Shifting sociality during primate aging

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Abstract

Humans exhibit major age-related shifts in social relationships along with changes in social and emotional psychological processes that underpin these behavioral shifts. Does social aging in nonhuman primates follow similar patterns, and if so, what are the ultimate evolutionary consequences of these social shifts? Here we synthesize empirical evidence for shifts in social behavior and underlying psychological processes across species. Focusing on three elements of social behavior and cognition that are important for humans—propensities to *engage* with others, the positive versus negative *valence* of these interactions, and capabilities to *influence* others, we find evidence for wide variation in the trajectories of these characteristics across primates. Based on this, we identify potential modulators of the primate social aging process, including social organization, sex, and dominance status. Finally, we discuss how comparative research can contextualize human social aging.

Keywords: aging, lifespan, primates, social behavior, social cognition

1. Introduction

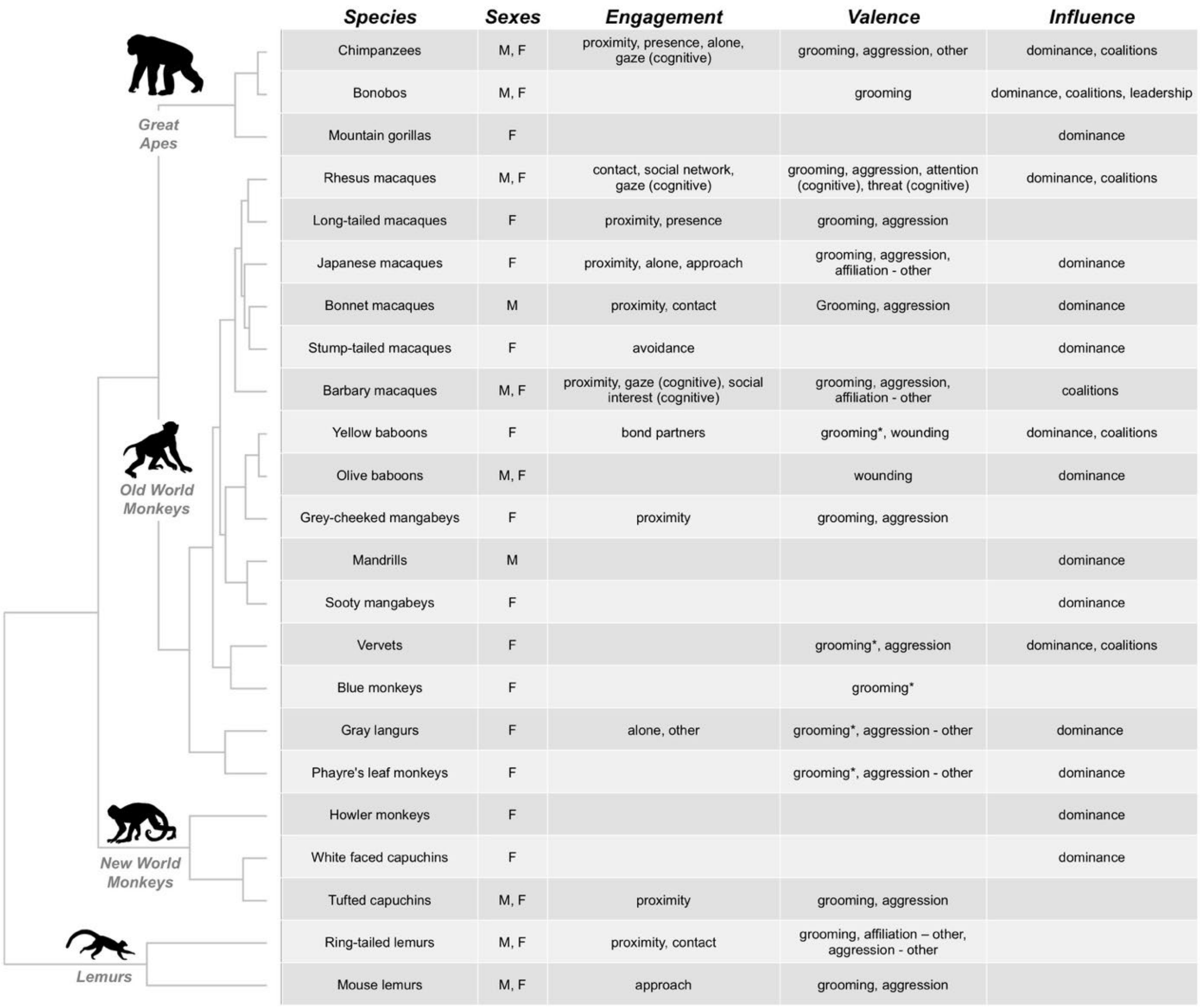
Humans are living into old age more than ever before, making it critical to understand the processes of aging. It is increasingly recognized that successful aging is not just a matter of physical health, but also depends on social functioning: people with strong social support experience enhanced wellbeing, health, and longevity [1-3]. Yet people also show complex patterns of decline, preservation, and even improvement in their social behavior and cognition during aging. For example, older adults tend to exhibit smaller social networks, yet have more emotionally-satisfying interactions, and exhibit greater skillfulness in solving social conflicts, compared to younger adults [4-8]. Variation across these different facets of sociality can therefore shape the dynamics and outcomes of successful aging.

One way to understand the consequences of these different aging trajectories is to contextualize humans in a broader comparative framework accounting for aging patterns across species. Other primates have provided crucial insights into the physiological aging process [9, 10], and can be a valuable comparative model for social aging as well due to their close genetic relatedness with humans, shared social complexity, and relatively long lifespans. Moreover, the observational techniques commonly used with animals allow for unparalleled records of natural social interactions, as well as opportunities for lifespan longitudinal studies that may be challenging to carry out in humans. Yet while recent work on primates has examined how variation in primate sociality impacts lifetime biological outcomes like fitness, health, and longevity [11-14], there has little systematic examination of how patterns of sociality themselves shift during the aging process. Rather, most work on primate social aging has focused on descriptive changes of different components of sociality, typically within a single species or sex studied in isolation.

In order to understand the processes of primate social aging, here we take a ‘bottom-up’ approach to synthesize current data from nonhuman primates. Our aim is to characterize patterns of social behavior and underlying proximate mechanisms across diverse primate species. First, we review age-related changes across different primate species in order to characterize variation in social aging trajectories. We then synthesize current data to examine the potential modulators of the primate aging process by identifying commonalities and divergences in patterns across species, between males and females, and according to dominance status—and further identify key gaps in current knowledge that are crucial areas for future research. Finally, we discuss how understanding primate social aging across different populations and individuals can inform human social aging.

2. Social aging patterns across primates

We examine studies tracking age-related changes in primates across three domains: (1) *social engagement*, or how socially active or reclusive an individual is, as a crucial pre-requisite for other social interactions; (2) the *valence of social interactions,* or the positive versus negative quality of their initiated behaviors; and (3) *social influence*, or an individual’s ability to flexibly impact other’s behavior. While these distinctions are not necessarily typically used to categorize social behavior in traditional approaches in primatology, they are important domains for understanding human aging, and conceptually capture different ways that individuals can adjust their social behavior during the aging process. Across these domains, we focus primarily on changes within adult age-classes, not just between juvenility and adulthood. Importantly, different studies of different populations often use different metrics (see Figure 1 for a summary of different relevant metrics we clustered under these domains, and ESM Tables S1-S3 for details about all metrics and studies). Given this variability in metrics, we focus on comparing aging trajectories within a study (increases, decreases or no change with age) rather than comparisons of absolute behavioral rates across species, sexes, or studies.



Species	Sexes	Engagement	Valence	Influence
Chimpanzees	M, F	proximity, presence, alone, gaze (cognitive)	grooming, aggression, other	dominance, coalitions
Bonobos	M, F		grooming	dominance, coalitions, leadership
Mountain gorillas	F			dominance
Rhesus macaques	M, F	contact, social network, gaze (cognitive)	grooming, aggression, attention (cognitive), threat (cognitive)	dominance, coalitions
Long-tailed macaques	F	proximity, presence	grooming, aggression	
Japanese macaques	F	proximity, alone, approach	grooming, aggression, affiliation - other	dominance
Bonnet macaques	M	proximity, contact	Grooming, aggression	dominance
Stump-tailed macaques	F	avoidance		dominance
Barbary macaques	M, F	proximity, gaze (cognitive), social interest (cognitive)	grooming, aggression, affiliation - other	coalitions
Yellow baboons	F	bond partners	grooming*, wounding	dominance, coalitions
Olive baboons	M, F		wounding	dominance
Grey-cheeked mangabeys	F	proximity	grooming, aggression	
Mandrills	M			dominance
Sooty mangabeys	F			dominance
Vervets	F		grooming*, aggression	dominance, coalitions
Blue monkeys	F		grooming*	
Gray langurs	F	alone, other	grooming*, aggression - other	dominance
Phayre's leaf monkeys	F		grooming*, aggression - other	dominance
Howler monkeys	F			dominance
White faced capuchins	F			dominance
Tufted capuchins	M, F	proximity	grooming, aggression	
Ring-tailed lemurs	M, F	proximity, contact	grooming, affiliation – other, aggression - other	
Mouse lemurs	M, F	approach	grooming, aggression	

Figure 1: Social aging metrics across species. Social metrics and phylogenetic distribution of current social aging data. Sex indicates if there ever is any data for both sexes (see ESM for detailed breakdown by metric). Social engagement metrics comprised time spent *alone*, *avoidance* of others, *approach* towards others spatial *proximity*, physical *contact*, *presence* in a party or group, number of *bond partners*, *social network* size, *gaze* following, and *social interest* in photographs and vocalizations. Social valence primarily comprised *grooming* given (*denotes a modified grooming index; *affiliation–other* indicates an alternative measure of affiliation described in ESM) and *aggression* given (*denotes a modified aggression index; *aggression–other* indicates an alternative measure of aggression described in ESM). Other metrics include rate of *wounding*, relative *attention* to positive versus negative stimuli, and *threat response* to emotional signals. Social influence metrics comprised *dominance rank*, *coalitions* (coalitionary aggression), and *leadership* of group movements. Primate phylogeny extracted from [15].

2.1 Social engagement

During aging, humans exhibit reductions in their social activity and interest. Older adults often report smaller social networks than younger adults [5, 16], and show declines in their general attention to other's social cues like gaze direction that track this general pattern of increasing social disengagement with age in experiments [17]. In nonhumans, these kinds of shifts have been assessed both in cognitive experiments and in natural behaviors (see Figure 1). Psychological traits can be measured by examining changes in primates' responses to and interest in social stimuli like conspecific photographs or vocalizations [18], as well as their propensity to respond to social cues in gaze-following tasks [19-21]. Observational metrics such as time spent alone, spatial proximity, or approaching others in natural behavior [22-24] can also capture an individual's willingness to socially engage with others by initiating interactions or allowing interactions to occur—because being around others is a pre-requisite for many other kinds of interactions.

Current data indicates that many primates become markedly less social with advancing age. This phenomenon has been best-studied amongst female-philopatric Old World monkeys, where females remain in their natal group and males disperse. For example, older rhesus macaques (*Macaca mulatta*) [25], stump-tailed macaques (*Macaca arctoides*) [26], Japanese macaques (*Macaca fuscata*) [26-30], and long-tailed macaques (sometimes called crab-eating macaques; *Macaca fascicularis*) [31, 32], and Barbary macaques (*Macaca sylvanus*) [18, 23] all exhibit reduced social engagement in terms of spatial distance to others, time spent alone, approaching others, or total network size. While there has been less work examining psychological mechanisms, older rhesus macaques also show a declining propensity to follow other's gaze [19, 20]. Several other catarrhines, platyrrhines, and strepsirrhines share this general pattern of increasing reclusiveness. For example, older gray langurs (sometimes called Hanuman langurs;

Semnopithecus entellus; previously called *Presbytis entellus*) [33, 34], grey-cheeked mangabeys (*Lophocebus albigena,* previously called *Cercocebus albigena*) [35], tufted capuchins (*Sapajus apella*) [22], ring-tailed lemurs (*Lemur catta*) [36], and gray mouse lemurs (*Microcebus murinus*) [37] are less likely to be in close proximity to others, or engage in fewer overall social behaviors.

Yet such social withdrawal is not universal, as some groups show steady rates of social engagement during aging. For example, male Bonnet macaques (*Macaca radiata*) exhibit no major age-related changes in social contact [38], and female yellow baboons (*Papio cynocephalus*) exhibit no changes in number of strong bond partners [39] (although they may reduce the number of weak bond partners). Notably, while older Barbary macaques show some declines in social contact, they nonetheless maintain steady profiles of interest in conspecific social stimuli such as photographs or vocalizations [18], and continue to follow other's gaze like younger monkeys [20]. Finally, older male chimpanzees (*Pan troglodytes*) are more likely to be alone, but exhibit *increased* sociality when they do engage: they are more likely to be in larger parties and in proximity to others compared to younger adults [40, 41]. In contrast, older female chimpanzees are less likely to be present in parties [42] (although note this study consisted of one old male and two old females), and show declines in gaze-following [21]. More generally, there may be important sex differences in social engagement: almost all of the studies of female-philopatric Old World monkeys to date focus on females, but males can show a different pattern. For example, whereas older female rhesus monkeys show declining social contact time and smaller networks, older males show steady or increasing social engagement [25, 43]. The reverse is true in ring-tailed lemurs: older females increase physical contact, whereas males show no changes [36].

The pattern of age-related change in current data indicate that there may not be intrinsic constraints on older individuals' ability to socially engage with others. While some primates show declines in engagement in line with the costs imposed by senescence—as physical declines may make it more difficult for older individuals to keep up with the rest of the group [44]—others may not change or even increase their social engagement. One possibility is that socioecological context impacts these patterns, as the socially dominant sex often has more preserved social functioning in old age when data exists from both sexes within a species. In particular, males are the dominant sex in both chimpanzees and macaques, and show greater social engagement during aging compared to females. In contrast, lemurs are one of the few primate taxa exhibiting female dominance [45], and female ring-tailed lemurs maintain or increase their sociality with age (note that mouse lemurs show a dispersed social system without comparable dominance patterns). Yet it is important to note that there is often only or more data from one sex (for example, females are much better studied amongst Old World primates; see Figure 1), so this could also reflect an overall difference in aging trajectories across species. To test this, it will be important to have more systematic comparisons across the sexes within-species, as well to compare closely-related taxa with variation in sexual dominance systems, such as *Eulemur* [45].

2.2. Valence of social interactions

Humans show age-related changes in not just the quantity but also the nature or quality of their social interactions. In particular, older adults show a well-documented bias in attention and memory for positive social information (e.g., looking longer at showing better recall for happy facial expressions compared to negative ones), a shift from the 'negativity' bias more commonly seen in younger adults [5, 7]. Importantly, this psychological shift has concordant behavioral manifestations: older adults exhibit a greater prioritization of positive social interactions, and show decreases in interpersonal conflicts [5, 46]. That is to say, older adults' social relationships get ‘better’ with age [47]. In animals, parallel shifts in the valence of behavioral interactions can therefore be assessed by examining the relative frequency of negative social interactions (such as aggression given) compared to positive interactions (such as grooming given). Finally, some work has experimentally tested animals’ attention or responses to emotionally-valanced information [48, 49], more closely mirroring human experimental work looking at attentional biases.

Current evidence suggests that, unlike in humans, an increasing *negativity bias* in behavior may be common across other primates. For example, multiple macaque species show a pattern of declining rates of grooming given, but relatively consistent engagement in aggression during aging. Older rhesus macaques show these changes in giving grooming and aggression even though older individuals continue to *receive* grooming from others at high rates, and are less likely themselves to be attacked [13, 25, 43, 50]. Similarly, older Barbary macaques [18, 23], long-tailed macaques [32], Bonnet macaques [38], and Japanese macaques [24, 27, 29, 30] also show declines in grooming given but initiate aggressive behaviors like younger adults. Macaques show similar shifts in their production of and responses to negative emotional signals or contexts: the production of negative emotional signals such as yawning and scratching increase in older adults [32]; production of conspecific threat signals generally stay consistent or increase in adult animals [43, 51], and older macaques can show exacerbated responses to external threats in controlled experiments [48]. This aligns with converging experimental evidence looking at cognitive biases, showing that older macaques attend relatively more to negative socioemotional stimuli (photographs of conspecific threat faces) compared neutral or positive expressions [49], similar to human research measuring looking responses to affective stimuli using similar paradigms [52, 53].

A general pattern of increasing behavioral negativity also appears in several other Old World monkey species. For example, olive baboons (*Papio anubis*) [54], vervet monkeys

(*Chlorocebus pygerythrus*) [55], gray langurs [34], mangabeys [35], and Phayre's leaf monkeys (*Trachypithecus phayrei*) [56] show steady initiation of aggression or risk of wounding from aggression across adulthood. Yet grooming declines in yellow baboons [57], blue monkeys (*Cercopithecus mitis*) [58], mangabeys [35], Phayre's leaf monkeys [33], and potentially gray langurs (although this is inconsistent [33]). The only New World monkey with comparable data are tufted capuchins, where aggression rates stay fairly consistent and grooming declines, especially in females [22]. Along the same lines, old mouse lemurs show declines in grooming and affiliation as well as increases in initiating aggression [37, 59], although ring-tailed lemurs do not show changes [36].

Overall, current evidence suggests that a relative negativity bias in behavior may be a widely conserved pattern across primates: multiple Old World monkeys (including species with different social organizations) as well as at least one New World monkey and one strepsirrhine species show a general pattern of steady aggression but declining grooming, and none show a relative positivity bias in behavior. Thus, the positivity bias seen in humans does not seem to be an intrinsic consequence of aging in primates. A clear exception to this predominant pattern is the valence of chimpanzee interactions. For example, old chimpanzees give less aggression than younger adults, but maintain affiliative social behaviors like grooming [40, 41, 60]. Similarly, agreeable personality traits increase in older chimpanzees, as in humans [61, 62]. While there are not comparable studies of aging in bonobos (*Pan paniscus*), adult male and female bonobos show age-related increases in grooming compared to subadults [63] (see also [64] for grooming networks in older adults), so there is a clear need for additional studies of bonobos.

Why might humans and chimpanzees exhibit increasing positivity while many other primates show increasing negativity (see Figure 2b)? One possibility is that this stems from the flexible fission-fusion social organization seen in both human and chimpanzees [65]. This social system means that male chimpanzees often have more flexibility in choice of whom they spend time with than primates that exhibit low fission-fusion dynamics such as macaques [66, 67]. Moreover, bonds amongst chimpanzees are not as strongly patterned by kinship compared to many female-philopatric Old World monkeys [65, 68]. Relationships with non-kin may require more time and effort to maintain than is the case for kin, given that kinship bonds intrinsically provide indirect fitness benefits and are important for many species [68], resulting in different patterns of affiliation and aggression during aging. Another relevant factor may be life history: chimpanzees are amongst the most long-lived nonhuman mammals in terms of total lifespan, and can live more than 60 years in the wild [69]. This means that chimpanzees, like humans, spend many years—even decades—as older individuals. During this period they can continue to obtain fitness benefits through affiliative strategies that require maintaining bonds with non-kin allies [70], a strategy that might be less relevant for other species. To test these possibilities, it is crucial to have data from other fission-fusion species (such as spider monkeys [71]), as well as from bonobos, who share life history and basic social organization with chimpanzees, and gorillas, who have reduced lifespans compared to chimpanzees [72].

2.3 Social influence

A final important change in human social relationships during aging concerns older adults' abilities to flexibly impact other's behavior. Older adults can exhibit general deficits in social cognition such as theory of mind skills, yet also can also show greater 'wisdom' and thus increasing skillfulness at addressing complex social conflicts [73-75]. Relevant changes have been assessed in nonhumans by examining strategic social behavior, such as acquisition of high dominance status, propensity to form coalitions, and leadership of group movements. Other relevant metrics such as third-party interventions like consolation [76], or experimental cognitive studies of strategic deception or other aspects theory of mind [77] and partner choice in cooperation [78], have not been studied in the context of aging to our knowledge (see also Figure 1).

Current evidence indicates that age-related changes in dominance rank, the best-studied metric to date, are highly variable across species. In many male primates, dominance exhibits an inverted-U-shape with age, such that the youngest and oldest adults are lowest ranking, while prime-aged adults achieve the highest status. This pattern is evident in male chimpanzees [79, 80] and many male Old World monkeys, including mandrills (*Mandrillus sphinx*) [81], olive baboons [82], yellow baboons [82-85], and some populations of Japanese macaques [86, 87]. While male rhesus macaques sometimes show this pattern [86], rank is also sometimes achieved through queueing, such that individuals with the longest tenure length have the highest rank [88-90] and rank correlates better with tenure than age [91]. In other cases, age had no effect on male rhesus dominance [86, 92]. Queueing is likely the result of synchrony in female reproductive cycles in this species, which reduces reproductive skew and thus the reproductive benefits of rank [93].

In females, in contrast, dominance often shows more linear changes. For example, rank declines with age in Phayre's leaf monkeys [33], gray langurs [34, 94], and howler monkeys (*Alouatta palliata*) [95]. But some species exhibit no overall change or even increases with age. For example, rank remains stable in female olive baboons [82], female stump-tail macaques [26], female vervet monkeys [55], and female sooty mangabeys (*Cercocebus atys,* previously called *Cercocebus torquatus*) [96]. An important consideration here is that matrilineal social organizations can create complex age effects. For example, among female baboons and macaques, daughters' dominance rank is inherited from their mother in inverse birth order, such that youngest daughter has the highest rank [97, 98]. Thus, rank within the matriline generally decreases with age as younger sisters reach maturity. An exception is the oldest female of each matriline, where age is positively related to status within the matriline [99, 100]. Lifespan pattern for these females are even further complicated when looking at overall rank within the whole group: if a female from the highest ranking matriline enters the group's adult hierarchy, members of all other matrilines accordingly drop in rank. Female white-faced capuchins (*Cebus capucinus*) also exhibit matrilineal rank, although the pattern matrilineal inheritance may be more relaxed [101, 102]. Finally, some female apes obtain rank via queuing: both female chimpanzees [103], and female bonobos exhibit increases in rank with age [104-106]. However, female mountain gorillas (*Gorilla beringei berengei*) exhibit the inverted-U pattern seen in many males [107].

There have been fewer studies looking at other aspects of social influence, but current evidence suggests that at least some other relevant behaviors also show these variable age patterns. For example, coalitionary aggression in male chimpanzees shows a U-shaped pattern, such that a greater proportion of aggression is coalitionary in younger and older individuals [108] (but see [80] for evidence of declines in an extremely large community). Thus overall lower-ranking age classes show more coalitions, even though these coalitions may have different consequences of rank and fitness for these different cohorts [109]. In other species, participation in coalitions does not shift much with age. For example, older female vervet monkeys maintain high rates of coalitionary aggression specifically in support of their daughters [55]. While this may be a common pattern for species with matrilineal dominance inheritance, where coalitionary interventions support close maternal kin [55, 110], this pattern is not consistent as coalitionary aggression which actually increases with age in female rhesus macaques [111]. Coalitionary aggression also increases for male Barbary macaques [112], and male baboons [113, 114] (although see [84]). which may be because coalitions help individuals maintain rank and access mating opportunities as they age, or because successful coalitions require social experience acquired with age [84, 114, 115]. The role of social experience could also explain why older female bonobos are more likely to lead group movements and form coalitions [64, 116].

Current data therefore suggests that social influence shows a complex pattern that varies across species and sexes (see Figure 2c). This may stem in part from how dominance affects an individual's access to resources like mates. In species with high despotism and reproductive skew, young adults entering the adult hierarchy will start to compete for high rank (and thus mating access) immediately. This competition is typically physical in nature for males, so age-related change in dominance follow an inverted-U: both younger and older males have less fighting ability than prime-aged males, either because they are still growing or loosing muscle mass. Thus, if rank strongly predicts reproductive success, a decline in rank with age (either linear or an inverted-U-shape) is likely due to a decline in physical status. This also intersects with philopatry: in male-philopatric species like chimpanzees, males start competing for rank as adolescents so peak rank is obtained later [79, 80, 108, 117], whereas males who immigrate into a group when they are already fully grown and thus can sometimes occupy their highest rank shortly after dispersal in female-philopatric species like macaques and baboons [118]. Finally, among species or age-sex classes with low despotism and reproductive skew, such that rank is less important for fitness, individuals often obtain rank through queuing rather than competition [119]. Consequently, older individuals are more dominant, as in female chimpanzees and bonobos [64, 103, 105, 106].

3. Comparative social aging: state of the art and future directions

There are many ways to be an old primate: social aging in primates is a complex phenomenon with great variation in how socially engaged older animals are, in the relative valence of their social interactions, and in the forms of social influence they can exert over others. While primate social aging is still a nascent field of study, here we synthesize some key findings from current data looking changes across different social domains. Then, we identify limitations of current work and consequent key areas for future study.

3.1 Modulators of the primate social aging process

Current data suggests some key themes concerning the pace and pattern of primate social aging across species (see Figure 2). First, social context can modulate the primate aging process: current data indicates that species differing in their social organization and philopatry can exhibit different aging trajectories. For example, older female macaques often exhibit declines in social engagement—as indexed by proximity or social network size—and an increasing negativity bias—with declines in giving grooming but consistent levels of aggression [13, 98]. This may be related to their female philopatric social organization: females in such species form bonds primarily with kin, so social networks may shrink as their aging kin die, yet older females can obtain fitness benefits by supporting their daughters in agonistic context [55]. Yet different species may show different patterns. For example, older male chimpanzees exhibit some age-related increases in social engagement, as well as an increasing positivity bias with increasing grooming. This might stem in part from the fact that chimpanzees exhibit fission-fusion groups with a high degree of social choice, and further that males may be more likely to form flexible, long-term bonds with both kin and non-kin [65], as discussed previously.

A related theme is that sex matters: males and females can have different aging trajectories. For example, while older primates generally withdraw from social interactions, the socially dominant sex may sometimes exhibit preserved social behavior, as is seen in representative species of apes, Old World monkeys, and strepsirrhines (e.g., male chimpanzees, male rhesus macaques, and female ring-tailed lemurs). This may be due in part to the differential importance of social bonds across sexes (although this would not necessarily explain declines in female macaques, given their strong female-female bonds [13]). Importantly, some of these apparent sex differences may also be due to differences in sex-specific mortality, with one sex outliving the other by several years [120] therefore revealing different patterns of change in behavior in old age. Yet given that current work often focuses on only one sex in isolation—especially in Old World monkeys where much work to date has focused on females (see Figure 1)—more direct comparisons across sexes are crucial to assess how and why sex modulates social aging.

Finally, social status both changes with age, and can impact other aspects of sociality. High rank is generally correlated with reproductive success [70, 109, 121-123], so age-related declines in social status presents a biological problem. As such, older animals may sometimes shift their social behavior to accommodate falling rank, such as how older chimpanzees with declining physical stature may increasingly exploit social bonds and coalitionary aggression to obtain fitness [70, 108, 124]. A corollary to this point is that it is important to assess dominance status in studies of social aging, as many primate studies have not directly accounted for rank effects on other aspects of sociality. For example, while young and old female Japanese macaques appear to have similar patterns of behavior at first glance, dominance and age have opposing effects: older low-ranking females have larger social networks but spend less time socializing, whereas older high-ranking females have smaller social networks and devote more time to social interactions [125].

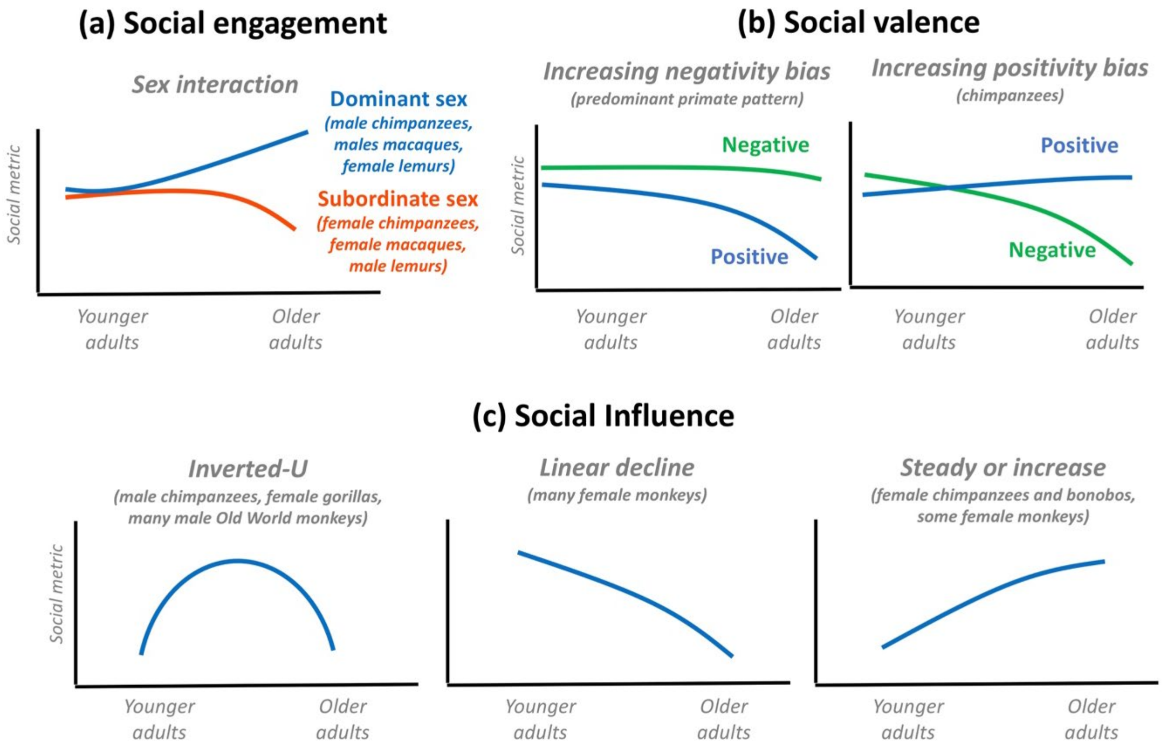


Figure 2: Comparative patterns of social aging. (a) Current data on social *engagement* indicate that the socially dominant sex (which depends on social organization) can show preserved functioning during aging, whereas the subordinate sex shows greater withdrawal. (b) The relative *valence* of social interactions in many primates shows increasing behavioral negativity, whereas chimpanzees (and humans) show relative positivity. (c) There are diverse trajectories for social *influence* such as dominance status, with major differences according to both sex, social organization, and philopatry.

3.2 Gaps in current data

To understand why and how different patterns of social aging emerge, there is a critical need to examine a phylogenetically diverse set of species. As such, an important limitation of primate social aging data to date concerns its phylogenetic distribution: there has been a much greater focus on work on female-philopatric Old World monkeys than other taxonomic groups (see Figure 1). For example, platyrrhines and strepsirrhines are under-represented in current work, yet exhibit social features that are uncommon in Old World primates, including female dominance in lemurs [45], and cooperative breeding in callitrichids. The lesser apes (gibbons and siamangs) are important examples of monogamy, and the great apes also show great diversity in social organization. While some of these limitations reflect the current state of primate research effort as a whole, some species like marmosets are well-studied models for physiological aging [126] yet are nonetheless not represented in current social aging work.

A second gap concerns within-species variation across sexes and populations. While both sexes of some species have been well-studied, in other groups like Old World monkeys there is often data from only one sex (see Figure 1 and ESM Tables S1-S3), which is an important caveat for interpreting potential sex differences. In addition, there have been few studies comparing across populations of the same species, which is another crucial test of how socioecological conditions shape aging. For example, among rhesus macaques and chimpanzees, males living in large groups can show different age-related patterns in dominance rank [86, 118] and coalitionary aggression [80, 108] than males in smaller groups. This may be because group size impacts reproductive skew: younger male macaques acquire top ranks in smaller groups with higher reproductive skew, whereas rank is acquired through queueing in larger groups [86, 118], likely because male rank has less of an impact on reproductive success when many males are present [93]. Along the same lines, changes in social aging patterns may vary across captive versus wild populations, for example due to differences in competition. For example, a fair amount of research on macaque species has focused on provisioned populations [e.g., 13, 18, 19, 23-29, 49, 112, 123, 125, 127, 128], which may show different aging patterns than in the wild due to socioecological effects.

A final gap concerns how social aging impacts different kinds of social domains and metrics. We differentiated between patterns of overall social engagement (being around or near others) and the emotional valence of social interactions (the positive versus negative quality of those interactions, as indexed by grooming versus agonism), in contrast to many approaches in primatology consider both proximity and grooming as examples of affiliation, so it is an important empirical question whether these behaviors are unified or dissociated during aging. Current data indicates that there can be differences in a given species' aging trajectories for engagement versus valence (see Figure 2), which suggests that these metrics may indeed reflect divergent processes. Second, a key aspect of human social aging concerns changes in social selectivity: older adults have smaller social networks but focus more on close, important social relationships [5, 16, 129]. While much recent high-profile work on primate behavior has focused on the fitness consequences of strong social bonds [11, 12, 38], its notable that most work to date on primate social aging has not accounted for the specific identity of the partner. Indeed, we could find only one study that specifically addressed strong social bonds during aging [39]. As such, a more nuanced approach differentiating between social bonds by the value and persistence over time is crucial.

4. Conclusions and implications for human aging

Social aging in nonhuman primates can provide novel insights into the human aging process because both social context and cognitive status are associated with differences in physical health and mortality in humans [4, 6, 11]. Current data indicates that primates show high levels of variation in aging trajectories across different sexes and social organizations, which can help pinpoint the kinds of social contexts that promote successful aging. For example, variation across primate social organization and philopatry can serve as a referential model for the impact of social support networks and presence of family members in human aging [4]. Similarly, the biological effects of sex on primate aging can help disentangle the effects of sex from culturally-mediated effects of gender in humans [19]. Finally, dominance status in primates [130] can provide a model for understanding how disparities due to socioeconomic status shape aging in humans.

A major challenge for human aging research is that humans have extremely slow life histories, so the processes of aging are difficult to study. As such, many common animal models have faster life histories that are more tractable for aging research [9, 126]. Yet a long lifespan may itself change the dynamics of aging, which highlights the crucial importance of understanding aging in other long-lived primates. For example, an important aspect of human social aging is that older adults show increasing social positivity bias towards positive socioemotional interactions [5, 7], yet current work suggests few other primate species show this kind of shift, besides potentially long-lived chimpanzees (see Figure 2). More generally, comparative work on long-lived nonhumans can address conceptual gaps in human work. For example, changes in human social functioning occur gradually over decades and thus are often studied with cross-sectional designs that introduce generational confounds like educational attainment and sociocultural experiences. In contrast, longitudinal approaches are a fundamental aspect of long-term primate field sites.

Finally, future studies of nonhuman primate aging can address open questions in the study of human aging concerning the links between causal mechanisms and real-world social behavior. For example, studies of socioemotional cognition are a key line of evidence in human social aging, yet there have been relatively few studies examining social cognition in aging nonhumans [18-21, 48, 49]. Yet promoting healthy social aging requires an understanding of both how aging plays out in natural social contexts, as well as the underlying mechanisms that might be amenable to targeted interventions. Recent studies of free-ranging primates combining both experiments and observations show how these approaches can be synthesized [18]. As such, nonhuman primates can provide a pathway for understanding changes in real world social behavior during aging, as well as inferring and intervening on causal mechanisms shaping these patterns.

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Electronic Supplementary Materials

Shifting sociality during primate aging

Z.P. Machanda & A.G. Rosati

Table S1: Summary of studies examining social engagement. These studies captured elements of whether engaged socially with others versus withdrew, including metrics like spatial proximity and time spent alone. Note that some of these are measures of social interest or engagement (e.g., spatial proximity) whereas other index withdrawal (e.g. time spent alone), which accordingly would show reverse shifts. Age-related change focused primarily on comparisons of younger versus older adults.

Taxa	**Species**	**Sex**	**Social metric**	**Age changes and references**
Apes	Chimpanzees *(Pan troglodytes)*	Males	Spatial proximity	Increase (Machanda et al., 2019; Rosati et al., under review)
			Time spent alone	Increase (Machanda et al., 2019; Rosati et al., under review)
			Presence in larger parties	Increase (Machanda et al., 2019; Rosati et al., under review)
		Females	Combined metric of presence in parties and proximity	Decrease (Huffman, 1990)
			Gaze following (cognitive)	Decrease (Lacreuse, Russell, Hopkins, & Herndon, 2014)
Old World monkeys	Rhesus macaques *(Macaca mulatta)*	Males	Physical contact	No change (Corr, 2000, 2003; Suomi, Novack, & Well, 1996)
			Social network size	No change (Corr, 2000, 2003)
			Gaze following (cognitive)	Decline (Rosati, Arre, Platt, & Santos, 2016; Rosati & Santos, 2017)
		Females	Physical contact	Decline (Corr, 2003; Suomi et al., 1996)
			Social network size	Decline (Corr, 2003)
			Gaze following (cognitive)	Decline (Rosati et al., 2016; Rosati & Santos, 2017)
	Long-tailed macaques (*Macaca fascicularis)*	Females	Spatial proximity (components of 'affiliation')	Decline (Veenema, Spruihit, Gispen, & van Hooff, 1997)
			Presence in main party	Decline (van Noordwijk & van Schaik, 1987)
	Japanese macaques *(Macaca fuscata)*	Females	Spatial proximity	Decline (Hauser & Tyrrell, 1984; Nakamichi, 1984, 1991)
			Time spent alone	Increase (Kato, 1999; Nakamichi, 1984, 1991)
			Rests alone	Increase (Hauser & Tyrrell, 1984)
			Approaches	Decline (McDonald Pavelka, 1990)

	Bonnet macaques (*Macaca radiata*)	Males	Physical contact	No change (Silk, 1994)
			Spatial proximity	No change (Silk, 1994)
	Stump-tailed macaques (*Macaca arctoides*)	Females	Avoids; ignores	Increase (Hauser & Tyrrell, 1984)
	Barbary macaques *(Macaca sylvanus)*	Males	Gaze following (cognitive)	No change (Rosati & Santos, 2017)
		Females	Gaze following (cognitive)	No change (Rosati & Santos, 2017)
			Interest in social stimuli (cognitive)	No change (Almeling, Hammerschmidt, Senn-Reulen, Freund, & Fischer, 2016)
			Spatial proximity	Decline (Almeling et al., 2016; Almeling, Senn-Reulen, Hammerschmidt, Freund, & Fischer, 2017)
	Yellow baboons (*Papio cynocephalus*)	Female	Number of strong bond partners	No change (Silk, Altmann, & Alberts, 2006)
	Grey-cheeked mangabeys (*Lophocebus albigena)*	Females	Spatial proximity	Decline (Wasser, 1978)
	Gray langurs *(Semnopithecus entellus)*	Females	Avoid interactions	Increase (Hrdy & Hrdy, 1976)
			Move away from group	Increase (Hrdy & Hrdy, 1976)
			Time alone	Increase (Borries & Koenig, 2008)
New World Monkeys	Tufted capuchins (*Sapajus apella*)	Males	Spatial proximity	Decline (Schino & Pinzaglia, 2018)
		Females	Spatial proximity	Decline (Schino & Pinzaglia, 2018)
Lemurs	Ring-tailed lemurs *(Lemur catta)*	Males	Spatial proximity	Decline (McGuire, 2017)
			Physical contact	No change (McGuire, 2017)
		Females	Spatial proximity	Decline (McGuire, 2017)
			Physical contact	Increase (McGuire, 2017)
	Mouse lemurs *(Microcebus murinus)*	Males	Approaches	Decline (Picq, 1992)
		Females	Approaches	Decline (Picq, 1992)

Table S2: Summary of studies examining social valence. These studies captured elements of how primate interactions were characterized by more positive (e.g., grooming) or negative (aggression) emotional states. We focused primarily on positive and negative behavior initiated by the focal animals whenever possible (e.g. grooming given or aggression given) but in a few cases indicated in the table only combined measures (e.g., all grooming) or a proxy (e.g., wounding risk) were reported. Age-related change focused primarily on comparisons of younger versus older adults; *Indicates studies with adult age variation but where the primary reported statistical comparison is between adults and subadults.

	Species	Sex	Valence	Social metric	Age change and references
Apes	Chimpanzees *(Pan troglodytes)*	Males	Positive	Grooming given	Increase (Machanda et al., 2019; Rosati et al., under review)
				Agreeableness	Increase (King, Weiss, & Sisco, 2008) (Altshul et al., 2018)
			Negative	Aggression given	Decline (Machanda et al., 2019; Rosati et al., under review)
		Females	Positive	Grooming given; grooming partners	Decline (Huffman, 1990)
				Agreeableness	Increase (Altshul et al., 2018; King et al., 2008)
	Bonobos *(Pan paniscus)*	Males	Positive	Grooming given	Increase (Franz, 1999)*
		Females	Positive	Grooming given	Increase (Franz, 1999)*
Old World monkeys	Rhesus macaques *(Macaca mulatta)*	Males	Positive	Grooming given	No change (Corr, 2000, 2003; Suomi et al., 1996)
				Attention to affiliative signals (cognitive)	No change (Rosati, Arre, Platt, & Santos, 2018)
			Negative	Aggression given	Increase (Bernstein & Ehardt, 1985a)*; No change (Suomi et al., 1996); Decline (Corr, 2000, 2003)
				Threats given	No change (Suomi et al., 1996)
				Attention to threat signals (cognitive)	Increase (Rosati et al., 2018)
		Females	Positive	Grooming given	Decline (Brent, Ruiz-Lambides, & Platt, 2017; Corr, 2000, 2003); No change (Suomi et al., 1996)
				Attention to affiliative signals (cognitive)	No change (Rosati et al., 2018)
			Negative	Aggression given	Increase (Bernstein & Ehardt, 1985a); No change (Corr, 2003; Suomi et al., 1996)
				Threats given	No change (Suomi et al., 1996)
				Attention to threat signals (cognitive)	Increase (Rosati et al., 2018)
				Responsivity to threat (cognitive)	Increase (Bliss-Moreau & Baxter, 2018)

	Long-tailed macaques (*Macaca fascicularis)*	Females	Positive	Grooming given	Decline (Veenema et al., 1997)
			Negative	Aggression given	No change (Veenema et al., 1997)
	Japanese macaques *(Macaca fuscata)*	Females	Positive	Grooming given	Decline (Nakamichi, 1984); No change (McDonald Pavelka, 1990)
				Affiliative signal production	Decline (McDonald Pavelka, 1990)
				Grooming given	Decline (Nakamichi, 1984, 1991)
				Grooming given to unrelated females	Decline (Nakamichi, 2003)
				Grooming given to related females	No change (Nakamichi, 2003)
			Negative	Aggression given	No change (McDonald Pavelka, 1990)
	Bonnet macaques (*Macaca radiata*)	Males	Positive	Grooming given	Decline (Silk, 1994)
			Negative	Aggression given	No change (Silk, 1994)
				Threats given	Decline (Silk, 1994)
	Barbary macaques *(Macaca sylvanus)*	Females	Positive	Grooming given	Decline (Almeling et al., 2016; Almeling et al., 2017)
				Number of grooming partners	Decline (Almeling et al., 2016; Almeling et al., 2017)
			Negative	Aggression given	No change (Almeling et al., 2017)
	Yellow baboons (*Papio cynocephalus*)	Females	Positive	Grooming - combined index	Decline (Archie, Tung, Clark, Altmann, & Alberts, 2014)
			Negative	Wounding risk	Increase (Archie, Altmann, & Alberts, 2014)
	Olive baboons *(Papio anubis)*	Males	Negative	Wounding risk	No change (MacCormick et al., 2012)
		Females	Negative	Wounding risk	No change (MacCormick et al., 2012)
	Grey-cheeked mangabeys (*Lophocebus albigena)*	Females	Positive	Grooming given	Decline (Wasser, 1978)
			Negative	Aggression given	No change (Wasser, 1978)
	Vervets *(Chlorocebus pygerythrus)*	Females	Positive	Grooming given to high ranking females	No change (Fairbanks & McGuire, 1986)
			Negative	Aggression given	No change (Fairbanks & McGuire, 1986)s
	Blue monkeys (*Cercopithecus mitis*)	Females	Positive	Grooming interactions per partner	Decline (Rowell, Wilson, & Cords, 1991)
	Gray langurs *(Semnopithecus entellus)*	Females	Positive	Grooming - combined index	No change or decline (Borries & Koenig, 2008)

			Negative	Intergroup aggression	No change (Hrdy & Hrdy, 1976)
	Phayre's leaf monkeys *(Trachypithecus phayrei)*	Females	Positive	Grooming - combined index	Decline (Borries & Koenig, 2008)
			Negative	Rate of agonistic initiative / winning	No change or decline (Lu, Borries, Gustison, Larney, & Koenig, 2016)
New World monkeys	Tufted capuchins (*Sapajus apella*)	Males	Positive	Grooming given	No change (Schino & Pinzaglia, 2018)
			Negative	Aggression given	No change (Schino & Pinzaglia, 2018)
		Females	Positive	Grooming given	Declines (Schino & Pinzaglia, 2018)
			Negative	Aggression given	No change (Schino & Pinzaglia, 2018)
Lemurs	Ring-tailed lemurs (Lemur catta)	Males	Positive	Grooming given	No change (McGuire, 2017)
				Affiliative events initiated	No change (McGuire, 2017)
			Negative	Aggression initiated	No change (McGuire, 2017)
		Females	Positive	Grooming given	No change (McGuire, 2017)
				Affiliative events initiated	No change (McGuire, 2017)
			Negative	Aggression initiated	No change (McGuire, 2017)
	Mouse lemurs *(Microcebus murinus)*	Males	Positive	Grooming given	Decline (Picq, 1992)
			Negative	Aggression given	Increase (Aujard & Perret, 1998; Picq, 1992)
		Females	Positive	Grooming given	Decline (Picq, 1992)
			Negative	Aggression given	Increase (Picq, 1992)

Table S3: Summary of studies examining social influence. These studies captured elements of how primates can influence others by obtaining high dominance status or forming coalitions. Age-related change focused primarily on comparisons of younger versus older adults.

Taxa	Species	Sex	Social metric	Age changes and references
Apes	Chimpanzees *(Pan troglodytes)*	Males	Dominance rank	Inverted-U (Hasegawa & Kutsukake, 2015; Watts, 2018)
			Coalitionary aggression	U-shaped (Muller et al., 2019); Decline (Watts, 2018)
		Females	Dominance rank	Increase (Foerster et al., 2016)
	Bonobos *(Pan paniscus)*	Females	Dominance rank	Increase (Furuichi, 1997; Ihobe, 1992; Stevens, Vervaecke, & van Elsacker, 2008)
			Coalitionary aggression	Increase (Tokuyama & Furuichi, 2016)
			Group movement leadership	Increase (Tokuyama & Furuichi, 2017)
	Mountain gorillas (*Gorilla beringei beringei*)	Females	Dominance	Inverted-U (Robbins, Robbins, Gerald-Steklis, & Steklis, 2005)
Old World monkeys	Rhesus macaques *(Macaca mulatta)*	Males	Dominance rank	Inverted-U (Sprague, 1998); No change: (Higham, Heistermann, & Maestripieri, 2011; Sprague, 1998); Increase (Berard, 1999; Bercovitch, 1997; Manson, 1995)
		Females	Dominance rank	Decline (Chikazawa & Gordon, 1979)
			Coalitionary aggression	Increase (Bernstein & Ehardt, 1985b)
	Japanese macaques *(Macaca fuscata)*	Males	Dominance rank	Inverted-U (Sprague, 1998; Takahashi, 2002); no change (Sprague, 1998)
	Bonnet macaques (*Macaca radiata*)	Females	Dominance rank	Increase (Silk, Samuels, & Rodman, 1981)
	Stump-tailed macaques (*Macaca arctoides*)	Females	Dominance rank	No change (Hauser & Tyrrell, 1984)
	Barbary macaques *(Macaca sylvanus)*	Males	Coalitionary aggression	Increase (Rathke, Berghänel, Bissonnette, Ostner, & Schülke, 2017)
	Yellow baboons (*Papio cynocephalus*)	Males	Dominance rank	Inverted-U (Alberts, Watts, & Altmann, 2003; Altmann et al., 1996; Noë & Sluijter, 1993; Packer, Collins, & Eberly, 2000)
			Coalitionary aggression	Increase (Bercovitch, 1988; Noe, 1992); Decline (Noë & Sluijter, 1993)
		Females	Dominance rank	Increase (Hausfater, Altmann, & Altmann, 1982)

	Olive baboon *(Papio anubis)*	Males	Dominance rank	Inverted-U (Packer et al., 2000)
		Females	Dominance rank	No change (Packer et al., 2000)
	Mandrills (*Mandrillus sphinx*)	Males	Dominance rank	Inverted-U (Setchell, Wickings, & Knapp, 2005)
	Sooty mangabeys (*Cercocebus atys*)	Females	Dominance rank	No change (Gust & Gordon, 1994)
	Vervets *(Chlorocebus pygerythrus)*	Females	Dominance rank	No change (Fairbanks & McGuire, 1986)
			Coalitionary aggression	No change (Fairbanks & McGuire, 1986)
	Gray langurs *(Semnopithecus entellus)*	Females	Dominance rank	Decline (Borries, Sommer, & Srivastava, 1991; Hrdy & Hrdy, 1976)
	Phayre's leaf monkeys *(Trachypithecus phayrei)*	Females	Dominance rank	Decline (Borries & Koenig, 2008)
New World monkeys	Howler monkeys (*Alouatta palliata*)	Females	Dominance rank	Decline (Clarke & Glander, 1984)
	White faced capuchins (*Cebus capucinus*)	Females	Dominance rank	Decline (Bergstrom & Fedigan, 2010; Perry, Manson, Muniz, Gros-Louis, & Vigilant, 2008)

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