SOCIALITY

Social selectivity in aging wild chimpanzees

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Humans prioritize close, positive relationships during aging, and socioemotional selectivity theory proposes that this shift causally depends on capacities for thinking about personal future time horizons. To examine this theory, we tested for key elements of human social aging in longitudinal data on wild chimpanzees. Aging male chimpanzees have more mutual friendships characterized by high, equitable investment, whereas younger males have more one-sided relationships. Older males are more likely to be alone, but they also socialize more with important social partners. Further, males show a relative shift from more agonistic interactions to more positive, affiliative interactions over their life span. Our findings indicate that social selectivity can emerge in the absence of complex future-oriented cognition, and they provide an evolutionary context for patterns of social aging in humans.

Social bonds have adaptive consequences over the life span; strong social support enhances health, longevity, and biological fitness (*1, 2*). In humans, old age is characterized by increasing selectivity for positive, meaningful social interactions, manifesting as a cluster of behavioral and cognitive features we call the human social aging phenotype. First, older adults across societies have smaller yet more emotionally fulfilling social networks than do younger adults, owing to an increasing focus on existing close relationships rather than new relationships (*3–6*). Second, older adults exhibit a positivity bias, showing greater attention to and memory for positive versus negative socioemotional information and reduced engagement in tension and conflicts (*7–9*). The origin of this social aging pattern is therefore a central issue both for evolutionary perspectives on the life course and for promoting well-being in old age.

Socioemotional selectivity theory, which argues that the central process generating life-span shifts in sociality is an explicit sense of future personal time and mortality (*10, 11*), has emerged as the most influential explanation for the human social aging phenotype. The core idea is that when individuals perceive the future as expansive (as in youth) they prioritize building new relationships and interacting with many partners, whereas when time is perceived as short (as in old age) people focus on existing, important social ties. In support of this view, older adults perceive a more limited future than younger adults; people who anticipate curtailed time horizons,

because of an illness diagnosis, natural disaster, or a geographic move, generally exhibit preferences similar to those of older adults; and experimental manipulation of future time perspective shifts socioemotional biases (*9, 11–13*). However, some evidence indicates that changes in socioemotional goals can be independent of future time perspective (*14, 15*). Thus, the role of shortened time perspectives in social selectivity during aging is currently unclear.

Here, we use a comparative approach to provide a test of the origins of human social aging patterns. Socioemotional selectivity theory proposes that changes in social goals and behavior during aging are causally dependent on an awareness of shortened personal time horizons. However, there is no evidence that any other species are aware of their own future mortality or can imagine far-off future experiences in this rich way. Some nonhumans do engage in forms of future-oriented planning, but only in short-term food acquisition contexts, such as saving a tool to access food hours or days later, and some of these instances may actually recruit lower-level cognitive mechanisms (*16, 17*). Even verbal young children show limitations in future-oriented cognition and can struggle to imagine their future selves (*18*). Accordingly, if this kind of subjective future time perspective is causally necessary to generate the human social aging phenotype, then other animals should not show these characteristic shifts.

An alternative possibility is that the human social aging phenotype is mediated by proximate mechanisms that are more widely shared across species. Cost-benefit trade-offs about whether to be social and with whom to socialize are critical for many animals. As aging imposes new constraints due to declines in physical condition, immunological health, and social status (*19–22*), older individuals might need to adjust their social choices. Accordingly, socioemotional selectivity in humans could represent an adaptive response where older adults focus on important social relationships

that provide benefits and avoid interactions that may have negative consequences. If so, other animals might also show social selectivity without necessarily possessing sophisticated future-oriented cognition like humans.

We test these alternatives by examining whether the key characteristics of the human social aging phenotype are shared with wild chimpanzees (*Pan troglodytes*). Chimpanzees are an ideal comparand because they are one of humans' two closest living relatives; have long life spans of 50 to 60 years in the wild; and form flexible, long-term social bonds. They have a high degree of choice about who to interact with owing to their large fission-fusion societies, which comprise temporary and fluid subgroups ("parties") that can range from one chimpanzee to almost an entire community. Our data come from Kibale National Park, Uganda, where we have documented social interactions in a community of wild chimpanzees on a near-daily basis for more than 20 years, providing longitudinal observations that are unparalleled in human research.

Using 78,000 hours of observations made between 1995 and 2016, we analyzed the social interactions of 21 male chimpanzees ranging in age from 15 (when males are physically mature and enter the adult hierarchy) to 58 years, with an average of 10.6 years of data per individual and 141.6 observation days per year. We examined males because they exhibit stronger bonds and more frequent social interactions than females, who are relatively asocial (*23, 24*). We used mixed models to test the importance of age in the longitudinal data. We always controlled for an individual's dominance rank, which has a pervasive effect on chimpanzee social interactions and declines in old age (*19, 25*). Few males had adult maternal brothers, so we did not account for kinship, but we did control for other predictors such as year or female presence, when appropriate for the social metric (see supplementary materials).

We first examined whether older chimpanzees focused their social interactions on important partners, a key signature of the human social aging phenotype. To characterize relationships, we used a spatial proximity metric indexing the time that pairs of individuals spend near each other. 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 (*1*). We indexed social preferences by examining how often two individuals were within 5 m of each other when in the same party. We then categorized male-male dyads as "mutual friends" (both showed a preference for sitting near the other, above their individual average rates of association), "one-sided friends" (one individual showed this preference, but their partner did not), or "nonfriends" (neither individual preferred to associate with

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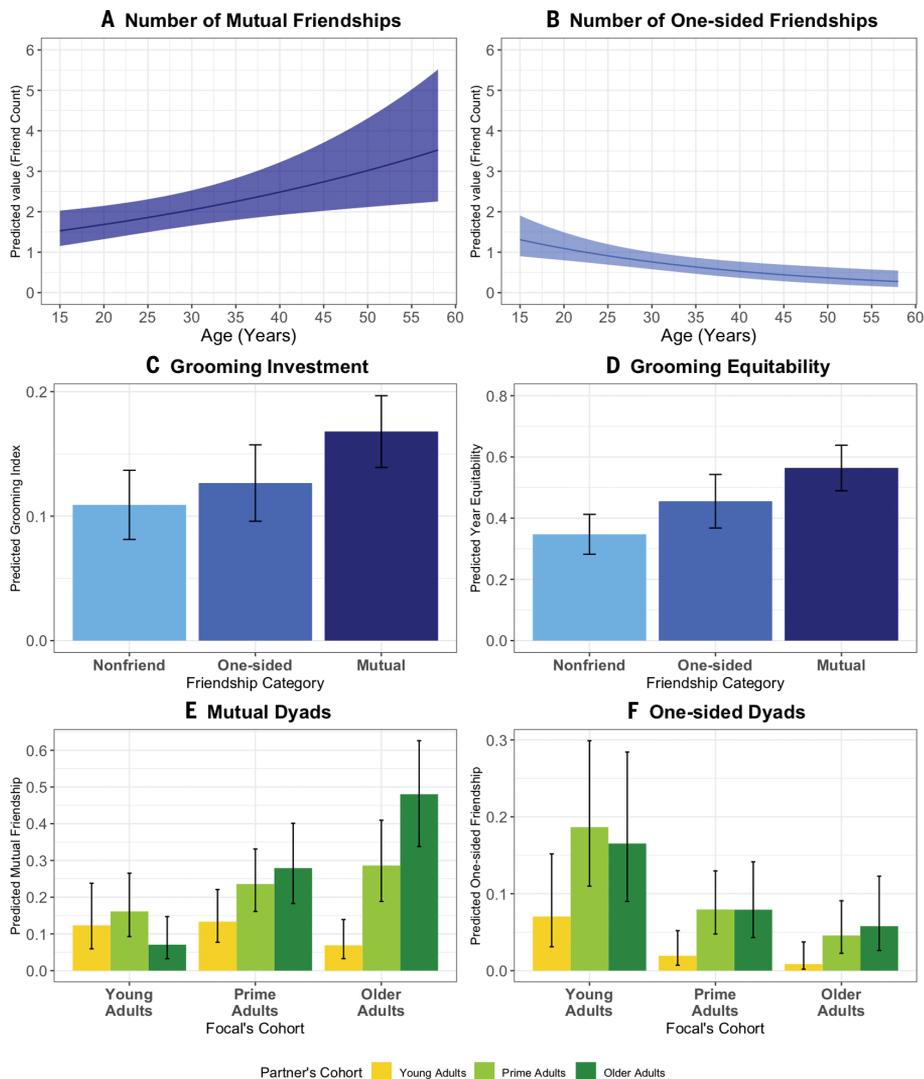*Corresponding author. Email: rosati@umich.edu (A.G.R.); zarin.machanda@tufts.edu (Z.P.M.)

A Number of Mutual Friendships

B Number of One-sided Friendships

C Grooming Investment

D Grooming Equitability

E Mutual Dyads

F One-sided Dyads

Partner's Cohort Young Adults Prime Adults Older Adults

Fig. 1. Friendships in aging chimpanzees. (**A** and **B**) Older males had more mutual friendships, whereas younger males had more one-sided friendships. (**C** and **D**) Chimpanzees invested more and had more equitable grooming patterns with mutual friends. (**E** and **F**) Older males (35+ years) were mutual friends with peers and were attractive partners for younger males' (15 to 20 years) and prime-aged males' (20 to 35 years) one-sided friendships. Ribbons and error bars indicate 95% confidence interval (CI) estimates.

the other). Thus, mutual friendships are reciprocated, whereas one-sided friendships are not. We found that the number of mutual friends increased with age [$\chi^2 = 6.89$, degrees of freedom (df) = 1, $P < 0.01$] (Fig. 1A), whereas one-sided friendships declined ($\chi^2 = 9.76$, df = 1, $P < 0.005$) (Fig. 1B). For example, 15-year-olds had an average of 2.1 one-sided friends and 0.9 mutual friends, whereas 40-year-olds had 0.6 one-sided friends and 3.0 mutual friends. Age and dominance had independent effects on relationships (see supplementary materials); higher rank and older age both predicted more mutual friendships but fewer one-sided friendships.

To test whether mutual friendships were high-value bonds like those prioritized by older humans, we then examined grooming, a prin-

cipal form of primate social investment (1). We first assessed whether mutual friends were more likely to groom each other and found that chimpanzees of all ages engaged in more total grooming with mutual friends than with one-sided or nonfriends ($\chi^2 = 94.38$, df = 2, $P < 0.0001$; $P < 0.0001$ for significant pairwise comparisons) (Fig. 1C), with similar results for grooming given and received (see supplementary materials). Second, mutual friends engaged in longer grooming bouts ($\chi^2 = 25.03$, df = 2, $P < 0.0001$; $P < 0.05$ for significant pairwise comparisons). Third, mutual friends had more equitable patterns of grooming, both within bouts of grooming ($\chi^2 = 38.23$, df = 2, $P < 0.0001$) and across the year ($\chi^2 = 58.13$, df = 2, $P < 0.0001$) (Fig. 1D). Using this dyadic data, we further found that

mutual friendships were more common among dyads of older males than dyads of prime-aged or younger males, but one-sided friendships were driven by younger males seeking out prime-aged and older partners (see Fig. 1, E and F, and supplementary materials). Thus, chimpanzees invested more, and invested more equitably, in mutual relationships than one-sided ones, and older adults had more mutual friendships than younger adults did.

Older human adults have smaller and more selective social networks, so we next examined how chimpanzee gregariousness changed with age. We assessed the likelihood that an individual was observed alone and found that although males were rarely alone (<1% of observation time), solitariness did increase with age ($\chi^2 = 4.51$, df = 1, $P < 0.05$). Yet when chimpanzees did socialize, age predicted an increased likelihood that they were in a party that included at least one other adult male, as opposed to only females or juveniles ($\chi^2 = 15.73$, df = 1, $P < 0.0001$) (Fig. 2A). Moreover, older males were observed in larger male parties ($\chi^2 = 19.50$, df = 1, $P < 0.0001$) and were more likely to be in close proximity of another adult male ($\chi^2 = 18.02$, df = 1, $P < 0.0001$) (Fig. 2B). For example, 15-year-olds were found in parties averaging 5.8 other males and were physically near another male in 36.6% of observations. In contrast, 40-year-olds were found in parties with 6.6 other males and in proximity to another male in 53.7% of observations. Thus, older males showed some declines in their overall tendency to be gregarious but were more likely to be in parties with and sit near important social partners when they did choose to socialize.

Our final set of analyses tested whether chimpanzees exhibit an increasing positivity bias, the other key component of the human social aging phenotype. We examined the overall rate at which individual male chimpanzees groomed all others in the community (as an index of positive social interaction) versus the rate at which they gave aggression to all others (as an index of negative interactions; comprising both directed aggression, where the individual targets another individual by hitting, biting, or chasing, and nondirected aggressive displays without specific targets). We found that whereas grooming remained fairly constant across the life span, aggression decreased with age ($\chi^2 = 69.09$, df = 1, $P < 0.0001$; $P < 0.0005$ for comparisons of age slopes) (Fig. 2C). Grooming and aggression received from others showed similar patterns (see supplementary materials). Chimpanzees therefore show a behavioral shift from relatively more negative interactions to more positive ones during aging, analogous to the human positivity bias.

Overall, our data provide the first evidence for social selectivity during aging in nonhumans. We found that older chimpanzees, like
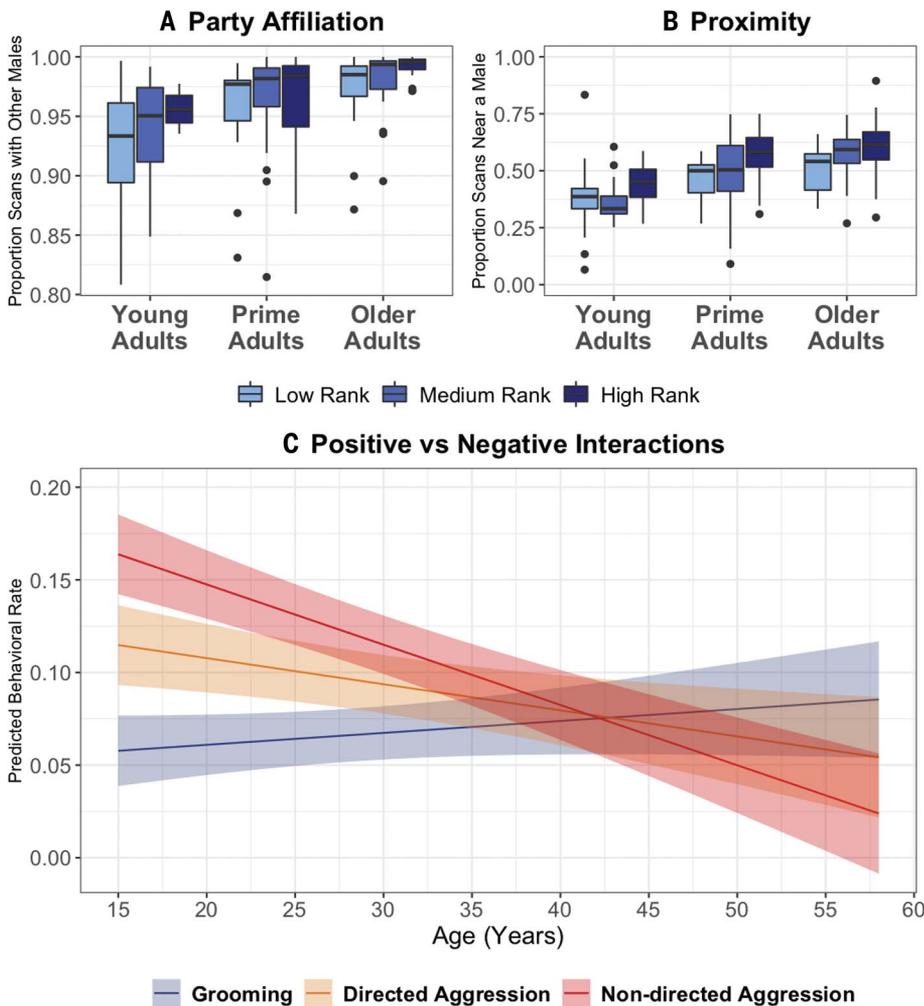
A Party Affiliation

B Proximity

C Positive vs Negative Interactions

Fig. 2. Gregariousness and positivity bias in aging chimpanzees. Older males were more likely than not to be observed (**A**) in parties with other males and (**B**) sitting in proximity to those males. (**C**) While both directed aggression (with specific targets) and nondirected aggression (displays) declined with age, grooming remained fairly constant. Ribbons indicate 95% CI estimates.

humans, prioritized high-quality relationships; whereas younger adults had more asymmetrical friendships characterized by reduced investment, older adults exhibited more mutual friendships characterized by high, equitable investment. Second, older chimpanzees were more likely to be observed alone but tended to socialize more with important partners by joining parties with other males, joining larger male parties, and sitting in close proximity to other males. Finally, chimpanzees exhibited an increasing positivity bias with age, showing consistent grooming but reductions in aggression across the life span. These patterns were notably independent of dominance rank; despite their falling status, older males were more likely to be mutual friends with each other and were targets of the one-sided advances of younger males. Together, our data indicate that chimpanzees demonstrate key behavioral signatures of the human social aging

phenotype, showing that increasing social selectivity can occur in the absence of a rich future time perspective.

These data support the view that senescence drives fundamental shifts in the costs and benefits of social interactions across species. Yet although many species face new constraints during aging, chimpanzees and humans show a response to these constraints that is not universal. In particular, several other primate species exhibit social withdrawal during aging—reducing social interactions overall without focusing on important partners—as well as a negativity bias characterized by declines in affiliation but steady rates of aggression (26–32). Why do aging chimpanzees and humans instead show social selectivity and a positivity bias? We propose that optimal social responses to aging depend on a species' social organization and life history. The relationships of many species are primarily based on kinship,

and senescence makes it difficult to form new relationships as close relatives die. Consequently, social withdrawal may be a common pattern. Yet social relationships are flexible, can occur outside of kinship, and last many years in long-lived humans and chimpanzees (23, 24). Thus, strongly established relationships may be more reliable for older chimpanzees than for other primates. This may be especially important for species with relatively low reproductive skew like chimpanzees, as older individuals can still obtain fitness benefits via cooperative alliances despite changes in health and social status (19–22).

A second question concerns the specific proximate mechanisms underpinning social selectivity in chimpanzees. Socioemotional selectivity theory proposes that the human social aging phenotype causally depends on an explicit sense of the self in time, but given that other animals have constrained future-oriented cognition (16, 17), other proximate mechanisms must play a role in nonhumans. In some primates, age-related shifts in social behavior have been proposed to stem from declining capacities to cope with stress (32), yet older chimpanzees do not exhibit major increases in sensitivity to either energetic or social stressors despite higher overall glucocorticoids (22). An alternative possibility is that chimpanzee social aging patterns are driven by shifts in emotional reactivity, given that an increasing capacity for emotional regulation is a feature of human aging (8, 14). Thus, a key question is whether older chimpanzees also exhibit shifts in affective processes, such as a less reactive temperament or lower rates of reactive aggression.

Our findings demonstrate how data from long-lived, socially flexible animals are crucial for disentangling the proximate and ultimate causes of human social aging patterns. In addition to testing how different species respond to the constraints of aging, comparative data can inform our understanding of the evolution of social roles. In other long-lived mammals such as cetaceans and elephants, older individuals serve as stores of ecological knowledge that benefit groupmates (33). This indicates that a prolonged life course can shape adaptive strategies for information processing and suggests that the social aging phenotype characteristic of chimpanzees and humans may be due in part to the social knowledge that long-lived, socially flexible species can acquire. Indeed, older adult humans exhibit greater crystallized intelligence and skillfulness at reasoning about social conflicts (34). Similarly, older chimpanzees might acquire social knowledge over their life span that makes them attractive social partners despite falling dominance status. In sum, although humans exhibit extraordinary cognitive features that allow for complex reasoning about the future, commonalities

in social aging between humans and other animals are key to understanding the evolution and function of these mechanisms.

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