Within-individual changes reveal increasing social selectivity with age in rhesus macaques

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Accumulating evidence in humans and other mammals suggests older individuals tend to have smaller social networks. Uncovering the cause of these declines can inform how changes in social relationships with age affect health and fitness in later life. While age-based declines in social networks have been thought to be detrimental, physical and physiological limitations associated with age may lead older individuals to adjust their social behavior and be more selective in partner choice. Greater selectivity with age has been shown in humans, but the extent to which this phenomenon occurs across the animal kingdom remains an open question. Using longitudinal data from a population of rhesus macaques on Cayo Santiago, we provide compelling evidence in a nonhuman animal for within-individual increases in social selectivity with age. Our analyses revealed that adult female macaques actively reduced the size of their networks as they aged and focused on partners previously linked to fitness benefits, including kin and partners to whom they were strongly and consistently connected earlier in life. Females spent similar amounts of time socializing as they aged, suggesting that network shrinkage does not result from lack of motivation or ability to engage, nor was this narrowing driven by the deaths of social partners. Furthermore, females remained attractive companions and were not isolated by withdrawal of social partners. Taken together, our results provide rare empirical evidence for social selectivity in nonhumans, suggesting that patterns of increasing selectivity with age may be deeply rooted in primate evolution.

aging | mammals | selectivity | social behavior | senescence

Social relationships change in quality and quantity across the lifespan (1, 2), a phenomenon that has been referred to as "social aging" (3, 4). Older people have commonly been observed to engage in less social activity and to have smaller social networks (1). Given the established health benefits of social integration (5, 6), this decline in network size with age has led to an increasing concern of an "epidemic" of social isolation among the elderly (7). However, research over the past several decades has suggested that reduced social network size may not simply be the result of unfavorable conditions in old age, such as increased frailty and reduced social competence (8). Instead, individuals may actively adjust their social decisions as they age to cope with new challenges in later life or take advantage of new opportunities (9).

In humans, aging individuals have been shown to become more selective in partner choice as they age and to proactively focus on meaningful relationships, such as close friends and relatives (10, 11). Intriguingly, social selectivity in older individuals may not be limited to humans. Several species of nonhuman primates have been suggested to show patterns of social aging that might indicate greater selectivity in social partners in later life (3, 4, 12, 13). Evidence for social selectivity in some of our closest living relatives could hint at deep evolutionary origins behind this phenomenon and may suggest that selectivity is an adaptive strategy that individuals use to cope with the physical and physiological limitations they face as they age.

Fundamentally, social selectivity is driven by within-individual changes in behavior with age. However, to date, most nonhuman studies have been cross-sectional in nature. That is, they have shown older animals differ from younger ones, but have either not had the longitudinal data needed to track changes within aging individuals or have not disentangled within-individual changes due to age from between-individual differences that might instead result from differences among cohorts or processes like selective disappearance (14, 15). For instance, if more social individuals are more likely to die because of increased exposure to disease or increased levels of competition, then an apparent age-related "decline" in sociality might appear at the population level without necessitating any within-individual change. Disentangling these mechanisms is a challenge that has long been recognized in other studies of senescence (14), but has received little attention in

Significance

The narrowing of social networks and prioritization of meaningful relationships with age is commonly observed in humans. Determining whether social selectivity is exhibited by other animals remains critical to furthering our understanding of the evolution of late-life changes in sociality. Here, we test key predictions from the social selectivity hypothesis and demonstrate that female rhesus macaques show within-individual changes in sociality with age that resemble the human social aging phenotype. Our use of longitudinal data to track how individuals change their social behavior within their lifetimes offers the most conclusive evidence to date that social selectivity is not a phenomenon unique to humans and therefore might have deeper evolutionary underpinnings.

the social aging literature (see 16 for a nice example of disentangling mechanisms of social aging). Studies of social selectivity that are unable to separate within- from between-individual effects therefore cannot conclusively demonstrate that selectivity is driving the observed age-related patterns.

In addition to being necessarily driven by changes within aging individuals, the social selectivity hypothesis implies that individuals proactively narrow their networks with age. It is, therefore, important to rule out alternative explanations for age-based reductions in sociality. For example, declines in social engagement might be driven by loss of social interest, motivation, or physical ability to engage (9). Alternatively, older individuals might be perceived as less valuable partners (e.g., due to declines in social status; 17, 18), resulting in reductions in network size as a result of withdrawal of social partners. Apparent preferences for related individuals with age might also reflect demographic changes and the loss of familiar, unrelated partners (such as age mates) due to mortality (19). Some progress has been made in generating evidence in favor of the occurrence of active social selectivity in nonhumans (see refs. 3, 4, 12 and 13 for examples), but differentiating between these alternative explanations necessitates a clear set of predictions for what we would expect to see if social selectivity were actively occurring as an individual ages and the data to test these predictions.

In this study, we used within-individual data from a longitudinal study of highly social rhesus macaques (*Macaca mulatta*) to explore two nonmutually exclusive explanations for changes in sociality with age: 1) within-individual selectivity with age and 2) selective disappearance. To explore whether social aging was driven by increasing selectivity in partner choice with age, we tested four main behavioral predictions we derived from the social selectivity hypothesis. Prediction 1: social networks will narrow as an individual ages, that is, individuals will interact with fewer social partners as they get older. Prediction 2: this narrowing will be driven by the aging individual in question rather than by the withdrawal (Prediction 2a) or death (Prediction 2b) of their social partners. Prediction 3: the aging individual will remain actively engaged with others. This prediction is intended to disentangle social selectivity from a narrowing of networks that might result from the loss of interest, motivation, or physical ability to engage socially. Prediction 4: older individuals will focus their social effort on important partners, including kin (Prediction 4a), strong partners (Prediction 4b), and stable partners (Prediction 4c). In the biogerontology literature, "important" relationships have typically been viewed as family and close friends because they are the most emotionally salient relationships (20). Increased focus on kin, strongly connected partners, and stable partners with age might also make sense from an evolutionary perspective since these are partners that commonly provide important direct and indirect fitness benefits (21–23). Finally, regarding our second hypothesis, we explored the possibility that variation in sociality with age was not driven by within-individual changes in behavior but instead by population-level trends. Specifically, we tested whether age-based differences in sociality might emerge as a consequence of the selective disappearance of more or less social individuals.

We tested these two alternative explanations using a long-term dataset spanning 8 years and 204 individuals. We collected two different types of social interaction data—grooming interactions and spatial proximity—which we used in our analyses as measures of social connectedness, in line with many other studies on Cercopithecine primates (21, 24–27). Our subjects were mature adult females aged 10–28 (mean age = 14.3) from six naturally formed mixed-sex social groups from the well-studied population living on the island of Cayo Santiago. For the 204 females that we monitored between 2010 and 2017, we had on average 2.8 y of data per individual with a range of 1–8 y (Fig. 1 *A–C*). We chose females who were 10–28 y old because we were specifically interested in looking at age-based changes in social behavior from prime adulthood onward. At 6 y, old females are deemed adults (28), and analyses from the Cayo Santiago population have shown that the median lifespan for females that survive to reproductive age is 18 y, with a maximum lifespan of about 30 y (29, 30). After reaching sexual maturity (~ age 6), female macaques on Cayo Santiago experience a steady increase in their probability of death (29). In addition to this increased risk of mortality, individuals aged 10 and beyond also exhibit extensive evidence of aging in activity, body mass index and body composition (31–33), prevalence of macular degeneration (34), bone mass (35), inflammation (36), and reproductive output (31), among other traits. It is, therefore, clear that females within the age limits of our sample exhibit marked age-dependent decreases across a wide range of systems and tissues. Given this clear evidence of aging in females ten and older, and because we were specifically interested in within-individual changes in behavior, we looked at how all females in our dataset adjusted their social behavior as they got older, regardless of what age those females entered the dataset or their age at last observation (see Fig. 1*A* for a distribution of age ranges over which each female was observed). Females with one data point could not contribute to this within-individual analysis but did contribute to the cross-sectional component of the analysis (see below).

To test whether patterns of social aging were driven by changes in behavior within an individual as they grew older (in line with social selectivity), or by selective disappearance, we used a within-individual centering approach (15). Studies of aging commonly distinguish between senescence and selective disappearance by including age and longevity in the same model (37). However, when some or all individuals are still alive in a dataset (as was the case with our data), then another (functionally equivalent) approach is needed (15, 38). We provide details of this approach in the *Methods* but briefly, within-individual centering can be used when lifespan is not known for all subjects and there is natural variation in the range of a given predictor variable (x) over which individuals are sampled (15). In this study, there was variation in the age ranges over which we had behavioral data for each female macaque. For example, we might have data from one female between the ages of 12 and 19, while for another female, we have data from 20 to 27 (see Fig. 1*A*). The inclusion of random intercepts in mixed models is useful in many circumstances, including helping to account for between-subject variation in the response variable y (i.e., a given metric of social behavior). However, under other circumstances, random intercepts alone are not always sufficient and, depending on the structure of the data, may not fully account for between-subject variation in x (i.e., age). Thus, in cases where there is individual variation in the x variable, an association between x and y might be driven by a within-subject effect of x on y (individuals change their social behavior as they age; i.e., in line with social selectivity) or by a between-subject effect of x on y (individuals with high average age also have high average sociality; i.e., selective disappearance; (15)).

To distinguish between these two alternative explanations, we fitted models where we separated age into two terms: the between-subject effect was obtained by taking the average age of each subject (called "average age" in the models) and the within-subject effect was calculated by subtracting average age from each age at which the individual was observed (called "within-individual age" in the models; see Fig. 1*D*). This "within-individual age" term therefore represents how an individual's deviation from
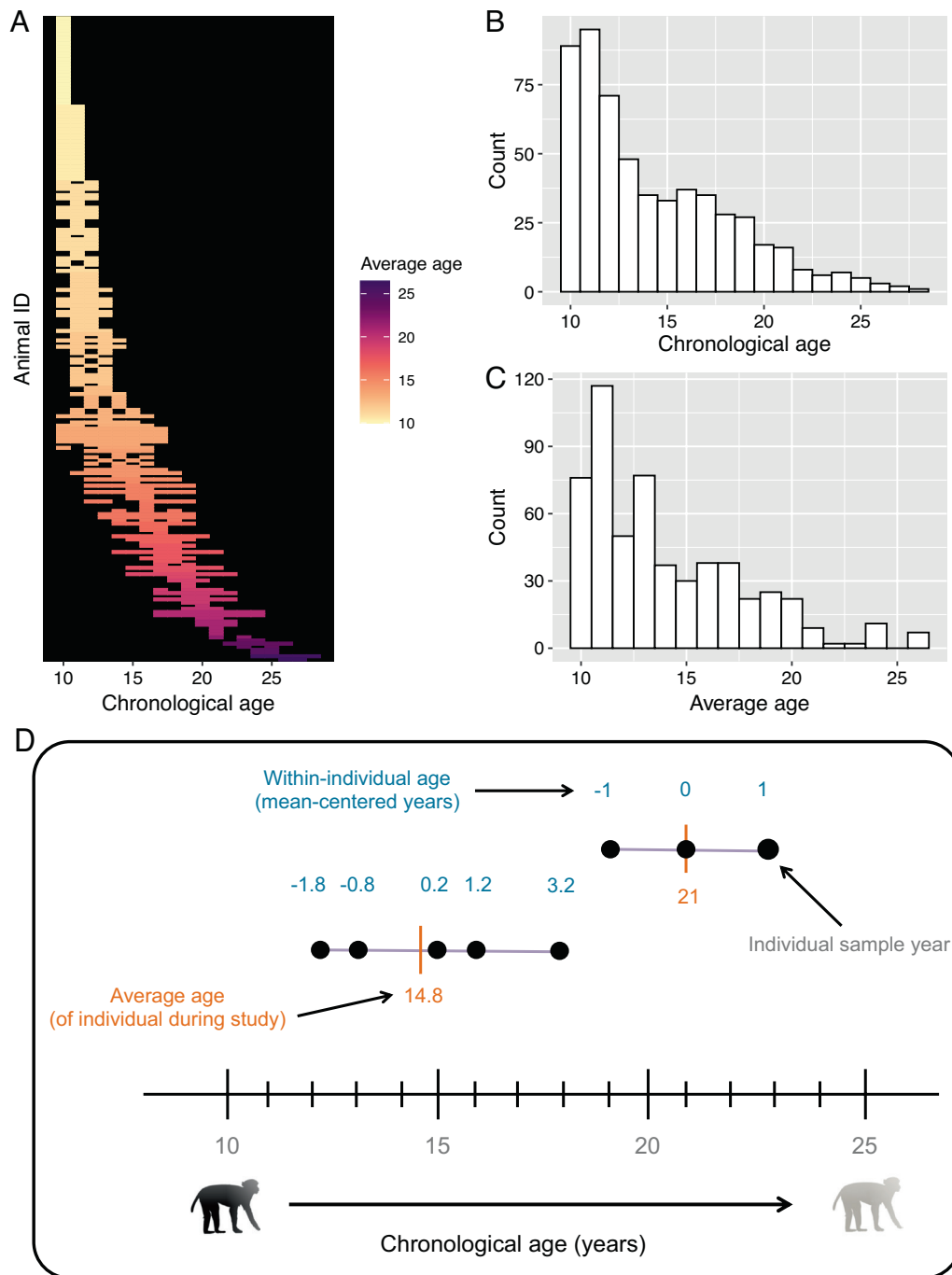
Fig. 1. (*A*) Heat map showing age ranges over which each individual was sampled. Each row represents one individual. (*B* and *C*) Histogram showing the number of individuals in each age (*B*) and average age (*C*) class. (*D*) Schematic showing how average age and within-individual age were computed for each subject.

its mean age affects its behavior, while the "average age" term reflects whether individuals who are on average older differ in their behavior from those who are on average younger (providing a cross-sectional comparison; (15)). Selective disappearance can then be tested for by assessing whether the "within-individual age" and "average age" terms differ significantly from one another (15, 38). In cases where these terms do not differ, it suggests that any between-individual differences in sociality are driven exclusively by within-individual changes in social behavior.

Additionally, because female rhesus macaques have a strict dominance hierarchy whereby daughters occupy ranks immediately below their mother (39), we tested for an interaction between rank and within-individual age in all of our models to assess whether

social status affected how individuals changed their social behavior as they aged (19, 40). Below, we only report this interaction term where it was significant. Finally, we fitted within-individual age as a random slope term over individual ID in all models to assess whether there was between-individual variation in how females changed their social behavior with age. Given the variation in age ranges across which individuals were sampled, we might expect that individuals who were on average older might exhibit more rapid changes in sociality with age. We present all effect sizes below by describing the expected within-individual change in social behavior over the study period (8 y) for a mid-ranking individual while holding average age constant at the mean (14.3 y). Our results offered no support for social aging being driven by selective disappearance

but provide evidence in a nonhuman animal that within-individual increases in social selectivity with age can lead to clear differences in sociality between younger and older individuals.

Results

Social Selectivity Hypothesis

Prediction 1: Social networks will narrow with age. Female rhesus macaques showed within-individual declines in their number of social partners with age. On an average, females reduced their number of grooming partners by 44% over an 8-y period (within-individual: β = –0.06; 95% CI = [–0.12, –0.01]; Fig. 2 *A* and *B* and *SI Appendix,* Table S1) and also reduced the number of partners that they spent time in proximity to, although this was modulated by dominance rank (Fig. 2 *C* and *D* and *SI Appendix,* Table S2). Relative to their mean age, low-ranking individuals reduced their number of proximity partners by 47% over an 8-y period, while high-ranking individuals only reduced their number of proximity partners by 8% (within-individual age: rankL: β = –0.07; 95% CI = [–0.13, –0.01]). We also found between-individual differences in number of social partners, where individuals who were on average older had fewer grooming (average age: β = –0.04; 95% CI = [–0.06, –0.02]; Fig. 2*B* and *SI Appendix,* Table S1) and proximity (average age: β = –0.03; 95% CI = [–0.04, –0.01]; Fig. 2*D* and *SI Appendix,* Table S2) partners than did younger individuals.

Prediction 2: Narrowing of social networks will be driven by the aging individual. Prediction 2a. Female macaques showed a within-individual decrease in the number of partners that they approached with age, which was modulated by rank (Fig. 3 *A* and *B* and *SI Appendix,* Table S3). Relative to their mean age, low-ranking individuals reduced the number of individuals they approached by 51% over an 8-y period, while high-ranking individuals reduced the number of individuals they approached by 15% (within-individual age: rankL: β = –0.08; 95% CI = [–0.14, –0.01]). However, females continued to be approached by similar numbers of partners as they aged regardless of rank (within-individual age: β = –0.02; 95% CI = [–0.07, 0.02]; Fig. 3 *C* and *D* and *SI Appendix,* Table S4). When comparing between individuals of different average ages, we found that older individuals approached (average age: β = –0.03; 95% CI = [–0.04, –0.01]; Fig. 3*B* and *SI Appendix,* Table S3) and were approached by (average age: β = –0.03; 95% CI = [–0.04, –0.01]; Fig. 3*D* and *SI Appendix,* Table S4) fewer individuals.

Prediction 2b. We also explored the possibility that reductions in the number of partners with age might be driven by demographic changes, that is, by partners dying and not being replaced. Specifically, we asked whether the number of grooming partners and proximity partners in the current year (year t) was predicted by the number of partners that died in the previous year (year t-1). The number of grooming partners in year t was not predicted by
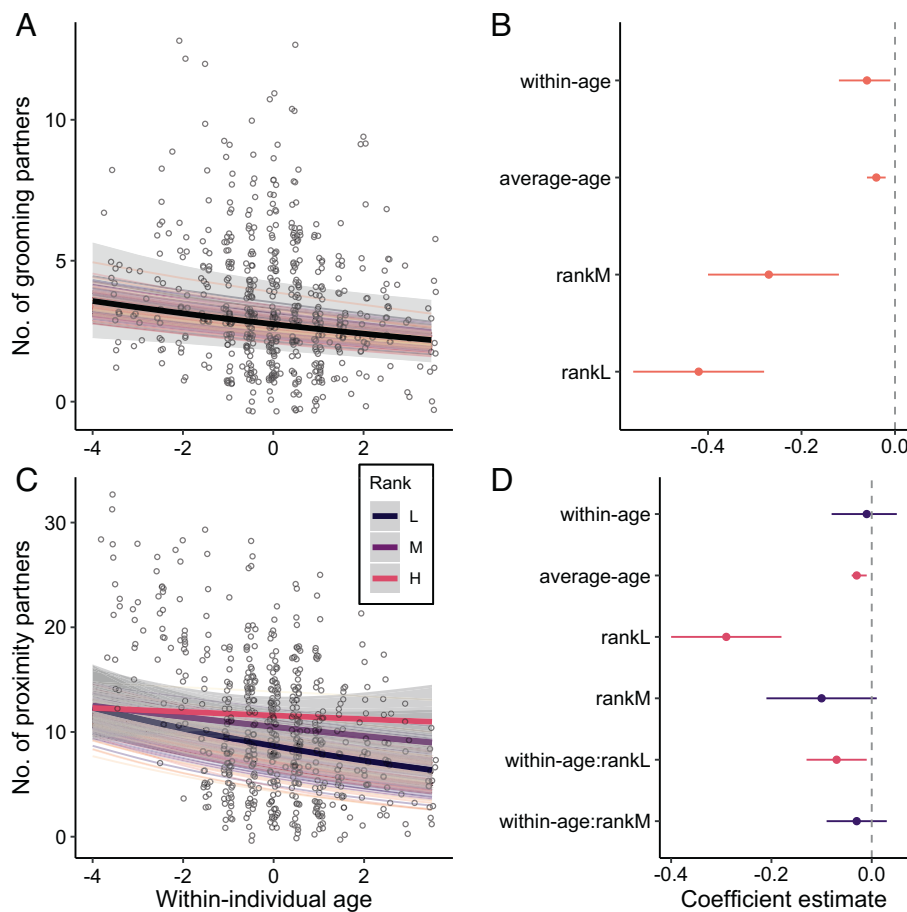

Fig. 2. Narrowing of social networks with age. (*A* and *C*) Females show within-individual declines in the number of (*A*) grooming partners and (*C*) proximity partners with age. Points represent raw data with a small amount of jitter introduced to show overlapping points. The thick solid lines show the average predicted within-individual change (dependent on rank where appropriate). Random slopes are shown using the thin colored lines to illustrate the amount of interindividual variation in a given social aging pattern. Shaded gray bars indicate 95% confidence intervals around the predicted values. (*B* and *D*) Parameter estimates (mean of the posterior distribution) and 95% credible intervals (CI) for all fixed effects for models that test the effect of age on the number of (*B*) grooming partners and (*D*) proximity partners. Instances where the 95% CI overlaps zero are colored in purple.
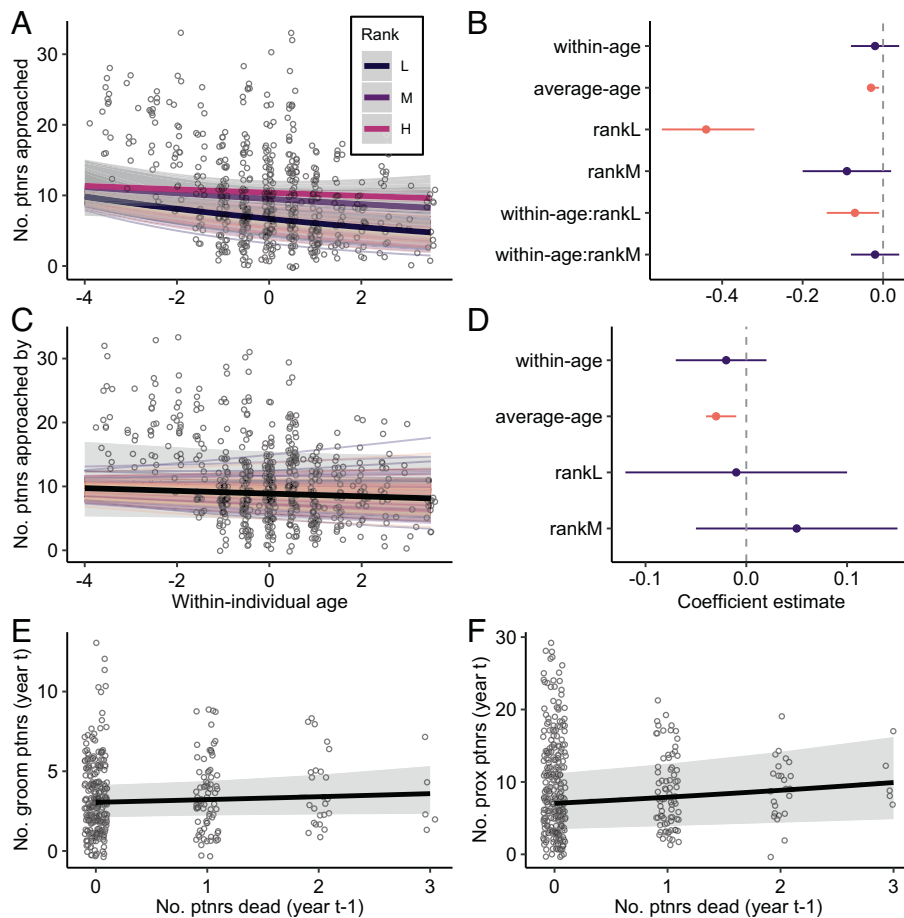
Fig. 3. Network narrowing is driven by the aging individual. (*A* and *C*) Females show (*A*) within-individual declines in the number of partners that they approached, but (*C*) no change in the number of partners that they are approached by with age. Points represent raw data with a small amount of jitter introduced to show overlapping points. The thick solid lines show the average predicted within-individual change (dependent on rank where appropriate). Random slopes are shown using the thin colored lines to illustrate the amount of interindividual variation in a given social aging pattern. Shaded gray bars indicate 95% confidence intervals around the predicted values. (*B* and *D*) Parameter estimates (mean of the posterior distribution) and 95% credible intervals (CI) for all fixed effects for models that test the effect of age on (*B*) number of partners approached and (*D*) number of partners approached by. Instances where the 95% CI overlaps zero are colored in purple. (*E* and *F*) Effect of the number of partners that died in the previous year on number of (*E*) grooming partners and (*F*) proximity partners in the current year. Points represent raw data with a small amount of jitter introduced to show overlapping points. Shaded gray bars indicate 95% confidence intervals around the predicted values.

the number of partner deaths in year t-1 (β = 0.06; 95% CI = [−0.04, 0.15]; Fig. 3*E* and *SI Appendix*, Table S5). The number of partner deaths in year t − 1 had a positive effect on the number of proximity partners in year t (females had more, not fewer, proximity partners in years following the death of their previous partners: β = 0.12; 95% CI = [0.05, 0.18], Fig. 3*F* and *SI Appendix*, Table S6). Therefore, the narrowing of networks with age appears to be driven by within-individual behavioral changes of the aging individual rather than by the deaths of partners or the withdrawal of partners from social interaction.

Prediction 3: Individuals will show continued engagement and interest in the social world as they age. Female macaques continued to give (within-individual age: β = −0.05; 95% CI = [−0.12, 0.03]; Fig. 4 *A* and *B* and *SI Appendix*, Table S7) and receive (within-individual age: β = 0.02; 95% CI = [−0.05, 0.09]; Fig. 4 *C* and *D* and *SI Appendix*, Table S8) similar amounts of grooming regardless of their age. Similarly, females did not show a change in the amount of time they spent in proximity to other individuals with age (within-individual age: β = −0.02; 95% CI = [−0.08, 0.05]; Fig. 4 *E* and *F* and *SI Appendix*, Table S9). Therefore, while females interacted with fewer partners as they aged, they continued to spend similar amounts of time on social behavior, suggesting that they remained motivated and engaged in

the social world. We also found no differences between individuals who were on average younger and those who were on average older in the amount of time spent giving (average age: β = −0.05; 95% CI = [−0.12, 0.03]; Fig. 4*B* and *SI Appendix*, Table S7) or receiving grooming (average age: β = −0.01; 95% CI = [−0.03, 0.01]; Fig. 4*D* and *SI Appendix*, Table S8) or in the amount of time spent in proximity (average age: β = −0.02; 95% CI = [−0.04, 0.00]; Fig. 4*F* and *SI Appendix*, Table S9).

Prediction 4: Individuals will focus on important relationships in later life. Previous research on rhesus macaques has shown that females preferentially form relationships with female kin (41, 42) and that females with strong and stable connections to favored social partners have significantly reduced mortality risk (21). It, therefore, seems likely that a) kin, b) strongly connected partners, and c) stable partners may all be important social relationships that females might strive to maintain in later life. To test whether females focused on important relationships as they aged, we quantified changes in these three types of "important" partners. We assessed first whether a) females increased their proportion of kin partners with age. Second, on a dyadic rather than individual level, we assessed whether, at their last time point in the dataset (i.e., their oldest age), females were more likely to choose partners b) to whom they had previously been strongly connected or c)
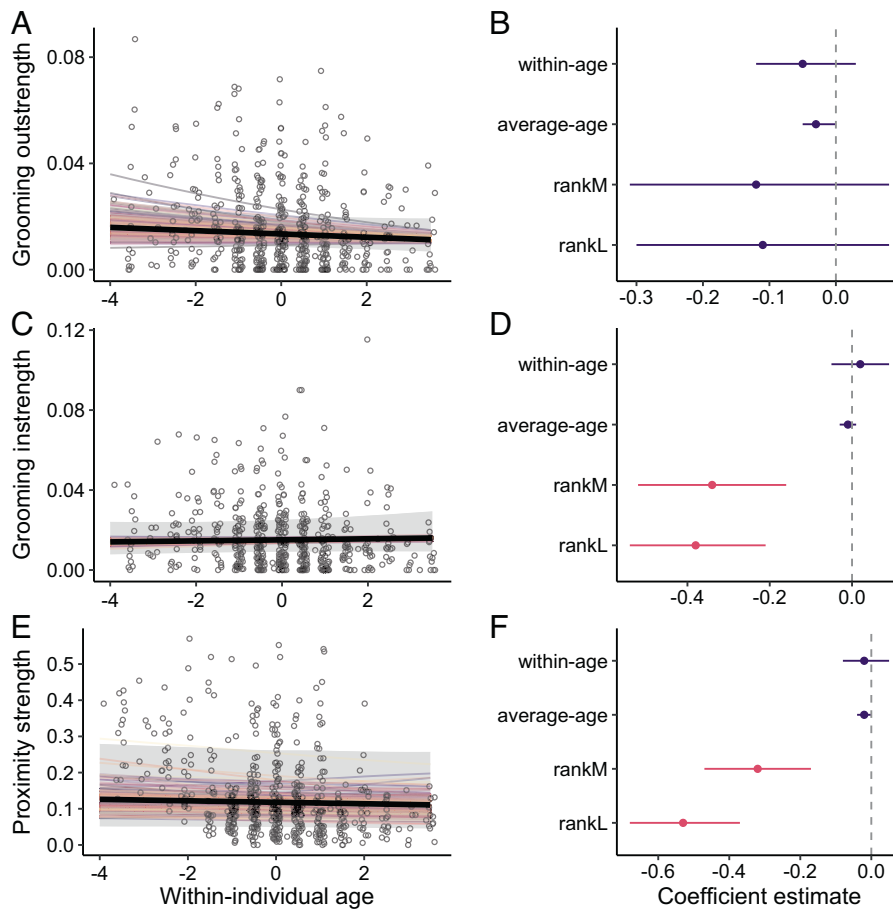
Fig. 4. Individuals show continued engagement and interest in the social world as they age. (*A*, *C*, and *E*) Females show no within-individual change in the amount of time spent (*A*) giving grooming, (*C*) receiving grooming, and (*E*) in proximity to other females as they age. Points represent raw data with a small amount of jitter introduced to show overlapping points. The thick solid lines show the average predicted within-individual change. Random slopes are shown using the thin colored lines to illustrate the amount of interindividual variation in a given social aging pattern. Shaded gray bars indicate 95% confidence intervals around the predicted values. (*B*, *D*, and *F*) Parameter estimates (mean of the posterior distribution) and 95% credible intervals (CI) for all fixed effects for models that test the effect of age on amount of time spent (*B*) giving grooming, (*D*) receiving grooming, and (*F*) in proximity to other females. Instances where the 95% CI overlaps zero are colored in purple.

with whom they previously had stable connections. For all the aforementioned analyses, we calculated social connectedness between a subject and each of their potential partners by combining pairwise grooming duration and spatial proximity into a dyadic sociality index (DSI) (43). DSI represents the relative rate at which a pair of individuals interact relative to the mean rate of interaction for all pairs of subjects in that given group and year. DSI can range from zero to infinity, with zero representing dyads that never interact and higher values representing dyads that spend more time interacting. We also ran these analyses separately for grooming and proximity and returned qualitatively similar results to those reported below (*SI Appendix*, Tables S13–S16 and Figs. S5 and S6).

Prediction 4a. We found that female macaques showed a substantial within-individual increase in their proportion of kin partners with age. Females more than doubled the proportion of kin they interacted with over an 8-y period (120% increase), even when accounting for the increasing availability of kin that occurs as females reproduce and contribute offspring to the group ((30); within-individual age: $\beta = 0.12$; 95% CI = [0.03, 0.19]; Fig. 5 *A* and *B* and *SI Appendix*, Table S10). When comparing between individuals of different average ages, we also found that older individuals had a greater proportion of kin in their social networks than did younger individuals (average age: $\beta = 0.05$; 95% CI = [0.03, 0.08]; Fig. 5*B* and *SI Appendix*, Table S10).

Prediction 4b & 4c. At a dyadic level, female macaques were also twice as likely to be partners with individuals to whom they had been strongly connected earlier in life (i.e., partners with whom they had a high mean DSI) and this effect was strongest in older females (mean DSI*age: $\beta = 0.01$; 95% CI = [0.01, 0.02]; Fig. 5 *C* and *D* and *SI Appendix*, Table S11). In older females, the most strongly connected individuals (those whose mean DSI values were greater than the "average" mean DSI value of 0.87) had on average a 39% chance of being a partner, while more poorly connected individuals (those with a mean DSI value < 0.87) only had on average a 17% chance of being a partner. Similarly, females were more than twice as likely to be partners with individuals with whom they had a stable social relationship earlier in life (i.e., partners with whom they had interacted for at least two consecutive years) ($\beta = 1.54$; 95% CI = [1.31, 1.77]; Fig. 5 *E* and *F* and *SI Appendix*, Table S12). Individuals who were not previously a stable partner had only a 21% chance of being a partner with females compared to individuals who were previously a stable partner and had a 56% chance of being a partner. This relationship was not age dependent; in other words, we found no interaction between partner stability and female age. This result indicates that females are consistently pairing with stable partners regardless of their age and so this emphasis on stable partners may not be a behavior that is unique to older individuals. Regardless, both of these findings suggest that aging females continue to interact with
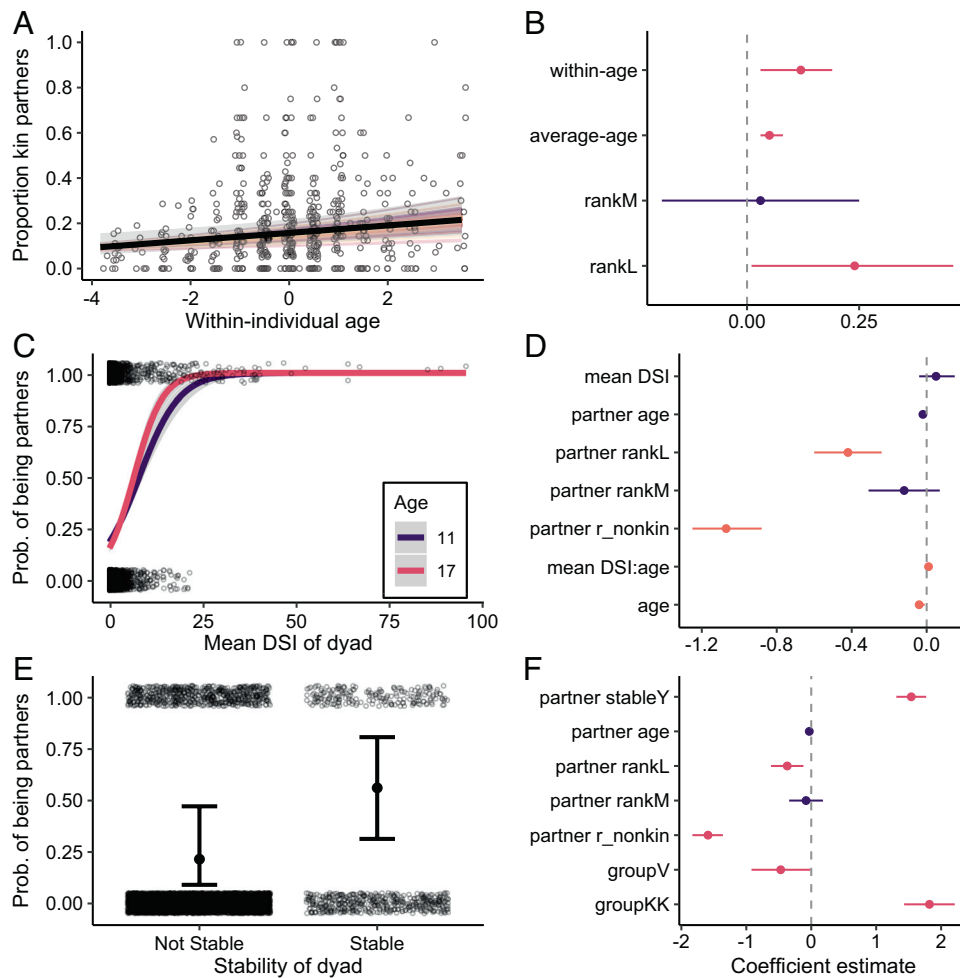
Fig. 5. Individuals focus on important partners later in life. (*A*) Females show a within-individual increase in the proportion of kin partners with age. (*C* and *E*) Average dyadic sociality index (DSI) of a dyad and the stability of dyad positively predict the probability of being chosen as a partner by a female in later life (i.e., at the last point the female was observed in the dataset). Points represent raw data with a small amount of jitter introduced to show overlapping points. Random slopes are shown using the thin colored lines to illustrate the amount of interindividual variation in a given social aging pattern. Shaded gray ribbons and error bars indicate 95% confidence intervals around the predicted values. (*B*, *D*, and *F*) Parameter estimates (mean of the posterior distribution) and 95% credible intervals (CI) for all fixed effects for models that test the effect of (*B*) age on proportion of kin partners, (*D*) mean DSI of a dyad on the probability of being partners with an older female, and (*F*) stability of a dyad on the probability of being partners with an older female. Instances where the 95% CI overlaps zero are colored in purple.

strong and stable partners when narrowing their networks in later life.

Little Evidence of Between-individual Variation in the Rate of Aging. In all the models that included a within-individual age term, we also included within-individual age as a random slope term over individual ID. We found little evidence of between-individual variation in individuals' rate of social aging. In other words, there was little variation between individuals in the slope of the within-individual age term. In all models, the random slope term for individual ID explained between 0.16% and 0.64% of the variance in the model (see *SI Appendix*, Tables S1–S4 and S7–S10 Model A), while the random intercept term explained between 1.7% and 8.4% of the variance in the model. Thus, there was much more variation in an individual's average social behavior than in how they changed their social behavior with age. The lack of variation among individuals in their slopes indicates that individuals change their behavior similarly throughout adulthood. In other words, an individual who ages from 12 to 18 is expected to show the same rate of change in social behavior as an individual who ages from 20 to 28. These findings seem to suggest either that social aging is very relative to the individual in question and is dependent more on biological age than chronological age, and/or that social aging

is not something that happens only to very old individuals but instead is a progressive decline from prime age onward.

Selective Disappearance Hypothesis. The above findings suggest that individuals show both within-individual declines in social behavior with age ("significant" within-individual age term) and between-individual differences in sociality across different ages ("significant" average-age term). To test whether selective disappearance was driving the observed between-individual differences in social behavior, we needed to assess whether the within-individual age and average-age terms differed significantly from one another (15, 38). We did this for all analyses by fitting a new model (Model B) where we replaced within-individual age (i.e., mean-centered age) in the original model (Model A; *SI Appendix* Equation 2) with chronological age (hereafter referred to as "age;" Fig. 1*D*; *SI Appendix* Equation 3; see *Methods* and *SI Appendix* for a more in-depth explanation). Therefore, this new model included both age and average-age as continuous covariates in the model (which is analogous to models which test for selective disappearance by including age and longevity in the same model; 37). If the coefficient of average age in Model B was "significantly" positive (or negative), it would indicate that the differences in

sociality between young and old individuals are not exclusively driven by within-individual changes with age but that individuals with low (or high) levels of the social behavior of interest also selectively disappear from the population, leading to between-individual differences in behavior (15, 36). The 95% credible intervals for the average-age term in Model B always overlapped zero (see *SI Appendix*, Tables S1–S4 and S7–S10 Model B), meaning there was no evidence of selective disappearance driving age-related patterns in any of the models. Instead, the between-individual differences in sociality we observed appear to be driven by within-individual changes in social behavior with age.

Discussion

Increasing selectivity in social relationships is a commonly observed phenomenon in aging humans. Whether this pattern is unique to humans or characterizes other taxa must be addressed to fully understand the evolution of social aging. Here, we explicitly disentangled two nonmutually exclusive explanations for social aging. By taking advantage of an underutilized statistical method, we were able to separate within-individual changes with age, which is a necessary prerequisite for social selectivity, from selective disappearance. In doing so, we show that within-individual changes in behavior across the lifespan can lead to increasing social selectivity in a nonhuman primate.

We tested four key predictions of the social selectivity hypothesis and found that our results supported all of these predictions. We found that as females aged, they reduced the size of their social networks and increased the proportion of kin in their social networks. Older females also prioritized strongly connected and stable partners, both of which have been shown to provide important fitness benefits (21). Females reduced the number of partners they approached as they aged, suggesting that this narrowing was an active decision by the aging individual. Meanwhile, older females remained appealing social partners as they continued to be approached by similar numbers of partners and received similar amounts of grooming. Although not part of our initial predictions, we followed up these results with a post hoc analysis to explore who approaches were directed toward or received from. We found that females at their oldest point in the dataset were more likely to approach and to be approached by kin, strong partners, and stable partners compared to nonkin, weak partners, and unstable partners (*SI Appendix*, Tables S17–S20 and Figs. S7 and S8). We were also able to show that the decline in the number of partners with age was not driven by the deaths of social partners. Despite the reduction in their number of partners as they aged, females remained actively engaged in the social sphere and continued to spend similar amounts of time grooming and in proximity to their social partners.

The distinction between within-individual change and between-individual differences is critical in providing evidence for social selectivity because apparent declines in an individual's network size or in other patterns of sociality can occur in the absence of behavioral changes across an individual's lifetime. Social selectivity is fundamentally a within-individual process. Therefore, demonstrating behavioral changes across the lifespan is necessary evidence for this phenomenon. Some recent work has used longitudinal data to look at age-based selectivity (3); however, demonstrating a relationship between age and social behavior at the population level does not necessarily imply within-individual change. Here, we demonstrate those within-individual changes and show that declines in social behavior across the lifespan can generate differences in sociality among individuals of different average ages, which are not the result of selective disappearance.

While the use of cross-sectional data is an important means to approximate age-related changes in behavior when longitudinal data are not available, such results must be interpreted with caution. Studies that only use cross-sectional data or that cannot distinguish between-individual differences from within-individual changes may conflate social selectivity (i.e., behavioral plasticity) with population-level processes like selective disappearance. Alternatively, such studies might conclude that there is no relationship between the social behavior of interest and age when there are actually two underlying associations of interest that counteract each other (15). Fundamentally, differentiating between within-individual changes in sociality with age and selective disappearance is important because it allows us to demonstrate that social behavior, just like other morphological, physiological, or genomic traits, is a feature that can change across an individual's lifetime. This perspective places sociality squarely within the larger aging phenotype and opens up the possibility of asking how and why these patterns of social aging have evolved and what their consequences are for other aspects of senescence.

The fact that we found that a reduction in the number of partners with age was not driven by the deaths of social partners was somewhat surprising to us given that we know females form strong, stable connections with their favored partners, and so we expected that these deaths should lead to declines in sociality. However, our results suggest that females may actively compensate for this loss. We observed that the more partners that died, the more females increased the number of partners they spent time in proximity to in the following year. It is also possible that the effect of partner loss on social declines may depend on the type of partner lost. Despite clear kin bias, females do frequently form relationships with nonkin (on average 79% of partners are nonkin; i.e., r < 0.125), but these relationships tend to be less stable (on average females only maintain a social relationship with their top nonkin partner for 1.26 y). As such, the loss of less stable nonkin partners (which can make up a large portion of a female's relationships) may have little or no effect on the partners females are choosing the following year.

Despite methodological differences, our results are consistent with many studies on humans and other animals that find older individuals tend to have fewer social partners and to prioritize important relationships (3, 12, 13, 19, 20, 40, 44–46). Our cross-sectional results recapitulate these findings, but also go beyond them by showing that between-individual differences are the consequence of individual changes in behavior with age. Similar to these studies, our findings indicate that nonhuman primates demonstrate patterns of social aging that resemble the human social aging phenotype. While studies in humans have suggested that social selectivity in older adults may arise from an awareness of limited time left in life (10), these findings add to a growing body of evidence suggesting that patterns of selectivity may also be underpinned by other biological pathways. Many mammals face increased constraints and limitations as they age, including physiological changes as well as physical, energetic, and cognitive declines that might limit the capacity for, or alter the costs and benefits of, social interaction (9). Being more selective in partner choice and focusing on important or preferred partners with age might therefore reflect an adaptive response to these constraints. For example, rhesus macaques show declines in their immune function with age (29), which is a common phenomenon in mammals (47). This might select for withdrawal from social interactions to avoid competition and minimize the chance of negative encounters, or a reduction in network size to avoid contracting disease or illness. Similarly, declines in physical mobility or energetic capacity might select for individuals to be more

discerning in which partners they spend their reduced effort and energy on. It is also possible that patterns of social selectivity are governed by much simpler processes, such as the transition from a naïve to an informed state as individuals age. For instance, when individuals are young, they may have to sample many partners to find their preferred ones. As females age, and become more informed about the social environment, they are more likely to continue to interact with those preferred partners. Meanwhile, partners that individuals interact with less are slowly pruned from their social sphere. Such simple mechanisms might produce patterns of selectivity not dissimilar to what we have observed here.

Our findings that some age-related changes in sociality in female rhesus macaques were rank dependent support the possibility that age-based changes in sociality may be an proactive response to senescence. Specifically, lower ranking females decreased the number of partners they sat near and approached more strongly with age. In this population, older low-ranking females are more likely to be injured, which is strongly associated with increased mortality risk (48). Furthermore, low-ranking individuals exhibit greater increases in inflammatory cells with age (36). Thus, it is possible that older low-ranking females reduce their social integration more strongly with age to mitigate injury risk and the associated costs given their immune-compromised state. Old, low-ranking individuals have also been shown to avoid unpredictable social partners (49). This behavior might result from declines in information-processing abilities, potentially as a result of elevated levels of adversity, which renders individuals unable to respond to social cues and adjust their behavior appropriately (49). Stronger declines in sociality with age among lower ranking individuals (40, 50) might therefore be an adaptive response to relatively greater cognitive and physiological constraints with age. It is also possible that lower-ranking individuals may experience more rapid senescence due to greater adversity (6, 51), which might accelerate declines in sociality with age.

Conclusively demonstrating that declines in sociality result from active selectivity with age remains challenging, and not only due to a lack of longitudinal data. Similar declines in sociality with age might occur as physical or mental deterioration inhibits an individual's ability to interact with others or leads to reduced desirability of older individuals as social partners (9). Previous research has worked to disentangle these alternative hypotheses by showing, for instance, that Barbary macaques maintain an interest in vocal and visual social stimuli in later life (12, 52). Similar to our results, some studies have found that, despite interacting with fewer partners in later life, older individuals continue to receive the same or more affiliation from conspecifics, indicating that old individuals remain valuable social partners (12, 13, 30). In other cases, older individuals have been shown to engage in fewer energy-demanding activities (4, 52) or exhibit changes in space use with age (16) alongside reductions in social behavior. This invites the possibility that decreases in affiliation are not a proactive response to aged physiology, but are instead a direct consequence of deteriorating physical condition. Alternatively, social connectedness might be less strongly selected for at older ages, or declines in sociality could occur because enhanced social experience and skill among aged individuals free them from reliance on social capital to successfully navigate their environment (9). Previous research in this system has shown that the fitness benefits of social affiliation are stronger in prime-age females than that in old-age females (30), in support of these possibilities.

Distinguishing between alternative explanations for social aging remains an important avenue for future research. In this study, we derived a clear set of predictions to test the social selectivity hypothesis. This approach increases confidence in the conclusion

that social selectivity underlies the observed age-related declines in sociality in this macaque population and mitigates other potential explanations including reduced energy for social interactions, loss of social interest, reduced social desirability, loss of social partners, or selective disappearance. Nevertheless, future work on social aging will benefit from studies in which longitudinal changes in sociality with age can be measured alongside physical, energetic, and cognitive changes to enable a fuller understanding of whether senescence precedes or follows changes in sociality across the lifespan. Perhaps even more critically, the fitness consequences of social aging will need to be explored to understand the adaptive nature of these changes. Future work should seek to assess age-specific selection on, and genetic architecture of, social traits to provide deeper insights into the evolution of age-dependency in sociality. Our study only investigates changes in same-sex adult relationships. Future research on how relationships with juvenile animals and individuals of the opposite sex change across the lifespan may also deepen our understanding of the processes leading to age-based changes in sociality (9).

Given the well-established role that social integration plays in health and survival (6), understanding how social behavior changes with age and its associated fitness consequences will facilitate a deeper understanding of the mechanisms driving demographic aging under natural conditions. While social senescence is a topic that has been most extensively studied in primates (cf. refs. 16, 53), there are many other group-living animals for whom social relationships are also critical for securing access to resources. As a result, age-related changes in sociality might play a pivotal role in life history tradeoffs between reproductive investment and somatic maintenance, thereby shaping senescence. Thus, there is an increasing need to incorporate social behavior into our broader understanding of the aging process across species if we are to better appreciate the forces shaping intra- and inter-individual variation in patterns of senescence.

Materials and Methods

Study Site and Population. We studied a population of free-ranging rhesus macaques on the island of Cayo Santiago off the southeastern coast of Puerto Rico. The animals are descendants of 409 Indian-origin rhesus macaques that were introduced to the island in the late 1930's. The current population is maintained by the Caribbean Primate Research Centre (CPRC). All animals were food supplemented and provided with ad libitum access to water. There are no predators on the island and there is no regular medical intervention for sick or wounded individuals, thus the major causes of death are illness and injury (54). Demographic data were collected up to 5 d per week by the CPRC staff and there was minimal dispersal from the island, allowing for dates of birth and death for all individuals to be known to within a few days.

We began collecting behavioral data on individuals when they were considered to be "adults" (i.e. ≥age 6), but here we focused on 204 females aged 10 y and older because we were specifically interested in behavioral changes from prime adulthood onward. Previous research on the Cayo Santiago population has shown that the median lifespan for females that survive to reproductive age is 18 y with a maximum lifespan of about 30 y (29, 30). We focused on females that were alive between 2010 and 2017 and for whom we had detailed behavioral data, resulting in 563 macaque years of data, with an average of 2.8 y of data per individual (range: 1–8 y; Fig. 1).

During this period, we collected behavioral data from different study groups in different years (group F 2010–2017; group HH 2014; group KK 2015; group R 2015–2016; group S 2011; group V 2015–2016). We collected behavioral data using 10-min focal animal samples and recorded all behaviors continuously (55). We recorded the duration of grooming behavior along with the identities of the interactants and the direction of grooming. To establish spatial proximity, we conducted three scans at evenly spaced intervals during each focal sample and recorded the identities of all individuals within two meters of (but not in physical

contact with) the study subject. We collected behavioral data between 07:30 and 14:00, and data collection was stratified to ensure equal sampling of individuals throughout the day and over the course of the year.

For the purposes of this study, we included only interactions between adult females. We did not include interactions with males or juveniles of either sex as we wanted to avoid capturing changes in sociosexual behavior with age, and the behavior of juveniles' is commonly influenced by their lack of independence from their mother. We established dominance ranks for all females in a given year by using the direction and outcome of agonistic and submissive interactions (as per (21)(25)). Rank was assigned as "high" (≥80% of other females dominated), "medium" (50 to 79% of other females dominated), or "low" (≤ 49% of other females dominated).

Quantifying Social Metrics

Prediction 1: Social networks will narrow with age. To quantify changes in the size of an individual's social network with age, we explored changes in grooming degree and proximity degree. For each female in a given year, we calculated grooming degree as the number of unique individuals that a female gave grooming to or received grooming from and we calculated proximity degree as the number of unique individuals that a female was observed sitting in proximity to. We predicted to see declines in both grooming and proximity degree with age.

Prediction 2: Narrowing of social networks will be driven by the aging individual.

Prediction 2a. To determine if changes in network size were driven by the focal individual or by changes in the behavior of the social partners, we counted the unique number of individuals that the focal approached each year (approach outdegree) and the unique number of individuals that the focal was approached by each year (approach indegree). We predicted to see a decline in approach outdegree with age but no change in approach indegree with age.

Prediction 2b. We also assessed whether changes in network size were driven by the deaths of social partners. We did this by counting the number of partners that died the previous year (where a partner was an individual with a dyadic sociality index (DSI) > 0, see below) and looked to see whether this predicted the number of grooming or proximity partners a female had the following year. If social selectivity were driving age-based reductions in sociality, we predicted that the deaths of social partners would not affect a female's network size.

Prediction 3: Individuals will show continued engagement and interest in the social world as they age. We quantified changes with age in the amount of grooming given (grooming outstrength) and received (grooming instrength) and the amount of time spent in proximity to other individuals (proximity strength). We calculated dyadic grooming outstrength and instrength as the total duration of grooming given and received by a subject (in seconds) divided by the total amount of time that both the subject and their partner were observed (in seconds). These dyadic measures were then summed across all pairs to give a total measure of individual grooming outstrength and instrength for each subject in each year. We calculated proximity strength in the same fashion. On a dyadic basis, we first calculated the number of scans that pairs of individuals were in proximity to each other relative to the total number of scans done on both individuals. We then summed those dyadic measures across all pairs to give a total measure of individual proximity strength for each subject in each year. We predicted to see no change in the amount of time spent giving or receiving grooming or the amount of time spent in proximity with age.

Prediction 4: Individuals will focus on important relationships in later life. To test whether females focused in on important relationships with age, we looked at three metrics: a) whether females increased their proportion of kin partners with age, b) whether older individuals were more likely to choose partners to whom they had previously been strongly connected, and c) whether older individuals were more likely to choose partners with whom they had previously had stable social connections. We calculated social connectedness between a subject and each of their potential partners by combining grooming duration and spatial proximity into a DSI (43). Grooming and spatial proximity are two positively correlated (Pearson's r = 0.37 in this study) affiliative social interactions that have been widely used to quantify the strength of dyadic bonds in primates (21, 24–27). We calculated total grooming duration between pairs of individuals and divided this by the total amount of time that both individuals were observed. This dyadic grooming rate was then divided by the mean grooming rate in that group/year. For proximity, we again calculated the total number of scans that both

individuals were in proximity and divided this by the total number of scans of both individuals. This dyadic proximity rate was then divided by the mean proximity rate in that group year. For each dyadic pair, these standardized grooming and proximity rates were then summed and divided by the total number of behaviors (two) as per (43) to give the DSI.

Prediction 4a. To assess changes in the proportion of kin partners with age, we assigned all partners as either kin or nonkin using a cutoff of r ≥ 0.125, as this is the level at which kin discrimination occurs for affiliative interactions in rhesus macaques from this population (56). Relatedness coefficients were calculated in the kinship2 package in R (version 1.8.5; (57)) using the long-term pedigree maintained by the CPRC. We predicted to see an increase in the proportion of kin partners with age.

Prediction 4b. To assess whether older females were more likely to choose partners to whom they were strongly connected, we subset our data to only include the last year of data that we had for all subjects. For all subjects and their partners present in this "last-year" dataset (N = 11,050 dyads), we calculated the mean DSI using all previous years of data for the subject and their partner (range = 0–7 y, mean = 2 y of previous data on each dyad). Note that only subjects with at least 2 y of behavioral data could be included in this analysis (185 individuals), but we kept all potential partners in the last year dataset, including those that were observed in the group for the first time and so had a mean DSI of zero with the subject. It was important to account for the possibility that individuals appearing in the dataset for the first time might be chosen as partners by the subject despite not having previously been strongly connected. For this reason, it is possible for dyads to have zero years of previous data. It should be noted, however, that it is possible that some of these mean DSI values of zero may be false zeros. That is, because we only collected behavioral data on adults (i.e., ≥ age 6), it is possible that the focal individual and partner had a previously established relationship when the partner was a juvenile that was not captured in our dataset. However, the inclusion of these zeros only makes our analysis more conservative, and our results remained the same even when these potential partners with zero years of previous data were removed from the analysis. We predicted that individuals who were strongly connected to the subject earlier in life would be more likely to be partners with the subject in later life than individuals who were previously weakly connected to the subject.

Prediction 4c. For all subjects present in the last-year dataset, we also assessed whether their partners were "stable" social partners (recorded as a categorical variable no/yes). Dyads were considered to be stable partners if they had a DSI > 0 for at least two consecutive years. Note that this means that only subjects with at least 3 y of behavioral data could be included in this analysis (113 individuals). For example, if a subject had 2 y of data, 1 y would be used in the last-year dataset, leaving only 1 y of previous data from which to calculate the stability of social relationships. This means that by default all relationships with that subject would have been unstable as there would have been insufficient sampling time for stable social relationships to be established. As above, we kept all potential partners in the last-year dataset (N = 6,893 dyads). It was important to account for the possibility that individuals appearing in the dataset for the first time might be chosen as partners by the focal individual despite their lack of a stable relationship (again false zeros are possible because behavioral data collection began when individuals were adults). On average, each dyad was observed for 2.7 y prior to the final year of data (range 0–7 y). Our results remained the same even when potential partners with only one or 2 y of data were removed from the analysis (i.e., partners with whom the subject did not have time to establish a stable relationship). We predicted that individuals who were stable partners with the subject earlier in life would be more likely to be partners with the subject in later life than individuals who were not stable partners previously.

Statistical Analyses

We used a suite of generalized linear mixed-effects models in a Bayesian framework with different error structures and random effects to quantify changes in social behavior and partner preference with age. We conducted all analyses using R version 4.1.0 (58) and fitted all models in the Bayesian software STAN (59) using the brms package (version 2.15.0; (60)). All fixed effects were given weakly informative priors (see *SI Appendix* for more details). We ran all models for 10,000 iterations across two chains

with a warm-up period of 2,000 iterations. We assessed model convergence by examining traceplots to assess sampling mixing and by ensuring Rhat = 1. We considered estimates of fixed effects to be significantly different from zero when the 95% credible intervals of the posterior distribution did not overlap zero.

Social Selectivity Hypothesis

Predictions 1-2a and 3-4a. For Predictions 1-2a and 3-4a, all analyses were conducted at the level of the individual and we fitted two models for each analysis. In these analyses, we were specifically interested in how social behavior changes across an individual's lifetime, that is, in the within-subject effect of age. To separate the within- from the between-subject age components, we used a within-subjects centering approach (as per 15; see *SI Appendix* for details). Model A included within-individual age (to capture within-individual changes in behavior) and average age (to capture between-individual differences in behavior) as continuous fixed effects (see Eq. 2 in the *SI Appendix*) as well as rank as a categorical fixed effect (*SI Appendix*, Tables S1–S4 and S7–S10). We tested for an interaction between rank and within-individual age in all models to see whether how social behavior changed across the lifespan was influenced by an individual's social status and removed the interaction when not significant. We included a random effect of group and year to account for variation in social behavior that might be due to differences between groups or years, and also included a random intercept term for individual ID, to account for repeated observations of the same females. We included within-individual age as a random slope term over individual ID, which allowed us to assess whether there was variation in how individuals changed their social behavior with age. Although we did not expect nonlinearities in the relationship between age and the response variable given that we were looking at changes in behavior from prime adulthood to old age, we nevertheless fitted a model with smoothing terms for within-individual age and average age and compared that model fit to the model with only linear age terms using leave-one-out cross-validation in the brms package (version 2.15.0; (60)). Including smoothing terms in the model never improved the model fit and so was not considered further. For Predictions 1-2a (grooming degree, proximity degree, approach outdegree and indegree), we fitted all models with a Poisson error distribution (log link). For Prediction 3 (grooming outstrength and instrength, proximity strength), models were fitted using a zero-inflated beta regression error distribution (logit link). For Prediction 4a (proportion of kin partners), we fitted the model with a binomial error distribution (logit link) and also included proportion of kin in the group as an additional offset term to account for the increasing availability of kin with age.

Prediction 2b. To assess whether reductions in the number of grooming and proximity partners with age were driven by the aging individual rather than by deaths of social partners (Prediction 2b), we fitted two models with a Poisson error distribution (log-link) where the response variables were number of grooming partners and number of proximity partners, respectively (*SI Appendix*, Tables S5 and S6). In both models, we fitted the number of partners that died in year t-1 as a continuous fixed effect (where a partner was any individual with a DSI > 0). We also included group as a categorical fixed effect since there were only three groups with at least 2 y of continuous data (R, V, and F). In all models, we checked for an interaction between number of dead partners and female age to assess whether the effect of partner deaths was dependent on the age of the female. The interaction was not significant in either model and so was not considered further. As with all of the previous models, we included year and individual ID as random effects.

Predictions 4b and 4c. For Predictions 4b and 4c, all analyses were conducted at the level of the dyad. We fitted whether or not individuals were partners (coded as 0/1) as the response variable in both models and used a Bernoulli error distribution (logit link). For Prediction 4b, the predictor variable of interest was the mean DSI for the focal individual and their partner––calculated based on all previous years of interaction. This was included in the model as a continuous fixed effect. For Prediction 4c, the predictor of interest was whether or not the focal individual and partner were stable social partners in previous years (no/yes). We included this in the model as a categorical fixed effect. We also included the partner's age (continuous), the partner's rank (categorical), and whether or not the partner was kin or nonkin (categorical) as fixed effects in both models (*SI Appendix*, Tables S11 and S12). In each model, we checked for an interaction between the predictor of interest (mean DSI and partner stability) and focal individual age to assess whether the likelihood of choosing a strong or stable partner was dependent on a female's age. We removed the interaction term from the model when it was not significant. As above, we included group and year as random effects to account for variation in partner choice that might be due to differences between groups or years. Individual ID and partner ID were included as random effects in a multimembership grouping term (61). This multimembership grouping term accounts for the inherent multilevel structure of the data and allows each sample (dyad) to belong to more than one individual in a random effect at the same time.

Selective Disappearance Hypothesis. We tested for selective disappearance by fitting a second model (Model B) for all the aforementioned models used for Predictions 1-2a and 3-4a above (*SI Appendix*, Tables S1–S4 and S7–S10). Model B included age and average age (see Eq. 3 in the *SI Appendix*) as well as the same fixed and random terms as Model A, but did not include age as a random slope term over individual ID. In Model B, the effect of age will be equivalent to the effect of within-individual age in Model A and the average age term now represents the difference between the between and within-subject effects. In cases where average-age term is significant in Model B, the between- and within-individual slopes significantly differ, providing evidence for selective disappearance.

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1. C. Wrzus, M. Haenel, J. Wagner, F. J. Neyer, Social Network changes and life events across the life span: A meta-analysis. *Psychol. Bull.* **139**, 53–80 (2013).
2. Z. P. Machanda, A. G. Rosati, Shifting sociality during primate ageing. *Philos. Trans. R. Soc. B Biol. Sci.* **375**, 20190620 (2020).
3. A. G. Rosati *et al.*, Social selectivity in aging wild chimpanzees. *Science* **370**, 473–476 (2020).
4. L. Almeling, H. Sennhenn-Reulen, K. Hammerschmidt, A. M. Freund, J. Fischer, Social interactions and activity patterns of old Barbary macaques: Further insights into the foundations of social selectivity. *Am. J. of Primatol.* **79**, e22711 (2017).
5. J. Holt-Lunstad, T. B. Smith, J. B. Layton, Social relationships and mortality risk: A meta-analytic review. *PLoS Med.* **7**, e1000316 (2010).
6. N. Snyder-Mackler *et al.*, Social determinants of health and survival in humans and other animals. *Science* **368**, eaax9553 (2020).
7. A. Steptoe, A. Shankar, P. Demakakos, J. Wardle, Social isolation, loneliness, and all-cause mortality in older men and women. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 5797–5801 (2013).
8. E. Cumming, W. E. Henry, *Growing Old, the Process of Disengagement* (Basic Books, New York, 1961).
9. E. R. Siracusa, J. P. Higham, N. Snyder-Mackler, L. J. N. Brent, Social ageing: Exploring the drivers of late-life changes in social behaviour in mammals. *Biol. Lett.* **18**, 20210643 (2022).
10. L. L. Carstensen, D. M. Isaacowitz, S. T. Charles, Taking time seriously. A theory of socioemotional selectivity. *Am. Psychol.* **54**, 165–181 (1999).
11. L. L. Carstensen, The influence of a sense of time on human development. *Science* **312**, 1913–1915 (2006).
12. L. Almeling, K. Hammerschmidt, H. Sennhenn-Reulen, A. M. Freund, J. Fischer, Motivational shifts in aging monkeys and the origins of social selectivity. *Curr. Biol.* **26**, 1744–1749 (2016).

13. G. Schino, M. Pinzaglia, Age-related changes in the social behavior of tufted capuchin monkeys. *Am. J. Primatol.* **80**, e22746 (2018).
14. D. H. Nussey, T. Coulson, M. Festa-Bianchet, J. M. Gaillard, Measuring senescence in wild animal populations: Towards a longitudinal approach. *Funct. Ecol.* **22**, 393–406 (2008).
15. M. van de Pol, J. Wright, A simple method for distinguishing within- versus between-subject effects using mixed models. *Anim. Behav.* **77**, 753–758 (2009).
16. G. F. Albery *et al.*, Ageing red deer alter their spatial behaviour and become less social. *Nat. Ecol. Evol.* **6**, 1231–1238 (2022).
17. S. B. Hrdy, D. B. Hrdy, Hierarchical relations among female hanuman langurs (primates-colobinae, presbytis-entellus). *Science* **193**, 913–915 (1976).
18. D. P. Watts, Male dominance relationships in an extremely large chimpanzee community at Ngogo, Kibale National Park, Uganda. *Behaviour* **155**, 969–1009 (2019).
19. M. Nakamichi, Age-related differences in social grooming among adult female Japanese monkeys (Macaca fuscata). *Primates* **44**, 239–246 (2003).
20. S. T. Charles, L. L. Carstensen, Social and emotional aging. *Annu. Rev. Psychol.* **61**, 383–409 (2010).
21. S. Ellis, N. Snyder-Mackler, A. Ruiz-Lambides, M. L. Platt, L. J. N. Brent, Deconstructing sociality: The types of social connections that predict longevity in a group-living primate. *Proc. R. Soc. B* **286**, 20191991 (2019).
22. W. D. Hamilton, The genetical evolution of social behaviour. I. *J. Theor. Biol.* **7**, 1–16 (1964).
23. J. B. Silk, "Evolutionary Perspectives on the Links between close Social Bonds, Health, and Fitness" in *Sociality, Hierarchy, Health Comparative Biodemography*, M. Weinstein, M. A. Lane, Eds. Washington, DC: National Academies Press (US); 2014, pp. 121–144.
24. E. A. Archie, J. Tung, M. Clark, J. Altmann, S. C. Alberts, Social affiliation matters: Both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proc. R. Soc. B* **281**, 20141261–20141261 (2014).
25. L. J. N. Brent *et al.*, Genetic origins of social networks in rhesus macaques. *Sci. Rep.* **3**, 1361–1368 (2013).
26. R. McFarland *et al.*, The `strength of weak ties' among female baboons: Fitness-related benefits of social bonds. *Anim. Behav.* **126**, 101–106 (2017).
27. J. B. Silk, Social bonds of female baboons enhance infant survival. *Science* **302**, 1231–1234 (2003).
28. G. E. Blomquist, D. S. Sade, J. D. Berard, Rank-related fitness differences and their demographic pathways in semi-free-ranging rhesus macaques (macaca mulatta). *Int. J. Primatol.* **32**, 193–208 (2011).
29. K. L. Chiou *et al.*, Rhesus macaques as a tractable physiological model of human ageing. *Philos. Trans. R. Soc. B* **375**, 20190612 (2020).
30. L. J. N. Brent, A. Ruiz-Lambides, M. L. Platt, Family network size and survival across the lifespan of female macaques. *Proc. R. Soc. B* **284**, 20170515–7 (2017).
31. C. L. Hoffman, J. P. Higham, A. Mas-Rivera, J. E. Ayala, D. Maestripieri, Terminal investment and senescence in rhesus macaques (Macaca mulatta) on Cayo Santiago. *Behav. Ecol.* **21**, 972–978 (2010).
32. W. A. Draper, Free-ranging rhesus monkeys: Age and sex differences in individual activity patterns. *Science* **151**, 476–478 (1966).
33. S. M. Schwartz, J. W. Kemnitz, Age- and gender-related changes in body size, adiposity, and endocrine and metabolic parameters in free-ranging rhesus macaques. *Am. J. Phys. Anthropol.* **89**, 109–121 (1992).
34. G. M. Hope *et al.*, A primate model for age related macular drusen. *Br J. Ophthalmol.* **76**, 11–16 (1992).
35. C. J. DeRousseau, Aging in the musculoskeletal system of rhesus monkeys: III. Bone loss. *Am. J. Phys. Anthropol.* **68**, 157–167 (1985).
36. M. R. S. Rosado, Sociodemographic effects on immune cell composition in a free-ranging non-human primate. *bioRxiv* (2021). 10.1101/2021.12.06.471383.

37. M. van de Pol, S. Verhulst, Age-dependent traits: A new statistical model to separate within- and between-individual effects. *Am. Nat.* **167**, 766–773 (2006).
38. S. Verhulst, M. Geerdink, H. M. Salomons, J. J. Boonekamp, Social life histories: Jackdaw dominance increases with age, terminally declines and shortens lifespan. *Proc. R. Soc. B* **281**, 20141045–20141045 (2014).
39. S. Datta, The acquisition of dominance among free-ranging rhesus monkey siblings. *Anim. Behav.* **36**, 754–772 (1988).
40. H. C. Veenema, B. M. Spruijt, W. H. Gispen, J. A. R. A. M. van Hooff, Aging, dominance history, and social behavior in java-monkeys (Macaca fascicularis). *Neurobiol. Aging* **18**, 509–515 (1997).
41. I. S. Bernstein, P. G. Judge, T. E. Ruehlmann, Kinship, association, and social relationships in rhesus monkeys (Macaca mulatta). *Am. J. Primatol.* **31**, 41–53 (1993).
42. A. Widdig, P. Nürnberg, M. Krawczak, W. J. Streich, F. B. Bercovitch, Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proc. Natl. Acad. Sci. U.S.A* **98**, 13769–13773 (2001).
43. J. Silk, D. Cheney, R. Seyfarth, A practical guide to the study of social relationships. *Evol. Anthropol.* **22**, 213–225 (2013).
44. W. Bruine de Bruin, A. M. Parker, J. Strough, Age differences in reported social networks and well-being. *Psychol. Aging* **35**, 159–168 (2020).
45. F. R. Lang, L. L. Carstensen, Close emotional relationshisp in late life: Further support for proactive aging in the social domain. *Psychol. Aging* **9**, 315–324 (1994).
46. J. Corr, Social behavior in aged rhesus macaques. *Coll. Antropol.* **27**, 87–94 (2003).
47. A. Peters, K. Delhey, S. Nakagawa, S. Aulsebrook, S. Verhulst, Immunosenescence in wild animals: Meta-analysis and outlook. *Ecol. Lett.* **22**, 1709–1722 (2019).
48. M. A. Pavez-Fox, Reduced injury risk links sociality to survival in a group-living primate. *bioRxiv* (2022). 10.1101/2022.04.05.487140.
49. H. C. Veenema, J. A. van Hooff, W. H. Gispen, B. M. Spruijt, Increased rigidity with age in social behavior of Java-monkeys (Macaca fascicularis). *Neurobiol. Aging* **22**, 273–281 (2001).
50. E. Kato, Effects of age, dominance, and seasonal changes on proximity relationships in female japanese macaques (Macaca fuscata) in a free-ranging group at Katsuyama. *Primates* **40**, 291–300 (1999).
51. R. M. Sapolsky, The influence of social hierarchy on primate health. *Science* **308**, 648–652 (2005).
52. E.-M. Rathke, J. Fischer, Social aging in male and female Barbary macaques. *Am. J. Primatol.* **83**, e23272 (2021).
53. S. B. Kroeger, D. T. Blumstein, J. G. A. Martin, How social behaviour and life-history traits change with age and in the year prior to death in female yellow-bellied marmots. *Philos. Trans. R. Soc. B* **376**, 20190745 (2021).
54. A. Widdig *et al.*, Genetic studies on the Cayo Santiago rhesus macaques: A review of 40 years of research. *Am. J. Primatol.* **78**, 44–62 (2016).
55. J. Altmann, Observational study of behavior: Sampling methods. *Behaviour* **49**, 227–267 (1974).
56. E. Kapsalis, C. M. Berman, Models of affiliative relationships among free-ranging rhesus monkeys (Macaca Mulatta) II. Testing predictions for three hypothesized organizing principles. *Behaviour* **133**, 1235–1263 (1996).
57. J. P. Sinnwell, T. M. Therneau, D. J. Schaid, The kinship2 R package for pedigree data. *Hum. Hered.* **78**, 91–93 (2014).
58. R. Core Team, R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria, 2021), https://www.R-project.org/
59. Stan Development Team, "RStan: the R interface to Stan." R package version 2.21.7 (2022), https://mc-stan.org/
60. P. C. Bürkner, brms: An R package for Bayesian multilevel models using Stan. *J. Stat. Sof.* **80** (2017), 10.18637/jss.v080.i01.
61. M. Tranmer, D. Steel, W. J. Browne, Multiple-membership multiple-classification models for social network and group dependences. *J. R. Stat. Soc. Ser. A Stat. Soc.* **177**, 439–455 (2014).