



## Review

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# Shifting sociality during primate ageing

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Humans exhibit major age-related shifts in social relationships along with changes in social and emotional psychological processes that underpin these behavioural shifts. Does social ageing in non-human 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 behaviour and underlying psychological processes across species. Focusing on three elements of social behaviour 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 ageing process, including social organization, sex and dominance status. Finally, we discuss how comparative research can contextualize human social ageing.

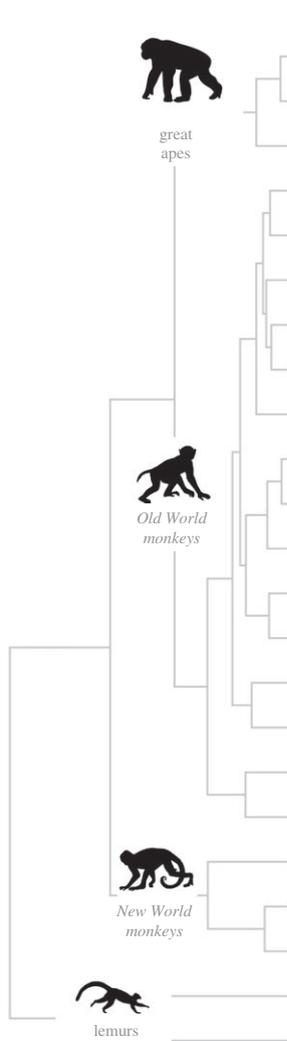
This article is part of the theme issue 'Evolution of the primate ageing process'.

## 1. Introduction

Humans are living into old age more than ever before, making it critical to understand the processes of ageing. It is increasingly recognized that successful ageing 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 behaviour and cognition during ageing. 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 with younger adults [4–8]. Variation across these different facets of sociality can therefore shape the dynamics and outcomes of successful ageing.

One way to understand the consequences of these different ageing trajectories is to contextualize humans in a broader comparative framework accounting for ageing patterns across species. Other primates have provided crucial insights into the physiological ageing process [9,10], and can also be a valuable comparative model for social ageing owing to their close genetic relatedness with humans, shared social complexity, and relatively long lifespans. Moreover, the observational techniques commonly used with animals allow 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 ageing process. Rather, most work on primate social ageing 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 ageing, here we take a 'bottom-up' approach to synthesize current data from non-human primates. Our aim is to characterize patterns of social behaviour and underlying proximate mechanisms across diverse primate species. First, we review age-related changes across different primate species in order to characterize variation in



species	sex	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*	
grey 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 ageing metrics across species. Social metrics and phylogenetic distribution of current social ageing data. Sex indicates if there ever are any data for both sexes (see electronic supplementary material, 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 the electronic supplementary material) and *aggression* given (\*denotes a modified aggression index; *aggression—other* indicates an alternative measure of aggression described in the electronic supplementary material). 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].

social ageing trajectories. We then synthesize current data to examine the potential modulators of the primate ageing 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 ageing across different populations and individuals can inform human social ageing.

## 2. Social ageing 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 behaviours; and (3) *social influence*, or an individual's ability to flexibly impact others' behaviour. While these distinctions are

not necessarily typically used to categorize social behaviour in traditional approaches in primatology, they are important domains for understanding human ageing, and conceptually capture different ways that individuals can adjust their social behaviour during the ageing 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 electronic supplementary material, tables S1–S3 for details about all metrics and studies). Given this variability in metrics, we focus on comparing ageing trajectories within a study (increases, decreases or no change with age) rather than comparisons of absolute behavioural rates across species, sexes or studies.

### (a) Social engagement

During ageing, 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 others' social cues like gaze direction that track this general pattern of increasing social disengagement with age in experiments [17]. In non-humans, these kinds of shifts have been assessed both in cognitive experiments and in natural behaviours (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 behaviour [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 indicate that many primates become markedly less social with advancing age. This phenomenon has been best-studied among 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], 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 grey 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 grey mouse lemurs (*Microcebus murinus*) [37] are less likely to be in close proximity to others, or engage in fewer overall social behaviours.

Yet such social withdrawal is not universal, as some groups show steady rates of social engagement during ageing. 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 with younger adults [40]. By contrast, older female chimpanzees are less likely to be present in parties [41] (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

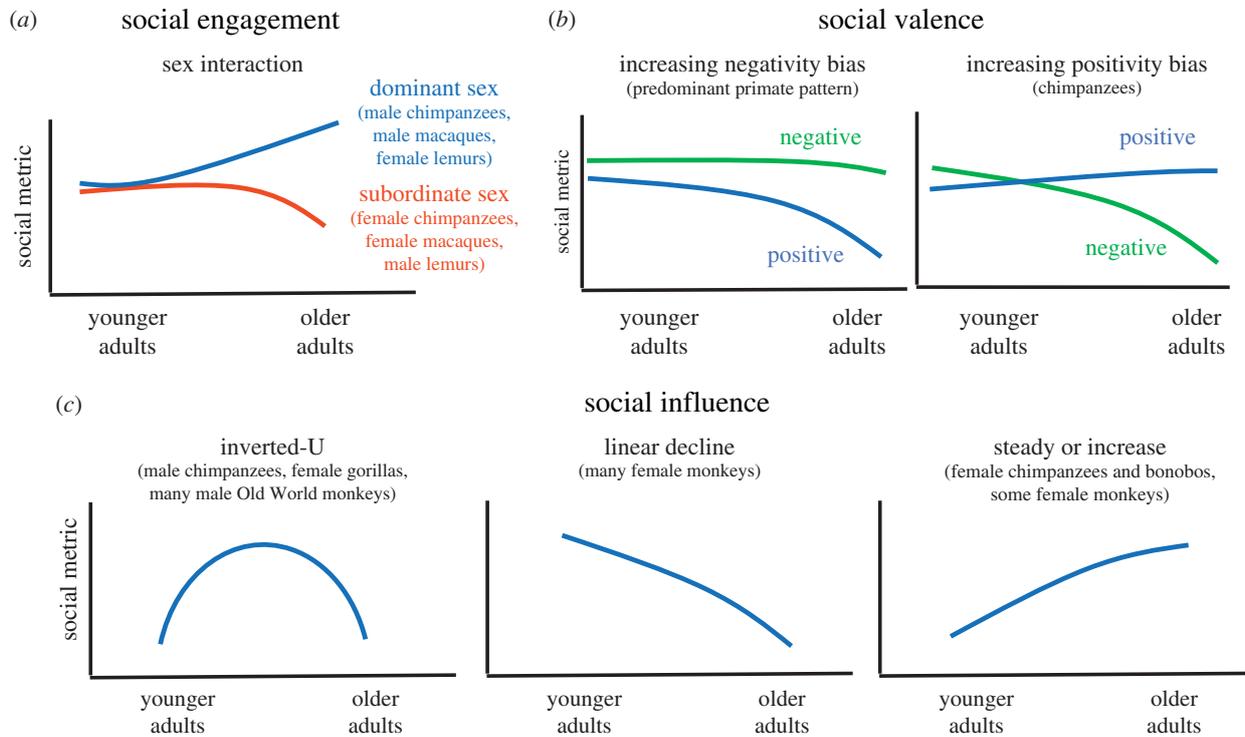
or increasing social engagement [25,42]. The reverse is true in ring-tailed lemurs: older females increase physical contact, whereas males show no changes [36].

The pattern of age-related change in current data indicates 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 [43]—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 exist from both sexes within a species. In particular, males are the dominant sex in both chimpanzees and macaques, and show greater social engagement during ageing compared with females. In contrast, lemurs are one of the few primate taxa exhibiting female dominance [44], 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 among Old World primates; figure 1), so this could also reflect an overall difference in ageing trajectories across species. To test this, it will be important to have more systematic comparisons across the sexes within-species, as well as to compare closely related taxa with variation in sexual dominance systems, such as *Eulemur* [44].

### (b) 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 and showing better recall for happy facial expressions compared with negative ones), a shift from the 'negativity' bias more commonly seen in younger adults [5,7]. Importantly, this psychological shift has concordant behavioural manifestations: older adults exhibit a greater prioritization of positive social interactions, and show decreases in interpersonal conflicts [5,45]. That is to say, older adults' social relationships get 'better' with age [46]. In animals, parallel shifts in the valence of behavioural interactions can therefore be assessed by examining the relative frequency of negative social interactions (such as aggression given) compared with positive interactions (such as grooming given). Finally, some work has experimentally tested animals' attention or responses to emotionally valenced information [47,48], more closely mirroring human experimental work looking at attentional biases.

Current evidence suggests that, unlike in humans, an increasing *negativity bias* in behaviour 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 ageing. 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 [13,25,42,49]. 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 behaviours like younger adults. Macaques show similar shifts in



**Figure 2.** Comparative patterns of social ageing. (a) Current data on social *engagement* indicate that the socially dominant sex (which depends on social organization) can show preserved functioning during ageing, whereas the subordinate sex shows greater withdrawal. (b) The relative *valence* of social interactions in many primates shows increasing behavioural 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 sex, social organization and philopatry.

their production of and responses to negative emotional signals or contexts: the production of negative emotional signals such as yawning and scratching increases in older adults [32]; production of conspecific threat signals generally stays consistent or increases in adult animals [42,50]; and older macaques can show exacerbated responses to external threats in controlled experiments [47]. This aligns with converging experimental evidence looking at cognitive biases, showing that older macaques attend relatively more to negative socio-emotional stimuli (photographs of conspecific threat faces) compared with neutral or positive expressions [48], similar to human research measuring looking responses to affective stimuli using similar paradigms [51,52].

A general pattern of increasing behavioural negativity also appears in several other Old World monkey species. For example, olive baboons (*Papio anubis*) [53], vervet monkeys (*Chlorocebus pygerythrus*) [54], grey langurs [34], mangabeys [35] and Phayre's leaf monkeys (*Trachypithecus phayrei*) [55] show steady initiation of aggression or risk of wounding from aggression across adulthood. Yet grooming declines in yellow baboons [56], blue monkeys (*Cercopithecus mitis*) [57], mangabeys [35], Phayre's leaf monkeys [33] and potentially grey langurs (although this is inconsistent [33]). The only New World monkey with comparable data is the tufted capuchin, 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 [37,58], although ring-tailed lemurs do not show changes [36].

Overall, current evidence suggests that a relative negativity bias in behaviour 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 shows a relative positivity bias in behaviour. Thus, the positivity bias seen in humans does not seem to be an intrinsic consequence of ageing 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 behaviours like grooming [40,40,59]. Similarly, agreeable personality traits increase in older chimpanzees, as in humans [60,61]. While there are not comparable studies of ageing in bonobos (*Pan paniscus*), adult male and female bonobos show age-related increases in grooming compared with subadults [62] (see also [63] 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 (figure 2b)? One possibility is that this stems from the flexible fission–fusion social organization seen in both humans and chimpanzees [64]. 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 [65,66]. Moreover, bonds among chimpanzees are not as strongly patterned by kinship compared with many female-philopatric Old World monkeys [64,67]. 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 [67], resulting in different patterns of affiliation and aggression during ageing. Another relevant factor may be life history: chimpanzees are among the most long-lived non-human mammals in terms of total lifespan, and can live more than 60 years in the wild [68]. 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 [69], 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 [70]), as well as from bonobos, who share life history and basic social organization with chimpanzees, and gorillas, who have reduced lifespans compared with chimpanzees [71].

### (c) Social influence

A final important change in human social relationships during ageing concerns older adults' abilities to flexibly impact others' behaviour. 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 [72–74]. Relevant changes have been assessed in non-humans by examining strategic social behaviour, 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 [75], or experimental cognitive studies of strategic deception or other aspects of theory of mind [76], and partner choice in cooperation [77], have not been studied in the context of ageing 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 [78,79] and many male Old World monkeys, including mandrills (*Mandrillus sphinx*) [80], olive baboons [81], yellow baboons [81–84] and some populations of Japanese macaques [85,86]. While male rhesus macaques sometimes show this pattern [85], rank is also sometimes achieved through queueing, such that individuals with the longest tenure length have the highest rank [87–89] and rank correlates better with tenure than age [90]. In other cases, age had no effect on male rhesus dominance [85,91]. 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 [92].

In females, in contrast, dominance often shows more linear changes. For example, rank declines with age in Phayre's leaf monkeys [33], grey langurs [34,93] and howler monkeys (*Alouatta palliata*) [94]. But some species exhibit no overall change or even increases with age. For example, rank remains stable in female olive baboons [81], female stump-tail macaques [26], female vervet monkeys [54] and female sooty mangabeys (*Cercocebus atys*, previously called *Cercocebus torquatus*) [95]. 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 [96,97]. 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 [98,99]. Lifespan patterns 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 matrilineal lines accordingly drop in rank. Female white-faced capuchins (*Cebus capucinus*) also exhibit matrilineal rank, although the pattern of matrilineal inheritance may be more relaxed [100,101]. Finally, some female apes obtain rank via queueing: both female chimpanzees [102], and female bonobos exhibit increases in rank with age [103–105]. However, female mountain gorillas (*Gorilla beringei beringei*) exhibit the inverted-U pattern seen in many males [106].

There have been fewer studies looking at other aspects of social influence, but current evidence suggests that at least some other relevant behaviours 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 [107] (but see [79] 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 for rank and fitness for these different cohorts [108]. 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 [54]. While this may be a common pattern for species with matrilineal dominance inheritance, where coalitionary interventions support close maternal kin [54,109], this pattern is not consistent as coalitionary aggression actually increases with age in female rhesus macaques [110]. Coalitionary aggression also increases for male Barbary macaques [111] and male baboons [112,113] (although see [83]), 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 [83,113,114]. The role of social experience could also explain why older female bonobos are more likely to lead group movements and form coalitions [63,115].

Current data therefore suggest that social influence shows a complex pattern that varies across species and sexes (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 follows an inverted-U: both younger and older males have less fighting ability than prime-aged males, because they are either still growing or losing 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 [78,79,107,116], whereas males who immigrate into a group when they are already fully grown can sometimes occupy their highest rank shortly after dispersal in female-philopatric species like macaques and baboons [117]. 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 queueing rather than competition [118]. Consequently, older individuals are more dominant, as in female chimpanzees and bonobos [63,102,104,105].

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

There are many ways to be an old primate: social ageing 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 ageing is still a nascent field of study, here we synthesize some key findings from current data looking at changes across different social domains. Then, we identify limitations of current work and consequent key areas for future study.

#### (a) Modulators of the primate social ageing process

Current data suggest some key themes concerning the pace and pattern of primate social ageing across species (figure 2). First, social context can modulate the primate ageing process: current data indicate that species differing in their social organization and philopatry can exhibit different ageing 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 [13,97]. 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 ageing kin die, yet older females can obtain fitness benefits by supporting their daughters in agonistic contexts [54]. 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 [64], as discussed previously.

A related theme is that sex matters: males and females can have different ageing trajectories. For example, while older primates generally withdraw from social interactions, the socially dominant sex may sometimes exhibit preserved social behaviour, 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 [119] and therefore revealing different patterns of change in behaviour 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 (figure 1)—more direct comparisons across sexes are crucial to assess how and why sex modulates social ageing.

Finally, social status both changes with age, and can impact other aspects of sociality. High rank is generally correlated with reproductive success [69,108,120–122], so age-related declines in social status presents a biological problem. As such, older animals may sometimes shift their social behaviour to accommodate falling rank, such as how older chimpanzees with declining physical stature may increasingly exploit

social bonds and coalitionary aggression to obtain fitness [69,107,123]. A corollary to this point is that it is important to assess dominance status in studies of social ageing, 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 behaviour 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 [124].

#### (b) Gaps in current data

To understand why and how different patterns of social ageing emerge, there is a critical need to examine a phylogenetically diverse set of species. As such, an important limitation of primate social ageing data to date concerns their phylogenetic distribution: there has been a much greater focus on work on female-philopatric Old World monkeys than other taxonomic groups (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 [44], 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 ageing [125] yet are nonetheless not represented in current social ageing 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 are often data from only one sex (figure 1 and electronic supplementary material, 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 ageing. For example, among rhesus macaques and chimpanzees, males living in large groups can show different age-related patterns in dominance rank [85,117] and coalitionary aggression [79,107] compared with 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 [85,117], likely because male rank has less of an impact on reproductive success when many males are present [92]. Along the same lines, changes in social ageing patterns may vary across captive versus wild populations, for example, owing to differences in competition. For example, a fair amount of research on macaque species has focused on provisioned populations [e.g. 13,18,19,23–29,48,111,122,124,126,127], which may show different ageing patterns from the wild owing to socioecological effects.

A final gap concerns how social ageing 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 that consider both proximity and grooming as examples of affiliation. It is, therefore, an

important empirical question whether these behaviours are unified or dissociated during ageing. Current data indicate that there can be differences in a given species' ageing trajectories for engagement versus valence (figure 2), which suggests that these metrics may indeed reflect divergent processes. Furthermore, a key aspect of human social ageing concerns changes in social selectivity: older adults have smaller social networks but focus more on close, important social relationships [5,16,128]. While much recent high-profile work on primate behaviour has focused on the fitness consequences of strong social bonds [11,12,38], it is notable that most work to date on primate social ageing has not accounted for the specific identity of the partner. Indeed, we could find only one study that specifically addressed strong social bonds during ageing [39]. As such, a more nuanced approach differentiating between social bonds by the value and persistence over time is crucial.

#### 4. Conclusion and implications for human ageing

Social ageing in non-human primates can provide novel insights into the human ageing process because both social context and cognitive status are associated with differences in physical health and mortality in humans [4,6,11]. Current data indicate that primates show high levels of variation in ageing trajectories across different sexes and social organizations, which can help pinpoint the kinds of social contexts that promote successful ageing. For example, variation across primate social organization and philopatry can serve as a referential model for the impact of social support networks and the presence of family members in human ageing [4]. Similarly, the biological effects of sex on primate ageing can help disentangle the effects of sex from culturally mediated effects of gender in humans [19]. Finally, dominance status in primates [129] can provide a model for understanding how disparities due to socioeconomic status shape ageing in humans.

A major challenge for human ageing research is that humans have extremely slow life histories, so the processes of ageing are difficult to study. As such, many common animal models have faster life histories that are more tractable for ageing research [9,125]. Yet a long lifespan may itself

change the dynamics of ageing, which highlights the crucial importance of understanding ageing in other long-lived primates. For example, an important aspect of human social ageing 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 (figure 2). More generally, comparative work on long-lived non-humans 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. By contrast, longitudinal approaches are a fundamental aspect of long-term primate field sites.

Finally, future studies of non-human primate ageing can address open questions in the study of human ageing concerning the links between causal mechanisms and real-world social behaviour. For example, studies of socioemotional cognition are a key line of evidence in human social ageing, yet there have been relatively few studies examining social cognition in ageing non-humans [18–21,47,48]. Yet promoting healthy social ageing requires an understanding of both how ageing plays out in natural social contexts, and 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, non-human primates can provide a pathway for understanding changes in real-world social behaviour during ageing, as well as inferring and intervening on causal mechanisms shaping these patterns.

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