Intake rate effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95) along with the SE and ranges for 50% and 95% confidence intervals.

	variable	estimate	SE	CI.low	CI.high	overlap
1	age	0.87	1.06	0.78	0.97	no overlap
2	community (West)	1.07	1.08	0.92	1.24	95% overlap
3	estrus females	0.99	1.03	0.94	1.06	50% overlap
4	feeding bout progress	0.92	1.06	0.82	1.03	95% overlap
5	intercept	5.26	1.35	2.92	9.48	no overlap
6	item = leaf	1.18	1.56	0.49	2.84	50% overlap
7	low quality	0.51	1.11	0.42	0.63	no overlap
8	party size	1.01	1.04	0.93	1.1	50% overlap
9	rank (Elo)	1.19	1.05	1.08	1.31	no overlap

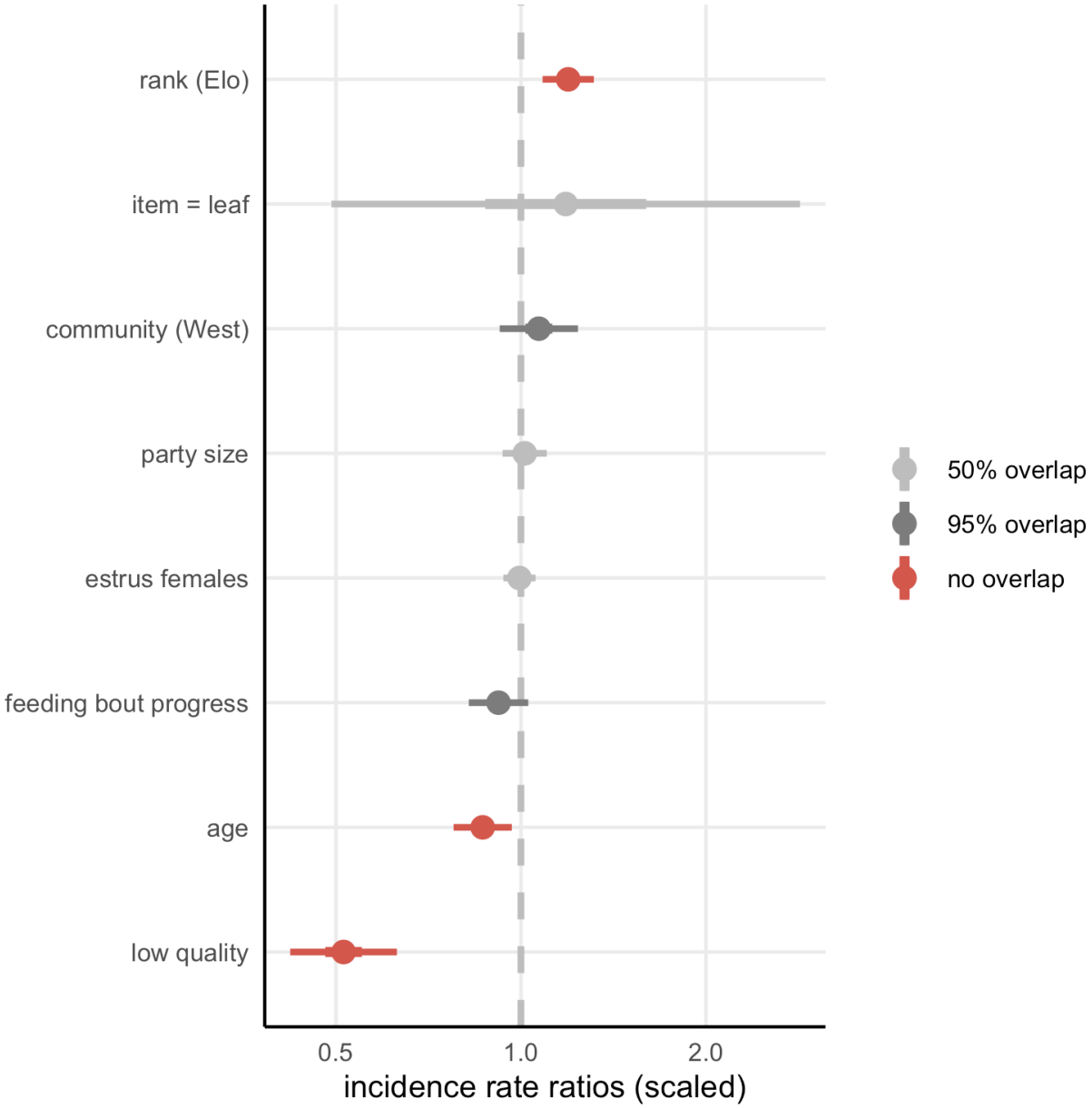

Figure S6. Intake rate complete coefficient plot from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S8. Undigested material back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95) along with the SE and ranges for 50% and 95% confidence intervals.

variable	estimate	SE	CI.low	CI.high	overlap
% high quality fruit	1.42	1.12	1.14	1.78	no overlap
age^2	1.33	1.1	1.09	1.61	no overlap
age^2 * % high quality fruit	0.87	1.22	0.59	1.29	95% overlap
age^2 * rank	0.97	1.13	0.77	1.22	50% overlap
community (West)	1.04	1.08	0.89	1.21	50% overlap
community * rank	0.93	1.18	0.68	1.29	50% overlap
date	1.02	1.14	0.79	1.31	50% overlap
date (sin(pi*date))	0.97	1.11	0.79	1.19	50% overlap
intercept	0.27	1.05	0.24	0.3	no overlap
intercept	0.62	1.05	0.56	0.68	no overlap
rank (Elo)	1.06	1.1	0.87	1.28	50% overlap
rank * % high quality fruit	0.97	1.11	0.79	1.19	50% overlap

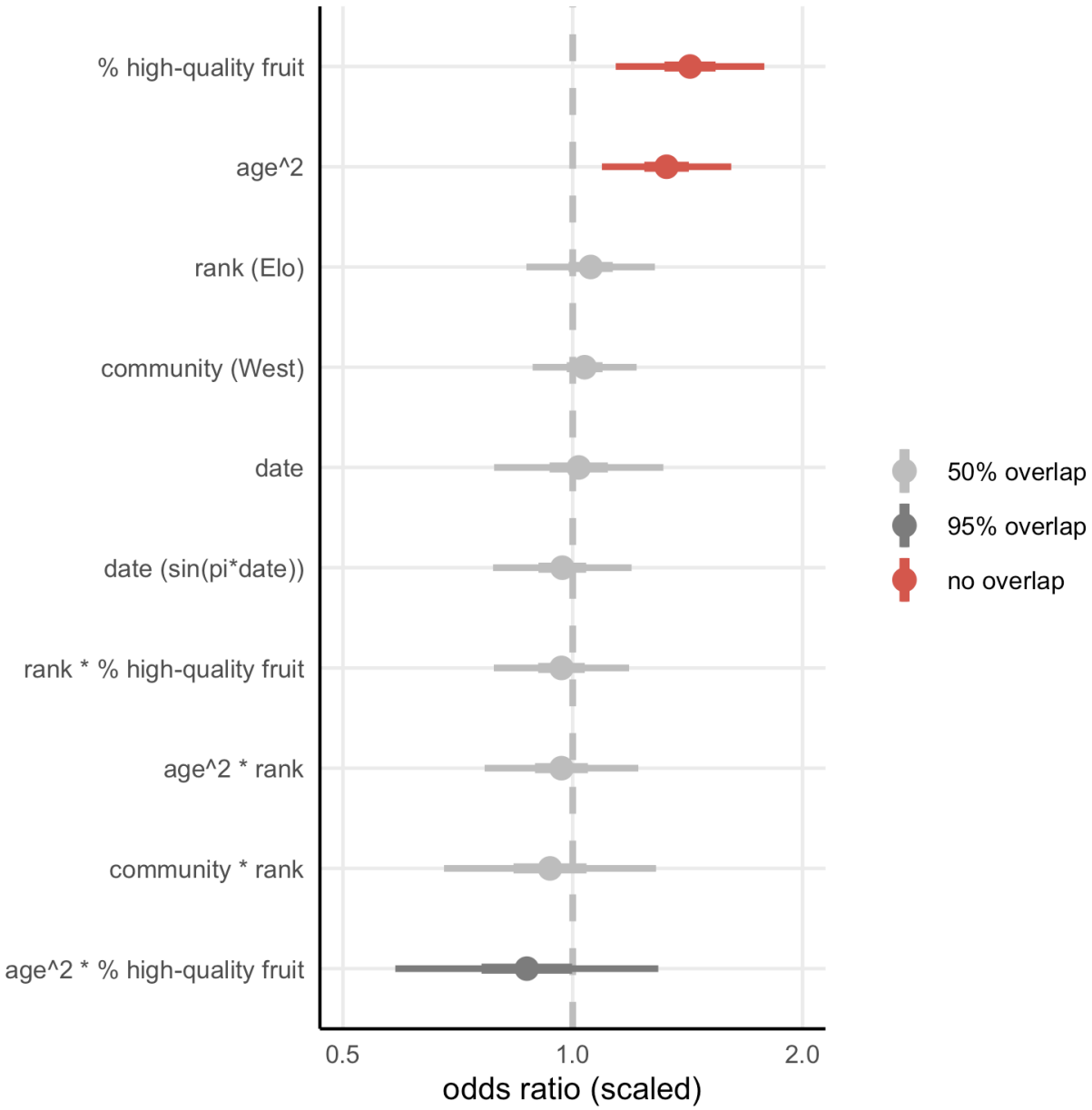

Figure S7. Undigested material complete coefficient plot from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

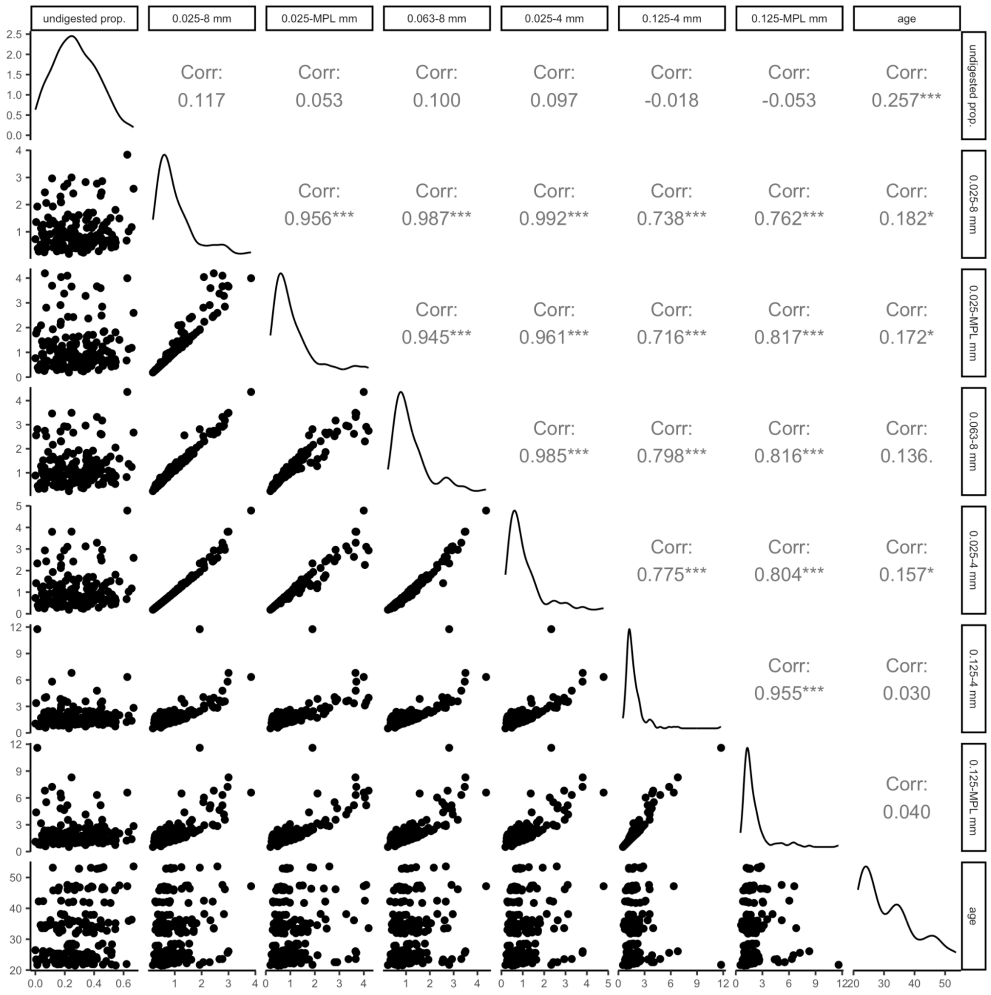

Figure S8. Fecal particle size dMeans pairwise correlations with proportion of undigested material and age.

Table S9. Fecal particle size model effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95) along with the SE and ranges for 50% and 95% confidence intervals.

variable	estimate	SE	CI.low	CI.high	overlap
% high quality fruit	0.53	1.15	0.4	0.7	no overlap
age	1.29	1.09	1.1	1.52	no overlap
age * % high quality fruit	1.04	1.12	0.83	1.31	50% overlap
age * rank	0.99	1.07	0.86	1.14	50% overlap
community (West)	1.02	1.06	0.91	1.13	50% overlap
community * rank	1.02	1.08	0.88	1.18	50% overlap
date (cos(pi*date))	1.44	1.13	1.13	1.83	no overlap
date (sin(pi*date))	1.41	1.1	1.18	1.69	no overlap
intercept	0.95	1.04	0.87	1.03	95% overlap
intercept	0.52	1.05	0.47	0.57	no overlap
processing time	1.07	1.17	0.79	1.44	50% overlap
rank (Elo)	0.92	1.09	0.78	1.09	95% overlap
rank * % high quality fruit	0.99	1.06	0.88	1.12	50% overlap

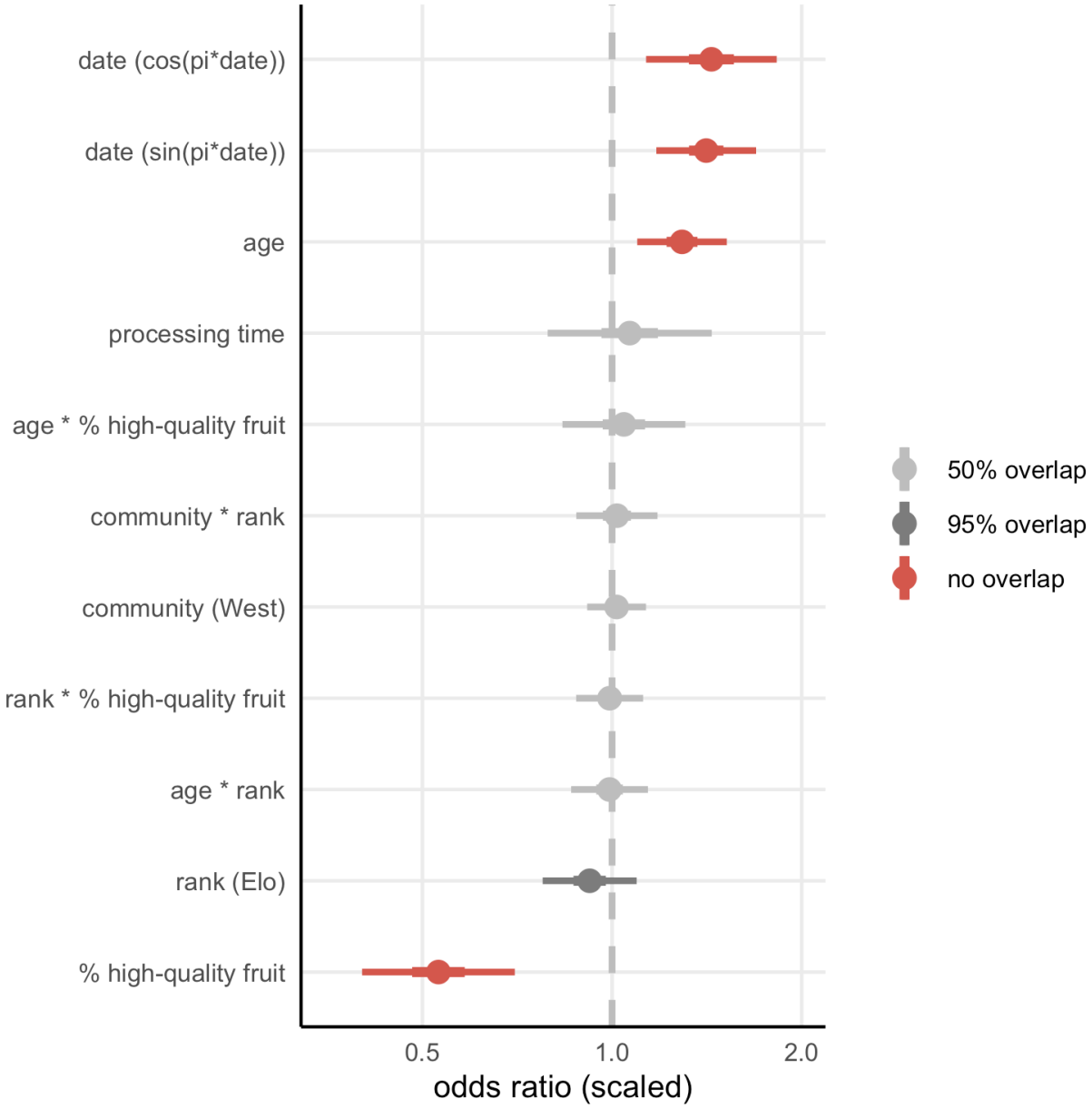

Figure S9. Fecal particle size complete coefficient plot from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

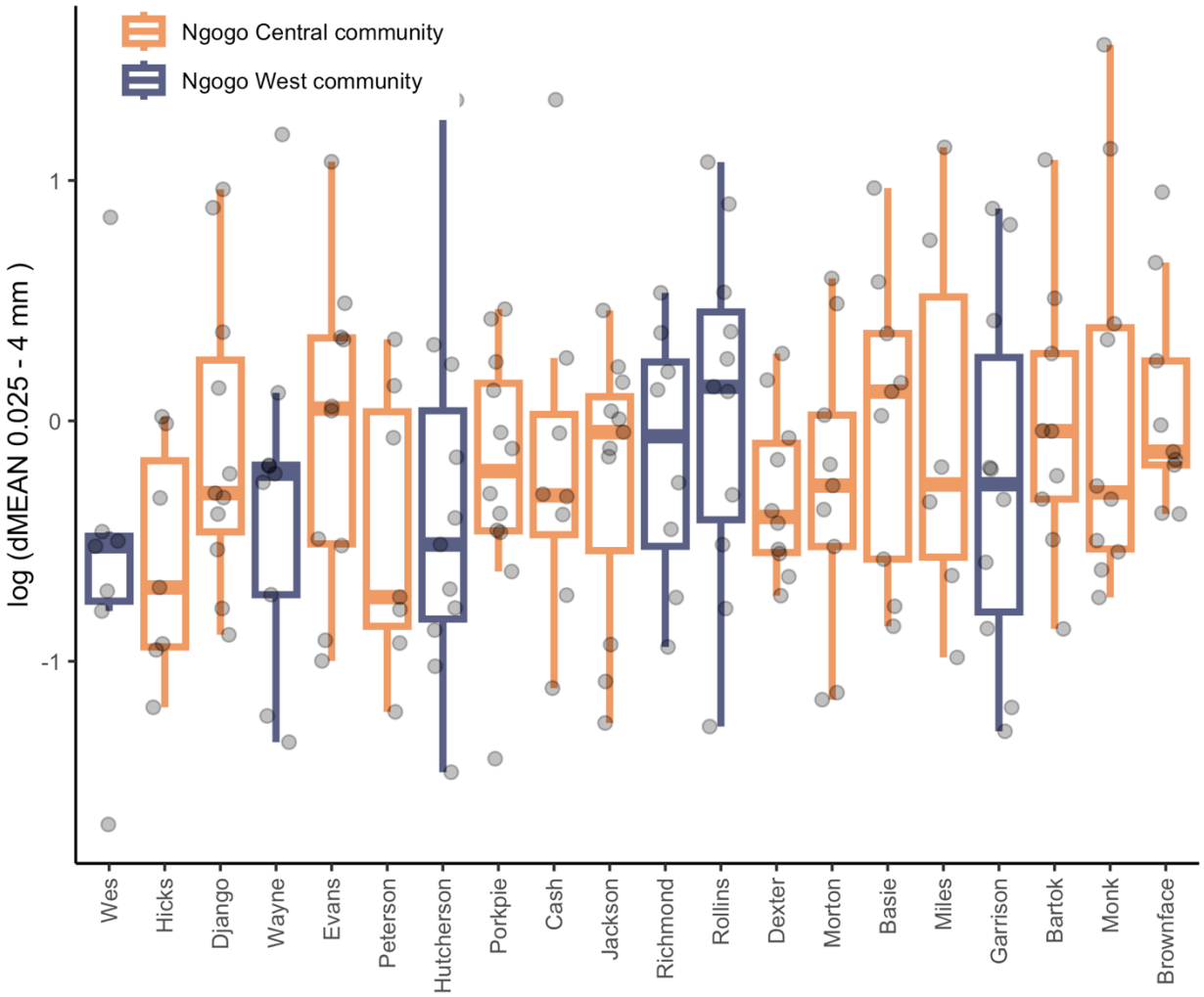

Figure S10. Fecal particle size and subject ID in order of increasing age (left to right) (ages 21-53) and boxplots depicting log ($dMEAN_{0.025–4\ mm}$). Each point depicts a fecal sample's dMEAN value.

Chapter 3.

Tradeoffs in Aging Chimpanzees:

Activity, But Not Condition, Declines in Old Males

Abstract

The reproductive success of wild animals often declines at the end of life, but the proximate mechanisms underlying this pattern are not well understood. In response to shifting physiology and tradeoffs between reproduction and maintenance, late-life animals may allocate relatively more (terminal investment) or fewer (terminal restraint) resources into reproduction. While the senescence of systems related to acquisition and expenditure can further alter resource allocation, it is unclear how such changes may influence such life history strategies late in life. Chimpanzees (*Pan troglodytes*) are especially long-lived primates. Adult male chimpanzees seem to maintain condition into old age but exhibit declines in fecundity and dominance. Understanding how these patterns relate to tradeoffs between resource acquisition, reproduction, and maintenance can help inform our understanding the longevity of chimpanzees and other

organisms. I investigated measures of physiological condition and activity in a particularly long-lived cohort of 20 adult male chimpanzees from two communities at Ngogo in Kibale National Park over 12 months. During a food abundant period, old male chimpanzees showed no declines in energetic status as measured by C-peptide insulin, or testosterone, and they climbed trees just as often as did younger adult males. Old males, however, spent less time moving and more time resting than did younger individuals. Additionally, old chimpanzees spent more time foraging when in large parties and foraged less in small parties. When controlling for important factors such as rank, the social displays of old males were less frequent and covered shorter distances. In times of food abundance, old males also copulated less often than their younger counterparts. These results suggest that old male chimpanzees may strategically restrict activity to maintain reproductive condition, while engaging less in reproductive behaviors overall. These findings provide a proximate explanation for why, despite seemingly maintaining body condition, old male chimpanzees reproduce less than younger individuals.

Introduction

Life history theory proposes that organisms optimally allocate resources to different purposes to maximize fitness (Stearns 1989, Roff 1992). Once organisms reach reproductive maturity — often considered “adulthood”— these trade-offs are between current reproduction and maintenance for future reproduction (Hamilton 1966). The cost of reproduction is the basis of the disposable soma theory of aging, which proposes that longevity is the result of favoring somatic protection and maintenance

over reproduction (Kirkwood 1977, Kirkwood & Austad 2000). How organisms optimize their age-specific allocation to reproduction to maximize fitness represents a central issue in the study of the evolution of aging (Finch 2010, Shefferson et al. 2017). Such questions are of particular importance for long-lived organisms such as primates and, specifically, humans (Kaplan et al. 2000, Gurven & Gomes 2017). Investigations into the nature of tradeoffs in such long-lived organisms can help inform our understanding of the evolutionary relationships between late-life reproductive effort and longevity.

An important prediction from life history theory on the age-specific allocation to reproduction is that iteroparous organisms should invest less in current reproduction when costs to future reproduction outweigh its benefits (William 1957, Stearns 1989). Accordingly, young animals with high residual reproductive value are expected to allocate less to current reproductive effort when they have subsequent chances to reproduce (the 'restraint' hypothesis, Elliot et al. 2014). Reproductive effort is the amount of time and energy that is invested in physiology and behavior that directly increases reproductive output, usually at the expense of other physiological demands (Clutton-Brock 1984, Ellison 2003, Burger et al. 2010). Because the probability of future reproductive output decreases with advancing age, 'terminal investment' is predicted; as organisms approach the end of their life, reproductive effort should increase (Williams 1966, Clutton-Brock 1984). Previous research demonstrates that reproductive investment frequently increases from reproductive maturation through adulthood (Coulson & Fairweather 2001), and especially when mortality risk is high (Clutton-Brock 1984). For instance, reproductive effort increases in compensatory response to declines in physiological condition in long-lived birds (*Sula nebouxii)* Velando et al. 2006) and

female primates (*Macaca mulatta*) (Hoffman et al. 2010). Importantly, individuals who invest heavily in reproductive effort are expected to face costs in terms of survival, future reproduction, or both (Reznick 1985).

In contrast to the terminal investment hypothesis, the 'reproductive restraint' hypothesis predicts that organisms adaptively invest less in reproduction as they age (Curio 1983, McNamara et al. 2009). Because reproductive effort contributes to the accumulation of damages and longevity may be limited by physiological condition (Bribiescas 2020), reproducing less intensively late in life may permit organisms to decrease the probability of dying and gain additional time for future reproduction (McNamara & Houston 1996, McNamara et al. 2009). Empirical evidence consistent with reproductive restraint is scarce but may be apparent when old organisms forego reproductive investment during particularly stressful times (Lecomte et al. 2010, Elliot et al. 2014, Jehan et al. 2020). For instance, in a study of long-lived wild sea birds (*Rissa tridactyla*, *Uria lomvia*), old birds showed reduced reproductive effort when stressed (Elliot et al. 2014). Although not a test of a restraint hypothesis, a 47-year study of female baboons found that those who produced surviving offspring at a slower rate had longer lifespans than those who reproduced at a faster rate (McLean et al. 2019). Evidence for late-life tradeoffs in primates could help clarify whether long-lived animals adaptively shift reproductive effort over the lifespan.

A challenge for studies of tradeoffs in wild animals is that while the 'principle of allocation' (Cody 1966) predicts negative correlations between life history tradeoffs such as reproduction and maintenance (Stearns 1992), empirical studies have often shown that intraspecific phenotypic correlations between these two resource investments are

often positive or nonsignificant (Glazier 1999, McLean 2021). If individuals differ in their average resource acquisition, then allocation tradeoffs can be masked phenotypically (Van Noordwijk & de Jong 1986). Consequently, Jong & van Noordwijk (1992) examined the life history impact of variation at the ‘acquisition‘ and ‘allocation loci.’ Regarding the acquisition loci, foraging may be a particularly important component of life history because acquisition determines the amount of resources that animals can allocate (Boggs 1992); individuals that acquire more resources will be able to allocate more, in absolute terms, to both current and future reproduction than individuals who acquire fewer resources. Such observations have led to the increased incorporation of within-species behavioral variation in life history models (Dammhahn 2018, Laskowski et al. 2021). While inter-individual variation is often attributed to a quality ‘syndrome’, in which some individuals may be more efficient foragers (Cam et al 1998, Weladji et al. 2008, McLean 2019), the same framework may apply to intra-individual variation over the lifespan. For instance, foraging performance may decline with age in a variety of taxa including insects (*Apis mellifera:* Dukas 2008, Higginson & Barnard 2004), birds (*Thalassarche & Diomedea spp.*: Catry et al. 2006, Lecomte et al. 2010, Clay et al. 2016, Frankish et al. 2020), and mammals (*Alces alces*: Montgomery et al. 2013; *Rangifer tarandus*: Skogland 1988, Veiberg et al. 2009; *Canis lupus*: Macnulty et al. 2009) including primates (*Lemur:* King et al. 2005*; Homo sapiens*: Kaplan et al. 2000, *Pan troglodytes*: see Chapter 2.*)*. Consequently, the consideration of age-related changes in energetics may be essential to understanding the nature of tradeoffs in late life, although to my knowledge no studies have explicitly tested hypotheses at both acquisition and allocation loci in primates. Moreover, considering acquisition and

allocation separately can help distinguish reductions in late-reproduction due to restraint or alternatively due to simply senescence. On one hand, senescing individuals may reduce late-life reproduction as a side effect of somatic deterioration, associated with an age-dependent decline in energetic balance. Alternatively, reduced late-life reproduction due to reproductive restraint should be associated with somatic protection (Jehan et al. 2020).

Aging in chimpanzees

Senescence shapes a variety of characteristics in later life for humans, but the extent to which it determines physiological and behavioral outcomes in our closest ape relatives remains unclear (Finch 2010, Emery Thompson 2020a). Although progressive deterioration is more pronounced in terrestrial mammals than the flying “Methuselahs,” birds and bats (Munshi-South & Wilkinson 2009), chimpanzees (*Pan troglodytes*) appear to present phenotypes largely unaltered by the passage of several decades of adult life. For instance, survivorship may not dramatically decrease with age across adulthood (Wood et al. 2017). As in other primates (Alberts et al. 2014), male chimpanzees experience declines in body mass with age after peaking in their early thirties (Pusey et al. 2005, Emery Thompson et al. 2012), but there is little evidence to link such to declines to negative health outcomes. Even after body mass began to decline, aging chimpanzees showed no declines in rates of travel or resting, and individuals appeared to maintain good body condition until close to death (Emery Thompson et al. 2020a).

Such findings may be at odds with other observed age-specific declines. For example, aging primates experience increased susceptibility to disease due to immune senescence (Haberthur et al. 2010). Old chimpanzees in the wild exhibited increased immune-burdens with greater immune-activation and viral richness (Negrey et al. 2020, 2021). There is evidence that mounting an immune response is itself energetically costly because the metabolic requirements of producing immune cells and the indirect consequences of immune upregulation divert resources from other functions such as reproduction (Sheldon & Verhulst 1996, Ilmonen et al. 2000) and survival (Hanssen et al. 2004). In addition, while male chimpanzees can continue to reproduce late in life, reproductive success is lower in old males. At Ngogo in Kibale National Park, Uganda, male fertility has an age-specific decline after approximately age 30 (Langergraber unpublished data). This decrease in reproduction appears concomitant with declines in dominance (Wroblewski et al. 2009); male chimpanzee social rank has a ∩-shape curve, decreasing in middle to late adulthood (Watts 2018). Falling dominance rank may be due to decreased fighting ability, as is often the case across primates (Perlman et al. 2016). Whether old male chimpanzees, faced with declining social rank, make different tradeoffs to maximize their fitness is unclear.

Chimpanzees face environmental stressors that can shape the costs and benefits associated with sociality and constrain reproduction (Wrangham 1980, Markham & Gesquiere 2017). Chimpanzees have a fission-fusion social organization that allows the formation of temporary subgroups of varying sizes (Nishida 1968, Goodall 1986). One primary determinant of party size is food availability, as smaller parties allow individuals to reduce feeding competition (White & Wrangham 1988,

Sakura 1994, Mitani et al. 2002). Importantly, older males are more likely to be alone (Rosati et al. 2020). Increased solitariness could reflect increased costs of sociality with age. Yet, despite being more solitary, old chimpanzees also socialize more with important social partners (Rosati et al. 2020). Incorporating information on resource availability may help explain this seemingly contradictory finding because taken together with the findings of foraging senescence in chimpanzees (see Chapter 2.), resource availability and party size may differentially affect prime and old age chimpanzees' behaviors, particularly those devoted to resource acquisition, i.e. foraging.

In sum, chimpanzees seem to maintain their condition into old age but exhibit declines in fecundity and dominance and associated shifts in sociality. Understanding how these patterns relate to tradeoffs between resource acquisition, reproduction, and maintenance is key to understanding the longevity of chimpanzees and other organisms.

Study design and hypotheses

In this chapter, I investigate whether senescence imposes tradeoffs for the physiology and behavior of wild male chimpanzees, and how they navigate them. I examine a suite of behavioral and physiological traits in a cohort of particularly long-lived male chimpanzees at Ngogo in the Kibale National Park, Uganda (Wood et al. 2017). I employ a framework to explore how adult organisms may make tradeoffs in the face of senescence at two loci: acquisition – or management of the resource pool – and allocation between terminal investment (reproduction) and terminal restraint (maintenance).

How do aging chimpanzees manage their resource pool from which allocations are made? To compensate for decreased foraging returns and potentially increased energetic costs from immune-activation, old chimpanzees may increase foraging investment (the 'terminal acquisition' hypothesis). If old male chimpanzees face greater energetic constraints, they may adopt a strategy to increase intake. Indeed, animals can adjust for physiological aging by adopting behavioral strategies that are less affected by their physical decline. For instance, humans with worn-down teeth spend more time chewing (Naka et al. 2014). Given observed declines in food processing with age (see Chapter 2), I predict that old chimpanzees may invest absolutely more time in resource acquisition. I also predict that increased foraging behavior will be positively associated with environmental stressors, i.e. more apparent during poor quality food periods because during such times, individuals invest more time in food processing (Coiner-Collier et al 2016). Because 'terminal acquisition' aims to compensate for changing payoffs, I predict that it will not be accompanied by any change in energetic status. C-peptide of insulin reflects energy balance, the amount of energy available to an organism, or the net of energy intake minus energy expenditure (Ellison 2003). C-peptide tracks energy balance in nonhuman primates (Ellison et al. 2003, Deschner et al. 2008, Emery Thompson et al. 2008, Gigard-Buttoz al. 2011) and has been shown to vary in wild chimpanzees according to ecological and behavioral conditions (Emery Thompson et al. 2009, Wessling et al. 2018). Even short-term changes in foraging behavior can impact urinary C-peptide, as levels correspond to hourly variance in fruit intake (Georgiev et al. 2012).

Alternatively, old male chimpanzees may compensate for increased energetic challenges by restricting expenditure, decreasing energetically expensive behaviors (the 'terminal restriction' hypothesis). According to the 'rate of living' theory of aging (Pearl 1928), old organisms may engage in strategic restriction as they are likely to encounter energy-related senescence. If energy expenditure causes senescence, individuals more likely to die of senescence-related causes should limit metabolic activity. This is one functional explanation for observed metabolic declines with age (Pontzer et al. 2021), which predicts that aging organisms should reduce components of energy overall to reduce their rate of senescence. To investigate this possibility, I examined several behaviors relevant to shifting energetic costs or changes in body condition, such as bone and muscle loss. Traveling in general is metabolically demanding, and climbing into trees is more expensive than terrestrial movement (Pontzer & Wrangham 2004), which offers a potential explanation for why aging primates may climb less (but not move less) overall (Shively et al. 2012). These considerations lead me to predict that if adult males restrict metabolic activity, then resting will increase while non-reproductive behaviors such as foraging, traveling, and vertical climbing heights will decrease. Energetic status, assayed by C-peptide of insulin, will remain unchanged because the overall energetic differential is unaffected (see summary of framework and hypotheses in **Figure 3**).

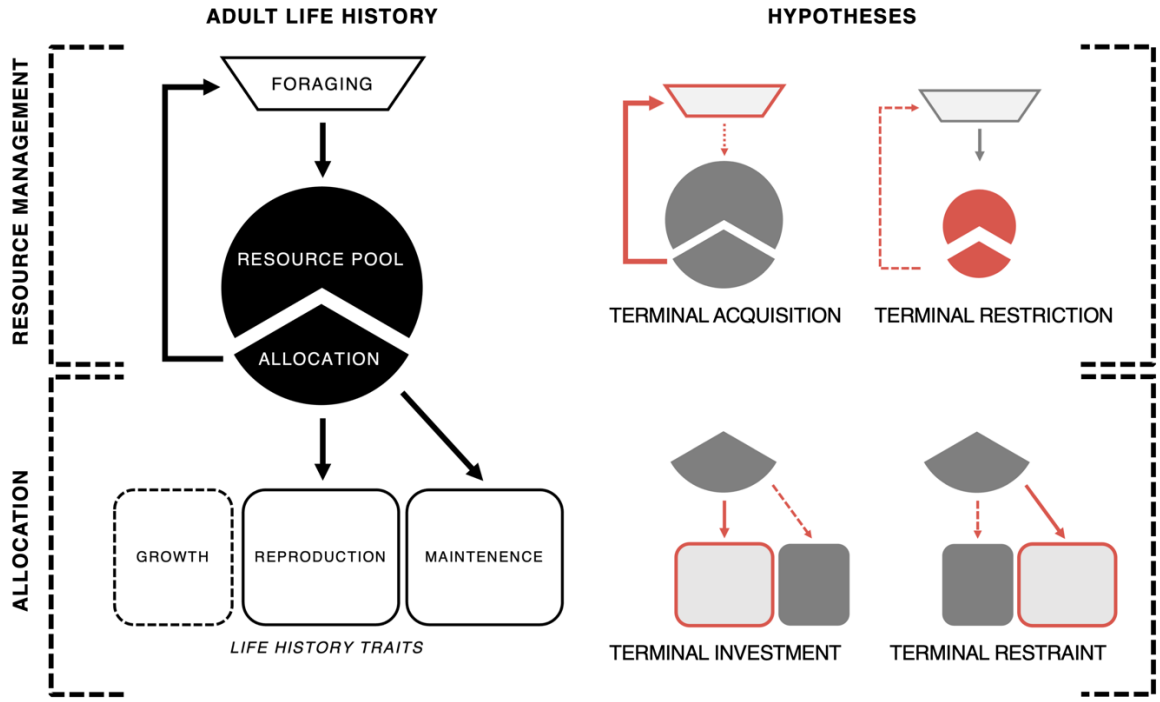

Figure 3. Life history framework and hypotheses. The left side depicts interconnections among foraging, allocation, and life history traits in sexually mature organisms (adults) where allocation to growth has ceased. The right side includes representations of four hypotheses with respect to the resource management and allocation loci, the top and bottom half of the left diagram respectively. Highlighted orange elements represent arenas of predictions for that hypothesis. These are the resource management strategies to increase intake (terminal acquisition) or reduce expenditure (terminal restriction), in addition to the hypotheses of whether adult organisms prioritize allocation to reproduction (terminal investment) or alternatively maintenance (terminal restraint). Figure inspired by figure from Boggs (1992) with adapted language from de Jong & van Noordwijk (1992).

At the resource allocation loci, I examine whether old male chimpanzees prioritize reproduction (terminal investment) or maintenance (terminal restraint). In accordance with the terminal restraint hypothesis, I predict that male chimpanzees should prioritize reproduction, and thus a suite of reproductive behaviors should increase or stay the same, reflecting increased relative investment in old age (Williams 1966, Clutton-Brock 1984). Agonistic displays are a common component of male

dominance displays. These displays make use of exaggerated locomotion and often object manipulation such as branch swaying or buttress drumming (Goodall 1986, Muller & Mitani 2005). High-ranking males display more often than lower-ranking individuals (Bygot 1979, Boesch & Boesch-Achermann 2000, Muller and Wrangham 2004a). While the energetic costs of such displays have not been measured, running speed is positively associated with energy expenditure in mammals (Taylor et al., 1982), which may explain why older primates move more slowly (Shively et al. 2012). Therefore, displays represent a reproductive investment with substantial costs, and I predict that social display frequency and distance will have a positive or no association with age under the terminal investment hypothesis, as will social activity budget and copulation rates. I am unaware of any study that explicitly considers the terminal investment hypothesis in adult male chimpanzees. However, Fessler et al. (2005) examined the maternal age, parity, and birth weight, of female chimpanzees and concluded there was no evidence of terminal investment.

To further investigate the terminal investment hypothesis in male chimpanzees, I consider testosterone as a proxy for reproductive effort. Testosterone is an important and costly physiological moderator of traits salient to male vertebrate reproductive effort. Testosterone promotes musculature (Muller & Wrangham 2004, Bribiescas 2001) and spermatogenesis (Weinbauer 2004). In primates, testosterone varies positively with mating behavior (Highley et al. 1996, Girard-Buttoz et al. 2009, Ostner et al 2011) and dominance rank acquisition (Beehner et al. 2005, 2009). Because aggression plays a prominent role in mating effort, testosterone increases during periods of reproductive competition (Wingfield 1990, Ketterson & Nolan 1999). Importantly, high circulating

levels of testosterone impose substantial costs including increased metabolic rates (Muehlenbein & Bribiescas 2005) and immunosuppression (Prall & Muehlenbein 2014), and intestinal parasite richness (Muehlenbein & Watts 2010). Thus, testosterone production may come at the expense of long-term survival (Hau 2007).

The relationships between testosterone and reproduction are well studied in wild vertebrates including primates, yet the precise nature of the mechanisms through which testosterone mediates aggression and dominance in chimpanzees remains uncertain and may vary based on social and ecological conditions (Muller & Wrangham 2004; Muehlenbein, et al. 2004; Sobolweksi et al. 2013). Recent work suggests that lean muscle mass, not aggression, mediates the relationship between dominance rank and testosterone in chimpanzees (Negrey et al. 2023). Negrey et al. (2023) found that testosterone was negatively correlated with aggression. Nonetheless, investments in sexually dimorphic tissue including muscle come with especially high metabolic costs (Adelman et al. 1988; Alonso-Alvarez et al. 2004, 2007). Testosterone senescence may reflect such costs as older males may compete less intensely for reproductive opportunities (Wroblewski et al. 2009). In several primate species, male testosterone peaks around the maximum of age-specific fertility and then declines (Muller 2017). In chacma baboons (*Papio hamadryas*) and geladas (*Theropithicus gelada*), for example, testosterone peaked at the age of first sexual consortship, and decreased with advancing age and declining reproduction (Beehner et al. 2009). For chimpanzees, this peak may be around 17-18, and subsequent decreases track the age-specific decline in fertility, but appears less steep than in other species such as baboons (Muller 2017). Consequently, testosterone senescence may play an important role in sarcopenia and

general loss of body condition for aging males (Emery Thompson et al. 2020a). Taken together, the preceding considerations suggest that if old male chimpanzees prioritize reproduction, they will exhibit increased or maintained testosterone levels, reflecting greater relative investment in old age. Because reproductive investment comes at the cost of physiological condition, I predict that energetic status will be inversely associated with testosterone.

If instead old chimpanzees engage in 'terminal restraint, they should prioritize maintenance (future reproduction) at the expense of current reproduction (McNamara et al. 2009). For elderly male chimpanzees with limited reproductive access, the benefits of investing in somatic maintenance to reduce senescence-related risks may be more certain than the benefits of investing in immediate reproduction, particularly during poor food periods when individuals are under greater energetic constraints. In this case, I predict that age will be negatively associated with reproductive investments of social display frequency and distance, social activity, and testosterone, particularly during poor food times. By contrast, there should be no association between age and energetic balance.

In sum, I test whether old age male chimpanzees manage their resource pool by strategies of terminal acquisition or terminal restriction, and whether they allocate resources in response to shifting payoffs late in life by terminal investment or terminal restraint. **Table 3** summarizes the predictions.

Table 3. Summary of hypotheses, predictions, and findings according to each response variable and their correlation with subject age. Symbols for correlations are as follows: "—" no correlation; "↓" negative correlation; "↑" positive correlation. To determine whether these correlations with age are state dependent, I added interaction effects with diet quality to assess how ecology might mediate these life history decisions. Δ denotes predicted interaction effect with diet quality.

response variable	description of measure [data class]	*resource management prediction with age*		*allocation prediction with age*		*findings with age*	
		acqusition	restriction	terminal investment	terminal restraint	main effect	interaction effect
forage activity	behavioral scan activity category [categorical]	↑ Δ	↓			–	↑ with party size
rest activity	behavioral scan activity category [categorical]		↑	↓	↑	↑	
move activity	behavioral scan activity category [categorical]		↓		↓	↓	
climbing distance	|Δheight| between scans [continous, zero inflated]		↓		↓	(↓)	
C-peptide of insulin	urinary C-peptide, energy balance (ng/ml-SG) [continuous]	—	—	↓	—	—	
testosterone	urinary tesoterone (pg/ml-SG) [continuous]			— / ↑	↓	—	
social activity	behavioral scan activity category [categorical]			— / ↑	↓	—	
display frequency	count of social displays per focal [discrete]			— / ↑	↓	↓	
display distance	social display distance traversed [continuous]			— / ↑	↓	↓	
copulation	count of copulations per focal [discrete]			— / ↑	↓	↓	↓ with foraging time

Methods

Study site and subjects

I observed chimpanzees at Ngogo in Kibale National Park, Uganda (between 0°13′–0°41′ N and 30°19′–30° 32′ E) from August 2018 to August 2019. The Ngogo study site is surrounded by other chimpanzee communities and covered by mature, mid-altitude rainforest interspersed with secondary growth, swamp forest, and grasslands (Struhsaker 1997, Lwanga 2003). Researchers have studied the Ngogo chimpanzee community since 1995 and all subjects were well-habituated to human observation (Watts 2012). In January 2018, the Ngogo community split into the Ngogo Central and Ngogo West communities (Sandel & Watts 2021). Together, the communities occupy territories that cover approximately 35 km^2. For the majority of the study period, Ngogo Central comprised 121 individuals, including 24 adult males and 40

adult females. Ngogo West consisted of 84 individuals, including 7 adult males and 24 adult females.

Subjects were 20 adult males ranging from age 21 to 53 years old at the start of study (mean age = 32 years) (**Figure S10**). While young adulthood includes individuals 16-20 years old, this period has been characterized as a distinct social life stage (Goodall 1983, Kawanaka 1989). I excluded young adults from analyses because their continued physical and social maturation might influence life history tradeoffs. The ages of males born in 1995 or later are known with a precision of between one day and a few months. For males born earlier (17 of 20 subjects), this study uses ages provided by Wood et al. (2017). These estimates are based on comparison of the appearance of males when first observed to that of known-aged males; visual assessment of when males who were immature at the study's start attained full, adult body mass; and comparisons among those who were already adults with respect to visible traits associated with senescence (e.g., muscle mass). Genealogical information for most males born before 1995 is known from an ongoing, long-term genetic study of the Ngogo chimpanzees (Langergraber et al. 2007, 2013). These data furnish an additional, key source of information to estimate the age of males born before 1995 (see Wood et al. 2017).

Behavioral data collection

Sharifah Namaganda and I observed subjects via continuous focal animal sampling (Altmann 1974). Focal sessions typically lasted 2 hours, after which we switched to new focal subjects. When no other focal subject was present, we remained with the current subject. Some focal sessions terminated early when chimpanzees were

lost, and in these situations, we included observations if subjects were followed for at least 30 minutes. Because chimpanzees live in fission–fusion societies and form temporary sub-groups known as parties, not all males were available for observation every day. We attempted to equalize the number of focal follows by rotating through subjects opportunistically, prioritizing males that had been observed less often than others during any given month. All observations were recorded digitally on a handheld device using *HanDbase IOS* software. Together, we conducted 1288 hours of focal observations on subjects (mean 64.4 ± SD:10.3 hours per subject), in which all behavioral outcomes were observed. I conducted an additional 132 hours of focal observation on non-focal adults, which were incorporated to generate dietary indices that were used as predictors of behavioral and physiological outcomes.

We collected behavioral data during scans every 15 minutes (n=5111 scans). This included food items consumed and whether subjects were arboreal, defined as ≥ 3m off of the ground. During scans, I collected additional data regarding subject height above the forest floor. I used a Haglöf clinometer to estimate the vertical angle of chimpanzees from my position and combined this with their visually assessed horizontal distance to calculate heights relative to the forest floor (Bezanson et al. 2012). I measured consecutive heights to calculate the change in height between scans (|∆height|, n=2761).

Namaganda and I recorded all instances of displays by the focal subject and when feasible, visually estimated the distance between the start and end location of the display (n=748 displays, n=644 with distance estimations). Because my research questions focus on energetic tradeoffs, I considered a broad definition of social displays.

These included any accelerated movement featuring at least one of the following: pant-hooting, pilo-erection, buttress drumming, log or other object dragging, and charging another chimpanzee. The maximum display distance estimation was 50 meters due to limited visibility, so any distances greater than that were recorded as 50 m. We also recorded all copulations by the focal subject (n=154).

Urine collection and assays

Namaganda and I collected fresh urine samples from study subjects opportunistically throughout the day by pipetting droplets from low-lying vegetation or a plastic substrate immediately after excretion. We stored the samples on ice until approximately 1800 h, at which time they were transferred to a −20°C freezer at the camp site. Samples were transported on dry ice to the United States and then stored at -80°C at the Comparative Human and Primate Physiology Center at the University of New Mexico (see Emery Thompson et al. 2009). We measured the specific gravity of each urine sample using a handheld refractometer (Antago PAL-10S) and corrected C-peptide and testosterone values for water content (Miller et al 2004).

I measured urinary C-peptide insulin to track changes in energetic condition (n=619; mean samples/subject 31 ± SD:3.9; mean concentration 1891 ±SD 1471 ng/ml-SG). C-peptide has been validated as an energetic measure in chimpanzees and other primates (Deschner et al. 2008; Emery Thompson et al. 2009), against measures of weight loss and gain (Girard-Buttoz et al., 2011), dietary quality (Georgiev et al. 2011), food availability (Emery Thompson & Knott 2008), estimated caloric intake (Emery Thompson & Knott 2008), and activity levels (Higham et al. 2011). I measured C-

peptide levels with commercial radioimmunoassay kits (Millipore Sigma, Burlington, MA, USA) following the manufacturer's instructions. The interassay CV of the low- and high-quality controls were 11.8% and 11.4% respectively (n=18 assays) and the mean intra-assay CV of samples was 5.5 ±1.8%. Assay sensitivity was 200 pg ml-1 and no samples fell below this threshold, whereas the maximum assay value was 10000 pg ml-1 and thus any values at this point were set to the 99.5th quantile, or 9901 ng ml-1 (n=3). Assay accuracy was determined by the recovery of a sample added in duplicate to all points of the standard curve.

I measured urinary testosterone from immunoassays (n=264; mean samples/subject 13.3 ±SD 4.2; mean concentration 88573 ±SD 48917 pg/ml-SG). Samples were deconjugated by treatment with beta-glucuronidase (Helix pomatia, Calbiochem, <2% aryl sulfatase activity) followed by ether extraction. Immunoreactive testosterone was assayed in triplicate using enzyme-immunoassay protocols and reagents provided by the University of California at Davis Clinical Endocrinology Laboratory. The polyclonal antibody R156/7 cross-reacts 100% with testosterone, 57.4% with 5alpha-dihydrotestosterone, and less than 0.3% with other androgens. The assay has a sensitivity of ~15 pg/ml, but chimpanzee urine has high concentrations of testosterone, requiring a 50-200x dilution. No samples fell below this sensitivity threshold whereas the maximum assay value was 30,000 pg ml-1 and thus any values at this point were set to the 99.5th quantile, or 289,804 pg ml-1 (n=2). Interassay CVs were 2.5% for high and 8.6% for low control and the mean intra-assay CV of samples was 6.0% ±0.6% (n=4). One sample with an outlier CV value (>99th quantile) was excluded.

Covariates and predictors

I employed the same covariates as predictors in model construction as the studies in Chapter 2 (summarized in **Table 4**). In addition, I included a measure of *foraging context* for the analysis of climbing distance. Because arboreal locomotion occurs while feeding (Goodall 1986), controlling for the foraging context during vertical height displacements will likely improve model performance. To do so, I incorporated an ordinal score that quantified the extent of foraging activity that occurred over the 15-minutes period during which vertical height displacements occurred. A score of one was assigned to the following conditions: if the end-scan's behavioral state was recorded as foraging, if the start-scan's behavioral state was recorded as foraging, and if a feeding bout occurred in the period in-between the start- and end-scans. The foraging context score was then the sum of those values, which ranged from 0–3, wherein a higher score corresponds to a greater extent of foraging behavior associated with the vertical distance.

Table 4. Description of predictors for measure outcomes and when they were included in the full model employed in dredge(). I employed pretests to identify and mutually exclude highly correlated variables ($r \geq 0.7$) from the same models.

Description of predictors for outcome measures			included in models						
type	predictor	description	activity	climbing distance	C-peptide	testosterone	display frequency	display distance	copulation frequency
fixed	date	three date terms: nuermic date of sample, cos(pi * date), and sin (pi * date) [numeric, continuous]	▪	▪	▪	▪	▪	▪	▪
	time	three time terms: numeric time of sample, cos(pi * time), and sin (pi * time) [numeric, continuous]	▪	▪	▪	▪	▪	▪	▪
	observer	observer identity: BJF or SN [categorical]	▪				▪	▪	▪
	community	identity of chimpanzee communinity: Ngogo Central or Ngogo West [categorical]	▪	▪	▪	▪	▪	▪	▪
	% high-quality fruit	daily population-wide index of the proportion of ripe non-fig fruit and *Ficus mucuso* fruit in the diet. Generated as predictions from GAM of time spent feeding on high-quality fruit per focal as a function of date [numeric, continuous]	▪	▪	▪	▪	▪	▪	▪
	% time spent foraging	daily population-wide index of the proportion of time spent foraging. Generated as predictions from GAM of time spent within foraging bouts per focal as a function of date and community [numeric, continuous]		▪	▪	▪	▪	▪	▪
	age / age^2	subject age or age^2 at sample, selection from preliminary analysis of per-variable sum of model weights [numeric, continuous]	▪	▪	▪	▪	▪	▪	▪
	rank	daily dominance rank (Elo score) [numeric, continuous]	▪	▪	▪	▪	▪	▪	▪
	party size	the number of chimpanzees in association throughout the day, excluding dependents younger than age 8 [numeric, discrete]	▪	▪	▪	▪	▪	▪	▪
	estrus female in association / number of estrus females	the number of sexually receptive parous female chimpanzees in association throughout the day [numeric, discrete] or a binary of whether a female was in association [binary], selection from preliminary anaylsis of per-variable sum of model weights	▪	▪	▪	▪	▪	▪	▪
	foraging context	a score [0,3] of how much foraging activity occurred in the 15-minute period of and between scans [ordinal]		▪					
random	subject ID	male identity [categorical]	▪	▪	▪	▪	▪	▪	▪
offset	focal sample duration	duration of focal follow [numeric, continuous]					▪		▪

Data analysis

I conducted preliminary data exploration, analysis, and data visualization in R (version 4.2.2; R Core Team 2022) via RStudio version 2022.12.0 (RStudio Team, 2022). To determine the effects of age on various physiological and behavioral outcomes, I adopted an information theoretic approach using generalized linear mixed models (GLMMs) to model variation in each outcome. I fit models using {lme4} (Bates et

al. 2004), {glmmTMB} (Brooks et al. 2017), {mclogit} (Elff 2022), and {gamlss} (Rigdy & Stasinopoulos 2005) to support a variety of distributions for outcome variables. For instance, I used a zero inflated model to fit the probability of no climbing (binomial distribution) and the distance when climbing did occur (*ziGamma* distribution) because the distribution of meters climbed had many zeros. For all analyses I fit ecologically plausible models (including interactions when warranted) with alternative distributions appropriate to the outcome of interest, (e.g. binomial for binary outcomes, ordered logit for categorical outcomes, gamma distributions for continuous outcomes). Following model fitting with the complete model (see **Table 4**), I performed model selection using the dredge() function {MuMIn} package (Bartón 2009), which employs an information theoretic multi-model selection approach based on Akaike's Information Criterion (AIC), or when n/K > 40, indicating a high number of terms relative to small sample size, AICc (Burnham & Anderson 2004). I then performed model averaging across models with cumulative weight of 0.95 using function model.avg() {MuMn}, which averaged predictions on their link scale to obtain weighted averaged estimates for each predictor for a complete model average (when a predictor was absent from a given model, the beta value is considered to be 0).

I considered predictors to be reliable when the 95% confidence intervals of their effect sizes did not overlap the null effect. To control for the non-independence of samples, I included random effects for subject ID. Prior to model fitting, I examined pair-wise correlation plots (see supplementary materials) to ensure highly correlated variables ($r \geq 0.7$) were not included in the same model to avoid issues with model convergence with the exception of date and time harmonic terms. Thus, *percent high-*

quality fruit and *percent time foraging* were not included together in any model. In preliminary analysis, I compared the performance of these dietary predictors and in the complete model included only the one with a greater performance according to AIC. Similarly, I conducted preliminary analyses to determine whether to include *age* or age^2 and *number of estrous females* or the binary *estrous female in association* in model construction. All continuous predictors were centered on the mean and standardized to permit direct comparison of effect size magnitude. Offsets were transformed according to their respective model's link function to place them on the same scale as the outcome. The outcome variables (**Table 3**) were: 1) activity budget (resting, foraging, moving, or socializing), 2) absolute vertical displacement, 3) urinary C-peptide insulin concentration, 4) urinary testosterone concentration, 5) social display counts per focal, 6) display distance, and 7) copulation counts per focal.

Results

Old chimpanzees foraged more in large parties, rested more, and spent less time moving

Adult male chimpanzees were classified as resting in 44% of scans, foraging in 27%, moving in 15%, and socializing in 13%. Age had a state-dependent effect on foraging frequency via an interaction with party size: on days with large parties foraging frequency increased with age and on days with small parties foraging frequency decreased with age (**Figure 4B**). In addition, the rate of moving relative to resting

decreased by 0.79(±1.13) times for each SD increase in age (equivalent to 9.6 years) (**Figure 4C, Table S11**). The top model according to AIC (weight = 0.65) predicted a decrease in moving frequency and increase in resting by approximately 1.2% for each 10 years of life. In contrast, there was no reliable relationships between age and rates of socializing behaviors. The latter increased by 1.37(±1.13) times for each SD increase in party size. Additionally, the proportion of high-quality fruit in the diet had a consistent effect across behaviors, as an additional SD in high-quality fruit proportion decreased the frequency of foraging (by 0.66±1.15 times) and socializing (by 0.62±1.20 times) (**Figure 4A**). This latter effect is surprising given that periods of high fruit abundance are often associated with increased socialization.

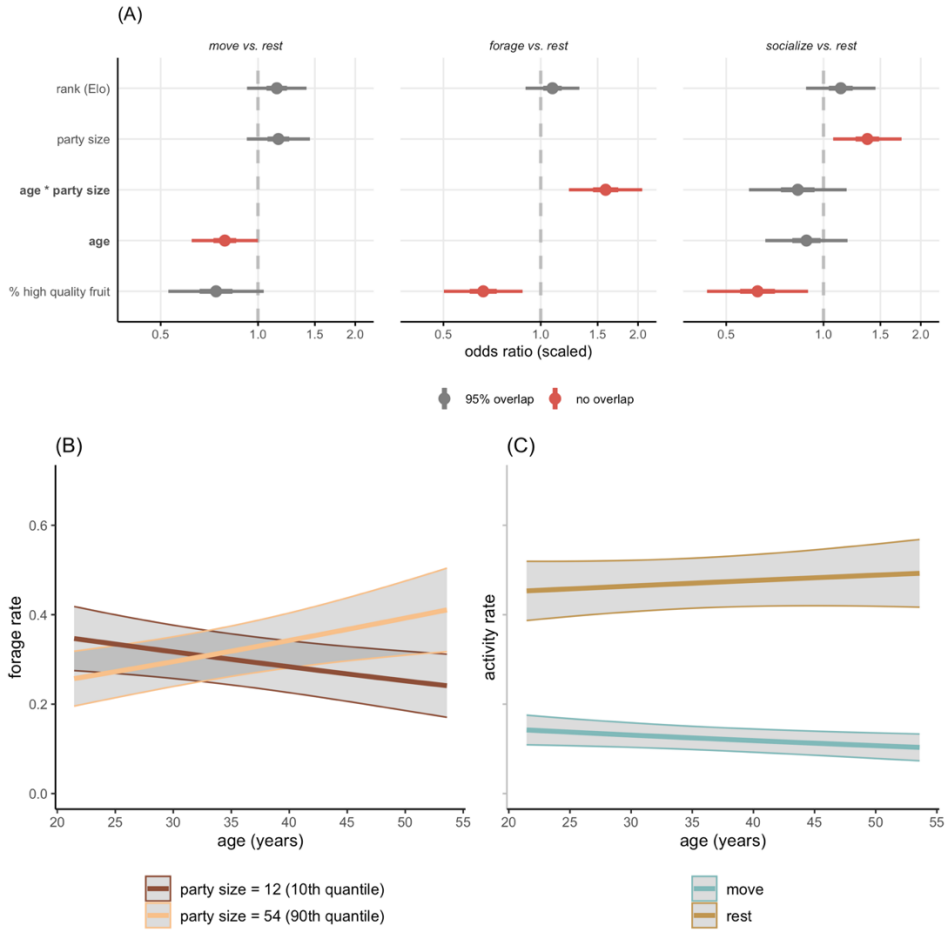

Figure 4. Activity varied with age based on focal behavior in behavioral scan (n=5111). All coefficient values and activity rate predictions are generated from the top model according to AIC (weight = 0.65). (A) Coefficient plot with back-transformed (exponentiated) beta-coefficients. Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect. Coefficient plots exclude control predictors (time of day predictors, date, and observer) and predictors with 50% CI overlap other than age for visual clarity. For complete coefficient plot see Figure S11. Bolded terms indicate effects of age and its interactions. Predictors are centered and standardized so the magnitude of beta coefficients are directly comparable. (B) Foraging rates according to age and party size: foraging increased with age in large parties and decreased with age in small parties. (C) Rates of moving and resting, which decreased and increased with age, respectively.

Old chimpanzees did not climb shorter vertical distances

Subjects traversed a mean absolute vertical distance of 4.5 m every 15 minutes (±SD 8.8 m). The effects of age on distance climbed (*mu*) and the probability that height

climbed was greater than zero (*nu*) were both unreliable, with 95% confidence intervals overlapping null effect. Both were nevertheless directionally consistent with each other and the prediction of decreased climbing with age (**Figure 5A**). For each 1SD increase in age, the model average predicted a 1.25(±1.23) times increase in the probability of no vertical displacement and that when this displacement was greater than zero, it predicted that the distance was 0.94(±1.07) times shorter (**Table S12**). The weighted model average (cumulative weight ≥0.95) predicted that climbing distance per 15-minute interval would decrease by only 0.54 meters for each additional 10 years of life (**Figure 5B**). The proportion of high-quality fruit in the diet was negatively correlated with the probability of climbing; for each SD increase in high-quality fruit, the probability of climbing decreased by 0.55(±1.15) times. The number of parous estrous females in association was positively correlated with distance climbed, with adult males climbing 1.17(±1.08) times more for each SD increase in the number of estrous females. Time predictors had reliable effects on the probability of climbing, but not the distance, whereas climbing probability and distance increased in foraging contexts.

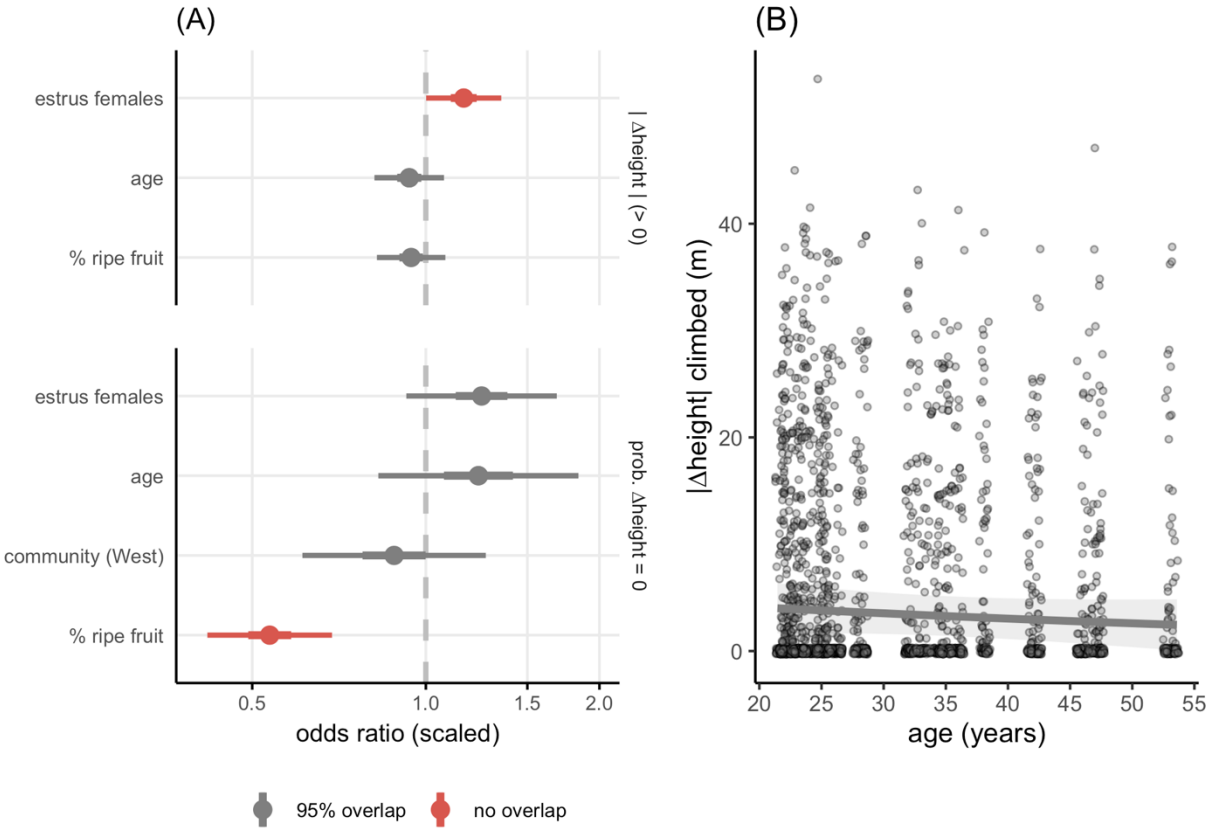

Figure 5. Absolute vertical climbing distances as measured by difference in heights between 15-minute scans (n=2761 scan pairs). (A) coefficient plots for zero-inflated distributions, which separately estimates 1) the probability that no climbing occurred (bottom plot: probability ΔHeight = 0) and 2) the absolute vertical displacement when climbing did occur (top plot: |ΔHeight| > 0). Coefficient plots depict back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect. Coefficient plots exclude control predictors (time of day predictors, date) and predictors with 50% CI overlap other than age for visual clarity. For complete coefficient plot see Figure S12. Predictors are centered and standardized so the magnitude of beta coefficients are directly comparable. (B) |ΔHeight| between scans with predicted height from model average.

Urinary C-peptide Insulin did not vary with age

There was no relationship between age and the C-peptide of adult males (**Figure 5**). The only reliable predictor of C-peptide levels was the sinusoidal term of date (**Table S13**), which suggests seasonal variation in energetic status that was not explained by

measures of dietary quality or group composition. I present results here from an analysis of urine samples associated with complete predictor values (n=619), however, I also conducted a supplementary analysis with additional urinary C-peptide samples (n=713), which excluded party composition predictors due to missing values. In this supplementary analysis with a larger sample size, once again there was no correlation between C-peptide and subject age.

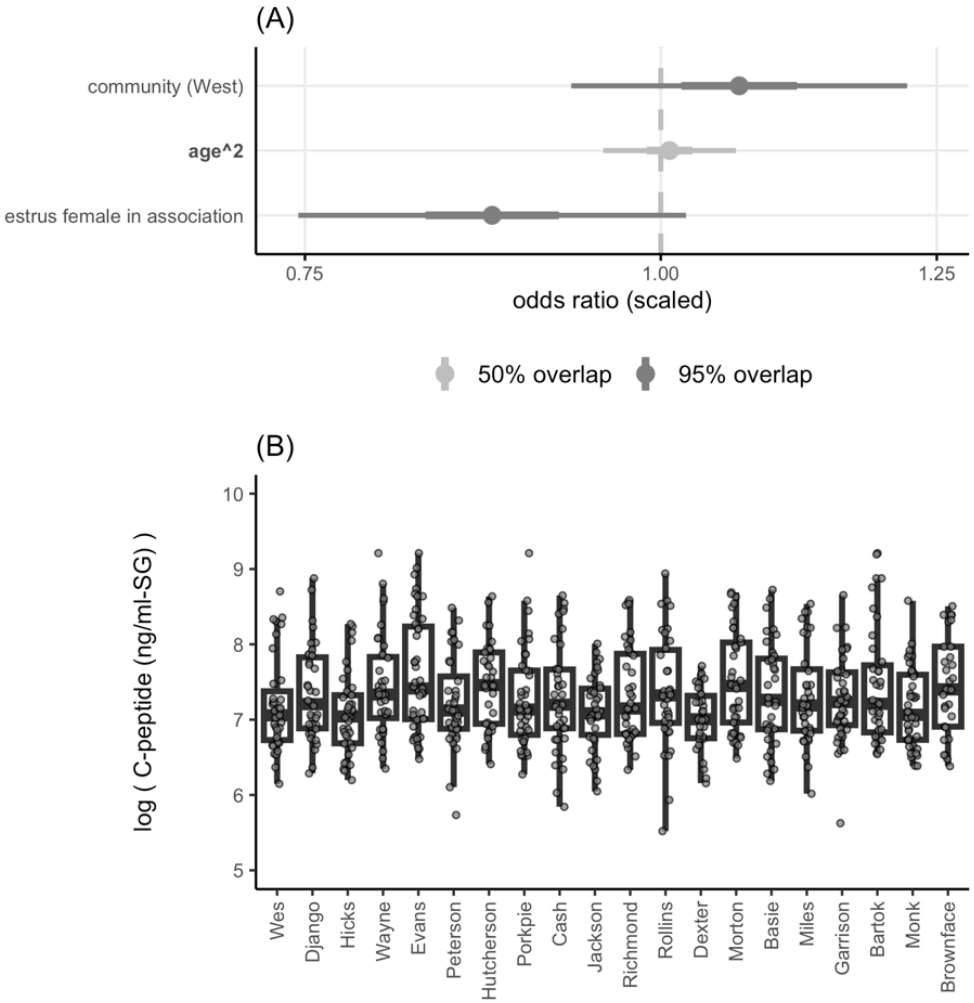

Figure 6. Urinary C-peptide Insulin: there was no relationship between age and urinary C-peptide (n=619). (A) coefficient plot with back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect. Coefficient plots exclude control predictors (time of day, date) and predictors with 50% CI overlap other than age for visual clarity. For complete coefficient plot see Figure S13. Predictors are centered and standardized so the magnitude of beta coefficients are directly comparable. Bolded terms indicate effects of age^2. (B) C-peptide by subject in order of increasing age (21 to 53 years).

Urinary testosterone did not decline in old age chimpanzees

There was no reliable relationship between age and the testosterone of adult males (**Figure 7**), although the maximum likelihood estimate predicted that testosterone decreased by 0.96±1.06 times for each SD increase in age (equivalent to 9.6 years) (**Table S14**). There was a reliable effect of community on testosterone, indicating that testosterone concentration was by 1.49(±1.12) times higher in the Ngogo West than Ngogo Central. Rank was also uncorrelated with testosterone. Both date and time predictors were the most reliable correlates of testosterone, even after controlling for percent foraging time and party composition. I present results here from an analysis of testosterone samples associated with complete predictor values (n=264), however, I also conducted a supplementary analysis with additional urinary testosterone samples (n=318), which excluded party composition predictors due to missing values. In this supplementary analysis with a larger sample size, once again there was no correlation between testosterone concentration and subject age.

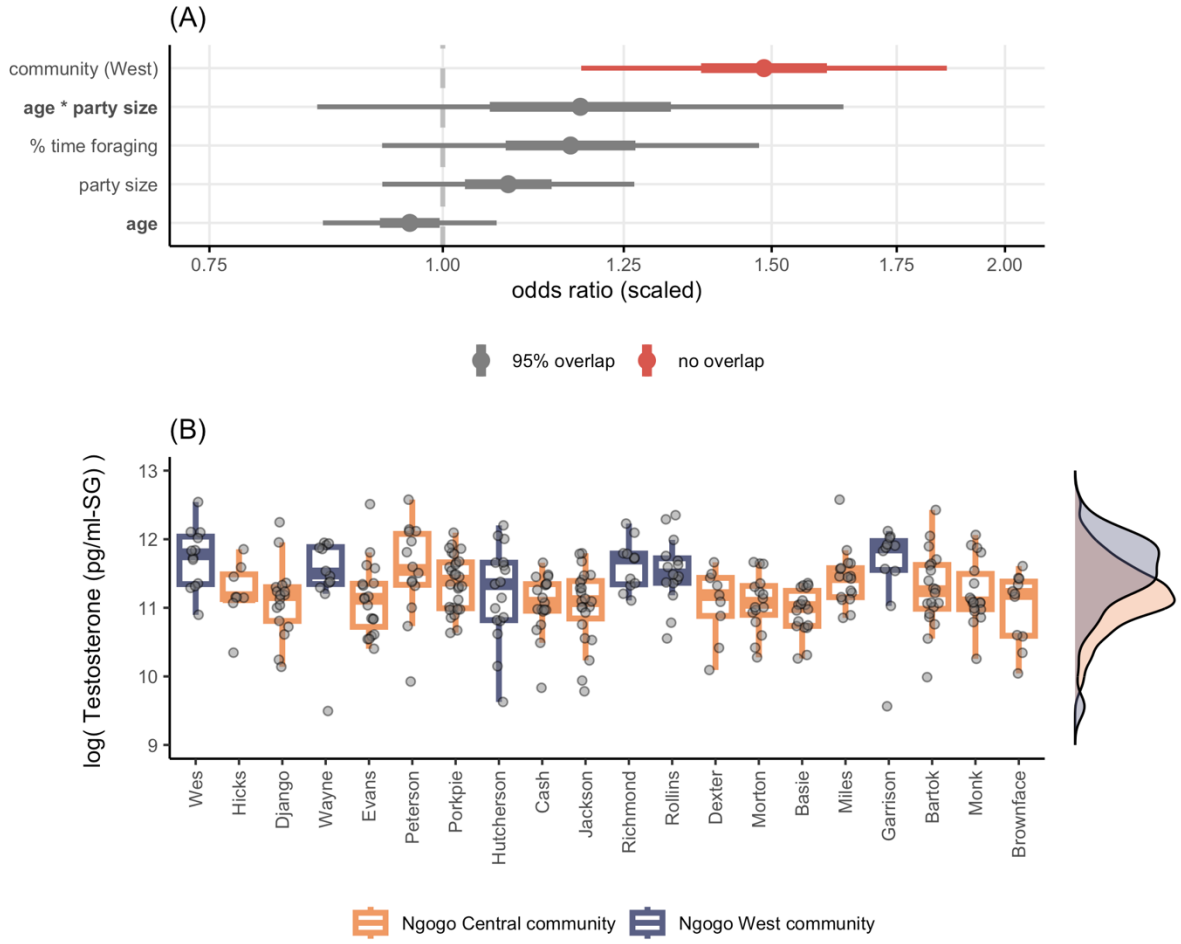

Figure 7. Urinary testosterone. There was no reliable relationship between age and the testosterone of adult males (n=264). (A) coefficient plot with back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect. Coefficient plots exclude control predictors (time of day) and predictors with 50% CI overlap other than age for visual clarity. Bolded terms indicate effects of age and its interactions. For complete coefficient plot see Figure S14. Predictors are centered and standardized so the magnitude of beta coefficients are directly comparable. (B) Testosterone by subject in order of ascending age left-to-right, color coded for the two Ngogo communities with a density distribution by community.

Old chimpanzees displayed less often and over shorter distances

On average, adult male chimpanzees displayed approximately 0.58 times per hour and traversed an average of 7.5(±8.6 SD) meters during displays. Display frequency decreased with age^2 as for each SD increase, display count decreased by 0.56(±1.20) times (**Figure 8A**). Consequently, the predicted per hour display rate was 0.8 for a 22-year-old and 0.4 for a 47 year old (the 10th and 90th subject age quantiles) (**Figure 8B**). Display frequency was also negatively correlated with the percent of time spent foraging, a potential inverse-proxy of diet quality, while counts decreased by 0.34(±1.20) times for each additional SD percentage increase in percent time spent foraging (**Table S15**).

Similarly, display distance was negatively correlated with age; for each SD increase in age, display distance decreased by 0.72(±1.16) times (**Figure 8C, Table S15**). Consequently, the predicted per hour display rate decreased by 1.9m meters for each additional 10 years of life (**Figure 8D)**. Display distance was also negatively correlated with rank, but rank interacted with party size, indicating that in large parties, higher ranking chimpanzees displayed over longer distances (**Figure 8C**).

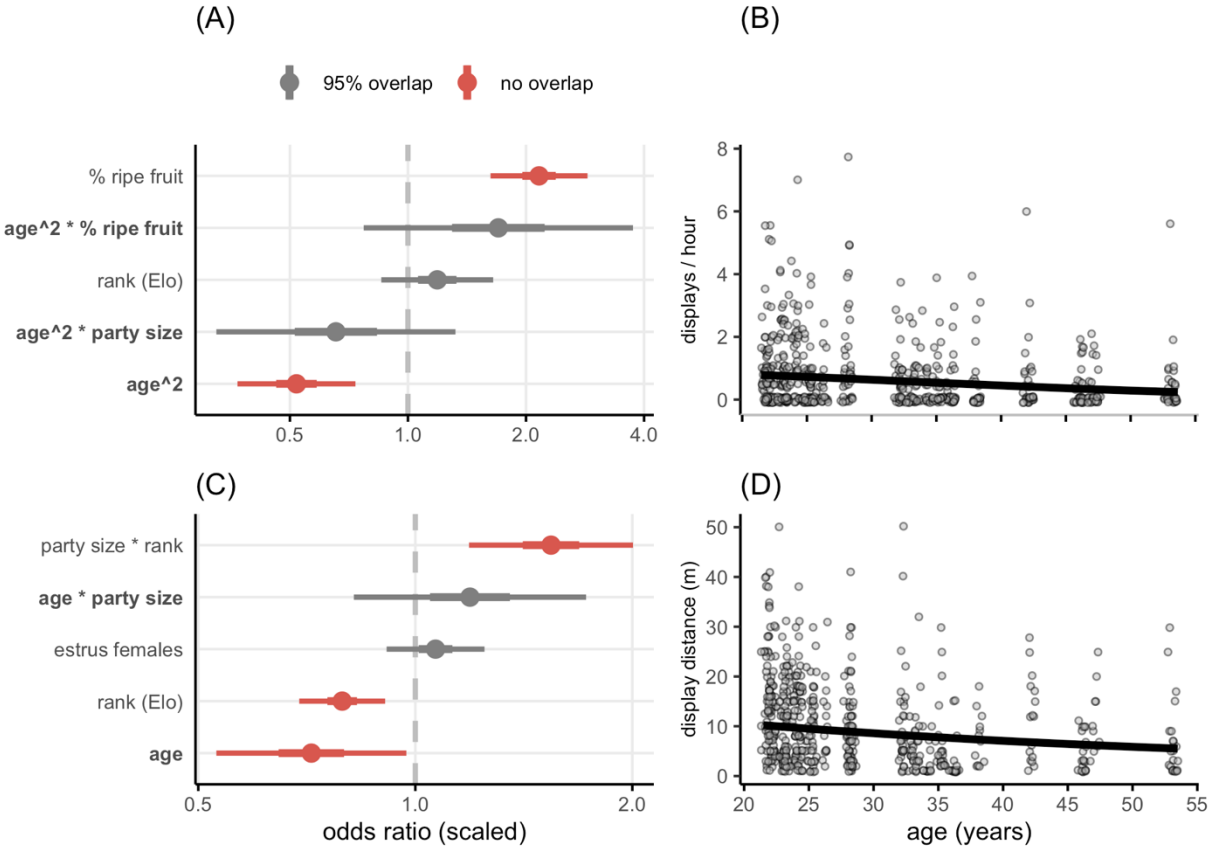

Figure 8. Social display counts (A, B) (n=767 display counts over 1288 focal observation hours) and distance (C, D) (n=593 displays of known distance) which were negatively correlated with age. (A) and (C) coefficient plots with back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect. Coefficient plots exclude control predictors (focal duration offset, date, observer) and predictors with 50% CI overlap other than age for visual clarity. For complete coefficient plots see Figures S15, S16. Bolded terms indicate effects of age or age^2 and their interaction. Predictors are centered and standardized so the magnitude of beta coefficients are directly comparable. (B) and (D) depict predictions from model averages with all other predictors held at their mean. Each data point in (B) represents a focal (n=689) and each data point in (D) represents a display (n=593)

Older males mated less because younger males copulated more during high quality food periods

Across the study period, adult male chimpanzees copulated 2.2 times every 10 hours. Age^2 had a state-dependent effect on copulation frequency via an interaction with percent time spent foraging, an inverse-proxy for diet quality; younger males copulated more in good food times, days with low amounts of time spent foraging (**Figure 9A)**. Meanwhile, copulation rates were consistently low across all ages during poor quality food times characterized by large amounts of foraging. Copulation frequency was also positively correlated with the number of estrous females in association (1.66±1.20 times higher for each SD increase in the number of estrous females) (**Table S17**).

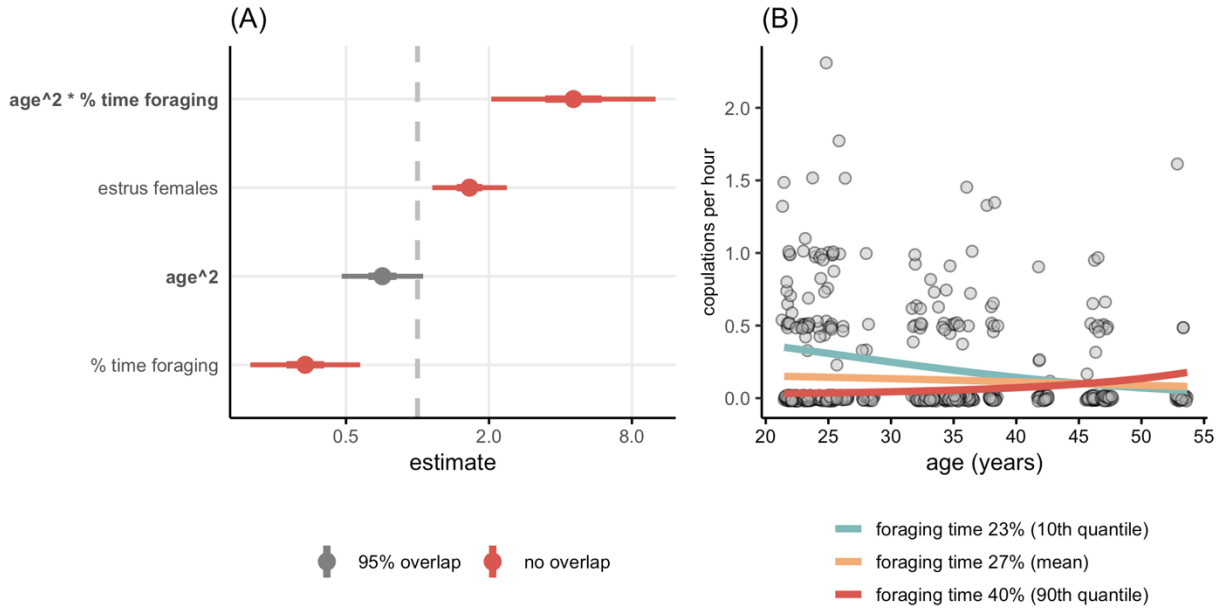

Figure 9. Adult male copulation rates (n=154 copulations over 1302 focal observation hours). (A) depicts coefficient plot and (B) depicts age effect predictions, both from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Predictors are centered and standardized so beta coefficients are comparable. Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect. Coefficient plot excludes control predictors (date and observer) and predictors with 50% CI overlap for visual clarity. For complete coefficient plot see Figure S17. Predictors are centered and standardized so the magnitude of beta coefficients are directly comparable. (B) Relationship between age, foraging time, and copulation rate according to model average predictions. Each data point depicts the rate of copulations for a focal (n=689).

Discussion

This study examines a suite of behavioral, but not physiological shifts with age in a cohort of particularly long-lived adult male chimpanzees. Neither C-peptide of insulin (**Figure 6**), a measure of energetic status, nor testosterone (**Figure 7**), a costly hormone and proxy for reproductive investment, varied reliably with age. In contrast, the rate of foraging increased with age in large parties and decreased in small parties (**Figure 4A)**. Old chimpanzees spent more time resting and less time moving regardless of environmental factors (**Figure 4C**), yet vertical climbing distances did not vary reliably with age (**Figure 5**). Meanwhile, display frequency (**Figure 8A**) and distance (**Figure 8C)** both declined with age, in addition to copulation rates during good food periods (**Figure 9**). I interpret these results in consideration of my hypotheses on shifting tradeoffs with age and considering two life history loci: resource pool management and allocation (see **Figure 3** for a conceptual diagram and **Table 3** for a summary of predictions and findings). My results provide insights into the potential tradeoffs between physiology and behavior that old chimpanzees may make as they balance

deteriorations of age with an observed capacity to maintain condition and survivorship until late in life (Emery Thompson et al. 2020a, Wood et al. 2017).

Regarding resource management, there is no evidence to support the 'acquisition' hypothesis that old chimpanzees prioritize obtaining resources to compensate for either increased energetic costs and diminished foraging performance. Contrary to my prediction, old chimpanzees only foraged more when in association with a large number of chimpanzees, and actually foraged less when in association with few chimpanzees. This effect controlled for a measure of diet quality (proportion of high-quality fruit in the diet), which is positively correlated with party size. Old chimpanzees may forage more in larger parties because of increased costs of sociality with age which could include increased feeding competition, increased energetic costs of socializing, and greater costs from social stress (Emery Thompson 2014). Older males also did not socialize less or more than prime-aged males (**Figure 4A**), which may provide circumstantial support for this explanation. Because there was no interaction between age and diet quality on foraging activity, it is unlikely that these patterns are directly attributable to foraging senescence.

Results were more consistent with the 'restriction' hypothesis, in which old male chimpanzees limit metabolic activity. Here, I predicted that various energetically expensive behaviors would decline with age. Time devoted to resting increased and moving decreased with age. There was no reliable evidence, however, that vertical climbing distance decreased with age. Taken together, these findings accord with modern adaptations of the 'rate of living' theory of aging (Pearl 1928), which links increased metabolic activity to increased oxidative stress (Costantini 2008) and predicts

that old organisms should engage in strategic restriction when they are likely to encounter energy-related senescence. This is because high levels of metabolism (oxidative phosphorylation) are linked to higher rates of damage (senescence) (Finkel & Holbrook 2000). While these findings are not immediately distinguishable or mutually exclusive from a terminal restraint strategy of allocation, they reflect distinct underlying mechanisms. Old chimpanzees may either decrease energetic expenditure in proportion to their overall diminished resource pool or invest relatively less in activity to increase investment in maintenance via somatic tissue or immune function in the face of shifting tradeoffs with reproduction.

Regarding the allocation locus, I found consistent support for the terminal investment hypothesis. Reproductive behaviors – social display distance, frequency, and copulation rates – all were negatively associated with age. Energetic status as measured by C-peptide insulin did not decline with age, which was predicted if old male chimpanzees increased reproductive investment at the cost of somatic maintenance. In contrast, testosterone, a costly proxy for reproductive investment, was maintained into old age showing no relationship with subject age. The conservation of testosterone into old age suggests that aging males maintain secondary sex characteristics to take advantage of reproductive opportunities, even if they are less frequent in old age. Given that testosterone increases metabolic rates in muscle cells (Tsai & Sapolsky 1996), the maintenance of testosterone suggests that older males are investing *relatively* more compared to their declining activity.

Conversely, the decreases in allocation to reproductive behaviors and maintenance of energetic status provided stronger support for the terminal restriction

hypothesis in which old male chimpanzees prioritize maintenance and somatic condition to maximize future reproduction by minimizing potential mortality costs of expenditure. Additionally, in accordance with predictions, old males also spent more time resting and less time moving. In contrast to the terminal restriction predictions, there was no indication that old individuals were sensitive to environmental stressors as state-dependent interaction effects between measures of investment with diet quality were absent from top models. Old male chimpanzees did not appear to restrain activity differentially with dietary quality. A state-dependent effect of age on copulation rate indicated that prime-aged males were, on the other hand, better able to take advantage of good food periods during which they copulated more than old males.

I considered the relationship between the behavioral and physiological outcomes with either linear age or the quadratic age^2 based on preliminary analyses. Outcomes where linear age was a reliable predictor (activity budgets, display distance) suggest that effects of senescence may accumulate steadily over the lifespan of subjects (age 21-53). When outcomes had quadratic age^2 as a reliable predictor (display and copulation frequency), the effects of senescence increasingly play a role over the lifespan.

Old chimpanzees reduced certain energetically expensive behaviors

I found that resting behaviors increased while movement decreased in old chimpanzees (**Figure 4C**). While prior studies have shown that declines in physical condition were accompanied with moderate changes in physical activity (Alberts et al. 2014), a study of the Kanyawara chimpanzees only found declines in foraging behavior,

not movement or resting (Emery Thompson et al. 2020a). My analyses showed that while foraging behavior did not change with age alone, old chimpanzees spent more time foraging than their prime-aged counterparts when in large parties and controlling for diet quality (**Figure 4B**). Rather than reflecting increased costs of sociality, an alternative explanation is that because fission-fusion allows for flexible group choices, old chimpanzees may only choose to be in larger parties when conditions permit increased foraging and decreased resting. Because I defined party size at the level of daily association, this coarse resolution may limit the interpretation of this party size effect; the party size predictor does not capture the intra-day variation in sociality. For instance, my measure of party size would not capture the degree to which a chimpanzee may be peripherally associated at the edge of the group, and thus from the perspective of foraging competition, may be in a small party size. A study that incorporates a less coarse measure of party size could more accurately assess feeding competition and more detailed social decisions throughout the day. Such patterns could provide insight into the patterns of social senescence of old chimpanzees, who appear to be both more solitary - spending more time alone - and also more prosocial - engaging in increased proximity and grooming (Rosati & Machanda 2020).

Social aging patterns do not explain why foraging time decreased when in smaller parties, a finding consistent with the longitudinal study of aging at Kanyawara (Emery Thompson et al. 2020a). One possibility is that if old chimpanzees are less proficient at extracting resources from lower quality food items, then this shift could signal that old chimpanzees invest less in foraging when returns are lower. Emery Thompson et al. (2020) attributed foraging shifts with age to differences in arboreality:

old chimpanzees were more terrestrial and thus they suggested that “climbing may have been the key limitation on feeding.” However, I found no consistent differences in climbing behavior. This result coincides with other findings that the Ngogo chimpanzees did not forage more terrestrially with age and did not climb less while foraging (see Chapter 2). Consequently, while not limited by climbing behavior, I found that old chimpanzees still foraged differently, with reduced movement and increased resting.

The analyses of display frequency and distance demonstrate that after controlling for rank, party composition, and other factors, old chimpanzees invested less in social displays (**Figure 8**). Such results are consistent with prior findings that mobility, particularly movement speed, decreases with age in primates (Shively et al. 2012) and that older males are less aggressive (Rosati et al. 2020). I also observed declines in copulation rates with age during high-quality food times when controlling for rank (**Figure 9**). Yet older males still represented a sizable proportion of copulation counts: 29 of 154 observed copulations (18%) were from five oldest subjects (age > 38 years) and all subjects were observed copulating multiple times.

Old males maintained testosterone levels

Urinary testosterone showed no association with age regardless of seasonality or time of day (**Figure 7**). Considering the decreases in behaviors associated with reproductive investment (social displays and copulation), it is notable that testosterone did not decline in tandem. Testosterone is commonly considered the quintessential physiological modulator of aggressive behaviors employed to promote reproductive effort (Wingfield 1990, Ketterson & Nolan 1999). Prior studies have found correlations

between aggressive behaviors like displays and reproductive behaviors including copulations with testosterone in a variety of primates including chimpanzees (Muller & Wrangham 2004, Mueller 2017). Observations in this chapter are consistent, however, with other findings from the same population of chimpanzees that did not document an association between testosterone and display rate (Muehlenbein & Watts 2004) and that testosterone may act as a mediator of dominance via body size, not aggression (Negrey et al. 2023). Because, testosterone comes with substantial costs including increased metabolic rates (Muehlenbein & Bribiescas 2005) and immunosuppression (Prall & Muehlenbein 2014), testosterone is thought to come at the expense of long-term survival (Hau 2007). Given the costly nature of testosterone, it should offer reproductive benefits if aging males incur relatively greater costs to maintain it. Yet testosterone senescence is not evident in my findings. The age-specific peak and then decline of testosterone in accordance with fertility is well-documented across a number of primate species (Beehner et al. 2009, Muller 2017). Given the decline in male fertility at Ngogo (Langergraber unpublished data), the lack of a relationship between age and testosterone in my sample was not predicted. While there is well-documented evidence for testosterone senescence in both humans (Harman et al. 2001) and non-human primates (Beehner et al. 2009, Muller 2017), there is substantial variation in this decline. Within humans, American males tend to exhibit a decline after age 40 (Gray et al. 1991), while other populations are characterized by either more modest declines or none at all (Ellison et al. 2002). Interspecies comparison suggests that factors like reproductive skew may influence rates of testosterone senescence; testosterone senescence is much more pronounced in baboons than chimpanzees (Beehner et al.

2009, Muller 2017). Future work to clarify these relationships would likely also explain the clear group difference between the two Ngogo chimpanzee communities, although that is beyond the scope of this study.

According to my analysis, testosterone did not covary with dietary measures. This result is consistent with prior findings that social factors, rather than changes in energy availability, were associated with testosterone production (Muller & Wrangham 2004). Indeed, the only reliable non-control predictor of testosterone was community. Notably, I did not find an effect of dominance rank on testosterone. While testosterone has been positively associated with rank in chimpanzee studies (Muller & Wrangham 2004) including at Ngogo (Muehlenbein, et al. 2004), this is not always the case (Sobolweksi et al. 2013). Further, I found that neither party size nor the presence of parous estrous females had a reliable effect, although their presence did improve model performance, suggesting that these factors explain a degree of the variation in testosterone. A notable drop in testosterone around the month of May remains unexplained. Because testosterone decreases in response to immune system challenges (Muehlenbein et al. 2006), I hypothesized that this drop may coincide with a contagious illness, but assessing the validity of this explanation is beyond the scope of this study.

What explains variation in energetic status?

Urinary C-peptide insulin did not vary with age, indicating that old males were in equivalent energetic condition to prime-aged males (**Figure 6**). Urinary C-peptide insulin tracks energetic status in primates including chimpanzees (Ellison et al. 2003, Deschner

et al. 2008, Emery Thompson et al. 2009). Because old chimpanzees have potentially greater energetic demands from increased immune burdens (Negrey et al 2020, 2021) and potentially lower energetic returns due to foraging senescence (see Chapter 2), I predicted that energetic status would decline with age, which was not the case. Old chimpanzees also have decreased muscle mass (Emery Thompson et al. 2012), which is energetically expensive to maintain (Zurlo et al. 1990, Bribiescas 1996, Mitani et al. 1996). Emery Thompson et al. (2020a) found that estimated lean body mass increased through the early 30s, and then sharply declined such that by age 40, males had lower lean body mass than at previous adult age. It is possible that physiological declines associated with increased immune burden, decreased energetic returns, but lower metabolic costs from muscle mass could have offset one another so that there was no net decline in energetic balance. A similar phenomenon was observed in deep-diving thick-billed murres (*Uria lomvia*), where older birds had both lower blood oxygen stores and oxygen utilization rates, but the two counteracted one another so that dive performance was unchanged (Elliot et al 2015). A longitudinal study of chimpanzee glucocorticoids as a proxy for stress found that while overall levels increased with age, old chimpanzees were not more sensitive to energetic stress (Emery Thompson et al. 2020b). Consequently, while old chimpanzees may be able to maintain both behavioral and energetic performance with age, it could be increasingly challenging to do so.

The result that C-peptide concentrations were not reliably associated with any socioecological predictors was surprising and may be attributed to the ability of subjects to successfully balance their energetics, the high-quality resources available at Ngogo generally, and/or the large amounts of ripe fruit that characterized the study period. Ripe

fruits are considered high quality diet items for chimpanzees and their contribution to diet is associated with decreased dietary diversity (Watts et al. 2012), greater C-peptide levels (Emery Thompson et al. 2009), and in this study, decreased foraging times. Yet other studies have shown mixed results in ripe fruit's ability to explain C-peptide variation (e.g. Wessling et al. 2018). At Ngogo, ripe fruits are associated with an increase in territorial and hunting patrols (Mitani et al. 2003), which are energetically expensive behaviors. These findings coincide with observations from my study period, in which the lowest C-peptide values corresponded to a *Uvariopsis* fruit masting event, during which the chimpanzees engaged in daily hunts of a multi-day period, a "hunting binge," which is associated with high travel rates (Watts & Mitani 2002). After controlling for party composition, however, the negative effect of this high-quality fruit disappeared. This result reinforces the importance of considering both ecological and social environments in analyzing energetics (as recommended in Emery Thompson et al, 2014). An important factor to consider in future studies is daily travel distance, especially because chimpanzee's day ranges can be greater than any other non-human primate (Chapman et al. 1995).

The lack of relationship between C-peptide and numerous predictors including diet quality and party composition in this sample may suggest that these subjects have ample access to food and thus are not food stressed. This is consistent with prior findings of Ngogo's abundant ripe fruit resources (Potts et al. 2011), higher intake rates (Potts et al. 2015), and higher C-peptide levels (Emery Thompson et al. 2009) than the Kanyawara chimpanzee community, where associations between diet seasonality and C-peptide may be clearer (Emery Thompson 2012). Of particular note, this study took

place over a 12-month period, which appeared to be a particularly high-quality food period featuring large proportions of high-quality fruit in the diet. Consequently, it is possible that these data did not capture particularly poor food seasons when associations between diet quality and C-peptide may have become apparent. Similarly, the absence of stressful dietary periods during this study may also illuminate the mixed support for the terminal restraint hypothesis; to properly examine whether old males strategically reduce reproduction for the sake of reducing mortality risk should include poor food periods.

Maintaining condition and alternative reproductive tactics

Senescence has a litany of degenerative effects on the physiology of wild animals that result ultimately in decreased fertility and increased mortality with age (Nussey 2013 and Jones et al. 2014). Yet in this study, old male chimpanzees managed to maintain several physiological measures and investment in the face of almost certainly increased costs, particularly those associated with testosterone. I observed concomitant reductions in energetically expensive behaviors such as movement and displays, which I propose is consistent with strategies to prioritize both terminal restriction in resource management and terminal restraint in resource allocation. In this way, old chimpanzees may adjust their behavior in the face of changing payoffs to compensate for increased costs of maintaining physiological condition, thereby extending the 'healthspan.' However, the maintenance of elevated testosterone with age suggests old apes continue to invest in reproductive fitness at the expense of continued lifespan.

While I suggest here that decreases in social displays may represent terminal restraint, it is possible that the reproductive tactics of old males shift in the face of changing payoffs. Male reproductive tactics are known to vary within a species (Oliveira et al. 2008), and sometimes with age (Gross 1996). For instance, in primates, old yellow baboons (*Papio anubis)* (Silk et al. 2020) and rhesus macaque (*Macaca mulatta*) (Langos et al. 2013) males who have declined in rank may become more prosocial with females or their own offspring. Silk et al. (2020) hypothesize that old baboon males obtain increasing opportunities through becoming primary associates of females and increase their fitness via paternal care. While it is unlikely chimpanzees are able to discriminate paternal relatives given their polygynandrous mating system (Langergraber et al. 2007), one study found that old males at Ngogo are more likely to associate and groom with adolescents, especially their sons (Sandel et al. 2019). Because the evolution of longevity necessitates both late-life fitness and selection for the prioritization of maintenance, understanding how tradeoffs can shift reproductive tactics away from costly competition may inform the evolution of extended lifespans. Whether this could be the case for male chimpanzees who become less aggressive with age (Rosati et al. 2020) remains to be explored.

Limitations and alternative explanations

By collecting data from the same individuals at the same time, this study avoids confounding effects of interannual variability in resources. Nevertheless, the findings of cross-sectional studies such as the one performed here should be interpreted cautiously when applied to senescence (Nussey et al. 2008). Given this, there are important

alternative explanations that these observed correlations with age do not represent shifting strategies or tradeoffs. Rather, shifts may be reflective of the various decreased capacities with age, non-adaptive decline, and/or the result of survivorship bias.

First, declines in activity with age may be accurately attributed to decreased physical mobility and/or strength without invoking energetic restriction or changing payoffs. For instance, proximate causes for the decrease in display distance with age include decreased musculoskeletal strength or diminished motivation to engage in aggression. Yet such explanations are not alternative or mutually exclusive from the ones I present here. Prioritizing one such explanation to reject another would commit the fallacy to separate complementary levels of analysis – causal mechanisms from their ultimate effects (Tinbergen 1965). Regardless of the mechanistic undergirding, when old chimpanzees decrease and otherwise alter their activities, they shift their investments, which can provide insight into their strategy to maximize fitness after their prime. A focus on functional consequences, not just causes, is necessary for a comprehensive understanding of aging's evolutionary history (Beehner & Bergman 2022).

Because aging evolved through the greater selective pressure at reproductive maturity than later in life (Medawar 1952, Hamilton 1966), it is certainly possible for emergent characteristics of old age such as behavioral shifts to be non-adaptive. In other words, antagonistic pleiotropy predicts the existence of phenotypes that do not maximize fitness late in life, which calls into question the utility of employing an adaptive framework to understand the tradeoffs of old male chimpanzees. However, this explanation is not entirely consistent with the observed patterns of aging in adult male

chimpanzees as I describe them here because of the timing of the declines and the absence of declines in these physiological measures. First, observed changes occurred across adulthood, with many decreases being linear effects. Because male chimpanzees in this community continue to reproduce until late in life, with 5% of offspring sired by individuals over the age of 45 (Langergraber unpublished data), the tradeoffs described here are likely still under selective pressure.

Prior studies have found that individuals show more pronounced senescent phenotypes immediately preceding death (Coulson & Fairweather 2001), including in chimpanzees for whom poor condition was acutely associated with illness and death (Emery Thompson et al. 2020a). This was not the case for the subjects described here. As data presented in this paper were collected in 2018-2019, I can now assess mortality proximity post-hoc. Of the 20 subjects, 13 were still alive as of November 2022. Of the deceased, four were killed by conspecifics (Hicks DOB 1997, Basie DOB 1983 killed in 2019; Porkpie DOB 1994 killed in 2001, and Jackson DOB 1991 killed in 2022) and three from unknown causes. Of the latter, Cash (1993) is suspected to have succumbed to disease in April 2021, as he displayed chronic signs of a skin infection, during the study period. The two remaining individuals, Bartok (1973) and Monk (1972) were considered old age, and their bodies were not recovered after disappearing in May 2020 and July 2020. Thus, I cannot rule out that their behavior during the study period was shaped by proximity to death, although they survived at least another 9 to 11 months from the end of the study period. Notably, the oldest subject, Brownface (born est. 1966), was still alive as of November 2022A. Brownface displayed an apparently senescent phenotype and has been nearly toothless since at least 2012 (Finkel

unpublished data). His perseverance suggests that individuals can survive, and potentially reproduce, for long periods with senescent phenotypes. Lastly and importantly, the study subjects were shown to maintain physiological status via C-peptide insulin and testosterone. Therefore, while mortality proximity may putatively explain some of the activity shifts with age documented here, it is unlikely to explain its extent or consistency across subjects.

In my view, the most plausible alternative explanation of my results is that they represent survivorship bias. Mortality selection could mean that this study is one of exceptional survivors, chimpanzees who may have necessarily senesced more slowly than their peers (Vaupel et al. 1979). For instance, if chimpanzees who invest less in reproduction are more likely to survive to old age – there some evidence of this in humans (Penn & Smith 2007), but not captive primates (Tidiére et al. 2017) – then a cross-sectional analysis could reveal apparent progressive senescence of reproductive investment due to the predominance of old age cohort chimpanzees. Diseases for which age positively predicts morbidity could contribute to such an effect, as may have been the case in a 2016-2017 outbreak of a reparatory virus where individuals ≥30 years old were 3.86 times as likely to die than younger adults (Negrey et al. 2019). However, an important source of mortality for adult males is extrinsic. Male chimpanzees make lethal coalitionary attacks on their neighbors (Mitani et al. 2010). Due to the stochastic nature of such deaths, this common mortality source likely has a weak selection signature against senescence and therefore there is little a priori justification to believe that the surviving members of older cohorts present an especially biased sample with respect to senescing phenotypes. Nonetheless, there is ample

evidence that high quality individuals survive longer, which has created the quality 'syndrome' wherein inter-individual variation masks tradeoffs, particularly in old age primates (McLean et al. 2019). Further research should explore longitudinal changes in tradeoffs among a larger sample of adult males to parse whether these observed correlations with age are the result of changing payoffs with age and shifts within the lifetime or attributable to inter-individual variation.

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Supplementary Materials

Table S10. Subject ID (n = 20) in order of increasing age. Age corresponds to age at study midpoint (February 2018) and ranks reflect the average Elo rating over the study period.

ID	age	birth year	community	Elo rating (mean)	ordinal rank
Wes	21.7	1997	West	-452.73	5
Django	22.1	1997	Central	-435.42	13
Hicks	22.1	1997	Central	-279.4	11
Evans	23.1	1996	Central	17.34	7
Wayne	23.1	1996	West	-674.24	6
Peterson	24.1	1995	Central	137.56	5
Hutcherson	25.1	1994	West	579.17	1
Porkpie	25.1	1994	Central	-130.61	9
Cash	26.1	1993	Central	-444.11	14
Jackson	28.1	1991	Central	696.64	1
Richmond	32.1	1987	West	197.56	2
Rollins	33.1	1986	West	-444.92	5
Dexter	34.1	1985	Central	-601.36	16
Morton	35.1	1984	Central	286.74	3
Basie	36.1	1983	Central	65.75	7
Miles	38.1	1981	Central	116.66	6
Garrison	42.1	1977	West	-304.48	4
Bartok	46.1	1973	Central	-17.73	8
Monk	47.1	1972	Central	-407.54	12
Brownface	53.1	1966	Central	-628.16	16

Table S11. Activity budget top model effects. Back-transformed (exponentiated) beta-coefficients from the top model (cumulative weight = 0.63) along with the SE and ranges for 50% and 95% confidence intervals.

variable	estimate	SE	CI.low	CI.high	overlap	parameter
% high quality fruit	0.66	1.15	0.5	0.88	no overlap	forage vs. rest
age	0.97	1.12	0.78	1.22	50% overlap	forage vs. rest
age * party size	1.59	1.14	1.22	2.06	no overlap	forage vs. rest
date	1.19	1.11	0.97	1.46	95% overlap	forage vs. rest
date (cos)	0.81	1.09	0.68	0.97	no overlap	forage vs. rest
Intercept	0.69	1.07	0.61	0.79	no overlap	forage vs. rest
observer (SN)	0.89	1.09	0.76	1.05	95% overlap	forage vs. rest
party size	1.05	1.11	0.86	1.28	50% overlap	forage vs. rest
rank (Elo)	1.09	1.1	0.9	1.32	95% overlap	forage vs. rest
time (cos)	0.65	1.06	0.58	0.72	no overlap	forage vs. rest
time (sin)	1.14	1.05	1.04	1.25	no overlap	forage vs. rest
% high quality fruit	0.74	1.19	0.53	1.04	95% overlap	move vs. rest
age	0.79	1.13	0.62	1	no overlap	move vs. rest
age * party size	1	1.19	0.72	1.4	50% overlap	move vs. rest
date	0.68	1.13	0.53	0.86	no overlap	move vs. rest
date (cos)	1.07	1.11	0.88	1.31	95% overlap	move vs. rest
Intercept	0.32	1.08	0.28	0.37	no overlap	move vs. rest
observer (SN)	1.36	1.1	1.12	1.64	no overlap	move vs. rest
party size	1.16	1.12	0.92	1.45	95% overlap	move vs. rest
rank (Elo)	1.14	1.11	0.93	1.41	95% overlap	move vs. rest
time (cos)	0.77	1.07	0.68	0.87	no overlap	move vs. rest
time (sin)	1.16	1.06	1.04	1.3	no overlap	move vs. rest
% high quality fruit	0.62	1.2	0.44	0.9	no overlap	socialize vs. rest
age	0.89	1.16	0.66	1.19	95% overlap	socialize vs. rest
age * party size	0.83	1.19	0.59	1.18	95% overlap	socialize vs. rest
date	0.76	1.14	0.59	0.99	no overlap	socialize vs. rest
date (cos)	0.98	1.12	0.79	1.23	50% overlap	socialize vs. rest
Intercept	0.24	1.09	0.2	0.29	no overlap	socialize vs. rest
observer (SN)	1.3	1.11	1.06	1.6	no overlap	socialize vs. rest
party size	1.37	1.13	1.07	1.74	no overlap	socialize vs. rest
rank (Elo)	1.13	1.13	0.88	1.45	95% overlap	socialize vs. rest
time (cos)	1.31	1.08	1.14	1.52	no overlap	socialize vs. rest
time (sin)	0.82	1.07	0.72	0.92	no overlap	socialize vs. rest

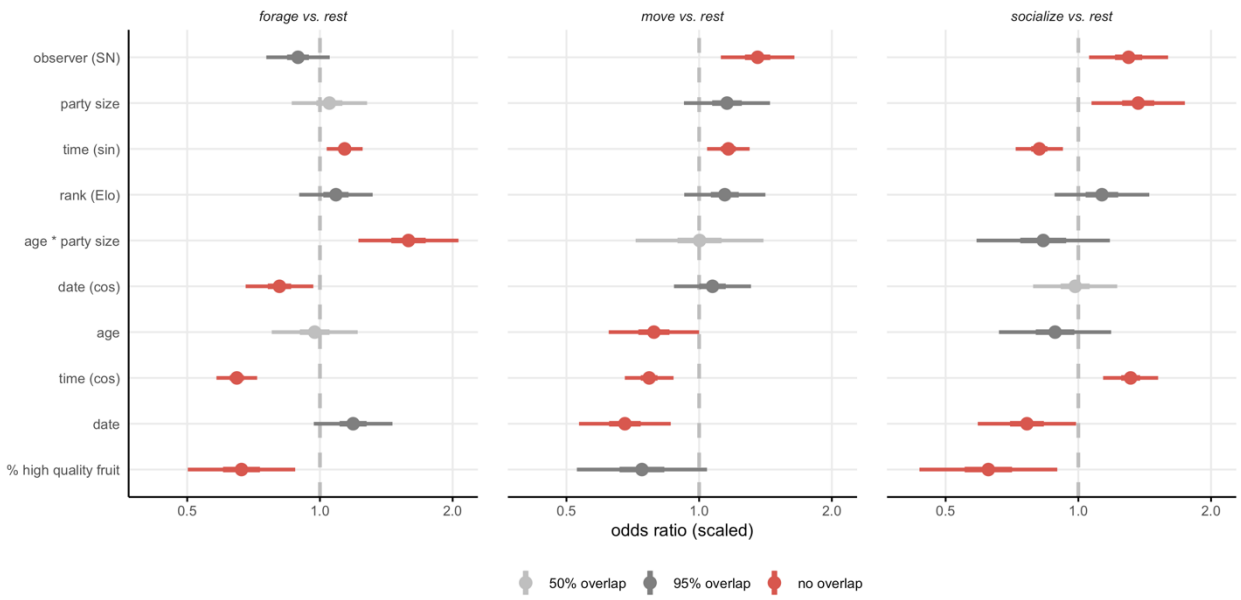

Figure S11. Activity analysis complete coefficient plot. Coefficient plot from back-transformed (exponentiated) beta-coefficients from top performing model (AIC weight ≥0.63). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S12. Climbing distance averaged model effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95).

variable	estimate	SE	CI.low	CI.high	overlap	parameter
% high quality fruit	0.55	1.15	0.42	0.73	no overlap	nu (|Δheight| = 0)
age	1.25	1.23	0.83	1.89	95% overlap	nu (|Δheight| = 0)
community (West)	0.87	1.22	0.59	1.27	95% overlap	nu (|Δheight| = 0)
estrus females	1.33	1.16	0.99	1.79	95% overlap	nu (|Δheight| = 0)
forage context 0	2.44	1.14	1.88	3.16	no overlap	nu (|Δheight| = 0)
forage context 1	0.74	1.1	0.61	0.89	no overlap	nu (|Δheight| = 0)
forage context 2	0.12	1.18	0.08	0.16	no overlap	nu (|Δheight| = 0)
intercept	1.39	1.12	1.12	1.73	no overlap	nu (|Δheight| = 0)
party size	0.93	1.14	0.71	1.21	50% overlap	nu (|Δheight| = 0)
time	1.36	1.1	1.13	1.64	no overlap	nu (|Δheight| = 0)
time (cos)	1.7	1.1	1.41	2.06	no overlap	nu (|Δheight| = 0)
% high quality fruit	0.94	1.08	0.81	1.09	95% overlap	mu (|Δheight| > 0)
age	0.94	1.07	0.82	1.08	95% overlap	mu (|Δheight| > 0)
estrus females	1.17	1.08	1	1.37	95% overlap	mu (|Δheight| > 0)
forage context 0	1.01	1.08	0.87	1.17	50% overlap	mu (|Δheight| > 0)
forage context 1	1.31	1.06	1.18	1.46	no overlap	mu (|Δheight| > 0)
forage context 2	1.36	1.1	1.14	1.63	no overlap	mu (|Δheight| > 0)
intercept	14.02	1.04	13.01	15.12	no overlap	mu (|Δheight| > 0)

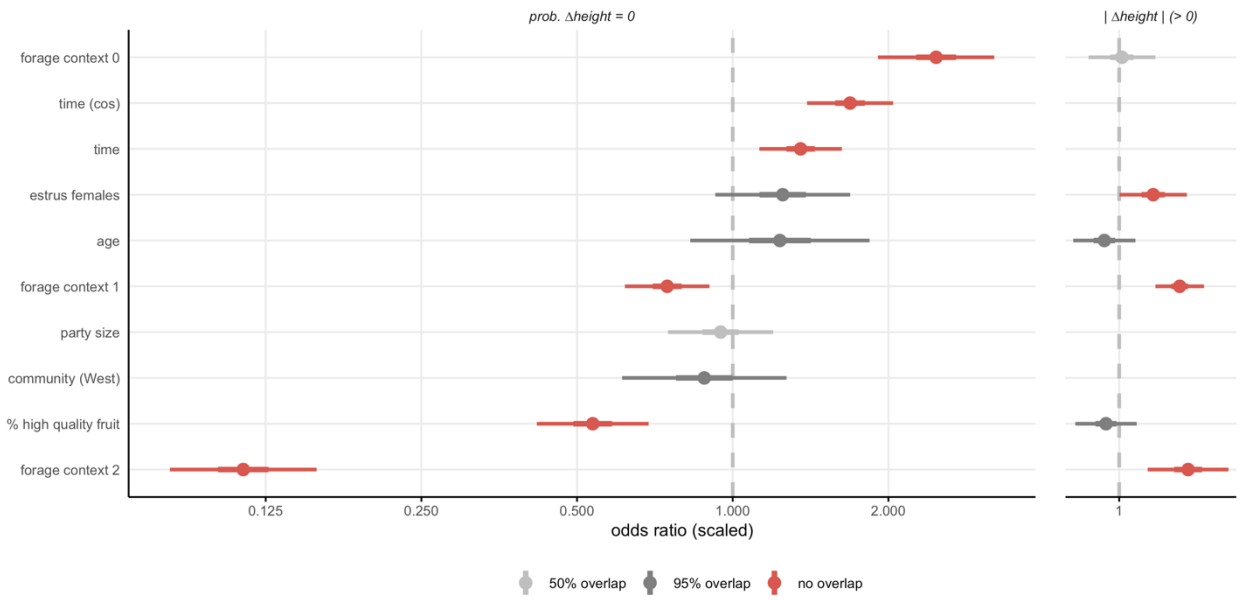

Figure S12. Climbing distance analysis complete coefficient plot. Coefficient plot from back-transformed (exponentiated) beta-coefficients from top performing model (AIC weight ≥0.63). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S13. C-peptide averaged model effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95).

variable	estimate	SE	CI.low	CI.high	overlap
% time foraging	0.95	1.08	0.82	1.09	95% overlap
age	1.01	1.03	0.95	1.06	50% overlap
community (West)	1.05	1.07	0.92	1.19	95% overlap
date (sin)	0.86	1.04	0.79	0.93	no overlap
estrus female * party size	0.91	1.14	0.7	1.19	50% overlap
estrus female * rank	1.05	1.09	0.88	1.24	50% overlap
estrus female in association	0.87	1.08	0.74	1.02	95% overlap
intercept	1091.42	1.08	942.32	1264.11	no overlap
intercept	0.57	1.03	0.54	0.6	no overlap
party size	1.01	1.12	0.82	1.26	50% overlap
rank (Elo)	1.02	1.07	0.89	1.18	50% overlap

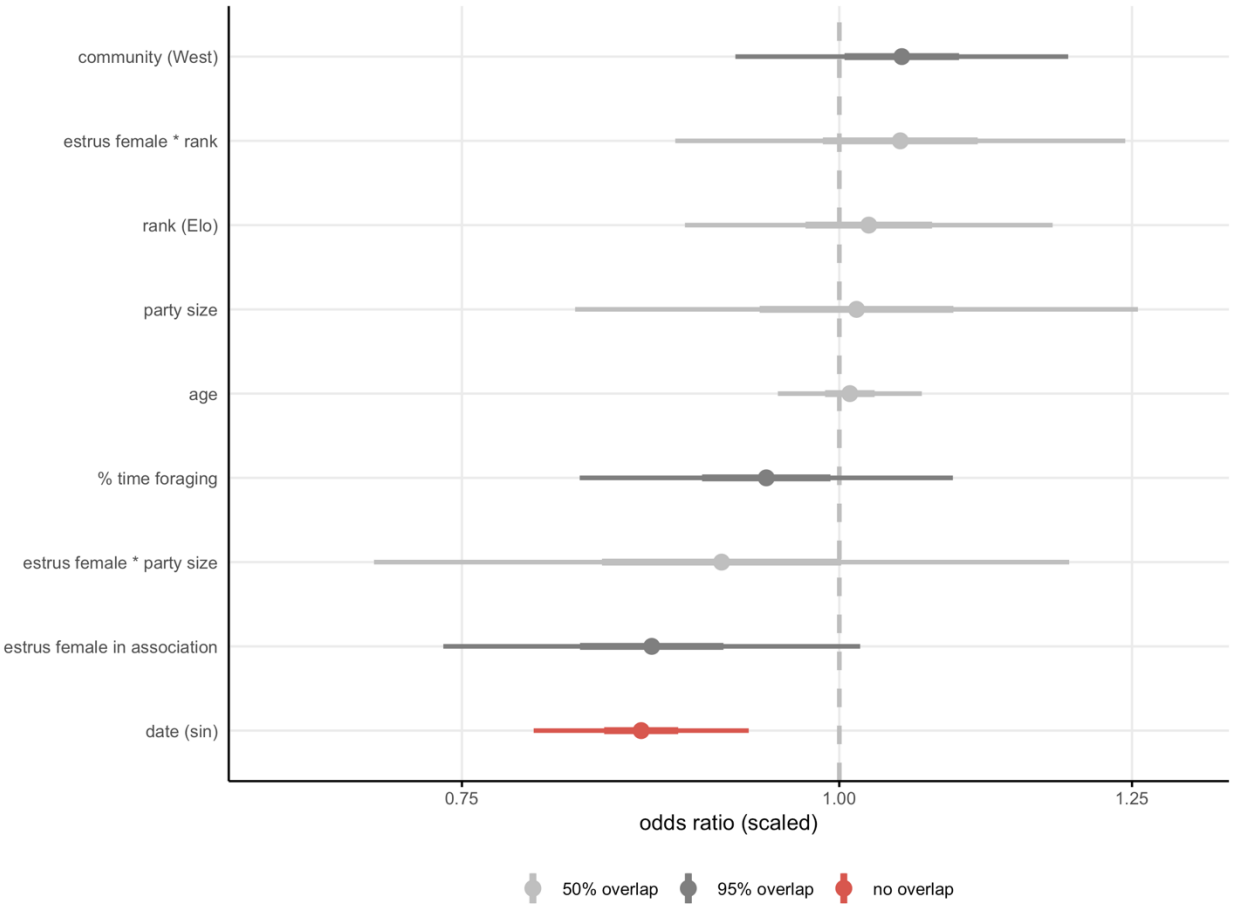

Figure S13. CP analysis complete coefficient plot. Coefficient plot from back-transformed (exponentiated) beta-coefficients from top performing model (AIC weight ≥0.63). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S14. Testosterone averaged model effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95).

variable	estimate	SE	CI.low	CI.high	overlap
% time foraging	1.17	1.13	0.93	1.48	95% overlap
age	0.96	1.06	0.86	1.07	95% overlap
age * % time foraging	0.92	1.14	0.72	1.19	50% overlap
age * estrus females	0.96	1.11	0.78	1.18	50% overlap
age * party size	1.18	1.18	0.86	1.64	95% overlap
alpha	0.93	1.12	0.75	1.16	50% overlap
community (West)	1.49	1.12	1.19	1.86	no overlap
date (cos)	1.22	1.08	1.06	1.41	no overlap
date (sin)	0.79	1.05	0.72	0.88	no overlap
estrus females	1.02	1.05	0.92	1.13	50% overlap
intercept	78466.71	1.05	71626.76	85959.84	no overlap
intercept (sig)	0.43	1.04	0.39	0.47	no overlap
party size	1.08	1.08	0.93	1.27	95% overlap
rank (Elo)	1.01	1.04	0.93	1.09	50% overlap
time (cos)	0.95	1.06	0.85	1.06	95% overlap
time (sin)	0.87	1.04	0.81	0.93	no overlap

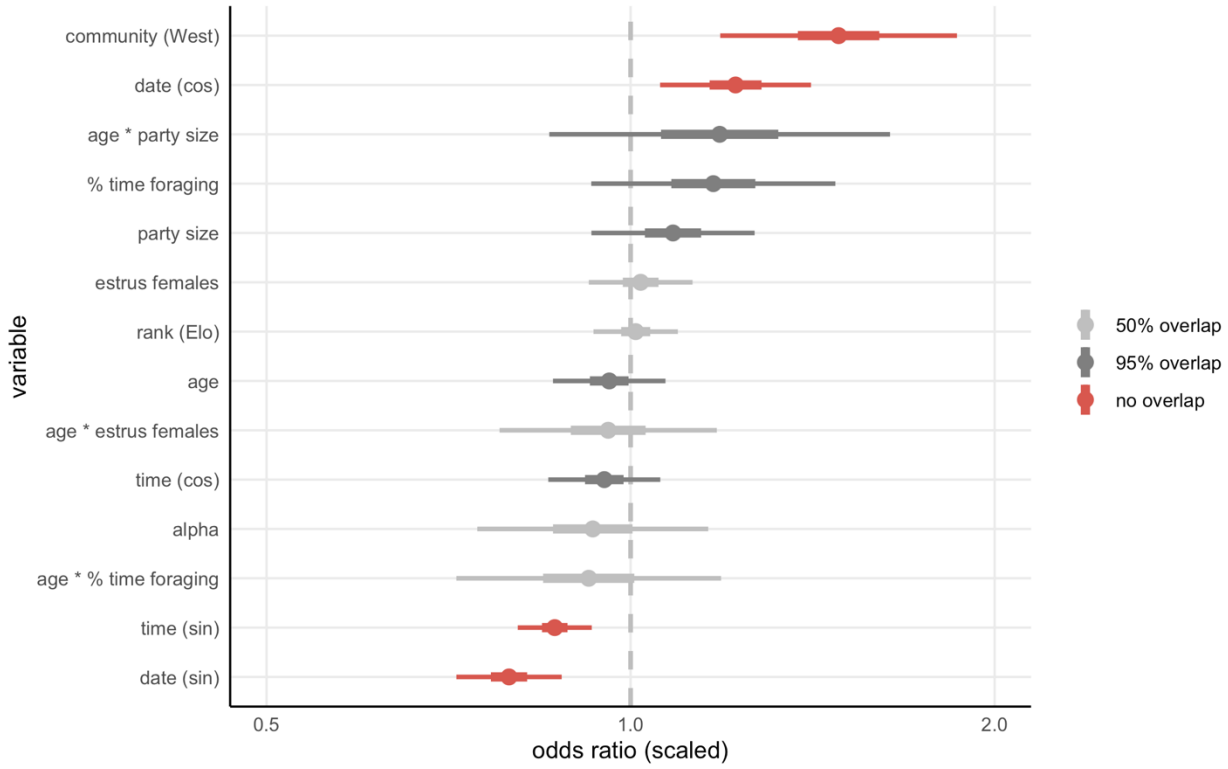

Figure S14. Testosterone analysis complete coefficient plot. Coefficient plot from back-transformed (exponentiated) beta-coefficients from top performing model (AIC weight ≥0.63). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S15. Display frequency averaged model effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95).

variable	estimate	SE	CI.low	CI.high	overlap	parameter
% time foraging	0.34	1.2	0.24	0.49	no overlap	beta
age	0.56	1.2	0.4	0.81	no overlap	beta
age * % time foraging	0.78	1.37	0.42	1.44	95% overlap	beta
date (sin)	1.49	1.17	1.09	2.03	no overlap	beta
estrus females	0.99	1.07	0.87	1.13	50% overlap	beta
Intercept	0.01	1.1	0.01	0.01	no overlap	beta
observer (SN)	0.75	1.16	0.56	0.99	no overlap	beta
party size	1.03	1.09	0.86	1.22	50% overlap	beta
rank (Elo)	1.24	1.2	0.86	1.78	95% overlap	beta

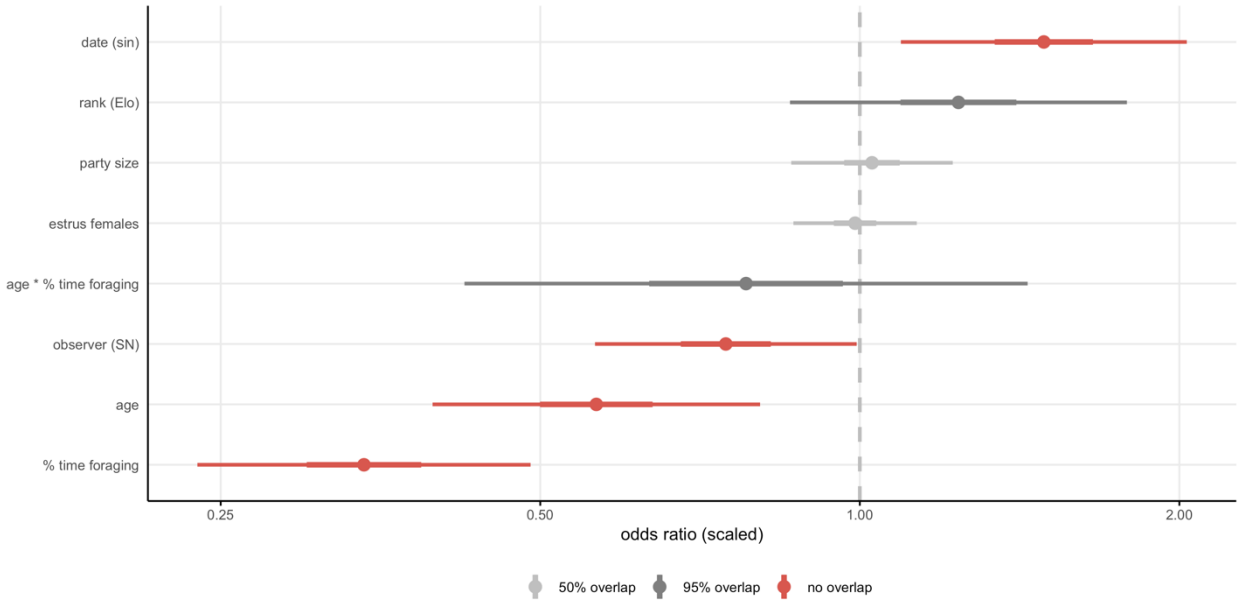

Figure S15. Display frequency analysis complete coefficient plot. Climbing distance analysis complete coefficient plot. Coefficient plot from back-transformed (exponentiated) beta-coefficients from top performing model (AIC weight ≥0.63). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S16. Display distance averaged model effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95).

variable	estimate	SE	CI.low	CI.high	overlap
% time foraging	1.01	1.04	0.93	1.1	50% overlap
age	0.72	1.18	0.53	0.99	no overlap
age * estrus females	1.13	1.21	0.78	1.64	50% overlap
age * party size	1.18	1.2	0.82	1.69	95% overlap
community (West)	1.04	1.08	0.89	1.2	50% overlap
estrus females	1.07	1.08	0.91	1.25	95% overlap
intercept	8.85	1.05	8.06	9.72	no overlap
intercept (sig)	0.79	1.03	0.75	0.83	no overlap
party size	0.99	1.08	0.84	1.16	50% overlap
party size * rank	1.55	1.14	1.19	2.01	no overlap
rank (Elo)	0.79	1.07	0.69	0.91	no overlap

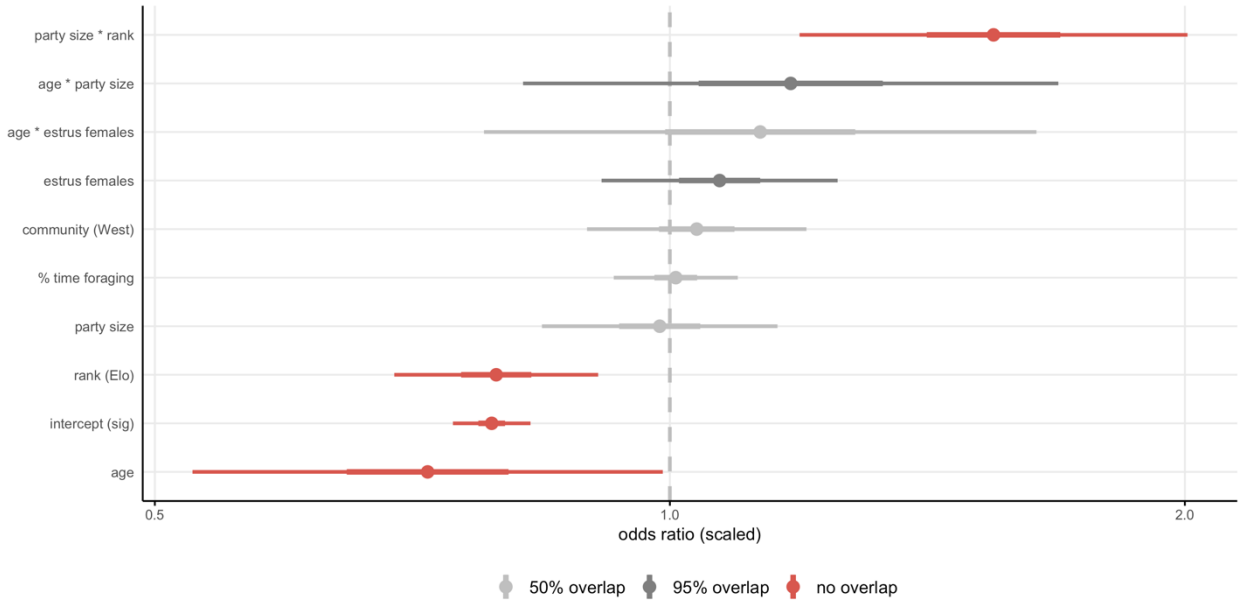

Figure S16. Display distance analysis complete coefficient plot. Climbing distance analysis complete coefficient plot. Coefficient plot from back-transformed (exponentiated) beta-coefficients from top performing model (AIC weight ≥0.63). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S17. Copulation frequency averaged model effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95).

variable	estimate	SE	CI.low	CI.high	overlap
% time foraging	1.01	1.04	0.93	1.1	50% overlap
age	0.72	1.18	0.53	0.99	no overlap
age * estrus females	1.13	1.21	0.78	1.64	50% overlap
age * party size	1.18	1.2	0.82	1.69	95% overlap
community (West)	1.04	1.08	0.89	1.2	50% overlap
estrus females	1.07	1.08	0.91	1.25	95% overlap
intercept	8.85	1.05	8.06	9.72	no overlap
intercept (sig)	0.79	1.03	0.75	0.83	no overlap
party size	0.99	1.08	0.84	1.16	50% overlap
party size * rank	1.55	1.14	1.19	2.01	no overlap
rank (Elo)	0.79	1.07	0.69	0.91	no overlap

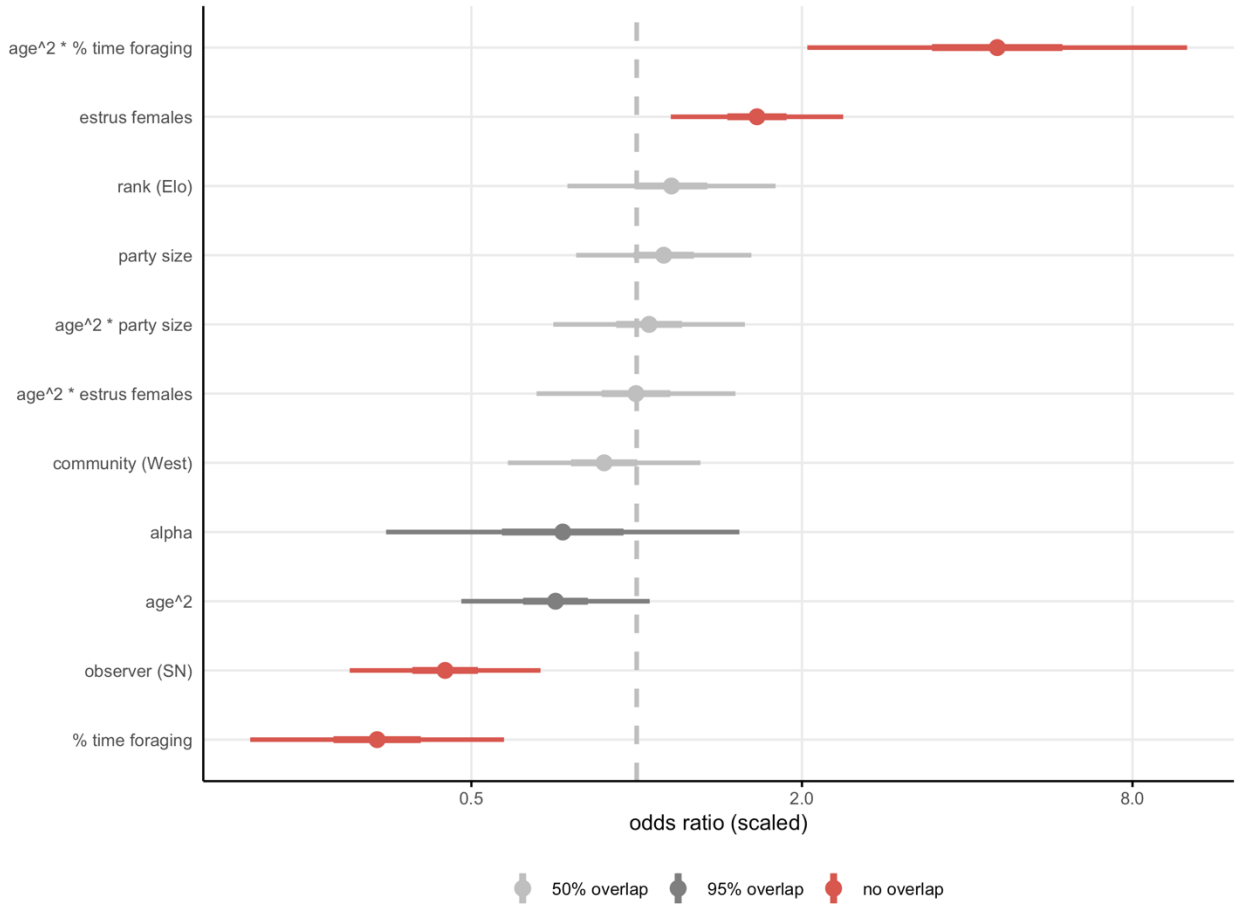

Figure S17. Copulation frequency analysis complete coefficient plot. Coefficient plot from back-transformed (exponentiated) beta-coefficients from top performing model (AIC weight ≥0.63). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Chapter 4.

Affiliative Behavior And Social Aging in Male Chimpanzees

Abstract

Maintaining social function and connection are crucial for healthy aging. Yet social aging patterns across humans and non-human primates indicate decreased social engagement with age. Despite interest, few studies have assessed links between social aging and physiological senescence, which could help identify proximate causes for declines in fitness with age. I analyze metrics of social engagement from a cohort of adult male chimpanzees and their correlations with socioecological variables to test hypotheses regarding how senescence affects social aging. Various measures of social engagement were positively associated with age: older males were less likely to be socially distanced, were in proximity to more adult males, groomed non-adults more, and received more grooming when in association with an estrous female. By contrast, old males groomed less with adult females and showed no change in the number of grooming partners. Both the number of adult males in proximity and time spent

grooming increased with age during high-quality food times, offering limited support for the hypothesis that energetic constraints may generate tradeoffs between maintenance and sociality for old male chimpanzees. I find no support for hypotheses that the sociality of old males may be limited by mobility or the avoidance of competition. I discuss preliminary evidence that older individuals may adopt alternative reproductive tactics in the face of changing payoffs as a result of senescence. The reproductive tactics of old males warrant special attention because maximizing late-life fitness is a precondition for the evolution of longevity.

Introduction

For humans, successful aging is not just contingent on physical health but also on social function and connection (Holt-Lunstad et al. 2010, Yang et al. 2016). A key insight from public health is that social isolation is an important predictor of mortality (Rafnsson et al 2020, Marmot 2020) and loneliness is a chief health concern, especially late in life (Hawkley & Cacioppo 2010, Gupta & Dhamija 2020). The negative impacts of social isolation appear to be shared with our primate relatives for whom social bonds predict improved health, survival, and reproduction (Silk 2007, Synder-Mackler et al. 2020).

How and why do social relationships change in old age for humans and other animals, and how do social ties affect health and longevity? Non-human primates can provide insights into these questions and the evolutionary foundations of social aging because we share similar life histories (Bronikowski et al. 2011), patterns of physiological senescence (Roth et al. 2004, Lowenstine et al. 2016, Shively et al. 2021),

and complex social lives. While recent research has described social aging across species, there still are relatively few examinations of how patterns of sociality change over the lifespan in wild primates and other long-lived organisms.

One pattern that has emerged, particularly in primates, is decreased social engagement with age (Machanda & Rosati 2020). In great apes, increased solitary behavior in aged individuals has long been reported (Goodall et al. 1985, Huffman 1990, Tarou et al. 2002), leading to the introduction of the concept of "social aging", which refers to a reduction in social activities associated with physical aging (Hosaka & Huffman 2015). Recent studies, particularly in catarrhine primates, have highlighted this phenomenon as older individuals are less likely to be in proximity to other individuals and/or engage in fewer social behaviors (Machanda & Rosati 2020). Such patterns may not be unique to primates because similar decreases have been documented in other taxa such as orca whales (*Ornicus orca*) (Weiss et al. 2021), red deer (*Cervus elaphus*) (Albery et al. 2021), and yellow-bellied marmots (*Marmota flaviventris*) (Wey & Blumstein 2010). Yet social withdrawal is not necessarily indicative of decreasing sociality overall; rather, it can be the result of increasing social selectivity. For instance, adult female macaques (*Macaca mulatta*) reduced the size of their social networks as they aged but spent similar amounts of time socializing (Siracusa et al. 2022a). Nevertheless, some studies describe no association between age and social engagement (*Macaca radiata*, Silk 1994; *Papio cynocephalus*, Silk et al. 2006), while others show a positive association. For example, old male chimpanzees (*Pan troglodytes*) were more likely to be alone, but also joined larger parties and were in proximity to more individuals (Rosati et al. 2020). Machanda & Rosati (2020) observe

that social organization, dominance, and sex appear to be modulators of primate social aging across species. However, more studies comparing across populations of the same species are necessary to determine how socioecological conditions shape aging. In particular, because age-related patterns in dominance, aggression, and reproduction can vary across populations, particularly between those with different group sizes, patterns of social aging can vary as well, though studies have yet to examine this.

Explanations for social aging have frequently focused on shifts in psychology, but few studies have assessed potential links to physiological senescence. In particular, various primate studies have adopted or assessed frameworks developed for human psychology such as socioemotional selective theory (Carstensen et al. 1999) (e.g. Rosati et al. 2020, Siracusa et al. 2022a); model of selection, optimization, and compensation (Freund & Baltes 1998) (e.g. Almeling et al. 2016); and the strength-and-vulnerability-integration model (Charles & Luong 2013) (e.g. Almeling et al. 2017, Rathke et al. 2022). To some degree, these studies all focus on describing age-related shifts in motivation and intentionality in humans, and such frameworks have been especially productive in comparing human and non-human aging. To develop a holistic understanding of social aging from a life history perspective, however, we must consider the role of physiological tradeoffs in shaping facets of social aging. Notably, these are not mutually exclusive explanations of age-related patterns. For instance, the selection, optimization, and compensation model describes successful aging as the management of *limited resources* across the lifespan by compensating for *potential losses* (Baltes & Baltes 1990). Life history theory and the study of senescence can help inform and identify the physiological nature of resource limitations and the potential losses

organisms face in late life. Moreover, a primary prediction of the strength and vulnerability integration model is that older adults will avoid stressful situations due to reduced physiological flexibility (Charles 2010). Identifying the mechanisms of reduced physiological flexibility can help us identify what constitutes stressful situations for wild animals as well as successful strategies to avoid them. Nonetheless, comparatively little work has examined how senescence or other patterns of aging correspond to late-life changes in social behavior (Siracusa et al. 2022b).

Study design and hypotheses

In this chapter, I present data on adult male chimpanzees from two communities at Ngogo in Kibale National Park, Uganda. Importantly, the Ngogo chimpanzees live only 10 km from the Kanyawara chimpanzees – whose social aging has been well described (Rosati et al. 2020) – but differ from them in distinct ways. The Ngogo chimpanzees occupy a territory with more ripe fruit (Potts et al. 2009), exhibit lower reproductive skew (Langergraber et al. 2010), live in much larger groups (Watts 2012), and live longer (Wood et al. 2017). I analyze metrics of social engagement from a cohort of adult males (ages 21 to 53 years) and their correlations with socioecological variables to test hypotheses regarding how senescence influences social aging. These data help address two gaps in the social aging literature: the lack of between-population comparisons and the shortage of tests on links between senescence and social aging.

There are well-established, age-specific changes in physiology and life history of wild chimpanzees that might contribute to social aging. Here, I hypothesize that physical deterioration in the form of (1) declining mobility, (2) energetic constraints, and (3)

increased costs of competition limit the social lives of old chimpanzees. Additionally, chimpanzees may (4) alter their behavior in old age to adapt to changing costs and benefits associated with senescence. Late-life male chimpanzees may adopt new reproductive tactics that produce novel social patterns.

First, because musculoskeletal health promotes active participation in social life via locomotion, deteriorations in these systems may lead to a decrease in social behaviors. Old chimpanzees, like humans, exhibit both muscle wasting (sarcopenia) and bone loss (osteoporosis), which are hypothesized to hinder locomotion (Morbeck et al. 2002). After peaking at approximately 30 years of age, male chimpanzees lose muscle mass (Emery Thompson et al. 2012; Emery Thompson et al. 2020a). Concurrently, age-related bone loss is observed across non-human primates (Madimenos 2015) and is hypothesized to impede locomotor performance in wild chimpanzees (Sumner et al. 1989). While older primates may move slower and climb less (Shively et al. 2012), there is limited evidence that this is the case in wild chimpanzees (c.f. Chapters 2 and 3). In a longitudinal study, old chimpanzees with lower lean body mass rested more often and were less arboreal, but did not otherwise differ in activity (Emery Thompson et al. 2020a). Nonetheless, potential declines in mobility may be especially consequential for chimpanzees who have greater day ranges than any other non-human ape (Chapman & Chapman 2000). Chimpanzees have a fission-fusion social organization that allows the formation of temporary subgroups of varying sizes (Nishida 1968, Goodall 1986). Consequently, if older individuals have a harder time keeping up with parties, then they may become more isolated. Based on the preceding considerations, I hypothesize that declining mobility limits old chimpanzees'

ability or opportunities to socialize. In particular, because arboreal movement is more costly than terrestrial movement (Pontzer & Wrangham 2004), I predict that old chimpanzees would be particularly less social in trees as young chimpanzees access more opportunities to socialize via arboreal locomotion.

Second, older organisms may lack the physical capacity to maintain high levels of energy intake or balance which may increase the relative costs of socializing and/or constrain social behavior due to allocation tradeoffs. Energetic status in chimpanzees is known to vary according to various environmental factors, including diet quality (Emery Thompson et al. 2009) and feeding competition (Georgiev et al. 2014). Late-life chimpanzees may experience greater energetic limitations due to the increased costs in immune function and decreases in foraging performance. Old chimpanzees at Ngogo exhibit increased immune-burdens with greater immune-activation and viral richness (Negrey et al. 2020, 2021). Mounting an immune response is itself energetically costly because the metabolic requirements of producing immune cells and the indirect consequences of immune upregulation divert resources from other functions, such as reproduction (Sheldon & Verhulst 1996, Ilmonen et al. 2000) and survival (Hanssen et al. 2004). Concurrently, both food intake and nutrient absorption decline with age (see Chapter 2.). Increased sensitivity to energetic requirements may impact sociality in several ways. Because movement is energetically expensive, chimpanzees could limit travel, which can reduce social connections (Almeling et al. 2017). Additionally, increased allocation to maintenance may come at the cost of social investment (Stearns 1989). In humans, acute hunger can reduce an individual's willingness to engage in prosocial behavior because of a shift towards self-preservation in the face of limited

energy stores (Dewall et al. 2008). These considerations lead to the hypothesis that old male chimpanzees may prioritize maintaining energetic status at the expense of socializing. If this is the case, then I predict that sociality should decrease with age during food-poor times when both returns on foraging effort and energetic condition may be lower. I also predict that old chimpanzees may be less social in foraging contexts because energetic sensitivity may make old individuals more vulnerable to feeding competition.

Third, senescence is associated with decreased benefits and increased costs from competition. In chimpanzees, male competition varies over time and as a function of female mating periods (Muller & Wrangham 2004b). Individual females mate during discrete estrous periods that last on average 12 days when they develop maximal sexual swellings (Matsumoto-Oda et al. 2007). Males compete for reproductive opportunities with estrous females within these relatively narrow windows (Wroblewski et al. 2009, Sobolewksi et al. 2013). Aggression associated with reproductive competition can be intense, especially over parous females (Muller et al. 2006). As a result, males exhibit increased testosterone levels (Sobolewksi et al. 2013), decreased energetic status (Emery Thompson et al. 2014), and increased glucocorticoid levels (Muller et al. 2021) when competing over parous estrous females, indicating that such mating opportunities are both stressful and come with high physiological costs. In addition to decreased fighting abilities observed in older primates (Bissonnette et al 2009, Berghänel et al. 2011), senescence may also diminish old primates' physiological capacity to cope with such stressors (Jensen et al 1980, Sapolsky & Altmann 1991). Relatedly, old chimpanzees may be more susceptible to stress, as indicated by

increasing glucocorticoid levels (Emery Thompson et al. 2020b), and older male chimpanzees may benefit less from such competition. Late-life males copulate (see Chapter 3) and reproduce less (Langergraber unpublished data), even after considering declines in rank (see chapter 2). The preceding observations suggest that old chimpanzees may be less social because of increased costs and diminished benefits associated with male-male competition. Accordingly, I predict that old male chimpanzees will be less social with other adult males with whom they compete and especially so when in association with parous estrous females.

Fourth, rather than generating limitations on activity, senescence may lead individuals to adopt new social patterns or compensatory adaptations in the face of changing payoffs (Siracusa et al. 2022b). Chimpanzees experience demographic senescence and age-related declines in fertility. At Ngogo, males over the age of 30 sire progressively fewer offspring (Langergraber unpublished data). This decrease in reproduction appears concomitant with declines in dominance (Watts 2018). Falling dominance rank may be due to decreased fighting ability, as is often the case across primates (Perlman et al. 2016). With declining competitive ability, shifts in reproductive tactics are predicted by life history theory (Gross 1996), but are not well documented in primates. One way that old males might make themselves attractive to mates by developing relationships with females and providing care for their offspring (Smuts 1982). Evidence for such a strategy comes from aging male yellow baboons (*Papio anubis)* (Silk et al. 2020) and rhesus macaques (*Macaca mulatta*) (Langos et al. 2013), who become more prosocial with females or their own offspring. Similarly, adolescent chimpanzees who have yet to climb the dominance hierarchy may adopt a similar

reproductive strategy, forming affiliative relationships with adult females to increase their chances of mating (Reddy & Mitani 2020). There are other anecdotal reports of old primate males interacting more often with immature individuals (e.g. van Schaik et al. 1996); in the Ngogo chimpanzees, older males are more likely to associate and groom with adolescents, especially their sons (Sandel et al. 2019). To continue to maximize fitness under the constraints of senescence, I hypothesize that late-life adult males may increase social investments with adult females (in order to increase mating opportunities) and with young chimpanzees who may be their offspring; both actions, I predict, come at the cost of socializing with other adult males. While I do not assess kinship in this study, male chimpanzees in a promiscuous mating system should not be able to recognize their offspring (hypotheses summarized in **Table 5**).

Table 5. Summary of non-exclusive explanations causing male chimpanzees to reduce or alter social behavior as they age. 'Sociality effect' refers to age's association with metrics of social behavior: proximity and grooming time. 'Partner effect' denotes predicted demographic changes in partners of social behavior or the absolute number of partners. To determine whether these associations are state dependent, I added interaction terms between age and potential confounding condition effects. Symbols for correlations are as follows: "—" no correlation; "↓" negative correlation; "↑" positive correlation.

mechanism	description	*prediciton with age*		
		sociality effect	state dependent effect	partner effect
1. mobility decline	Older individuals have hindered locomotion, which limits opportunities to socialize.	↓	↓ in trees	↓ partner n
2. energetic constraints	Older individuals priortize maintence due to energetic constraints at the cost of socializing with conspecifics.	↓	↑ with diet quality ↓ in foraging context	↓ partner n
3. competition/stress avoidance	Older individuals are less competitive and worse at coping with stress, motivating them to avoid conspecifics.	↓	↓ when estrous female present	↓ adult males
4. alternative reproductive tactics	Older individuals gain mating opportunities through increased association with adult females and/or indirect fitness through paternal care.	–	–	↑ adult females ↑ non-adults

Importantly, these four links between senescence and social aging are not mutually exclusive. Such relationships should be expected to operate simultaneously and potentially synergistically (Siracusa et al. 2022b). Their comparison here is to facilitate an understanding of their relative importance and relevance for social aging in adult male chimpanzees. Consequently, my goals in this chapter are to: 1) document patterns of social aging in males at Ngogo with a focus on comparison to those described in the nearby Kanyawara chimpanzees (Rosati et al. 2020), and 2) test hypotheses regarding how senescence shapes the sociality of old male chimpanzees.

Methods

Study site and subjects

I observed chimpanzees at Ngogo in Kibale National Park, Uganda (between 0°13′–0°41′ N and 30°19′–30° 32′ E) from August 2018 to August 2019. The Ngogo study site is surrounded by other chimpanzee communities and covered by mature, mid-altitude rainforest interspersed with secondary growth, swamp forest, and grasslands (Struhsaker 1997, Lwanga 2003). Researchers have studied the Ngogo chimpanzee community since 1995 and all subjects were well habituated to human observation (Watts 2012). In January 2018, the Ngogo community split into the Ngogo Central and Ngogo West communities (Sandel & Watts 2021). Together, the communities occupy territories that cover an approximately 35 km^2 area. For the majority of the study period, Ngogo Central comprised 121 individuals, including 24

adult males and 40 adult females, and Ngogo West had 84 individuals, including 7 adult males and 24 adult females.

Subjects were 20 adult males ranging from age 21 to 53 years old at the start of study (**Figure S18**). While young adulthood includes individuals 16 to 20 years old, this period has been characterized as a distinct social life stage (Goodall 1983, Kawanaka 1989). I excluded young adults from analysis because they had not yet socially matured. The ages of males born in 1995 or later are known with a precision of between one day and a few months. For males born earlier (17 of 20 subjects), this study uses ages provided by Wood et al. (2017). These estimates are based on comparison of the appearance of males when first observed to that of known-aged males; visual assessment of when males who were immature at the study's start attained full, adult body mass; and comparisons among those who were already adults with respect to visible traits associated with senescence (e.g., muscle mass). Genealogical information for most males born before 1995 is known from an ongoing, long-term genetic study of the Ngogo chimpanzees (Langergraber et al. 2007, 2013). These data furnish an additional, key source of information to estimate the age of males born before 1995 (see Wood et al. 2017).

Behavioral data collection

Sharifah Namaganda and I observed subjects via continuous focal animal sampling (Altmann 1974). Focal sessions typically lasted 2 hours, after which we switched to new focal subjects. When no other focal subject was present, we remained with the current subject. Some focal sessions terminated early when chimpanzees were

lost, and in these situations, we included observations if subjects were followed for at least 30 minutes. Because chimpanzees live in fission–fusion societies and form temporary sub-groups known as parties, not all males were available for observation every day. We attempted to equalize the number of focal follows by rotating through subjects opportunistically, prioritizing males that had been observed less often than others during any given month. Together, we conducted 1288 hours of focal observations on subjects (mean 64.4 ± SD 10.3 hours per subject). I conducted an additional 132 hours of focal observation, which were incorporated in the generation of the dietary indices that were predictors of social outcomes. All observations were recorded digitally on a handheld device using *HanDbase IOS* software.

I recorded chimpanzees within 5 meters proximity to focal subjects at 15-minute scan intervals (n=3205). Close proximity is an important marker of affiliation in primates, as it is a prerequisite for other cooperative interactions such as grooming, and signals social comfort (Silk 2007, Mitani 2009). Proximity counts excluded individuals younger than age eight as these include pre-adolescent infants, and juveniles who are still dependent on their mothers (Pusey 1990). Individuals were considered to be socially distanced when there was no other individual in proximity. Additionally, the age- and sex-class of individuals in proximity were considered to calculate the number of adult males in proximity, as adult males are the primary social partners of other adult males. Namaganda and I noted all instances of grooming given and received by focal subjects to the nearest half-minute.

Covariates and predictors

I employed the same covariates as predictors in model construction as the studies in Chapters 2 and 3 (summarized in **Table 6**). In addition, I included measures of *arboreal position* ("in tree") *and foraging context.* For analyses of proximity, I included whether the focal subject was considered arboreal or not if individuals were ≥3m above the forest floor. These data were only collected in scan sampling, and thus arboreality is not considered as a predictor of grooming behavior. Additionally, I included a measure of foraging context to assess whether sociality changes with age varied according to behavioral context. To help do so, I incorporated an ordinal score that quantified the extent of foraging activity that occurred over the 15-minute periods during which vertical height displacements occurred. A score of one was assigned to the following conditions: if the end-scan's behavioral state was recorded as foraging, if the start-scan's behavioral state was recorded as foraging, and if a feeding bout occurred in the period in-between the start- and end-scans. The foraging context score was then the sum of those values, which ranged from 0–3, wherein a higher score corresponds to a greater extent of foraging behavior associated with the vertical distance.

Table 6. Description of predictors for measure outcomes and when they were included in the full model employed in dredge(). I employed pretests to identify and mutually exclude highly correlated variables ($r \geq 0.7$) from the same models. Δ denotes where an interaction effect with age or age^2 was included in addition to the main effect.

description of predictors for sociality measures			included in models		
type	predictor	description	proximity	grooming time	n partners
fixed	date	three date terms: nuermic date of sample, cos(pi * date), and sin (pi * date) [numeric, continuous]	▪	▪	▪
	time	three time terms: numeric time of sample, cos(pi * time), and sin (pi * time) [numeric, continuous]	▪		
	observer	observer identity: BJF or SN [categorical]		▪	▪
	community	identity of chimpanzee communinity: Ngogo Central or Ngogo West [categorical]	▪	▪	▪
	% high-quality fruit in diet Δ	daily population-wide index of the proportion of ripe non-fig fruit and *Ficus mucuso* fruit in the diet. Generated as predictions from GAM of time spent feeding on high-quality fruit per focal as a function of date [numeric, continuous]	▪	▪	▪
	% time spent foraging Δ	daily population-wide index of the proportion of time spent foraging. Generated as predictions from GAM of time spent within foraging bouts per focal as a function of date and community [numeric, continuous]	▪	▪	▪
	in tree Δ	whether focal subject was arboreal (≥ 3m from forest floor) [binary]	▪		
	foraging context Δ	a score [1,3] of how much foraging activity occurred in the 15-minute period of and between scans [ordinal]	▪		
	age / age^2	subject age or age^2 at sample, selection from preliminary analysis of per-variable sum of model weights [numeric, continuous]	▪	▪	▪
	rank	daily dominance rank (Elo score) [numeric, continuous]	▪	▪	▪
	party size Δ	the number of chimpanzees in association throughout the day, excluding dependents younger than age 8 [numeric, discrete]	▪	▪	▪
	estrus females in association Δ	the number of sexually receptive parous female chimpanzees in association throughout the day [numeric, discrete]	▪	▪	▪
	partner age-sex class Δ	starting time of intake sample as proportion of way through feeding bout time [numeric, continuous]		▪	
random	subject ID	male identity [categorical]	▪	▪	▪
offset	focal duration	duration of focal sample [numeric, continuous]		▪	▪

Data analysis

I conducted preliminary data exploration, analysis, and data visualization in R (version 4.2.2; R Core Team 2022) via RStudio version 2022.12.0 (RStudio Team, 2022). To determine the effects of age on proximity and grooming outcomes, I adopted an information theoretic approach using generalized linear mixed models (GLMMs) to

model variation in each outcome. I fit models using {lme4} (Bates et al. 2004) to support a variety of distributions for outcome variables. I used a binomial model to fit the probability of no neighbors in proximity and negative binomial models to fit the counts of neighbors in proximity, count of minutes per focal spent grooming (as actor and receiver), and counts of grooming partners per focal. For all analyses I fit ecologically plausible models (including interactions when warranted) with alternative distributions appropriate to the outcome of interest. Following model fitting with the complete model, I performed model selection using the dredge() function {MuMIn} package (Bartón 2009), which employs an information theoretic multi-model selection approach based on Akaike's Information Criterion (AIC), or when n/K > 40, indicating a high number of terms relative to small sample size, AICc (Burnham & Anderson 2004). I then performed model averaging across models with cumulative weight of 0.95 using function model.avg() {MuMn}, which averaged predictions on their link scale to obtain weighted averaged estimates for each predictor for a complete model average (when a predictor was absent from a given model, its beta value was set to zero).

I considered predictors to be reliable when the 95% confidence intervals of their effect sizes did not overlap the null effect. To control for the non-independence of samples, I included random effects for subject ID. Prior to model fitting, I examined pair-wise correlation plots (see supplementary materials) to ensure highly correlated variables ($r \geq 0.7$) were not included in the same model to avoid issues with model convergence with the exception of date and time harmonic terms. Thus, *percent high-quality fruit* and *percent time foraging* were not included together in any model. In preliminary analysis, I compared the performance of these dietary predictors and in the

complete model included only the one with a greater performance according to AIC. Similarly, I conducted preliminary analyses to determine whether to include *age* or age^2 in model construction. All continuous predictors were centered on the mean and standardized to permit direct comparison of effect size magnitude. Offsets were transformed according to their respective model's link function to place them on the same scale as the outcome. The outcome variables were: 1) whether the number of neighbors in proximity was 0 (socially distanced), 2a) the count of adult males in proximity, 2b) the count of adult females in proximity, 3) count of minutes grooming as actor, 4) count of minutes grooming as recipient, 5) count of grooming partners per focal.

Results

Older males were more likely to be in proximity to others, particularly other adult males but not adult females

The probability of having 0 individuals in proximity during a scan or being socially distanced decreased by 0.70(±1.19) times for each SD increase in adult male age (equivalent to 9 years) (**Figure 10A, 10B**). The weighted model average (cumulative weight ≥ 0.95) predicted that a 23-year-old male was socially distanced in 52% of scans whereas a 47-year-old male was socially distanced in 41% of scans (the 10^{th} and 90^{th} quantiles of subject age, respectively) (**Table S19)**. The count of the number of adult males in proximity increased by 1.42(±1.19) times for each SD increase in age (**Figure 10C, Table S20**). Accordingly, the weighted model average predicted that a 23-year-old

male was in proximity to an average of 0.50 other adult males and a 47-year-old male was in proximity to 0.78 other adult males with all other predictors at their mean. In contrast, the number of adult females in proximity did not vary reliably with the main effect with age, nor did it appear to be condition-dependent (**Figure 10E**). Across proximity outcomes, the degree of sociality was negatively associated with arboreal position (“in tree”).

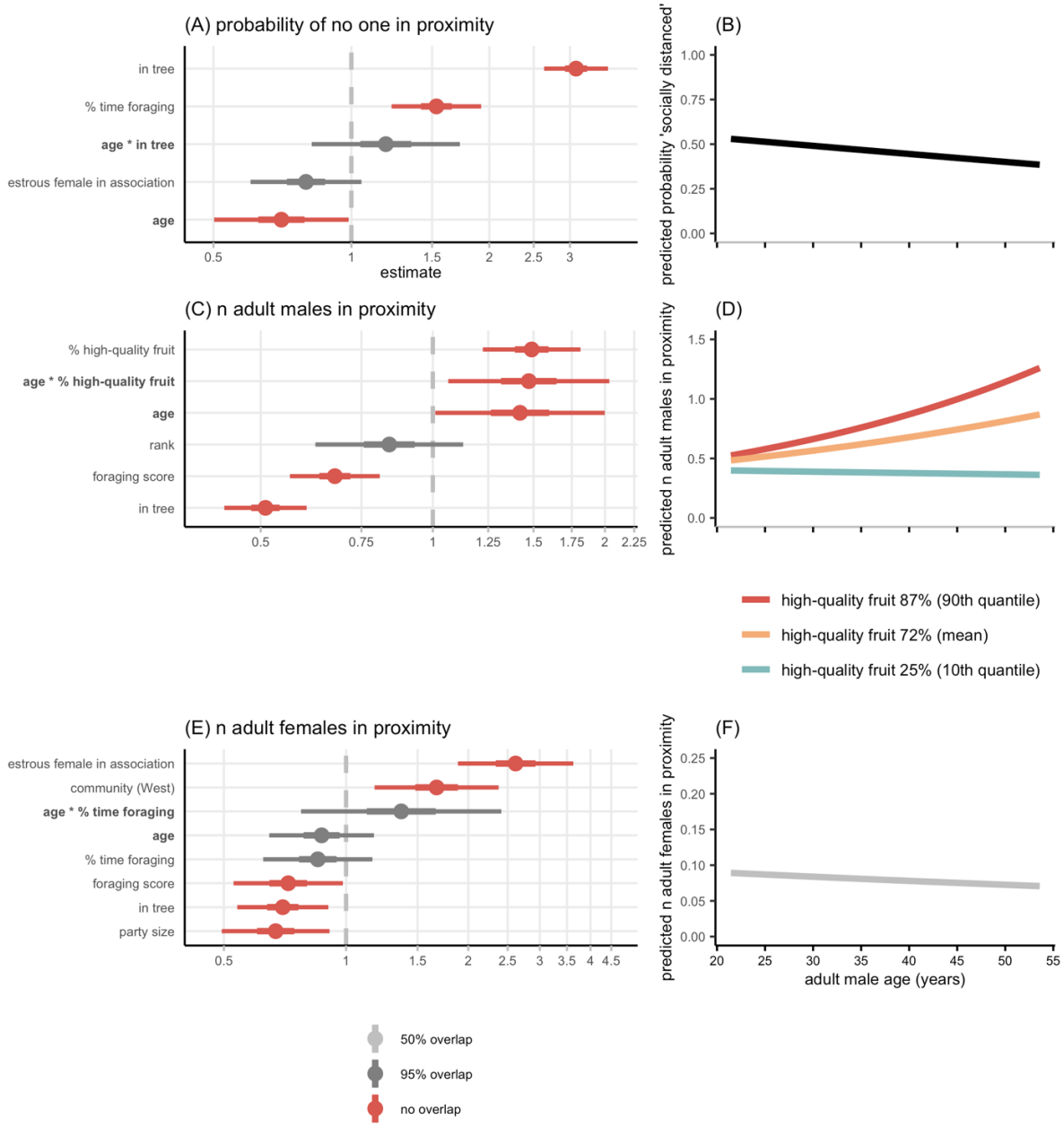
(A) probability of no one in proximity
in tree
% time foraging
age * in tree
estrous female in association
age
0.5
1
1.5
2
2.5
3
estimate
(B)
predicted probability 'socially distanced'
1.00
0.75
0.50
0.25
0.00
(C) n adult males in proximity
% high-quality fruit
age * % high-quality fruit
age
rank
foraging score
in tree
0.5
0.75
1
1.25
1.5
1.75
2
2.25
(D)
predicted n adult males in proximity
1.5
1.0
0.5
0.0
high-quality fruit 87% (90th quantile)
high-quality fruit 72% (mean)
high-quality fruit 25% (10th quantile)
(E) n adult females in proximity
estrous female in association
community (West)
age * % time foraging
age
% time foraging
foraging score
in tree
party size
0.5
1
1.5
2
2.5
3
3.5
4
4.5
(F)
predicted n adult females in proximity
0.25
0.20
0.15
0.10
0.05
0.00
20
25
30
35
40
45
50
55
adult male age (years)
50% overlap
95% overlap
no overlap

Figure 10. Compilation of coefficients and predictions from weighted model averages for proximity outcomes with respect to age Probability of being socially distanced (0 individuals in proximity) and number of individuals in proximity (≤ 5 m) to focal adult males in scans. Each row depicts results from a proximity measure outcome. The left column depicts coefficient plots and the right column depicts the corresponding age effect predictions, both from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Predictors are centered and standardized so the magnitude of beta coefficients are directly comparable. Thick bars represent 50% CI and thin bars represent 95% CI, whereas the coefficient plot color depicts the estimates' overlap with a null effect. Coefficient plots exclude control predictors (date, time) and predictors with 50% CI overlap for visual clarity. For complete coefficient plot see Figures S18, S19, S20. The right column depicts predictions from age and its interaction effects, if present, with all other predictors held at their mean. The display categories of foraging time and their respective colors (F) represent the minimum, mean, and maximum.

Older males were in proximity to more adult-males during high-quality food times

The daily score for percent time spent foraging – a potential inverse proxy for diet quality – was positively correlated with the probability of being solitary (**Figure 10A**). For each SD increase in the percent of time spent foraging (equivalent to 5.5%), the probability of being socially distanced increased by 1.53(±1.12) (**Table S19**). Similarly, the daily proportion of high-quality fruit in the diet was positively associated with the number of adult males in proximity (**Figure 10C**). For each SD increase in the proportion of high-quality ripe fruit in the diet, the number of adult males in proximity increased by 1.49(±1.11) times (**Table S20**). In addition, age had a positive interaction effect with the proportion of high-quality fruit in the diet; the proximity to other adult males was positively correlated with age in good food times (high proportion of high-quality fruit), while there was little correlation during poor food times (**Figure 10D**).

Potential proxies of diet quality were not reliably associated with the number of adult females in proximity. Patterns of sociality with females contrasted in other ways:

there was a community effect where male chimpanzees in Ngogo West were in proximity to 1.6(±1.20) times more adult females compared to Ngogo Central (**Table S21**). There was no effect of interaction terms between age and arboreality, foraging context, or estrus females in association.

Older males groomed others more in good food times, groomed adult females less and non-adults more

We recorded 125 hours of grooming in which adult male subjects groomed with other adult male partners 73% of the time, adult females 12% of the time, and non-adults 15% of the time. Age alone did not have a reliable effect on grooming time as actor (**Figure 11A**). However, age did have an interaction effect with the percent time spent foraging, indicating a state-dependent increase in grooming time: grooming time as actor increased with age when little time was spent foraging, while there was no change with age when more time was spent foraging (**Figure 11B**). Perhaps count-intuitively, time spent grooming was positively associated with the portion of time spent foraging; for each 5.5% increase in time spent foraging, subjects spent 1.62(±1.06) times as long grooming others. However, this controls for a correlated measure with diet quality, the presence of estrous females. An estrous female in association corresponded grooming times increasing by 1.44(±1.06) times (**Table S22**).

Old males groomed adult females especially less; for each SD increase in age, the time spent grooming adult females decreased by 0.71(±1.13) times (**Figure 11D, Table S22**). In contrast, a large and positive interaction coefficient between age and partner sex-class ‘non-adult’ indicates that grooming time as actor was positively

associated with age when grooming non-adults (males <16 and females <14); for each SD increase in age, the time spent grooming non-adults increased by 7.57(±1.17) times. Of the 38.4 hours of grooming by subjects under the age of 24 (the 25th percentile), only 3.4 hours was to a non-adult (approximately 9%). For males over the age of 36, 25% of grooming time was with non-adults. There was no reliable effect of interaction terms between age and arboreality, foraging context, or estrus females in association on grooming time as actor.

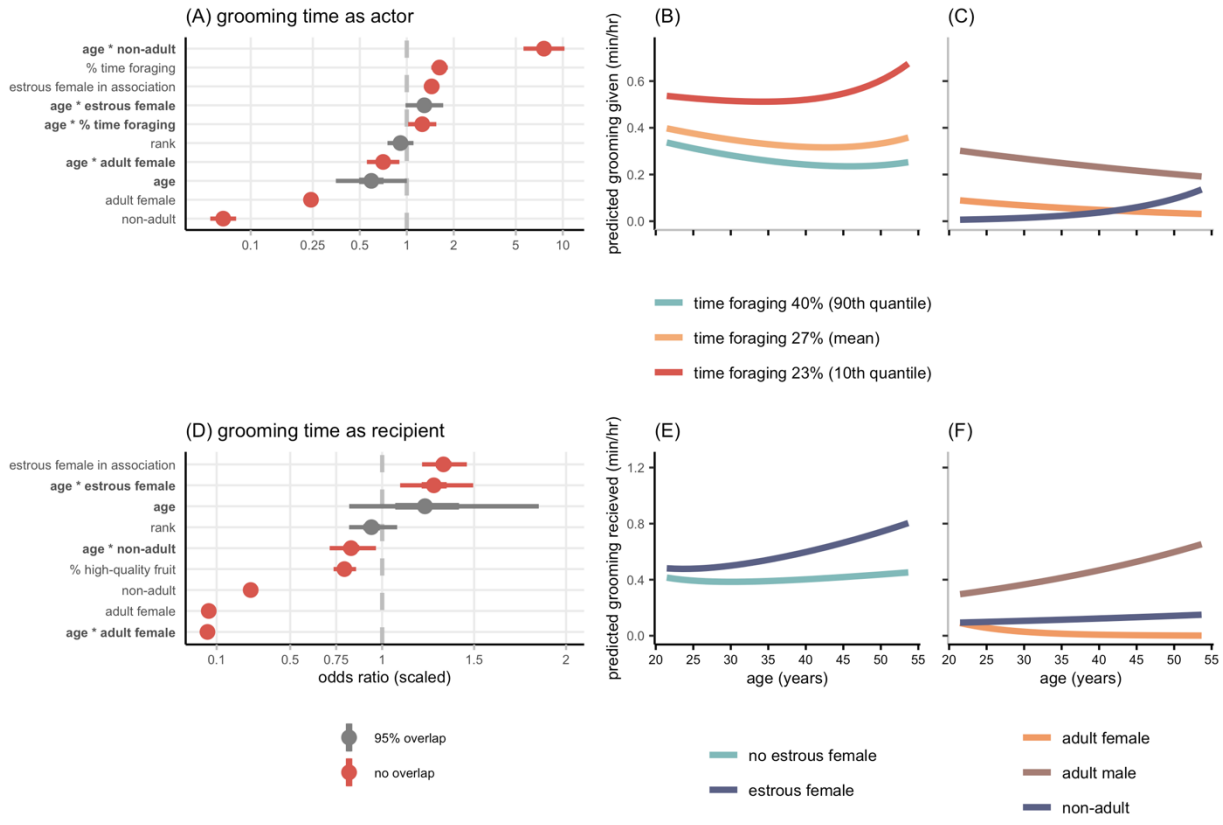

Figure 11. Grooming time per focal by partner age-sex class and grooming direction (n=125 hours over 688 focals). Each row depicts results from a grooming measure outcome. The left column depicts coefficient plots and the right column depicts the corresponding age effect predictions, both from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Predictors are centered and standardized so beta coefficients are comparable. Thick bars represent 50% CI and thin bars represent 95% CI, whereas color in the coefficient plots depicts the estimates' overlap with a null effect. Coefficient plots exclude control predictors (observer) and predictors with 50% CI overlap for visual clarity. For complete coefficient plot see Figures S21, S22. The right column depicts predictions from age and its interaction with partner age sex class, with all other predictors held at their mean.

Old male chimpanzees received more grooming in parties with estrous females, but almost none from adult females

The main effect of age was uncorrelated with amount of grooming received overall (**Figure 11D**). The effect of male age, however, was state-dependent on the

presence of at least one estrous female; old male received more grooming when in association with at least one estrous female (**Figure 11G**). In general, all subjects received 1.33(±1.05) times as much grooming when in association with at least one estrous female (**Table S23**). Again counterintuitively, the proportion of high-quality fruit in the diet was negatively correlated with grooming time; for each SD increase in proportion of high-quality fruit, the duration of grooming received decreased by 0.79(±1.04 times).

Grooming received from adult females was negatively associated with age; for each SD increase in age, the duration of grooming received from an adult female was 0.05(±1.27) times lower (**Table S23**). In fact, of the 30.3 hours of received grooming recorded for individuals over the age of 36, only 17.5 minutes were from an adult female (less than 1%). For males under the age of 24, 16% of received grooming came from adult females. With age, adult males also received less grooming from non-adults: for each SD increase in age, the duration of grooming received from a non-adult was 0.83(±1.08) times lower.

The number of grooming partners did not vary with age

Male age was not correlated with the number of grooming partners (**Figure 12**). The number of grooming partners was positively correlated with party size; for each SD increase in party size, the number of grooming partners in a focal increased by 1.29(±1.14) times (**Table S24**). The presence of an estrous female in the party also increased the number of grooming partners by 1.39(±1.12) times. Although not included here, I carried out supplementary analyses on the number of grooming partners as

either actor or recipient separately and they also indicated that there was no correlation with subject age.

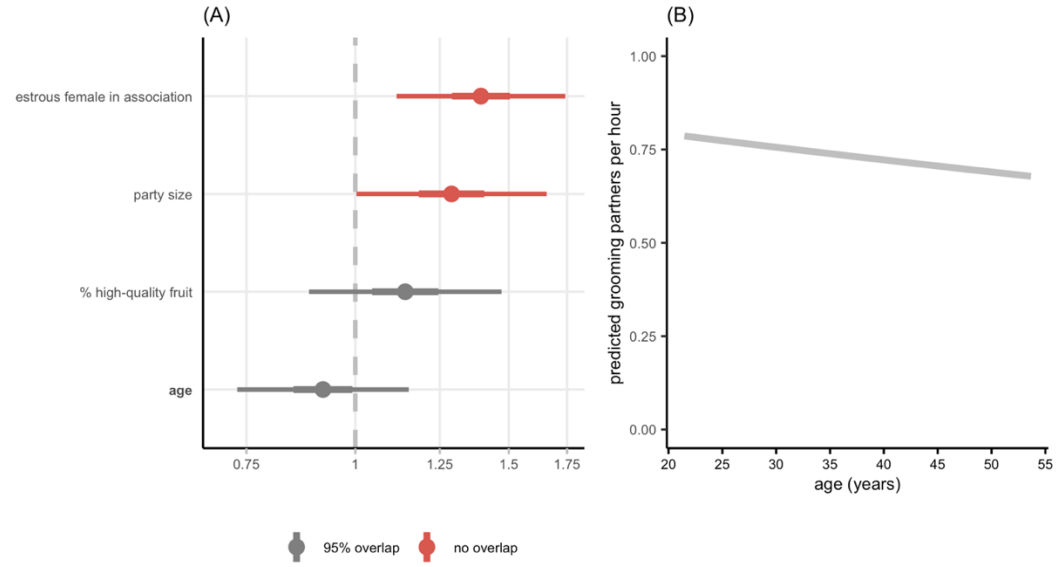

Figure 12. Number of grooming partners per focal (n=688 focals) did not vary with age. (A) Depicts the coefficient plot and (B) depicts the corresponding age effect predictions, both from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Predictors are centered and standardized so beta coefficients are comparable. Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect. Coefficient plots exclude control predictors (observer) and predictors with 50% CI overlap for visual clarity. For complete coefficient plot see Figure S23. (B) Depicts predictions from age with all other predictors held at their mean.

Discussion

In this chapter, I describe several patterns between age and sociality in adult male chimpanzees. I found that various measures of social engagement were positively associated with age: old males were less likely to be socially distanced (**Figure 10A**), were in proximity to more adult males (**Figure 10C**), spent longer time grooming others

during potentially food-rich times (**Figure 2B**), groomed non-adults more (**Figure 11C**), and received more grooming when in association with an estrous female (**Figure 11E**). Meanwhile, several social behaviors were negatively correlated with age: old males both groomed and received less grooming from adult females (**Figure 11C**) as well non-adults (**Figure 11F**). Other measures such as the number of social partners showed no change with age (**Figure 12**). These results — which control for rank and party composition — support prior findings that older male chimpanzees are more social in various measures like proximity (Rosati et al. 2020).

There is ongoing debate regarding the proximate mechanisms that underpin declines in fitness with advancing age or senescence. Because social relationships affect the reproductive success of social primates such as male chimpanzees, understanding the links between social aging and senescence may inform our understanding of why old organisms sometimes reproduce less. Yet little work has examined how senescence or other patterns of aging correspond to late-life changes in social behavior (Siracusa et al. 2022b). I interpret my findings in the context of hypotheses regarding the relationships between senescence and social aging (**Table 5**). Broadly, I find little evidence that sociality in late-life chimpanzees declines with age as few markers of sociality were negatively associated with age. A consistent prediction across hypotheses (1-3) was that proximity, grooming effort, and number of social partners should decrease, but this was not observed.

I do, however, find some support for the hypothesis that energetic constraints may influence sociality in late-life chimpanzees. I hypothesized that because late-life chimpanzees would experience greater energetic constraints due to factors like

increased costs in immune function (Ilmonen et al. 2000, Negrey et al. 2021) and decreases in foraging performance (see Chapter 2), they may face tradeoffs between maintenance and sociality. I found that both the number of adult males in proximity and time spent grooming others increased with age during potentially good food times; old chimpanzees appeared more social on days where less time was spent foraging and diets contained large amounts of high-quality fruit. I also predicted that old chimpanzees should be especially less social in foraging contexts to avoid feeding competition, but this was not the case. These findings may indicate that patterns of increased sociality in old males – particularly with other adult males – are facilitated during periods of abundant food, which could suggest that old males are sensitive to energetic or foraging requirements during food-poor times.

Alternative hypotheses for decreased sociality with age invoke mobility decline and competition avoidance. In the mobility decline hypothesis, I proposed that sociality in old individuals may be limited by movement because muscle (Morbeck et al. 2002) and bone loss (Madimenos 2015) are tied to age in wild chimpanzees and may impede locomotion (Emery Thompson et al. 2020a). This was not supported because sociality for old chimpanzees did not especially decline in arboreal contexts (i.e. old chimpanzees were not less social compared to their prime-aged counterparts). These findings are in line with longitudinal results from Emery Thompson et al. (2020) where the authors did not find an association between lower lean body mass and movement, although they did find that old chimpanzees were less arboreal (c.f. Chapter 2).

Because late-life male chimpanzees may see declines in competitive ability (Bissonnette et al 2009, Berghänel et al. 2011), competition payoffs, and capacity to

cope with stress (Jensen et al 1980, Sapolsky & Altmann 1991), I hypothesized that older individuals may avoid competition and stressful social interactions. The most common, intense form of male-male competition occurs in high mate-competition contexts – when a parous estrous female is present (Muller & Wrangham 2004b). Consequently, I predicted that older males should be less social when in association with an estrous female. However, I observed the opposite: older male chimpanzees did not groom less in high-competition contexts and in-fact received more grooming in those times. Additionally, because the only social competitors of adult males are other adult males, I predicted that with age, individuals may engage less with other adult males overall, but this was not supported by my results and is not consistent with the finding that there is a substantial increase in proximity to other adult males with age – a nearly two-fold increase over adulthood. In sum, I find no evidence that either mobility or competition avoidance limits the sociality of old male chimpanzee.

Another pathway through which senescence may shape social aging is through the generation of compensatory adaptations (Siracusa et al. 2022b). Accordingly, I hypothesized that older individuals may adopt alternative reproductive tactics in the face of changing payoffs. Chimpanzees experience demographic senescence, age-related declines in fertility. At Ngogo, the number of offspring sired sharply declines after age 30 (Langergraber unpublished data). This decrease in reproduction seems concomitant with declines in dominance (Watts 2018). As has been observed in other primates (Silk et al. 2020), aging males could first, gain mating opportunities through increased association with adult females or via increases indirect fitness through interactions with immature individuals who might be their offspring. Regarding the first prediction, there

was no evidence that aging males increased proximity nor grooming behavior with adult females; older males both groomed adult females less and in turn, adult females rarely groomed adult males at all.

The second prediction that older males increase affiliation with offspring is consistent with prior research at Ngogo that found increased association between adolescent sons and late-life fathers chimpanzees (Sandel et al. 2020). Yet this finding presents a puzzle as relationships with fathers are unexpected because chimpanzees are thought to be unable to discriminate paternal relatives given their polygynandrous mating system (Langergraber et al. 2007). I found that older males spent substantially more time grooming non-adults compared to their prime-aged counterparts. However, I did not consider the kinship of these infants, juveniles, and adolescents. Given the conjectural nature of the alternative reproductive tactics hypothesis (4), it will be necessary to incorporate information on kinship and the specific identity of grooming partners to determine whether old male chimpanzees regularly groom their potential offspring. Because maximizing late-life fitness is a precondition for the evolution of longevity, the reproductive tactics of old males warrant special attention.

Why are old male chimpanzees more social?

Consistent with prior research, I found that older male chimpanzees were more social according to measures like proximity (Rosati et al. 2020). Conversely, prior studies at various sites have found that older male chimpanzees are more solitary, or more likely to be alone (Goodall et al. 1984, Huffman 1990, Hosaka & Huffman 2015, Rosati et al. 2020). Because this chapter only analyzes proximity and interaction data,

assessing whether old males at Ngogo are more solitary is beyond the scope of this study. Because I defined party association based on daily association, observations in which individuals would be considered truly solitary (party size = 1) represented less than 1% of observation time, insubstantial for an analysis. While the low representation of solitary individuals is likely in part due to the methodological challenges of finding and following them, I did make particular effort to find and follow solitary individuals for this study. It is possible that the dearth of observations on solitary individuals may nonetheless reflect high degrees of sociality. Because party size is positively associated with resource quality (White & Wrangham 1988, Sakura 1994), one possible explanation is that the especially good ecological conditions at Ngogo promote increased sociality. Additionally, this study took place over a particularly high-quality diet period, featuring greater contributions of ripe non-fig fruit to the diet than historically observed. The importance of collecting data during such rare or otherwise infrequently observed events, such as truly solitary male chimpanzees, further emphasizes the importance of longitudinal studies.

A central finding of Rosati et al. (2020), supported by findings from other primates (Machanda & Rosati 2020, Siracusa et al. 2022a), is that there are increases in social selectivity with age. Old chimpanzees exhibited increased focus on mutual friendships characterized by equitable investment as well as increased affiliative interactions over agonistic ones, which they describe as social selectivity. While I did not directly evaluate selectivity, my findings furnish additional insights into whether old chimpanzees engage in social relationships selectively. I found no change in the number of grooming partners with age as would be expected with social selectivity.

However, I did find that old chimpanzees were in proximity more often with non-adult-males and groomed non-adults absolutely more, which is not fully explained by the hypothesis that with age males should prioritize only high-quality relationships, given their social bonds are most closely formed with other adult males. Rosati et al. (2020) also posit that established relationships may be particularly reliable for old chimpanzees, presenting high benefits of social interaction with few costs. Old male chimpanzees may be attractive social partners even if they do not offer as much grooming as their rates of aggression such as display rate decline (see Chapter 3). This explanation, however, may not account for the age-specific increase in rates of grooming non-adults, with whom old male chimpanzees have not had long-term established relationships, particularly as old males receive less grooming from non-adults than prime-aged males. The mechanism underpinning increased sociality, Rosati et al. (2020) propose, could be an increasing capacity for emotional regulation, such as a less reactive temperament with lower rates of aggression. Future studies should consider the function of aggression by old adult males and whether its patterns fit within the framework of increasing social appeal of old chimpanzees.

Limitations & future directions

By collecting data from the same individuals at the same time, this study avoids confounding effects of interannual variability in resources. Nevertheless, the findings of cross-sectional studies such as the one performed here should be interpreted cautiously when applied to senescence (Nussey et al. 2008). It is not possible to conclude that these observed correlations represent social aging, shifts across the lifespan. Rather,

shifts may reflect survivorship bias and inter-individual variation. Mortality selection suggests this study is one of exceptional survivors, chimpanzees who may have necessarily senesced more slowly than their peers (Vaupel et al. 1979). For instance, if chimpanzees who are more social, with strong social bonds, are more likely to survive to old age (Silk 2007, Synder-Mackler et al. 2020), then a cross-sectional analysis could reveal apparent increases in sociality due to the predominance of a cohort of old chimpanzees. A salient example of the value of social bonds for chimpanzee survival comes from a common extrinsic source of mortality: males chimpanzees make lethal coalitionary attacks on their neighbors and less social individuals more likely to be found alone will be vulnerable to such attacks (Mitani et al. 2010). A long-term study of this population is necessary to examine whether shifts in sociality with age are attributable to within individual shifts across the lifespan.

Additionally, chimpanzees at Ngogo have greater life expectancy than in any other chimpanzee community, including Kanyawara only 10km away (Wood et al. 2017). Notably at Ngogo, about 52% of male chimpanzees live past the age of 30, and 33% live past the age of 40 (Wood et al. 2017). A predominant explanation for the longevity of the Ngogo chimpanzees is the exceptional fruit supply (Potts et al. 2009, 2011, Watts et al 2012). Higher survival rates may promote sociality in old age because individuals simply have more known individuals with whom to interact. With increasing age, actuarial senescence ensures that elderly members of any population have fewer and fewer peers. Because male chimpanzees form stronger social bonds with peers relative to non-peers (Mitani 2009), it is possible that older males at Ngogo are more social because they live longer. However, the inverse is also worth consideration: that

older males at Ngogo live longer because they are more social. Understanding the factors associated with Ngogo's particularly long-life expectancy should consider how abundant resources may promote increased social connection.

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Supplementary Materials

Table S18. Subject ID (n = 20) in order of increasing age. Age corresponds to age at study midpoint (February 2018) and ranks reflect the average Elo rating over the study period.

ID	age	birth year	community	Elo rating (mean)	ordinal rank
Wes	21.7	1997	West	-452.73	5
Django	22.1	1997	Central	-435.42	13
Hicks	22.1	1997	Central	-279.4	11
Evans	23.1	1996	Central	17.34	7
Wayne	23.1	1996	West	-674.24	6
Peterson	24.1	1995	Central	137.56	5
Hutcherson	25.1	1994	West	579.17	1
Porkpie	25.1	1994	Central	-130.61	9
Cash	26.1	1993	Central	-444.11	14
Jackson	28.1	1991	Central	696.64	1
Richmond	32.1	1987	West	197.56	2
Rollins	33.1	1986	West	-444.92	5
Dexter	34.1	1985	Central	-601.36	16
Morton	35.1	1984	Central	286.74	3
Basie	36.1	1983	Central	65.75	7
Miles	38.1	1981	Central	116.66	6
Garrison	42.1	1977	West	-304.48	4
Bartok	46.1	1973	Central	-17.73	8
Monk	47.1	1972	Central	-407.54	12
Brownface	53.1	1966	Central	-628.16	16

Table S19. Probability of having no other independent individuals in proximity (≤5 m) in scan, weighted average model effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95).

variable	estimate	SE	CI.low	CI.high	overlap
% time foraging	1.53	1.12	1.22	1.92	no overlap
age	0.7	1.19	0.5	0.99	no overlap
age * % time foraging	0.91	1.16	0.68	1.22	50% overlap
age * in tree	1.19	1.21	0.82	1.73	95% overlap
community (West)	0.93	1.14	0.72	1.21	50% overlap
estrous female in association	0.8	1.15	0.6	1.05	95% overlap
in tree	3.09	1.09	2.63	3.63	no overlap
intercept	0.93	1.13	0.73	1.18	50% overlap
party size	1.15	1.14	0.88	1.5	95% overlap
rank	1	1.07	0.88	1.14	50% overlap
time (cos(pi*time))	0.75	1.08	0.64	0.87	no overlap

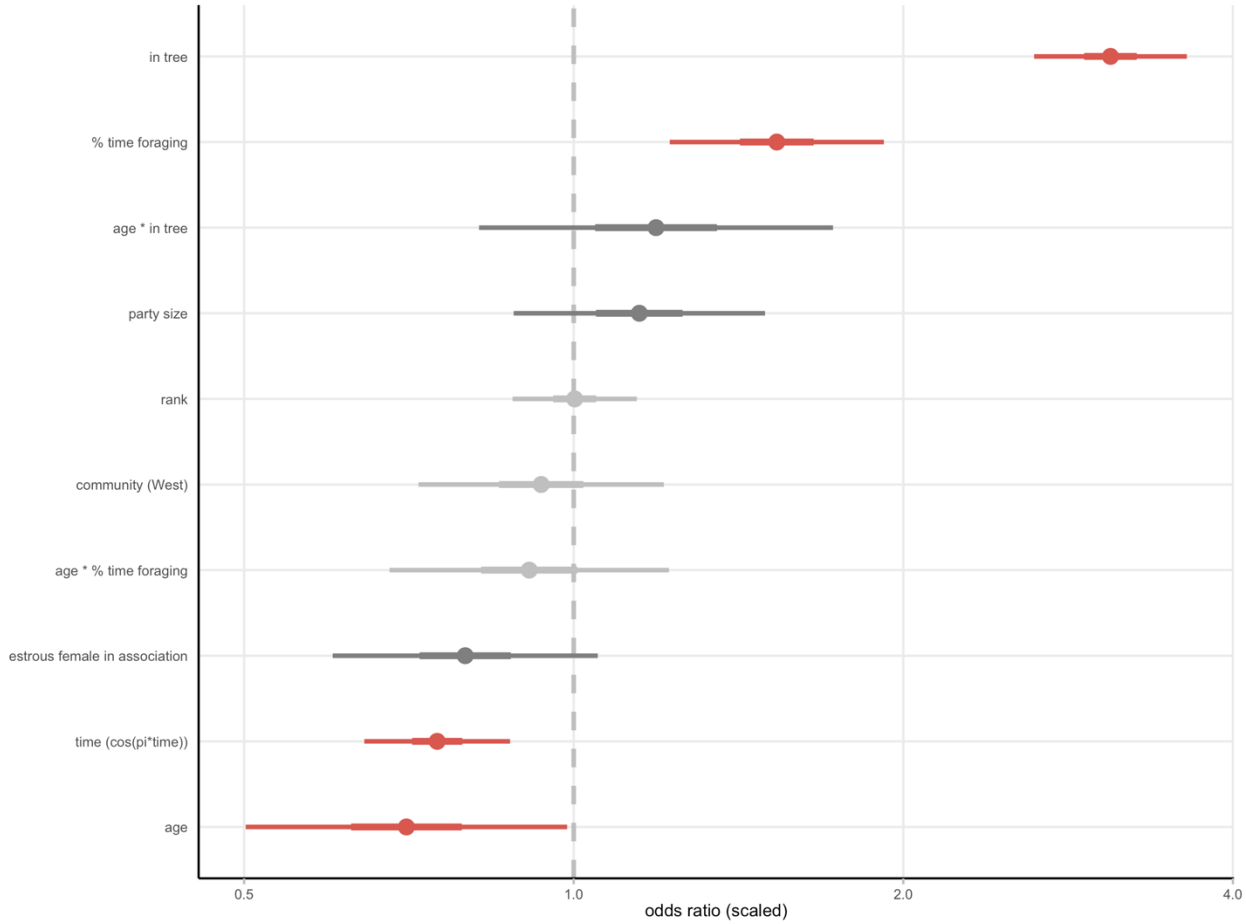

Figure S18. Probability of being alone (0 individuals in proximity) in 15-minute scans, coefficient plot from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S20. Number of adult males in proximity in 15-minute scans, weighted average model effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95).

variable	estimate	SE	CI.low	CI.high	overlap
% high-quality fruit	1.49	1.11	1.22	1.81	no overlap
age	1.42	1.19	1.01	2	no overlap
age * % high-quality fruit	1.47	1.18	1.06	2.04	no overlap
age * estrous female	1	1.05	0.9	1.1	50% overlap
age * foraging score	1.01	1.09	0.85	1.2	50% overlap
age * in tree	0.99	1.09	0.84	1.16	50% overlap
community (West)	0.99	1.1	0.83	1.19	50% overlap
date	0.92	1.08	0.79	1.08	95% overlap
estrous female in association	1.01	1.06	0.91	1.13	50% overlap
foraging score	0.67	1.1	0.56	0.81	no overlap
in tree	0.51	1.09	0.43	0.6	no overlap
intercept	0.59	1.1	0.49	0.71	no overlap
party size	1.03	1.07	0.9	1.18	50% overlap
rank	0.84	1.16	0.62	1.13	95% overlap
time (cos(pi*time))	1.33	1.06	1.18	1.5	no overlap

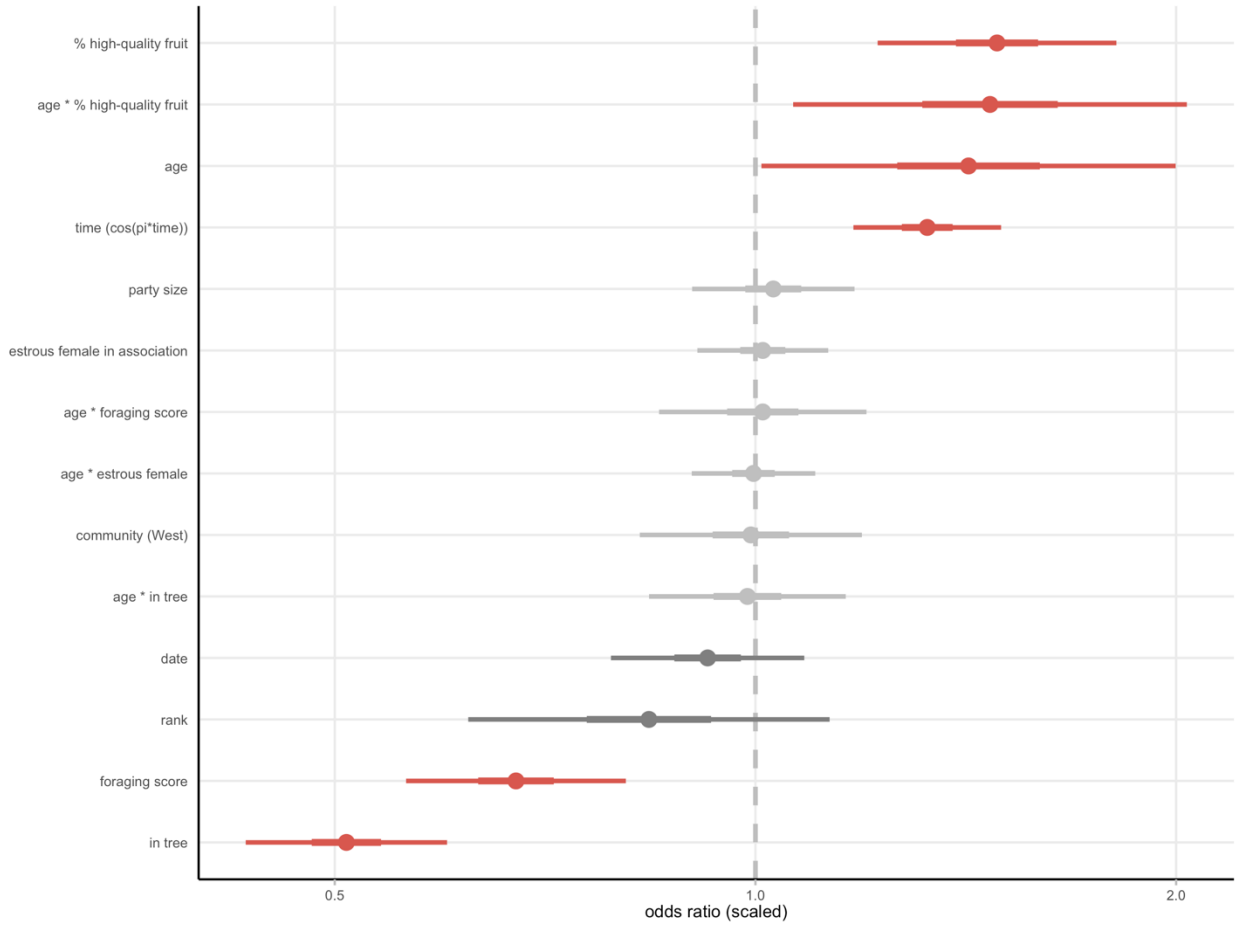

Figure S19. Number of adult males in proximity in 15-minute scans, coefficient plot from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S21. Number of adult females in proximity in 15-minute scans, weighted average model effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95).

variable	estimate	SE	CI.low	CI.high	overlap
% time foraging	0.85	1.17	0.62	1.16	95% overlap
age	0.87	1.16	0.65	1.17	95% overlap
age * % time foraging	1.37	1.34	0.77	2.41	95% overlap
community (West)	1.67	1.2	1.18	2.38	no overlap
date	0.96	1.09	0.81	1.14	50% overlap
estrous female in association	2.62	1.18	1.89	3.63	no overlap
foraging	0.72	1.17	0.53	0.98	no overlap
in tree	0.7	1.14	0.54	0.9	no overlap
intercept	0.08	1.17	0.06	0.11	no overlap
party size	0.67	1.17	0.49	0.91	no overlap
rank	1	1.07	0.87	1.15	50% overlap
time	1.24	1.11	1	1.53	no overlap

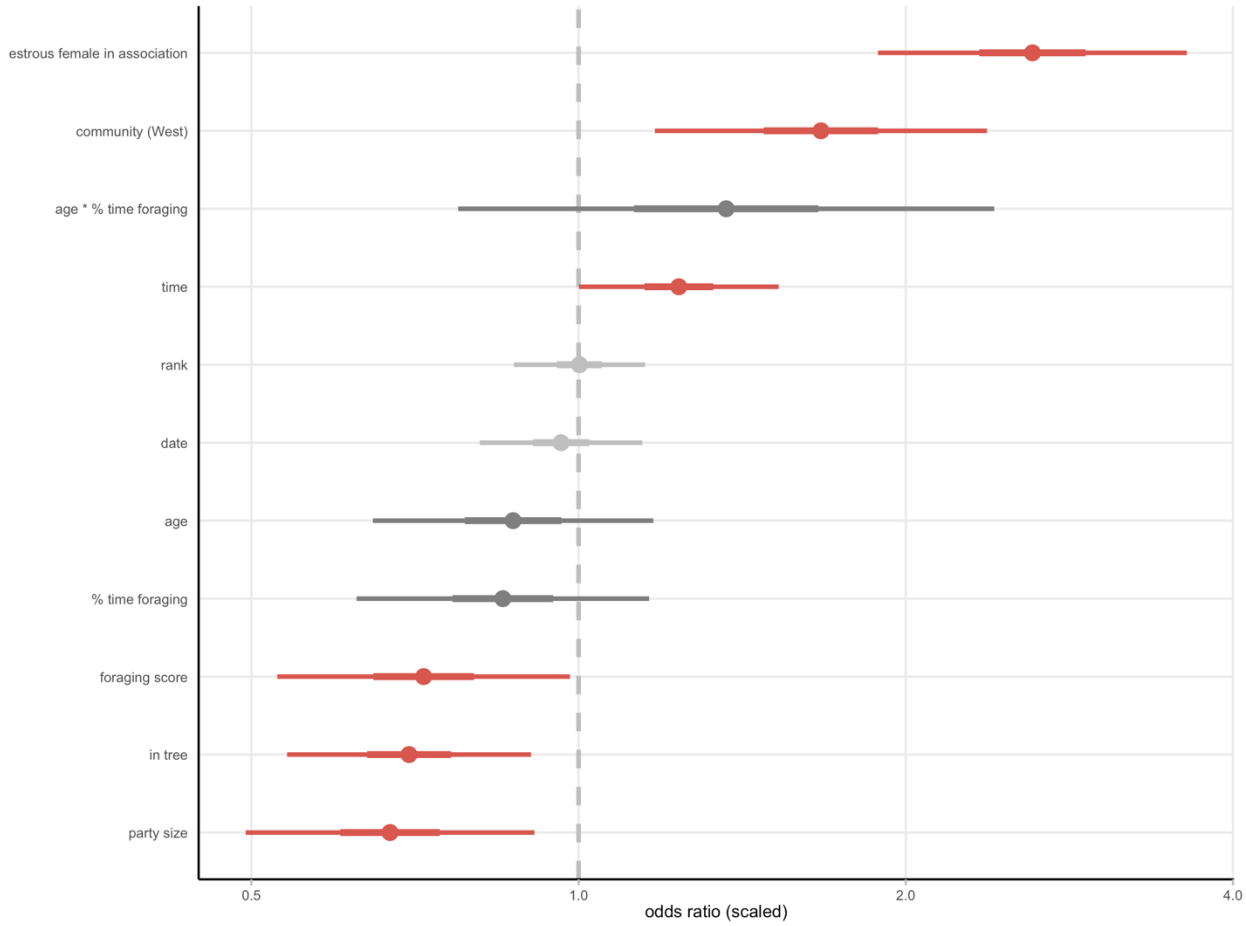

Figure S20. Number of adult females in proximity in 15-minute scans, coefficient plot from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S22. Grooming time as actor per focal weighted average model effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Offset coefficient for focal duration not shown.

variable	estimate	SE	CI.low	CI.high	overlap
% time foraging	1.62	1.06	1.44	1.83	no overlap
adult female	0.24	1.05	0.22	0.27	no overlap
age	0.59	1.31	0.35	1	95% overlap
age * % time foraging	1.26	1.11	1.02	1.55	no overlap
age * adult female	0.71	1.13	0.56	0.9	no overlap
age * estrous female	1.3	1.15	0.98	1.71	95% overlap
age * non-adult	7.57	1.17	5.6	10.25	no overlap
date (sin(pi*date))	0.64	1.06	0.57	0.71	no overlap
estrous female in association	1.44	1.06	1.29	1.62	no overlap
intercept	0.02	1.14	0.01	0.02	no overlap
non-adult	0.07	1.1	0.06	0.08	no overlap
party size	1.01	1.04	0.94	1.09	50% overlap
rank	0.91	1.1	0.75	1.1	95% overlap

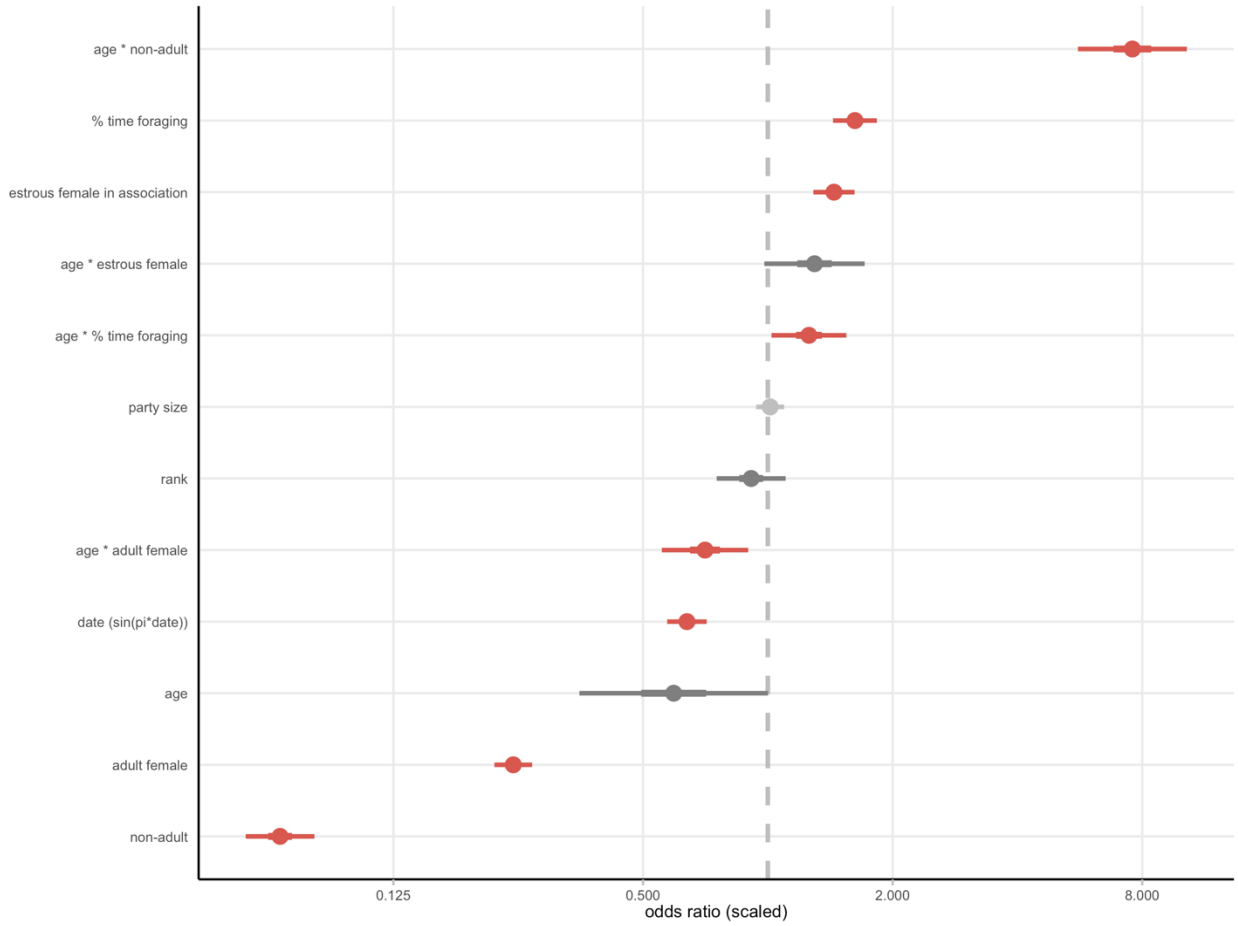

Figure S21. Grooming time as actor per focal, coefficient plot from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S23. Grooming time as recipient per focal weighted average model effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Offset coefficient for focal duration not shown.

variable	estimate	SE	CI.low	CI.high	overlap
% high quality fruit	0.79	1.04	0.74	0.86	no overlap
adult female	0.06	1.11	0.05	0.07	no overlap
age	1.23	1.23	0.82	1.85	95% overlap
age * % high quality fruit	1.01	1.04	0.94	1.08	50% overlap
age * adult female	0.05	1.27	0.03	0.08	no overlap
age * estrous female	1.28	1.08	1.1	1.49	no overlap
age * non-adult	0.83	1.08	0.71	0.97	no overlap
community (West)	0.89	1.21	0.61	1.3	50% overlap
estrous female in association	1.33	1.05	1.22	1.46	no overlap
intercept	0.03	1.13	0.02	0.04	no overlap
non-adult	0.29	1.04	0.26	0.31	no overlap
observer (SN)	1.13	1.04	1.05	1.21	no overlap
party size	0.99	1.03	0.93	1.05	50% overlap
rank	0.94	1.07	0.82	1.08	95% overlap

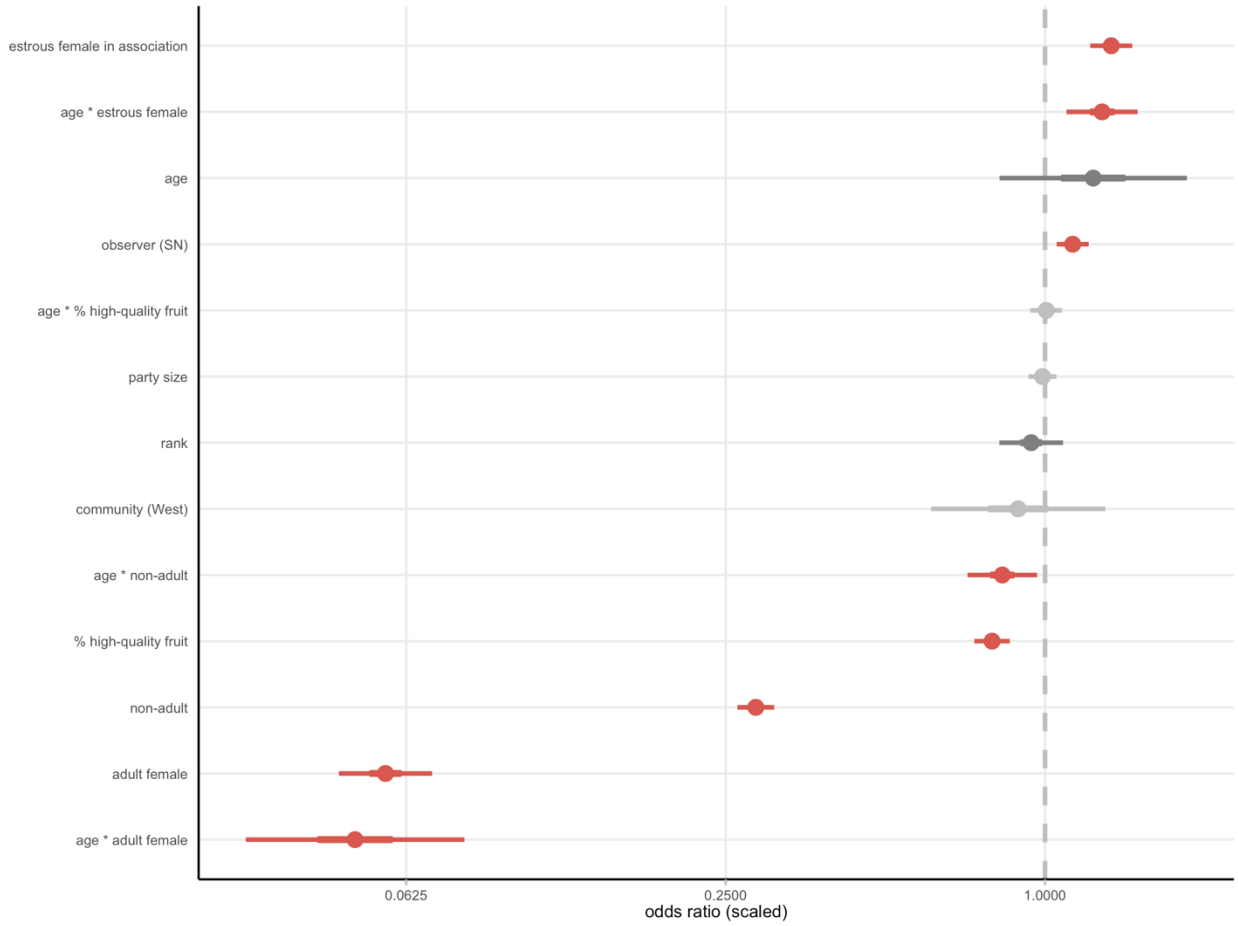

Figure S22. Grooming time as recipient per focal, coefficient plot from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Table S24. Number of grooming partners per focal weighted average model effects. Back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Offset coefficient for focal duration not shown.

variable	estimate	SE	CI.low	CI.high	overlap
% high quality fruit	1.14	1.14	0.88	1.47	95% overlap
age	0.92	1.12	0.73	1.15	95% overlap
age * % high quality fruit	1	1.06	0.9	1.11	50% overlap
age * estrous female	1.01	1.09	0.86	1.2	50% overlap
community (West)	1.01	1.06	0.91	1.13	50% overlap
date	0.96	1.08	0.82	1.11	50% overlap
estrous female in association	1.39	1.12	1.12	1.74	no overlap
intercept	0.01	1.1	0.01	0.02	no overlap
observer (SN)	0.76	1.09	0.64	0.89	no overlap
party size	1.29	1.14	1	1.66	no overlap
rank	1.03	1.07	0.91	1.16	50% overlap

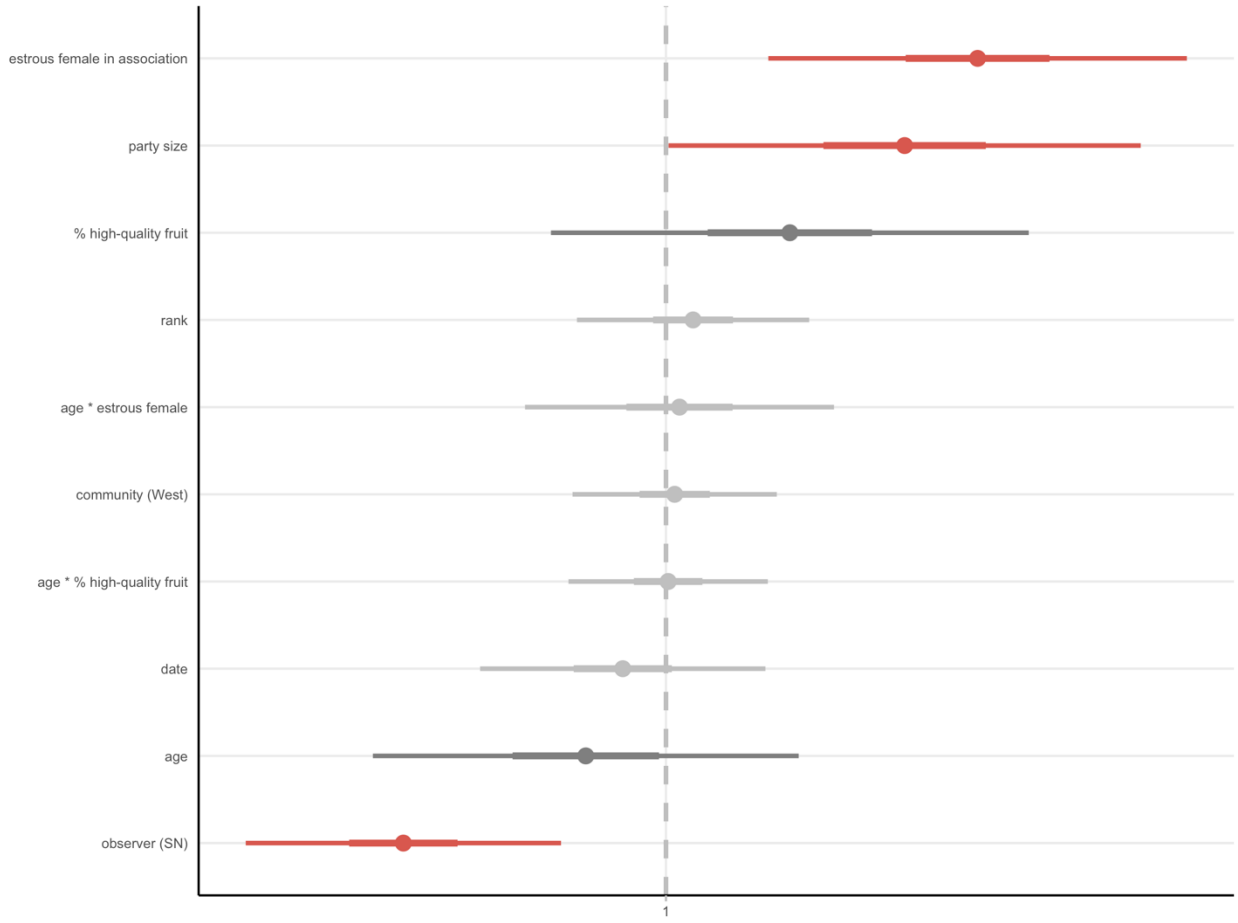

Figure S23. Number of grooming partners per focal, coefficient plot from back-transformed (exponentiated) beta-coefficients from weighted model averages (cumulative weight ≥0.95). Thick bars represent 50% CI and thin bars represent 95% CI, whereas color depicts the estimates' overlap with a null effect.

Chapter 5.

Conclusion & Future Directions

This dissertation investigated the patterns of aging in adult male chimpanzees, with an emphasis on how senescence may produce challenges for older adult males. I examine axes of variation in foraging behavior, life history tradeoffs, and social aging along with how they corresponded to subject age. While declines in fertility and dominance are well established in chimpanzees, this is one of the first studies to look at declining productivity and activity with age in chimpanzees. In this dissertation, I collected a novel dataset that examined multiple physiological and behavioral traits in a cross-sectional sample of adult males. I showed the first clear evidence that fecal particle size increases with age, and relatedly, that tooth wear may impede chewing efficacy in wild chimpanzees. My findings provide insights into how old male chimpanzees experience senescence, and in particular how they may adjust their behavior to compensate for the challenges it generates. The behavioral flexibility described across ages within this dissertation may help explain how chimpanzees manage to maintain both reproduction and survivorship late in life.

Chapter 2 highlights the relationship between age and a suite of foraging measures. I demonstrate that measures of food processing and ingestion were negatively correlated with age. In contrast to prior studies, old chimpanzees were not more terrestrial in foraging contexts, and I found only weak evidence that old chimpanzees climbed shorter vertical distances while foraging. I conclude that declining mobility, therefore, is unlikely to regularly limit most aging chimpanzees' access to foods. Diet item selection did not vary with age, but old chimpanzees may have been more likely to consume ripe figs. Consequently, old chimpanzees did not adjust behavior to prioritize different foods, such as more accessible foods with weaker mechanical properties. However, ingestion rates of both leaves and non-fig fruits were negatively associated with age**.** Notably, processing performance decreased with age across seasons and diets; both the amount of large undigested fecal material and fecal particle size increased with age. Both these and declines in ingestion rate may be linked to decreased chewing efficiency. If old chimpanzees take longer to chew and derive fewer resources from digesta, then senescence may limit energetic or nutritional yields. Taken together, these findings suggest that physiological deteriorations of age likely contribute to diminishing foraging performance, i.e., foraging senescence.

While there is widespread evidence of actuarial and reproductive senescence (Nussey et al. 2013), this study provides important data on functional senescence in the wild. Additionally, my findings support the idea that organisms' ability to extract energy from their environments could play an important role in shaping late-life fitness, consistent with Lecomte et al.'s (2010) proposal that feeding efficiency is a potential "cornerstone" of senescence in wild animals.

Chapter 3 highlights a suite of behavioral, but not physiological shifts with age in a cohort of particularly long-lived adult male chimpanzees. Neither C-peptide of insulin, a measure of energetic status, nor testosterone, a costly hormone and proxy for reproductive investment, varied reliably with age. In contrast, the rate of foraging increased with age in large parties and decreased in small parties. Old chimpanzees spent more time resting and less time moving regardless of environmental factors, yet vertical climbing distances did not vary reliably with age. Meanwhile, display frequency and distance both declined with age, as did copulation rates, but only during high-quality food periods. I interpreted these results with respect to hypotheses on shifting trade-offs with age and two life history loci: resource pool management and allocation. My results provide insights into the potential tradeoffs between physiology and behavior that old chimpanzees may make as they balance deteriorations of age (Emery Thompson et al. 2020a) with an observed capacity to maintain condition and survivorship until late in life (Wood et al. 2017). My results suggest that old male chimpanzees may strategically manage their resource pool under new constraints produced by senescence, while engaging in a degree of terminal restraint. Because testosterone is costly and said to come at the expense of long-term survival (Hau 2007), its maintenance across ages should offer reproductive benefits if aging males incur relatively greater costs to maintain it. Such findings may help explain why, despite seemingly maintaining body condition, old male chimpanzees exhibit declining fitness.

In Chapter 4, I present several patterns between age and sociality in adult male chimpanzees. I found that various measures of social engagement were positively associated with age: old males were less likely to be socially distanced, were in

proximity to more adult males, spent longer grooming others during high-quality food times, groomed non-adults more, and received more grooming when in association with an estrous female. Alternatively, several social behaviors were negatively correlated with age: old males groomed and received less grooming from adult as well non-adults. Other measures such as the number of social partners showed no change with age. These results — which control for rank and party composition — support prior findings that older male chimpanzees are more social in various measures like proximity (Rosati et al. 2020).

Because scant research has examined the relationship between senescence and late-life changes in social behavior, I evaluated hypotheses of mechanisms for how senescence may constrain sociality in old chimpanzees. Broadly, I find little evidence that senescence decreases sociality in late-life chimpanzees as few markers of sociality were negatively associated with age. I did, however, find some support for the hypothesis that energetic constraints may influence sociality in late-life chimpanzees. I hypothesized that because late-life chimpanzees may experience greater energetic stressors due to factors like increased costs in immune function (Negrey et al. 2021) and decreases in foraging performance (see Chapter 2), they may face tradeoffs between maintenance and sociality. I found that both the number of adult males in proximity and time spent grooming others increased with age, but only during high-quality food times; old chimpanzees appeared more social on days where less time was spent foraging and diets contained large amounts of high-quality fruit. These findings may indicate that patterns of increased sociality in old males – particularly with other adult males – are facilitated by periods of abundant food, which suggest that old males

are sensitive to energetic or foraging requirements during food-poor times. I discuss preliminary evidence that older individuals may adopt alternative reproductive tactics in the face of changing payoffs as a result of senescence.

These findings generate several questions. First regarding foraging senescence, what are the costs associated with decreased feeding efficacy? While such declines do not appear to have immediate energetic consequences as old chimpanzees neither forage absolutely more nor exhibit diminished energetic balance, it is possible that they impact both energetics and foraging behavior in other ways. For example, do decreases in chewing efficacy generate differential values of food items based on their mechanical and nutritional properties? While I found no evidence for my prediction that old chimpanzees may select different food items, I did find that old males were more likely to select ripe figs than their prime-aged counterparts. While this effect was small, a closer examination of diet and food item properties may reveal an important source of variation in the diet across ages in chimpanzees and other primates.

Another unanswered question concerns the observed declines in intake rate and fecal particle size with age. Are such declines directly attributable to dental wear as is the case in other herbivores? Given the lack of prior evidence that dental wear diminishes chewing ability in great apes, it will be necessary to confirm such findings with longitudinal data across populations. If chewing efficacy does decline with age, it will be of interest to understand how patterns of dental wear vary among individuals, as well as between males and females. Moreover, if foraging senescence is in fact, a ‘cornerstone’ of aging, what is its relationship to other functional declines such as immunosenescence? Do declines in foraging efficacy make old chimpanzees more

vulnerable to certain environmental conditions such as those that occur during poor quality food times?

Importantly, I can think of no a priori justification for why males, but not females, would experience foraging senescence. Female chimpanzees are subject to the same somatic deteriorations such as dental wear that may generate declines in various components of foraging proficiency. While rates of aging in females may be lower, their longer lifespans permits the accumulation of substantial damage, as seen in the bones of elderly female chimpanzees (Gunji et al. 2003). The disposable soma hypothesis predicts that the sex with a longer expected lifespan should invest more heavily in somatic structures. Given female chimpanzees' greater life expectancy, do they also show decreased rates of dental senescence because they invest more in enamel as predicted by the disposable soma hypothesis?

The lack of an association between age and physiological markers documented in Chapter 3 leads to several questions. The fact that there was little variation in the C-peptide insulin, or energetic balance, between individuals or seasons questions its utility as a broadly applicable proxy for energetic status. Is this because the Ngogo chimpanzees are able to adjust their behaviors in ways to consistently obtain adequate food? If this was the case during my study period, how often is it true under different ecological circumstances? Additionally, a potentially puzzling finding was that testosterone did not decline with age, but various behaviors associated with reproductive competition did. Prior studies have documented variation in testosterone senescence across biocultural contexts in humans. But how variable are patterns of testosterone senescence in humans, and what socioecological features shape it? If

testosterone is not associated with rates of reproductive investment in this sample of chimpanzees, why are older males incurring costs associated with maintaining high testosterone levels without apparent benefits? Additionally, what explains the large and persistent difference in testosterone levels between Ngogo West and Ngogo Central? Did group differences in mating competition and/or territorial defense affect my results?

Regarding the sociality of old male chimpanzees, I pose, but do not answer, the question of why old male chimpanzees may be more social as has been documented across sites, including now Ngogo. Like the Kanyawara chimpanzees, do the Ngogo chimpanzees display social selectivity with age, including an increasing investment in mutual rather than one-sided relationships? Analyses of dyadic relationships and how they change with age, for instance regarding grooming equitability, will generate useful data to help address this question. Rosati et al. (2020) suggest that adult males become less reactive and aggressive with age, which could make them more appealing social partners. Data from populations such as Ngogo could help determine if this is the case and whether this change in affect explains patterns of social aging. If changes in affect occur, is it useful to interpret them in an adaptive framework, in which old chimpanzees may be maximizing fitness late in life? Future studies should consider the function of aggression by old adult males and whether its patterns fit within the framework of increasing social appeal of old chimpanzees.

In Chapters 2 and 3, I provide evidence that locomotion does not vary substantially with age (such as climbing distance). However, in Chapter 3, I document that the frequencies of moving behaviors are negatively associated with age, more in accordance with prior findings that travel time and arboreality may increase with age

(Emery Thompson et al. 2020). In Chapter 4, I present some evidence that arboreal mobility does not seem to constrain sociality in old males. However, I did not consider travel distances and how they may shape social decisions differentially with age. Additional data, including on travel distances, may help reconcile these findings and clarify the role of locomotion in primate aging.

Because females live longer and exhibit greater rates of bone loss, does locomotion play a particular role in the senescence of female chimpanzees? Data on age-related bone loss may help address this and other questions. While bone loss is well documented for old female chimpanzees, such studies have relied on necropsied specimens (Gunji et al. 2003). A correlate of bone resorption (type 1 collagen, NTx) may provide a way to assess bone loss in vivo and was recently validated in chimpanzees (Sandel et al. 2023). What are the patterns of bone loss in wild chimpanzees, and does it impede locomotion as hypothesized (Madimenos 2015)? Do female chimpanzees experience greater bone loss than males and if so, why? Such data can inform our understanding of the evolution of sex-differences in aging and bone health.

Throughout this dissertation, I discuss the limitations of cross-sectional studies including the possibility that observed correlations with age are not the result of senescence, but rather survivorship bias. Chimpanzees that survive to old age may be exceptional in various ways (Vaupel 1979). Consequently, an essential inquiry is whether the observed declines with age in fact reflect within-individual senescence. Such a question can only be addressed via longitudinal studies.

Results of this research increase our understanding of senescence, foraging behavior, life history tradeoffs, and sociality in chimpanzees. My findings also have

important implications for our understanding of longevity in our own species. Data on aging from one of our closest relatives are critical to inform models of human evolution, particularly those that seek to explain our extended lifespans. Because maximizing late-life fitness is a precondition for the evolution of longevity, the reproductive tactics of old chimpanzees warrant special attention. Old chimpanzees move and eat differently than their younger counterparts, obtaining fewer resources from their food. Old males reproduce less and invest less in aggression like displays, yet find themselves socializing more with other adult males. For humans too, physical capacities and social lives change with age.

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