Social selectivity in aging wild chimpanzees

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Abstract

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 test 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 also socialize more with important social partners. Finally, males show a relative shift from more agonistic interactions to more positive, affiliative interactions over the lifespan. Our findings indicate that social selectivity can emerge in the absence of complex future-oriented cognition, and provide an evolutionary context for patterns of social aging in humans.

Main text

Social bonds have adaptive consequences over the lifespan: 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 term the human social aging phenotype. First, older adults across societies have smaller yet more emotionally-fulfilling social networks than younger adults, due 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 wellbeing in old age.

Socioemotional selectivity theory has emerged as the most influential explanation for the human social aging phenotype, arguing that the central process generating lifespan shifts in sociality is an explicit sense of future personal time and mortality (*10, 11*). 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—due to an illness diagnosis, natural disaster, or a geographic move—generally exhibit preferences like 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 new 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 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 tradeoffs 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 if 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 lifespans of

50-60 years in the wild, and form flexible, long-term social bonds. They have a high degree of choice about who to interact with due to their large fission-fusion societies which comprise temporary and fluid sub-groups (‘parties’) that can range from one chimpanzee to almost the 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 over 20 years, providing longitudinal observations that are unparalleled in human research.

We analyzed social interactions from 78,000 hours of observations from 1995-2016, comprising 21 male chimpanzees ranging from 15 years (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 relatively asocial females (*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*). Few males had adult maternal brothers so we did not account for kinship, but we controlled 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 pre-requisite for other cooperative interactions like grooming and signals social comfort (*1*). We indexed social preferences by examining how often two individuals were within 5m when in the same party. We then categorized male-male dyads as ‘mutual friends’ (both showed a preference to sit near the other, above their individual average rates of association), 'one-sided friends' (one individual showed this preference, but their partner did not), or 'non-friends' (neither preferred to associate with the other). Thus, mutual friendships are reciprocated, whereas one-sided friendships are not. We found that the number of mutual friends increased with age [$\chi^2=6.89$, 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. Finally, age and dominance had independent effects on relationships (see supplementary materials): both higher rank and older age 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 principal form of primate social investment (*1*). We first assessed whether mutual friends were more likely to groom, and found that chimpanzees of all ages engaged in more total grooming with mutual friends compared to one-sided and non-friends [$\chi^2=94.38$, df=2, $p<0.0001$; $p<0.0001$ for 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, $p<0.0001$; $p<0.05$]. Third, mutual friends had more equitable patterns of grooming, both within bouts [$\chi^2=38.23$, df=2, $p<0.0001$; Fig. 1d] and across the year [$\chi^2=58.13$, df=2, $p<0.0001$]. Using this dyadic data, we further found that mutual friendships were more common amongst 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. 1e-f and supplementary materials). Thus, chimpanzees invested more, and more equitably, in mutual than one-sided relationships, and older adults had more mutual friendships than younger adults.

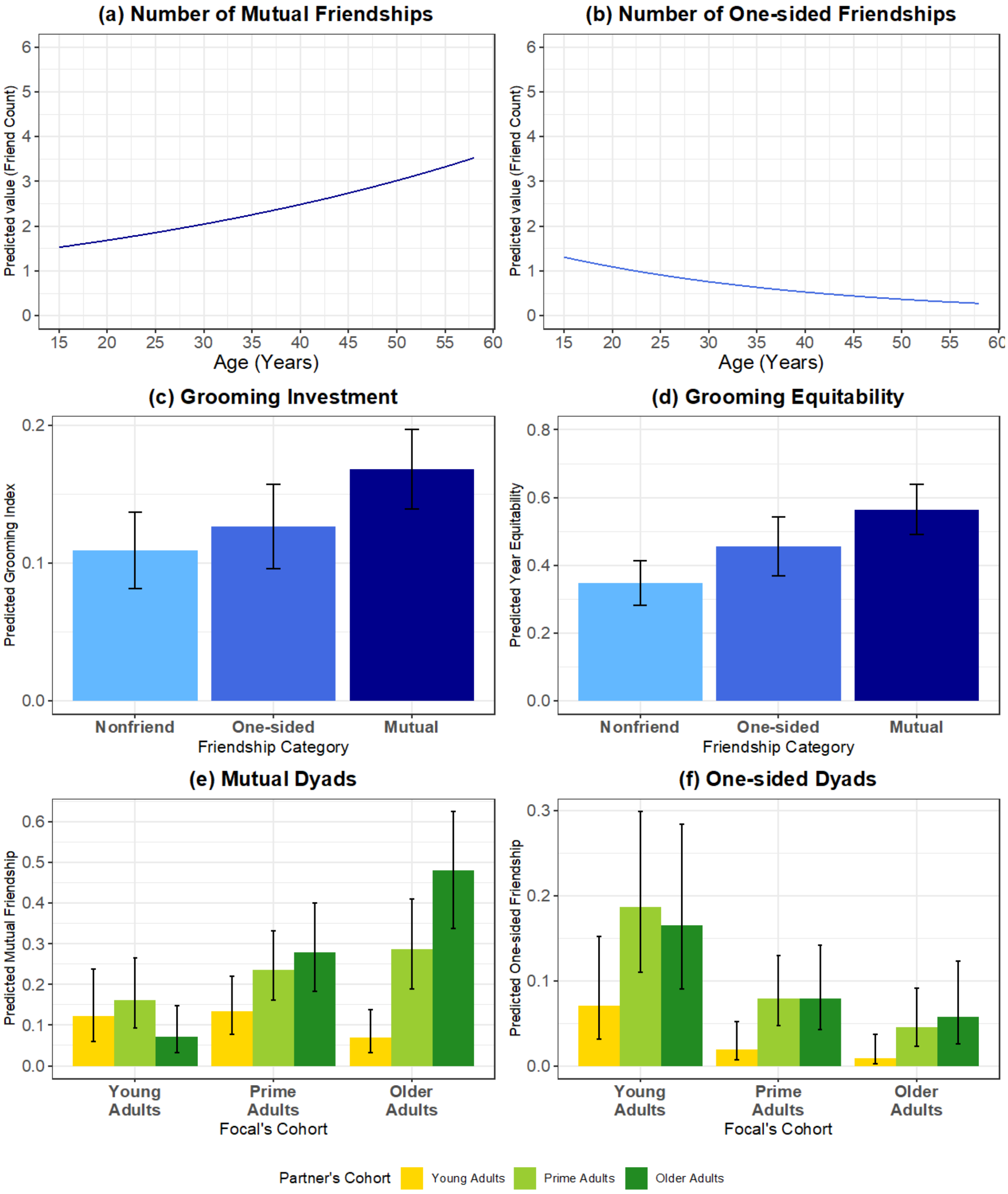

Figure 1: Friendships in aging chimpanzees. (a-b) Older males had more mutual friendships, whereas younger males had more one-sided friendships. (c-d) Chimpanzees invested more and had more equitable grooming patterns with mutual friends. (e-f) Older males (35+ years) were mutual friends with peers, and attractive partners for younger males' (15-20 years) and prime-aged males' (20-35 years) one-sided friendships. Ribbons and error bars indicate 95% CI estimates.

Older human adults have smaller but 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 (less than 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 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 on 36.6% of observations. In contrast, 40-year-olds were in parties with 6.6 other males, and in proximity to another male on 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 rates that individual male chimpanzees spent giving grooming to all others as an index of positive social interactions, versus rates they spent giving aggression as an index of negative interactions (comprising both directed aggression where the individual targets another specific individual by hitting, biting, or chasing them; and non-directed aggressive displays without particular targets). We found that whereas grooming remained fairly constant across the lifespan, aggression decreased with age [$\chi^2=69.09$, df=1, $p<0.0001$; Fig. 2c]. Grooming and aggression received from others showed similar patterns (see supplemental materials). Chimpanzees therefore show a behavioral shift from relatively more negative interactions to more positive interactions during aging, analogous to the human positivity bias.

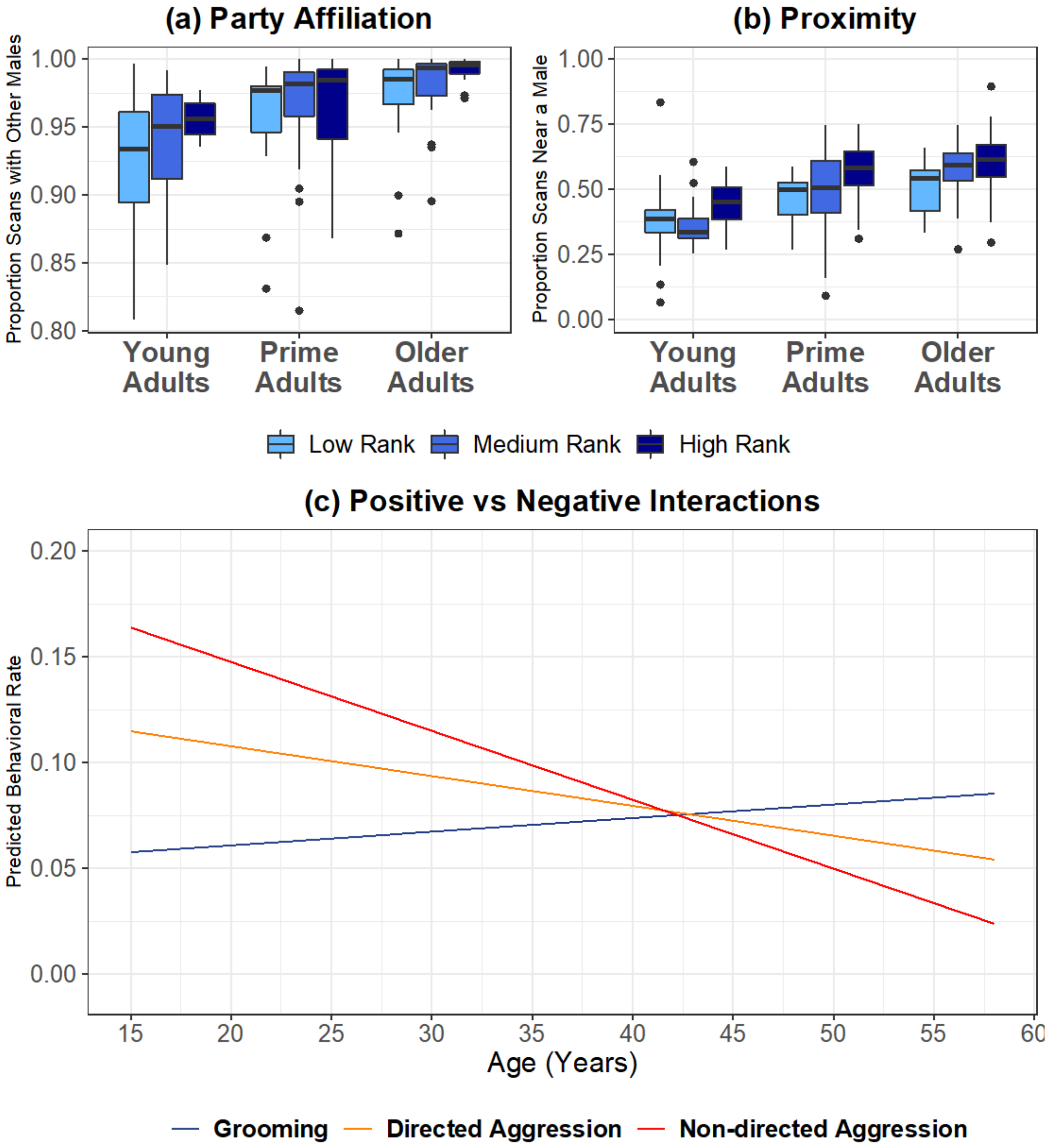

Figure 2: Gregariousness and positivity bias in aging chimpanzees. Older males were more likely to be (a) in parties with other males, and (b) sitting in proximity to those males. (c) While both directed aggression (with specific targets) and non-directed aggression (displays) declined with age, grooming remained fairly constant. Ribbons indicate 95% CI estimates.

Overall, our data provide the first evidence for social selectivity during aging in nonhumans. We found that older chimpanzees, like humans, prioritized high-quality relationships: whereas younger adults had more asymmetrical friendships characterized by reduced investment, older adults exhibited more mutual friendships characterized by a 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, showing consistent grooming but reductions in aggression across the lifespan. Importantly, these patterns were independent of dominance rank: despite their falling status, older males were more likely to be mutual friends with each other, and were the targets of 'one-sided' advances from 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 (*25-28*). 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 (*28*), 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 increasing capacities 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 to disentangle the proximate and ultimate causes of human social aging patterns. In addition to testing how different species respond to the constraints of aging, this can inform our understanding of evolution of social roles. In other long-lived mammals like cetaceans and elephants, older individuals serve as stores of ecological knowledge that benefit groupmates (*29*). 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 (*30*). Similarly, older chimpanzees might acquire social knowledge over their lifespan that makes them attractive social partners despite falling dominance status. In sum, while 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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Acknowledgments: We thank Felix Warneken and Toni Antonucci for feedback, and Corey Powell at CSCAR for statistical advice. **Funding:** NIH-R01AG04395, NSF-1926653, NSF-1926737, NSF-1926352, NSF-1355014, NSF-9807448, NSF-0416125, NSF GRFP DGE-0237002, Sloan Foundation FG-2019-12054, and long-term support from the Leakey Foundation and UNM. **Author contributions:** AGR and ZPM conceived the project; all authors performed the research; AGR and ZPM analyzed the data; AGR and ZPM wrote the paper with input from all authors. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** All data will be available at Dryad Digital Repository.

Supplementary Materials: Social selectivity in aging wild chimpanzees

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Study site and subjects

We conducted this study using long-term behavioral data from the Kibale Chimpanzee Project (KCP), which studies the wild Kanyawara chimpanzee community living in Kibale National Park, Uganda. Kibale is a semi-deciduous tropical rainforest in southwestern Uganda, and the Kanyawara chimpanzee territory occupies approximately 38 km^2 in the northwest quadrant of the park. All work had approval from the Institutional Animal Care and Use Committees of Harvard University (protocol #96-03), University of New Mexico (#19-200862-MC), and Tufts University (#M2019-83). Research permits were issued by the Uganda Wildlife Authority, and Uganda National Council for Science and Technology, and the research adhered to the legal requirements of Uganda.

Overview of field observational methods

At Kanyawara, trained Ugandan field assistants work in teams of 2-3 and enter the forest every morning and head to the location where the chimpanzees were sleeping the night before. One field assistant takes data at the party level, recording the identity of each chimpanzee in the party every 15 minutes. Additional field assistants record data on focal individuals. To equalize observation effort across individuals, the project attempts to focal every individual at least once a month, and as much as possible individuals are not followed two days in a row. We routinely calculate interobserver reliability tests between field assistants and find that their data scores above 95% in those tests.

From 1995 to August 2009, focal data took the form of ten-minute focal follows. For these, an individual was chosen (ideally one who had not been followed yet that day) and their behavior was recorded every 2 minutes, along with the identities of all individuals involved in joint behaviors with the focal such as grooming, and individuals within 5 meters of and nearest neighbor to the focal. After ten minutes, a new focal individual was chosen. To avoid biasing the choice of new focal to individuals engaged in interesting behaviors, we limit our dataset to the last 2-minute scan of each of the focals.

From August 2009, chimpanzees were observed using full-day focal follows where a focal individual is chosen who has ideally not been followed that month. One field assistant observes the focal individual and records their activity every minute along with the identity of other individuals who are involved in joint behaviors such as play or grooming. This field assistant also records the identity of every individual within 5 meters of the focal and the nearest neighbor to the focal every 15 minutes. The focal individual is followed for the entire day if possible. If the individuals are lost, field assistants search for the focal for up to 2 hours and then switch to a new individual. In the event of a party fission event, field assistants stay with the party of the focal.

Final dataset

The final dataset comprised data from 1995-2016, including 21 adult male chimpanzees ranging in age from 15-58 years old (see Table S1 for summary of data by subject). We focused on males because they exhibit stronger bonds and more frequent social interactions than relatively asocial females (*23*).

We analyzed social interactions from 78,000 hours of observations from 1995-2016 comprising party composition, grooming, and aggression. The community averaged 48 individuals per year (range: 41-53) with 10 adult males per year (range: 8-11). There was an average of 10.6 years of longitudinal observation for each individual (range: 1-22 years across individuals), and individuals were observed for an average of 141.6 days of observation per year (range: 20-278 days). All data will be made publicly available in Dryad Digital Repository upon publication.

Subject	**Age Range (in years)**	**Total years of observation**	**Days of observation / year**			**Number of scans / year**		
			Mean	***Min***	***Max***	***Mean***	***Min***	***Max***
1	21-40	20	147.5	87	226	4357.3	1730	7881
2	15-17	3	171.7	27	277	5473.0	790	9453
3	29-50	22	120.8	47	205	3503.3	1391	6774
4	29-32	4	71.5	53	111	1678.5	1017	2817
5	15-22	8	195.4	59	278	5610.8	1765	9425
6	15-28	14	194.4	77	275	5717.0	2002	9800
7	27-32	6	120.7	87	168	3041.0	1700	4782
8	15-33	19	205.2	138	274	6058.8	3485	9869
9	45-46	2	70.0	67	73	1652.5	1351	1954
10	20-35	16	156.4	82	247	4675.8	1810	8813
11	15-18	4	151.0	75	218	4133.8	1904	7050
12	15	1	118.0	118	118	3105.0	3105	3105
13	15-21	7	194.7	148	232	5357.1	3675	7343
14	16-25	10	180.6	84	257	5591.1	1999	9513
15	24-34	11	86.4	36	169	2231.4	518	5075
16	40-58	19	142.6	64	228	4181.2	1320	7743
17	31-36	6	96.5	23	160	2361.2	697	4167
18	15-21	7	172.9	81	226	4610.4	2469	6327
19	15-16	2	112.5	52	173	3355.5	1801	4910
10	35-54	20	103.7	20	211	3140.2	333	7170
21	22-43	22	161.0	71	250	4494.6	1677	8361
Mean	**-**	***10.6***	***141.6***	**-**	**-**	***4015.7***	**-**	**-**

Table S1: Summary of chimpanzee observations by individual. Age range, number of years of observation, number of days per year, and total number of scans per year for each individual included in the longitudinal dataset.

We analyzed two main kinds of data. First, some analyses focused on individual-level data compiling yearly overall averages for each individual in terms of their number of friends, counts of scans in different kinds of social parties, and rates of aggressive versus affiliative behavior (see below for the specific ways each of these metrics were calculated). This individual-level dataset allowed us to look at overall changes in patterning of social behavior within individuals (see Table S2 for summary of individual-level data used in this study). Subjects had to be observed for at least 20 hours over the course of 20 days in each year to be included in this dataset to ensure appropriate sampling of social behavior and calculate the metrics.

The second set of analyses focused on dyadic data comprising behaviors between pairs of individuals, to examine how focal individuals invested in different partners classified as mutual, one-sided, or non-friends, as well as how the personal characteristics of partners (e.g., rank, age, and their disparity in rank and age relative to the subject) influenced friendship patterns (see Table S2 for summary of individual-level and dyadic-level datasets used in this study). There were a total of 148 unique adult male-male dyads in this study. Of these only 3 dyads were maternal brothers; note that there is minimal evidence that chimpanzees or most other primates can identify paternal kin and a fairly limited evidence that affiliation is directed towards maternal kin (*24*). As a result of the small number of related dyads, we do not control for kinship in these analyses.

	Individual-level Dataset Variable	**Dyadic-level Dataset Variables**
Subject characteristics	• ID • Age • Dominance rank	• ID • Age • Dominance rank
Partner characteristics		• ID • Age • Dominance rank
Friendship metrics	• Total number of mutual friends • Total number of one-sided friends	• Is the partner a mutual friend? • Is the partner a one-sided friend?
Group metrics	• Total number of adult males • Average male party size • Average swollen female party size	
Individual sociality metrics	• Number of scans alone, versus in a social party • Number of party scans with another adult male, versus in a party with no adult males • Number of male party scans within 5m of another adult male, versus not	
Grooming metrics	• Overall rate of grooming given to all other individuals out of all possible time • Overall rate of grooming received by all other individuals out of all possible time	• Rate of grooming with partner • Rate of grooming given to partner • Rate of grooming received from partner • Total grooming time with partner • Bout length with partner • Equitability within a bout with partner • Equitability over the year with partner
Aggression metrics	• Overall rate of directed aggression given to all other individuals • Overall rate of non-directed aggression (displays without a target) • Overall rate of directed aggression received by all other individuals	

Table S2: Summary of social behavior datasets. The extracted social variables compared in the individual- and dyadic-level datasets. Each variable was calculated for each year of observation for that individual chimpanzee.

Overview of statistical analyses

We analyzed data in R version 3.6.1 (*35*). We implemented mixed models using either the *lmer* or the *glmer* function from the lme4 software package. In general, our analyses took the form of first constructing a base model with relevant control predictors, and then adding the subject's *age* to the full model to test its importance. Age was always treated as a continuous predictor, except in the analysis of dyadic friendship characteristics where we examined the interaction of age cohorts for both the subject and the partner (age cohorts here were defined as younger adults from age 15-20 years, prime-aged adults up to age 35 years, and older adults over 35 years following prior work).

We compared the fit of these different models using likelihood ratio tests (*36*), and post-hoc tests (both pairwise comparisons and age-related trends) were implemented used the *emmeans* package with a Tukey correction. Linear mixed models were automatically refit using maximum likelihood for these model comparisons. Graphs showing predicted effects and 95% confidence intervals from these models were calculated using the *effects* package in R, and reported parameter estimates are all unstandardized.

Statistical models always included random *subject* intercepts to account for repeated, unbalanced measurements within subjects in the longitudinal dataset. Across models, we also always controlled for an individual's *dominance rank category* (high, medium, or low rank), as dominance can strongly pattern primate social interactions, and declines during old age after a peak in prime adulthood. Finally, we controlled for several other variables as appropriate for specific metrics (see following sections for details for each specific metric and associated models). For example, we accounted for the *total number of males* in most models, either a predictor or an offset, given that the number of males in the group can constrain socializing opportunities. In models examining rates or counts of behaviors (such as grooming metrics, aggression metrics, or party membership metrics), we included random effects of *year* to account for any global shifts in association or social behavior due to changes in ecology, food distribution or data collection protocols. In contrast, friendship metrics (e.g., number of mutual or one-sided friends) already intrinsically accounted for yearly variation in gregariousness in the calculation of the metric itself. We also accounted for average number of *females with sexual swellings* in analyses of party size, since this is a known predictor of male party size. Finally, in analyses of dyadic friendships, we accounted for the *difference in rank* and *difference in age* between the subject and their partner, as males often show bonds with males of similar age and rank.

Calculation and analysis of behavioral metrics

To test the predictions of socioemotional selectivity theory using observational data from wild chimpanzees, we used standard metrics of nonhuman primate social behavior, including party presence, spatial proximity, grooming patterns, and aggression. As described below, we identified key features of primate social interactions that mapped onto features of human social aging data, and then analyzed how they changed with age in chimpanzees.

Dominance rank

Across all analyses of social aging, we always controlled for an individual's dominance rank; after an initial rise through prime age, rank declines in old age (*19, 25*). Chimpanzees give vocalizations called pant-grunts and pant-barks to formally signal their subordinance to dominant individuals. Field assistants at Kanyawara record all such vocalizations and the identities of the givers and receivers. We used these data, together with the results of the winners and losers of decided, dyadic agonistic interactions, to calculate Elo dominance scores (*37*) and then averaged the Elo score for each male in each calendar year. These were used to assign annual ordinal ranks to each male. As rank is often a major driver of patterns of social behavior in wild primates, all of our analyses controlled for rank category (high rank is positions 1 through 3, medium is ranks 4 through 7, and low is ranked 8 or less).

Categorizing dyadic friendships in chimpanzees

The first question we addressed was whether older chimpanzees showed increasing focus on important social partners. We first categorized chimpanzee relationships using patterns of spatial association. To do this, we adapted prior work on chimpanzee friendships or 'preferred social partners' (*38, 39*) using a combined association index that integrated metrics of dyadic presence in parties, dyads being within 5m spatial proximity if the two individuals were in the same party, and dyads being nearest neighbors or grooming each other if they were within 5 meters. Here we categorized friendships using this overall approach, but assessed dyads based on only the spatial association metric, as we used presence in parties as a separate metric of overall gregariousness, and then used grooming as an independent metric of relationship investment, in order to test different aspects of socioemotional selectivity theory as described more below. Thus, when both individuals show a consistent preference to sit near each other when present in the same party, they were considered to be mutual preferred social partners. In contrast, if only one individual shows this preference, then they are considered one-sided friends.

To implement this, for each male-male dyad in each year, we calculated a dyadic within 5-meter index. Proximity is an important marker of affiliation in primates, as it is a pre-requisite for other cooperative interactions like grooming and signals a level of social comfort (*1, 38*). The within 5-m index is a spatial association index that measures the frequency with which two individuals are within 5-meters of one another, when they are in the same party together and when one of the individuals is the subject of a focal follow. From 1995 to September 2009, we used the ten-minute focal data. In September 2009, we switched from ten-minute focal follows to full-day focal follows. To calculate indices for 2009 which are comprised of the two different kinds of data, we averaged the index we calculated from the ten-minute focal data from early in the year with the full-day focal index from the last half of the year. Unpublished analyses from this site show that when we randomly subsample the full-day focals to mimic the 10-minute focals, there is no statistical difference in the metrics calculated from these two methods. The spatial proximity between individuals A and B is calculated using the following formula:

$$5m_{ab} = \frac{A_f B_5 + B_f A_5}{A_f B_P + B_f A_p}$$

where $A_f B_5$ is equal to the number of focal scans where A is the focal and B is within 5 meters, $B_f A_5$ is the number of focal scans where B is the focal and A is within 5 meters, $A_f B_P$ is the number of focal scans where A is the focal and B is in the same party and $B_f A_p$ is the number of scans where B is the focal and A is in the same party. It is important to note that this measure is independent of the number of times individuals are observed, because it controls for the number of times the two individuals were in the same party. This means that a dyad that had not been seen together in the same party very often might still have a high 5-meter association if they were frequently within 5 meters of one another in those instances when they were in the same party. We only calculated a 5-meter association index for dyads that were in the same party together for at least ten scans. Therefore, some dyads did not have data available to calculate this index.

We then used the 5-meter index to assign individuals into friendship categories. For male A, we calculated the average within 5-meter index for each year. If the dyadic within 5-meter score with male B was above ¼ standard deviation from this average, then male B was categorized as a friend of male A. If male A was also about ¼ standard deviation above the average of male B, then they were categorized specifically as a *mutual friend*. However, if male A did not exceed ¼ standard deviation of male B's average, then male B was categorized as a *one-sided friend* of male A. Other dyads were then classed as *non-friends.* This allows for a dyad to be categorized as a friendship if the proximity scores for the dyad are high for that chimpanzee individually, denoting their social preference.

Individual variation in number of friends

To analyze changes in an individual's number of friendships with age (see Figure S1), we examined yearly friendship counts for each individual using generalized linear mixed models (GLMMs) with a Poisson function. Here we analyze number of *mutual friends* and number of *one-sided* friends in two separate sets of models. The base model for each analysis accounted for *subject identity* (as a random factor), the subject's *rank category* (as an ordinal factor; high, medium, or low), and included the total *number of adult males* in the group that year as an offset (to account for the total number of possible friendships in that year; implemented as log value). Offsets are used in Poisson regression models when the data can be modeled as proportion (e.g., here friendships are a proportion of total males in the group). The full model then added the individual's *age* as a linear predictor, to test if number of each friendship type shifted with age.

For mutual friendships, we found that including age improved fit [$\chi^2 = 6.89$, df = 1, $p < 0.01$]. In the full model both age [*estimate* = 0.019, *SE* = 0.007, *Z* = 2.812, $p < 0.01$] and linear rank category [*estimate* = 0.286, *SE* = 0.103, *Z* = 2.772, $p < 0.01$] were significant predictors, indicating that older males and higher-ranking males tended to have more mutual friends (see also Figure 1a from the main manuscript for a graph of this age effect).

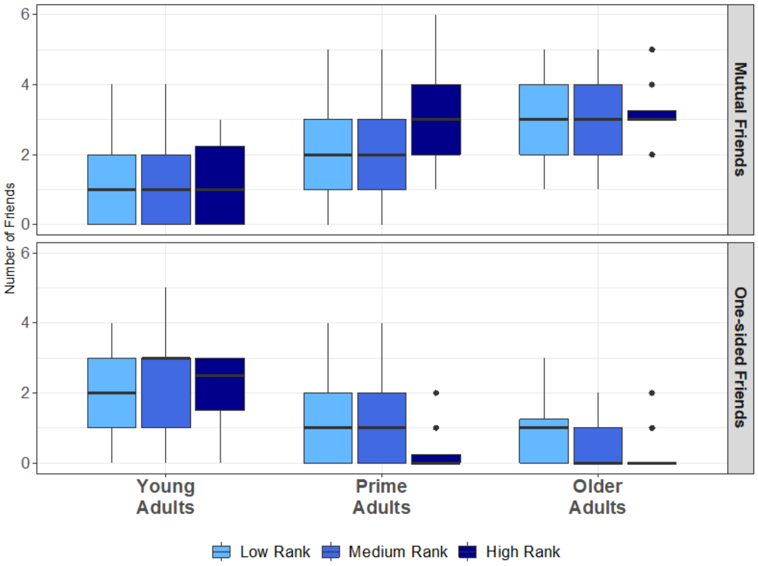

Figure S1: Lifespan changes in friendship types. Boxplots cluster data by age cohort and rank category; line indicates group median; whiskers reflect inter-quartile range; dots indicate outliers. Top panel shows average number of mutual friends, and bottom panel average number of one-sided friends.

In the models examining one-sided friendships, age also improved model fit [$\chi^2 = 9.76$, df = 1, $p < 0.005$]. However, here age [*estimate* = -0.036, *SE* = 0.011, *Z* = -3.429, $p < 0.001$] and linear rank category [*estimate* = -0.815, *SE* = 0.181, *Z* = -4.516, $p < 0.0001$] were both negative predictors: lower ranking and younger males tended to have more one-sided friends. Thus, old age and high rank have parallel impacts on mutual versus one-sided friendships: high rank and old age predict more mutual friends, whereas young age and low rank predict more one-sided friends. Note that since older male chimpanzees tend to fall in rank, this further indicates that old males maintain more mutual friends despite the opposing effects of their decreasing dominance rank.

Characteristics of chimpanzee friendship dyads

We next sought to replicate the above finding that older males have more mutual friends, but fewer one-sided friends, using the dyadic dataset. This dyadic dataset further allowed us to examine what characteristics of subjects and partners predicted whether specific dyads were categorized as mutual versus one-sided friends. To do so, we used GLMMs with a binomial function (logit link) to assess whether a given individual was categorized as a friend (either mutual or one-sided across different models) or not. For both mutual and one-sided friendships, the base model accounted for both *subject* and *partner* identity (both as a random factor), subject's *rank category* (as an ordinal factor; high, medium, or low), and the *rank difference* between the subject and the partner (as an absolute difference between their numerical rank; this predictor accounted for the possibility that males tend to associate with similar-status partners). In the second model, we then added *subject's age cohort* (young, prime-aged, or old as an ordinal factor) to confirm the friendship patterns we saw in the individual-level data. This is the only analysis that employed age as a categorical variable, which we did because we wanted to examine the interaction between focal age and partner age. Finally, in the full model we then added the interaction between *subject's age cohort* and *partner's age cohort,* to assess if individuals preferentially associated with peers versus younger or older chimpanzees. Note that we used age cohort rather than age in years for this particular analysis in order to parse the age effects stemming from the inclusion of this interaction.

For the analysis of mutual friendships, we found that including subject's *age cohort* improved fit [$\chi^2 = 18.95$, df = 2, $p < 0.0001$]: older males were more likely to be in a mutual friendship, aligning with the individual-level data results reported previously. In addition, the inclusion of the *subject's cohort X partner's cohort* interaction further improved fit [$\chi^2 = 61.93$, df = 6, $p < 0.0001$]. As also illustrated in Figure 2e in the main manuscript, post-hoc pairwise comparison using the *emmeans* function revealed that (1) dyads of two older males were more likely to be mutual friends than dyads of two prime-aged males [$p < 0.001$] or dyads of two younger males [$p < 0.005$]; (2) older males were more likely to be mutual friends with another older male, compared to with either a prime-aged male [$p < 0.05$] or a younger male [$p < 0.0001$]; (3) older males were also more likely to be mutual friends with prime-aged than younger males [$p < 0.0001$]; and (4) younger adults and prime-aged adults showed no clear preference for mutual friends according to age, in terms of preferring peers compared to differently-aged individuals. That is, older males were primarily attracted to other older males, and males in other age cohorts also showed an equal preference for older males compared to their peers. In the full model, rank difference was also a significant predictor [*estimate* = -0.182, *SE* = 0.027, *Z* = -6.747, $p < 0.0001$]: males were generally more likely to be mutual friends with similarly-ranked partners compared to males with a more disparate rank.

For the analysis of one-sided friendships, we found a different pattern. Here, including subject's *age cohort* as a predictor again improved fit [$\chi^2 = 17.67$, df = 2, $p < 0.0005$], but as in the individual-level data, older males were *less* likely to be in a one-sided friendship with other males. In addition, the inclusion of the *subject's cohort X partner's cohort* interaction further improved fit [$\chi^2 = 22.53$, df = 6, $p < 0.001$]. As also illustrated in Figure 2f in the main manuscript, post-hoc pairwise comparison using the *emmeans* function revealed that (1) young adults are more likely to seek a one-sided friendship with an old adult, compared to old adults seeking a one-sided friendship with a younger adult [$p < 0.001$]; (2) young adults are more likely to seek a one-sided friendship with a prime-aged-adult, compared to prime-aged adults seeking a one-sided friendship with a younger adult [$p < 0.0001$]; and (3) prime-aged and older adults showed no clear preference for one-sided friends by age, in terms of preferring peers compared to differently-aged individuals Overall this shows that one-sided friendships in chimpanzees typically involve younger males seeking out males that are older than them, whereas prime-aged and older males generally have few of these kinds of one-sided relationships. In the full model, subject's rank was also a significant linear predictor [*estimate* = -0.608, *SE* = 0.217, *Z* = -2.804, $p < 0.001$]: higher ranking makes were less likely to be in one-sided friendships than lower-ranking males.

Dyadic metrics of grooming investment

To confirm that mutual friendships represent high-value social bonds for chimpanzees, we then tested whether they show greater investment in individuals classified as different friendship categories by examining patterns of grooming. Grooming is well-recognized as a principle form of investment in a social bond in primates (*1, 23, 38, 39*). As grooming was not used for the friendship categorization, this allowed for an independent metric of relationship investment. To do this, for each male-male dyad in each year using either the ten-minute focal (1995-Aug 2009) or the full-day focal (August 2009-2016) data, we calculated a grooming index as follows:

$$Grooming_{ab} = \frac{A_f B_g + B_f A_g}{A_f B_5 + B_f A_5}$$

where $A_f B_g$ is equal to the number of focal scans where A is the focal and B a grooming partner, $B_f A_g$ is the number of focal scans where B is the focal and A is a grooming partner, $A_f B_5$ is the number of focal scans where A is the focal and B is within 5 meters of the focal and $B_f A_5$ is the number of scans where B is the focal and A is within 5 meters of the focal. This measure is independent of the within 5 index which was used to assign friendship categories, so that a dyad that has a high within 5 meter index doesn't necessarily have to have a high grooming index. For 2009, we averaged the ten-minute focal index with the full-day focal index.

To analyze these data, we used linear mixed models to test if this grooming index increased with age. The base model accounted for *subject identity, partner identity,* and *year* (as random factors; year accounted for any seasonal changes in the group's grooming patterns based on food availability or other global changes in the environment); subject's *rank category* and the absolute *rank difference* between the subject and the partner; and finally the absolute *age difference* between the subject and the partner (as a linear predictor, given the age interactions detected in the analyses of friendship reported above suggesting that many chimpanzees are preferentially associating with peers). In the second model, we then added *friendship category* (mutual, one-sided, or non-friends) to test how this shaped grooming patterns for that dyad. In the third model, we added subject's *age* to test if older chimpanzees show overall more grooming, and in the full model we finally added the interaction between subject's *age* and *friendship category* to assess if older males showed a different pattern of grooming towards different friend types than do younger males.

We found that the inclusion of *friendship category* improved model fit [$\chi^2 = 94.38$, df = 2, $p < 0.0001$]. Pairwise comparisons showed that chimpanzees groom more with mutual friends compared to both one-sided [$p < 0.001$] and non-friends [$p < 0.001$], and show a trend to groom more with one-sided friends than non-friends [$p = 0.086$]. Yet neither the inclusion of the subject's *age* [$\chi^2 = 1.54$, df = 1, $p > 0.21$, n.s.] nor the interaction between *age X friendship category* [$\chi^2 =$

2.27, df = 3, $p > 0.51$, n.s.] further improved model fit compared to the friendship-only model. This shows that chimpanzees generally groom their mutual friends more, independent of the individual's age; while older males have more mutual friends than younger males, they do not show any further shift in grooming (see Table S3 for parameters from the second, best-fit model).

	Grooming Index	**Bout Duration**	**Bout Equitability**	**Year Equitability**
Rank Category (Linear effect)	*Est.* = 0.007 *SE* = 0.006 $t = 1.069$ $p > 0.28$	*Est.* = -.971 *SE* = 0.541 $t = -1.796$ $p = 0.074$	*Est.* = 0.024 *SE* = 0.014 $t = 1.649$ $p > 0.10$	*Est.* 0.081 *SE* = 0.028 $t = 2.898$ **$p < 0.005$**
Rank Category (Quadratic effect)	*Est.* = -0.007 *SE* = 0.005 $t = -1.338$ $p > 0.18$	*Est.* = 0.457 *SE* = 0.410 $t = 1.113$ $p > 0.26$	*Est.* = -0.010 *SE* = 0.011 $t = -0.924$ $p > 0.35$	*Est.* = -0.036 *SE* = 0.022 $t = -1.620$ $p > 0.10$
Rank difference (Linear)	*Est.* = -0.007 *SE* = 0.001 $t = -6.190$ **$p < 0.0001$**	*Est.* = -0.050 *SE* = 0.091 $t = -0.548$ $p > 0.58$	*Est.* = -0.002 *SE* = 0.003 $t = -0.660$ $p > 0.50$	*Est.* = -0.010 *SE* = 0.005 $t = -1.882$ $p = 0.06$
Age difference (Linear)	*Est.* = -0.002 *SE* = 0.0003 $t = -5.331$ **$p < 0.0001$**	*Est.* = 0.015 *SE* = 0.021 $t = 0.682$ $p > 0.49$	*Est.* = -0.001 *SE* = 0.001 $t = -1.873$ $p = 0.062$	*Est.* = -0.004 *SE* = 0.001 $t = -3.138$ **$p < 0.005$**
One-sided friends (reference = non-friends)	*Est.* = 0.018 *SE* =0.008 $t = 2.127$ **$p < 0.05$**	*Est.* = 0.517 *SE* = 0.640 $t = 0.808$ $p > 0.41$	*Est.* = 0.037 *SE* = 0.018 $t = 2.069$ **$p < 0.05$**	*Est.* = 0.108 *SE* = 0.036 $t = 2.973$ **$p < 0.005$**
Mutual friends (reference = non-friends)	*Est.* = 0.059 *SE* =0.006 $t = 9.842$ **$p < 0.0001$**	*Est.* = 2.503 *SE* = 0.496 $t = 5.043$ **$p < 0.0001$**	*Est.* = 0.086 *SE* = 0.014 $t = 6.195$ **$p < 0.0001$**	*Est.* = 0.217 *SE* = 0.028 $t = 7.654$ **$p < 0.0001$**

Table S3: Predictors for grooming investment and grooming equitability within dyads. Parameters from the best-fit models examining different metrices of time spent grooming and distribution of grooming within dyads. The further addition of subject's age and the interaction between age and friendship category to subsequent models did not significantly improve model fit for these variables.

From 2009 using the full-day focal data, we were also able to calculate the total duration of grooming for each dyad. We first confirmed that the grooming index was a good proxy for total grooming time for those years where we could calculate both metrices, and in fact these were highly correlated [$r_p = 0.84$, $p < 0.0001$]. We then repeated the same analyses described above with total grooming time to check that the results held. In fact, as for the grooming index, the including of *friendship category* improved model fit [$\chi^2 = 28.02$, df = 2, $p < 0.001$]; pairwise comparisons showed that chimpanzees had more grooming with mutual compared to both one-sided [$p < 0.005$] and non-friends [$p < 0.001$]. There was a trend for the inclusion of subject's *age* to further improve model fit [$\chi^2 = 3.56$, df = 1, $p = 0.059$]; older chimpanzees exhibited slightly longer grooming durations. However, as with the analysis of grooming index, there was no improvement by including the interaction between *age and friendship* category [$\chi^2 = 1.10$, df = 2, $p > 0.57$, n.s.]. Overall, this analysis therefore largely confirmed the results from the grooming index.

As an additional check, we then examined grooming given and grooming received separately to assess if these above patterns were driven more by the behavior of the subject versus the partner. This analysis followed the procedure as for grooming index and grooming time, here using the full-day focal data where directionality of the grooming could be assessed with more accuracy, using durations instead of scan data. For grooming given, inclusion of *friendship category* improved model fit [$\chi^2 = 24.38$, df = 2, $p < 0.0001$], with more grooming given to mutual friends than either one-sided or non-friends. However, neither the inclusion of *age* [$\chi^2 = 0.002$, df = 1, $p > 0.96$, n.s.] nor the *age X friendship category* interaction [$\chi^2 = 1.33$, df = 3, $p > 0.72$, n.s.] further improved fit. For grooming received, we found similar patterns. The inclusion of *friendship category* improved model fit [$\chi^2 = 24.57$, df = 2, $p < 0.0001$], with more grooming received from mutual friends than either one-sided or non-friends. Here, the inclusion of *age* did improve fit [$\chi^2 = 9.24$, df = 1, $p < 0.005$]: older males received more grooming overall. As with the prior analyses, however, the *age X friendship* interaction did not improve fit [$\chi^2 = 1.33$, df = 2, $p > 0.51$, n.s.].

Finally, we were also able to calculate the average duration (in minutes) of grooming bouts between each dyad using the full-day focal data. A grooming bout was defined as continuous 1-minute scans involving the same two individuals that is not interrupted by another behavior by the focal or another individual involved in the grooming. We used the same analysis approach for grooming index and grooming time and found largely similar results: the inclusion of *friendship category* improved model fit [$\chi^2 = 25.03$, df = 2, $p < 0.0001$; see Table S3 for parameters from this best-fit model], with longer grooming bouts between mutual friends than either one-sided [$p < 0.05$] or non-friends [$p < 0.0001$]. As with most of the above analyses, neither the focal's *age* [$\chi^2 = 0.05$, df = 1, $p > 0.82$] nor the *age X friendship* interaction further improved fit compared to the second model with only friendship categories [$\chi^2 = 0.92$, df = 3, $p > 0.82$, n.s.]. Overall, then, all of these metrics indicate that males groomed more with their mutual friends across several relevant operationalizations of grooming investment.

Dyadic metrics of grooming equitability

From 2009 using the full-day focal data, we also examined how equitably grooming was divided between the individuals within each dyad, both over the course of a grooming bout and over the course of a year. To calculate bout equitability, we followed prior work on equitability in chimpanzee social bonds (*40*) and used the following formula:

$$Bout\ Equitability_{ab} = 1 - \left| \frac{Grooming_{A\ to\ B}}{Total\ Grooming_{AB}} - \frac{Grooming_{B\ to\ A}}{Total\ Grooming_{AB}} \right|$$

Here $Grooming_{A\ to\ B}$ is the number of minutes within a bout of grooming given by A to B, $Grooming_{B\ to\ A}$ is the number of minutes within a bout of grooming given by B to A and $Total\ Grooming_{AB}$ is the total number of minutes of grooming within a bout between A and B. In this measure, an index of 1 therefore indicates complete equitability and 0 indicates that one individual engaged in all of the grooming. This was averaged across all grooming bouts between a dyad in a given year. To calculate a yearly equitable index, we used the same basic formula as above, but used the sum of grooming given and received between a dyad over the course of a whole year. For both the bout equitability and year equitability indices, we only included unidirectional grooming and did not include instances of mutual grooming.

We analyzed these metrics of grooming equitability using the same procedure described above for our metrices of grooming investment, and found largely similar results. In general, the main predictor for how equitable grooming was distributed was friendship category. For bout equitability, the inclusion of *friendship category* improved model fit [$\chi^2 = 38.23$, df = 2, $p < 0.0001$; see Table S3 for parameters from this best-fit model], with more equitable grooming bouts between mutual friends than either one-sided [$p < 0.05$] or non-friends [$p < 0.0001$]. However, the inclusion of neither *age* [$\chi^2 = 1.04$, df = 1, $p > 0.30$, n.s.] nor the *age X friendship interaction* improved fit [$\chi^2 = 1.60$, df = 3, $p > 0.65$, n.s.] compared to the second model. For year equitability, the inclusion of *friendship category* improved model fit [$\chi^2 = 58.13$, df = 2, $p < 0.0001$; see Table S3 for parameters from this best-fit model], with more equitable long-term grooming between mutual friends than either one-sided [$p < 0.05$] or non-friends [$p < 0.0001$]. There was a trend for the inclusion of *age* to improve fit [$\chi^2 = 2.74$, df = 1, $p = 0.098$], but the *age X friendship* interaction did not [$\chi^2 = 0.07$, df = 2, $p > 0.96$, n.s.]. Overall, these metrics all indicate that males across the lifespan show more equitable patterns of grooming specifically with their mutual friends.

Overall level of individuals' sociality

We next addressed whether older males showed changes in their overall degree of sociality. To do so, we examined several metrics of their social behavior. First, we examined how often a given male was observed completely alone versus in a party. For each male in every year, we summed the number of 15-min scans that individuals were alone (with no other individuals) versus present with at least one other individual. Note that since individual chimpanzees are harder to track in the forest compared to louder and more visible groups, the amount of time an individual is observed alone is likely an underestimate of their actual alone time. Next, we examined the number of scans where they were present with at least one other individual who was an adult male, versus the number of scans that they were in a party without other males. Finally, we examined the number of scans where males were present in a party with an adult male and were within 5 meters proximity, versus were not within 5 meters, versus the number of scans that they were in a party with at least one other adult male. Note that each of these metrics (scans alone versus in a party; scans in a party with or without another adult male present; and scans in a party with adult males who are or are not within 5-meters) are therefore independent, distinct measures of sociality.

To analyze each of these dependent variables, we used GLMMs with a binomial function (logit link). The base model for each metric accounted for *subject identity* (as a random factor), *year* (as a random factor, to account for how annual changes in the environment might affect ranging and grouping patterns), subject's *rank category* (as an ordinal factor; high, medium, or low), and the total *number of adult males* in the group as a linear predictor. The full model then added the individual's *age* as a linear predictor. We found that including age improved model fit for scans alone versus in a party [$\chi^2 = 4.51$, df = 1, $p < 0.05$]: this metric increased with age and decreased with rank (see Figure S2, and Table S4 for parameters from the full model). Age also improved model fit for the comparisons of scans where the subject is in a party with other males, versus no other males [$\chi^2 = 15.73$, df = 1, $p < 0.0001$]: presence with other males increased with both older age and higher rank. Finally, inclusion of age improved model fit for likelihood of being in close proximity of another male within such parties [$\chi^2 = 18.02$, df = 1, $p < 0.0001$]; both age and rank were again significant positive predictors.

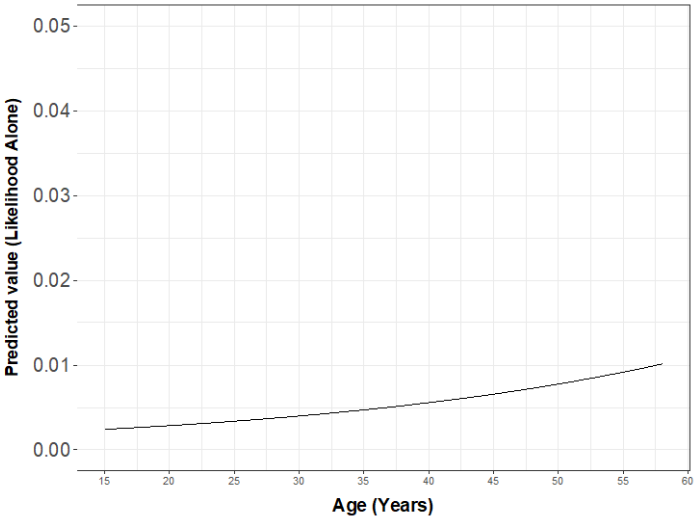

Figure S2: Lifespan changes in solitary behavior. Males could be observed either by themselves or in a social party with other individuals. While males are rarely observed alone overall, these observations increased with age. Ribbons indicate 95% confidence interval estimates from models.

We also calculated the average number of other males within a party, when the focal was in a party with at least one other male (see Figure S3). To analyze this, we used linear mixed models. Similar to the binomial GLMMs described above, the base model accounted for *subject* (as a random factor), *year* (as a random factor), subject's *rank category*, and included the total *number of adult males* in the group (as an offset; implemented as log value). We also controlled for the average number of *females with a sexual swelling* in a party, as such females tend to attract adult males to join the party (*23*). Including age improved model fit [$\chi^2 = 19.50$, df = 1, $p < 0.0001$]; in the full model only age [*estimate* = 0.016, *SE* = 0.003, $t = 5.455$, $p < 0.0001$] and swollen female party size [*estimate* = 1.291, *SE* = 0.129, $t = 9.988$, $p < 0.0001$] were significant predictors.

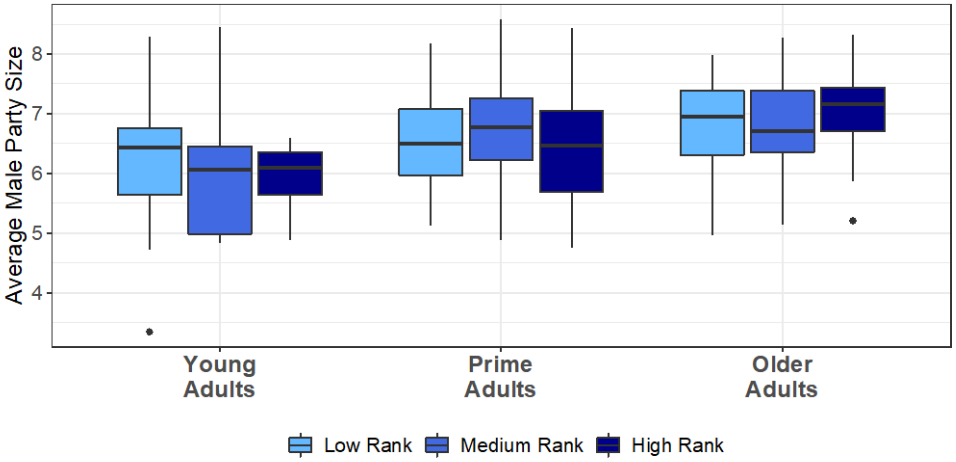

Figure S3: Lifespan changes in average party size. Boxplots cluster data by age cohort and rank category; line indicates group median; whiskers reflect inter-quartile range; dots indicate outliers.

	Being alone versus in a party with others	**Party with adult males versus without**	**Within 5m of an adult male versus not**
Total Adult Males (linear predictor)	$Est. = 0.115$ $SE = 0.123$ $Z = 0.934$ $p > 0.35$, n.s.	$Est. = -0.015$ $SE = 0.145$ $Z = -0.102$ $p > 0.91$, n.s.	$Est. = -0.061$ $SE = 0.072$ $Z = -0.845$ $p > 0.39$. n.s.
Rank Category (Linear effect)	$Est. = -0.487$ $SE = 0.032$ $Z = -15.408$ **$p < 0.0001$**	$Est. = 0.333$ $SE = 0.016$ $Z = 20.202$ **$p < 0.0001$**	$Est. = 0.258$ $SE = 0.026$ $Z = 10.059$ **$p < 0.0001$**
Rank Category (Quadratic effect)	$Est. = -0.413$ $SE = 0.024$ $Z = -17.394$ **$p < 0.0001$**	$Est. = -0.011$ $\mathrm{SE} = 0.012$ $\mathrm{Z} = -0.888$ $p > 0.37$, n.s.	$Est. = 0.034$ $SE = 0.020$ $Z = 1.762$ $p = 0.078$
Age in years (linear predictor)	$Est. = 0.033$ $SE = 0.016$ $Z = 2.146$ **$p < 0.05$**	$Est. = 0.040$ $SE = 0.008$ $Z = 5.259$ **$p < 0.0001$**	$\mathrm{Est.} = 0.016$ $SE = 0.003$ $Z = 5.433$ **$p < 0.0001$**

Table S4: Predictors for patterns of male sociality. Parameters from the full models examining scans of individuals alone versus in a party; in a party with or without other males; and scans where the subject was in a party with other males but were physically near another adult male or not.

Individual rates of positive versus negative social interactions

We finally examined changes in individuals' overall rates of affiliative (positive) behaviors versus agonistic (negative) behaviors across the lifespan**.** Unlike humans, several other primates (including several macaque species, capuchins, and lemurs) exhibit a pattern characteristic of a negativity bias during aging characterized by declines in affiliation but steady rates of aggression, as well as exhibit a cognitive negative bias by focusing more on negative socioemotional stimuli compared to neutral or positive stimuli (*26-31*). Here we tested if the same patterns are observed in chimpanzees.

To index positive social interactions, we looked at overall rates of grooming. Grooming is recorded as part of the focal behavioral data collection. When it is observed, the direction of the grooming is noted (is the focal grooming, being groomed or involved in simultaneous mutual grooming) along with the identity or identities of other individuals involved in grooming. If an individual is involved in chain grooming, such that chimpanzee A is grooming B and B is grooming C, then if the focal individual is B, we could count this as two separate dyadic grooming bouts between A and B and B and C. If the focal individual is A, then we would only consider the grooming bout between A and B. For aggression, all occurrence aggression is recorded by the field assistants as it happens. The identities of the aggressor and victim are recorded along with the action of the aggressor, the response of the victim and the duration. Chimpanzee aggression can be characterized as directed if the aggression is towards a particular victim and includes all chases, charges, stationary threats and attacks. However, aggression in the form of dominance displays which have no victim can be categorized as non-directed. To be certain that we were capturing aggression, we only included non-vocal displays and excluded vocal displays. Vocal displays are often given in response to distant calls and rarely escalate to higher levels of aggression unlike non-vocal displays.

For each male in each year, we calculated individual rates of both *directed aggression* and *non-directed aggression* by counting the number of either directed or non-directed aggressive events divided by the number of in view hours of observation (based on 15-minute scan data) for each individual. For the aggression given, we calculated a rate of directed or non-directed aggression by taking the number of events of either type of aggression and then dividing that by total observation time for the year. To assess individual changes in *grooming*, we calculated yearly rates of grooming given and received for each male. For 1995 to August 2009, we used the ten-minute focal data and calculated the proportion of total ten-minute focal scans that a focal male was giving or receiving grooming to or from another adult male. From August 2009 to 2016, we used the full-day focal data and calculated the proportion of total in view observation minutes that a focal male was giving or receiving grooming to or from another adult male. For 2009, we averaged the ten-minute focal index and the full-day focal index.

To analyze these different components of social behavior, we first directly compared rates of grooming, directed aggression, and non-directed aggression using linear mixed models. The base model accounted for *subject identity* (as a random factor), *year* (as a random factor), subject's *rank category* (as an ordinal factor; high, medium, or low), the *total number of adult males* in the group (as a linear predictor), the *number of days of observation* (to account for any variation in observation effort across individuals), and the *behavioral category* (grooming, directed aggression, or non-directed aggression). The second model then added *age* (as a linear predictor), and the full model then added the interaction between *age and behavioral category* to test whether negative behaviors and positive behaviors showed different age-related effects. We found that including both *age* [$\chi^2 = 7.33$, df = 1, $p < 0.01$] and the *age X behavior category* interaction [$\chi^2 = 69.09$, df = 2, $p < 0.0001$] improved model fit (see Table S5 for parameters from the full model). Post-hoc comparisons of age slopes using the *emtrends* function showed that both forms of aggression declined more with age than grooming with age [$p < 0.001$ in both cases], and further that non-directed aggression declined more than directed aggression with a target [$p < 0.005$].

	Estimate	***SE***	***t***	***p***
Days of Observation (linear predictor)	0.0001	0.0001	1.127	> 0.26
Total Adult Males (linear predictor)	-0.0001	0.004	-0.031	> 0.97
Rank Category (Linear effect)	0.016	0.006	2.806	**= 0.005**
Rank Category (Quadratic effect)	0.004	0.004	0.979	> 0.32
Age in years (linear predictor)	0.0006	0.0005	1.341	> 0.18
Directed aggression (reference = grooming)	0.088	0.015	5.727	**< 0.0001**
Non-directed aggression (reference = grooming)	0.165	0.015	10.724	**< 0.0001**
Age X Directed Aggression	-0.002	0.0005	-4.530	**< 0.0001**
Age X Non-Directed Aggression	-0.004	0.0005	-8.601	**< 0.0001**

Table S5: Predictors for rates of positive versus negative behaviors. Observations of grooming (affiliative behavior), directed aggression (agonistic behavior with a target), and non-directed aggression (agonistic behavior without a specific target). Number of *adult males*, *rank category*, and *behavioral category* were included in the base model; *age* and the *age X behavioral category* interaction were added to subsequent models to test their importance.

We also examined each of these behavioral metrics separately to confirm that these patterns held, since our manner of integrating grooming and aggression as rates to directly compare them involved combining data of somewhat different natures. For example, grooming rates are a true rate of behavior out of all observation time. Indeed, grooming bouts can last several minutes to even hours. In contrast, aggression tends to be fleeting or instantaneous events and therefore were calculated as a rate by dividing number of scans with aggression by number of total scans. The analysis approach for each of these metrics separately (grooming given, all aggression given, directed aggression given, and non-directed aggression given) paralleled the combined analysis: the base model for each metric accounted for *subject* (as a random factor), *year* (as a random factor), subject's *rank category* (as an ordinal factor; high, medium, or low), the *total number of adult males* (as a linear predictor), and the *number of days of observation* (to account for any variation in observation effort across different individuals). The full model then added *age* (as a linear predictor). For grooming given, we found that inclusion of age did not improve model fit [$\chi^2 = 1.51$, df = 1, $p > 0.21$, n.s.], again showing that grooming rates remain fairly consistent across the lifespan. In contrast, inclusion of age improved model fit for both all aggression given (combined rate of directed and non-directed aggression [$\chi^2 = 4.21$ df = 1, $p < 0.05$]) as well as directed aggression separately [$\chi^2 = 5.42$ df = 1, $p < 0.05$], showing a decline in behavioral rate with increasing age in both cases. Non-directed aggression did not [$\chi^2 = 1.16$, df = 1, $p > 0.28$, n.s.], possibly due to covariation with days of observation for this metric, as age trended to improve fit when observation days were removed [$\chi^2 = 3.75$, df = 1, $p = 0.053$]. Overall, these analyses of the behavioral metrics separately generally align with the results from the combined analysis.

We finally examined grooming received and directed aggression received to test whether older males were more often the targets of these behaviors (note that non-directed aggression by definition has no target). These analysis procedures were identical for those described above. For grooming received, we found that inclusion of *age* did not improve model fit [$\chi^2 = 0.21$, df = 1, $p > 0.64$, n.s.], again showing that grooming rates remain fairly consistent across the lifespan. In contrast, inclusion of age improved model fit for directed aggression received [$\chi^2 = 8.68$, df = 1, $p < 0.005$], showing a decline with increasing age similar to that seen for aggression given.

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