Social aging in male and female Barbary macaques

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Abstract
Aging brings about notable changes in sociality, with an increasing focus on essential partners in both humans and nonhuman primates. Several studies have shown that older nonhuman primates have fewer social partners and shift their types of interactions. The majority of these studies, however, involved only female individuals. Much less is known about the trajectory of social aging in males. We collected 2180 h of focal observation data in a large age-heterogeneous sample of 34 male and 50 female Barbary macaques (Macaca sylvanus; age range 5–30 years) living in two social groups at the outdoor enclosure at La Forêt des Singes in Rocamadour (France). To track age-related changes in social engagement of both sexes, we used classical behavioral and social network analysis to measure age-related variation in the number of partners, the frequency of affiliative interactions, and the position in the social network (eigenvector centrality and local clustering coefficient). We found that females were more central in most social network metrics than males, that is, had more social partners and were more engaged in affiliative interactions than males. We did not find notable sex differences with age: both sexes showed a similar decline in social activity and energy-demanding activities like jumping or running. Our results thereby extend our knowledge of older nonhuman primates’ social life and emphasize that age can have a similar impact on female and male social behavior.

KEYWORDS
aging, Barbary macaques, sex differences, social behavior, social network analysis

1 | INTRODUCTION

The growing proportion of older people in societies worldwide strongly impacts health systems and economic growth in the coming decades. With increasing life-span, a larger share of the population is afflicted by chronic ailments, such as diabetes or cardiovascular diseases (Christensen et al., 2009). In affluent societies, the proportion of people that are no longer working is also growing. Changes in individual physical status and daily routines have consequences for social life. Aging people often experience a decline in social network size, which may sometimes result in complete social isolation. Loneliness is perceived as a growing societal problem in older generations (Carstensen et al., 1993; Smith et al., 2018). A decline in social activity and social network size can be attributed to several factors, including the shift from work life to retirement, the loss of social partners due to mortality, that is, changes in opportunity, on the one hand, as well as shifts in the motivation to engage in social interactions on the other hand.
Several psychological theories have been put forward to account for age-related changes in human motivation and sociality (reviewed in Charles & Carstensen, 2010). The socioemotional selectivity theory (Carstensen et al., 1993) proposes that the awareness of a limited lifetime leads to an increased focus on fewer but more meaningful social partners. Recent studies on nonhuman primates have put this conjecture to the test (Almeling et al., 2016; Rosati et al., 2020). Nonhuman primates are a valuable model for studying the mechanisms underpinning motivational changes with age, as they share several physiological features with humans but are assumed to lack an awareness of their limited lifetime. If they would also experience a shrinking social network with age, this may indicate that motivational changes with age are not simply a result of one’s insight into a limited future time but may also be driven by more deeply rooted biological processes. There is now ample evidence that older subjects tend to rest more, spend more time on their own, and have fewer social partners (Almeling et al., 2016; Corr, 2003; Veenema et al., 1997).

What is less well understood to date is to which degree age-related changes in sociality differ between the sexes. Women continue to have more extensive social networks than men into old age, reflected by smaller social network size in single or widowed men compared with women in a similar situation, and being alone tends to have a greater impact on older men than on women (McLaughlin et al., 2010). Further, older women tend to have more widespread social networks than older men regarding related and unrelated social interaction partners (Cornwell, 2011). To better understand how age affects the social network structure from an evolutionary perspective, comparable data for males and females for different nonhuman primate species are needed.

A critical factor in the context of social aging is the identity of the dispersing sex. To date, most studies have focused on the philopatric sex. In female-philopatric species such as the members of the genus Macaca, females typically prefer to interact with the members of their matriline throughout their life (Roubová et al., 2015; Silk et al., 1999). Male macaques as the dispersing sex, in contrast, are prone to experience a variable network throughout life as they leave their natal group after reaching sexual maturity (Paul & Kuester, 1985). Note however, that even in captive conditions with potential male coalition partners and in females to increase mating opportunities (Bissonnette et al., 2011). Therefore, older males may invest more in affiliative interactions with potential male coalition partners and in females to increase mating opportunities (Bissonnette et al., 2011). In this case, males and females suggest that both sexes may experience substantial differences in sociality in old age.

We addressed the question of potential sex-dependent differences in aging trajectories in Barbary macaques living in the outdoor enclosure “La Forêt des Singes” in Rocamadour. This large park houses three social groups of Barbary macaques under near-natural habitat conditions. Due to food provisioning and the absence of predators, the monkeys have a much higher life expectancy than in the wild. The presence of an appreciable number of old subjects allowed us to study age-related changes in motivation and sociality with a decent sample size. Because the animals have ample space, we can also ask meaningful questions about the individuals’ gregariousness. The present study extends our previous work on aging in monkeys (Almeling et al., 2016, 2017; Rathke & Fischer, 2020).

To fill this knowledge gap on sex-dependent differences in social aging, we used a social network approach. We focused on four social network metrics, namely degree, strength, eigenvector centrality, and local clustering coefficient (hereafter clustering coefficient) derived from affiliative social interactions, such as grooming, contact sitting, hugging, touching, and other sex-specific affiliative interactions (see Section 2 for details). The degree represents the number of connections (edges) an individual (node) has to other individuals; in this study, the number of social partners. The strength of sociality is described by the frequency of interactions between two individuals (Lehmann & Ross, 2011; Newman, 2003). Considering indirect relationships, the eigenvector centrality measures how well-connected an individual’s partners are. High eigenvector centrality values indicate that the subject has many partners who themselves are connected to many partners. The clustering coefficient describes sub-grouping structures resulting from the connectedness of an individual’s partners. A high clustering coefficient reveals highly inter-connected partners, that is, an individual’s partners are also connected to each other (Brent, 2015; Newman, 2003; Sueur et al., 2011).

For females, and following previous findings, we expected a decrease in social activity with age. Old females should have fewer partners and spend less time in affiliative interactions (lower degree, lower strength). Concerning the indirect connections, we expected that older females would exhibit lower values in eigenvector centrality and clustering coefficient compared to younger females. For males, we considered two possibilities. If males become more selective in their social partners with age, potentially due to the unpredictability and potentially stressful social encounters, they should show similar age-related variation in sociality as females. A higher selectivity would be reflected in lower degree and strength values and more peripheral positions regarding the indirect metrics. Nevertheless, previous studies showed that older Barbary macaque males might maintain a high-ranking position when they invest in their social relationships (Henkel et al., 2010; Ostner & Schülke, 2014; Rathke et al., 2017). Therefore, older males may invest more in affiliative interactions with potential male coalition partners and in females to increase mating opportunities (Bissonnette et al., 2011).
should show greater variation in social activity with age, with some males continuing to hold central positions and others being reclusive.

We complemented the social network analysis by investigating the gregariousness of the subjects (number of individuals in 2 m proximity) and their social interest. To assess the latter, we recorded how frequently subjects uttered vocalizations in response to ongoing social interactions in the environment ("commenting behavior," Brumm et al., 2005). We analyzed the commenting behavior for aggressive and affiliative events. A previous study on females of the same population had not reported changes in commenting behavior with age. We, therefore, expected no such changes for females (Almeling et al., 2016, 2017) but considered whether old males show greater variation than females. Additionally, we investigated whether age impacts physical activity in energy-demanding behaviors, such as running, climbing, or jumping. In line with the idea that the age-related physiological decline appears to affect both sexes equally (Hamada & Yamamoto, 2010), we expected to find similar results for females and males.

## Methods

### Ethics statement

The research reported in this manuscript complies with the American Society of Primatologists’ principles for the ethical treatment of nonhuman primates. The study was exclusively noninvasive and solely based on observational data collection. It is in accordance with the European Directive 2010/63/EU and was further approved by the regulations of the private institution La Forêt des Singes, Rocamadour (France), where the study was conducted.

### Study site and subjects

We conducted behavioral observations during two consecutive field seasons from April to June and September to November in 2017 and 2018 at “La Forêt des Singes,” a 20-ha forested enclosure in Rocamadour, France (for the history of the population and more detailed information de Turckheim & Merz, 1984). The population comprised three social groups with 170 individuals in 2017 and 180 individuals in 2018. The monkeys are provisioned with cereal, fruits, and vegetables several times during the day. They also feed on natural food sources like leaves, grains, roots, and insects. Water is available ad libitum. Tourists can observe and feed the monkeys from designated routes, and the monkeys are well-habituated to behavioral observations. All individuals are identifiable by an inner-leg tattoo and distinctive physical characteristics, such as scars or facial pigmentation. The population is age-heterogeneous, with some monkeys reaching up to 30 years. We considered individuals as "young adult" up to the age of 10, as “middle-aged” when they were 11–19 years old, and as “old” when they were 20 years or older, following previous studies on macaques (Berghänel et al., 2010; Corr, 2003; Paul et al., 1993).

We collected data in two groups. In 2017, we studied the “Petit Bassin (PB)” group and in 2018 in the “Grand Bassin (GB)” group. The PB group had 61 group members (26 female); the GB group 51 group members (28 female). All animals were captive-born and the exact birth-dates are known. We included all females ≥5 years old and all males ≥seven years old in the study, resulting in 84 subjects (50 female). Of the 50 females, 16 were classified as young adult, 16 as middle-aged, and 18 as old. Of the 34 males, eight were classified as young adult, 16 as middle-aged, and ten as old (see Table S1 for a detailed overview). We used this categorization only for the descriptive statistics; in the statistical models, age was used as a continuous predictor variable (see below).

We recorded all affiliative behaviors, including grooming, contact-sit, hugging, touch, and sex-specific affiliative behaviors like "triadic interactions" (Taub, 1980) or “mounting” (Reinhardt et al., 1986) in males and “anti-parallel” greeting in females, a behavior during which females stand next to each other, grab or hug each other and teeth chatter at each other’s hind-quarters. In sum, we collected 2180 h of focal observations on all adult individuals using a 30 min continuous data sampling protocol (Altman, 1974; Martin & Bateson, 1986). The average observation time per subject was 25 h 54' (range: 24 38’–27 h 25’, except for one male (Z321) who died and was observed for 12 h 31’). Each focal protocol was preceded by an instantaneous scan in which we recorded the number of subjects observed in a 2 m radius. This number does not include individuals who were closer than 1 m and interacting with the focal individual to avoid doubling the strength measure.

Data collection took place 5 to 6 days a week, from 9 a.m. to 8 p.m. Focal observations were balanced across daytime and observer. We collected data using handheld computers (Samsung Galaxy Note 2), equipped with Pendragon Forms (Pendragon Software Cooperation). Aggressive interactions were collected during continuous focal observations and ad libitum sampling to establish the dominance hierarchy. To determine the dominance hierarchy, we used all dyadic and decided interactions, that is, explicit submission and no counter-aggression. We calculated the dominance rank based on the normalized David’s score, using the package EloRating in R (Neumann & Kulik, 2014).

### Data analysis

We used a weighted matrix for the social network analysis, including all affiliative behaviors observed during focal protocols. Network visualizations were generated using the Fruchterman Reingold layout (Fruchterman & Reingold, 1991). To determine the eigenvector centrality and clustering coefficient, we used the R package igraph 1.2.4.1 (Csárdi & Nepusz, 2006) with R 3.4.3 (R Core Team, 2019).

For both the number of partners (degree) and interaction frequency (strength), the direction of interaction can be described. We calculated how many partners engaged in affiliative interactions with an individual (indegree) and how many partners an individual affiliated with (outdegree). Similarly, we assessed the frequency of
received (instrength) or given (outstrength) affiliative behavior. These measures were obtained from the focal observation protocols.

To assess overall gregariousness, we calculated the mean number of partners per focal scan (proximity). For energy-intensive activities, we summed the frequencies of climbing, running, jumping, and “tree shaking” (individual count of each behavior). All occurrences of ‘commenting behavior’ per individual were used for the analysis of social interest.

2.4 Statistical analysis

Statistical analyses were carried out using R 4.0.3 (R Core Team, 2019). To analyze the impact of age and sex on degree, strength, activity, and commenting, we fitted generalized linear models (GLM) with negative binomial error distribution and log link function (McCullagh & Nelder, 1989). For eigenvector centrality and proximity (log-transformed; base e), we fitted linear models (LM) (i.e., assuming normally distributed and homogeneous residuals), and for clustering coefficient, we fitted a GLM with beta error distribution (Bolker, 2008) and logit link function. We included age and rank as quantitative predictor variables and sex as a categorical predictor variable. We included the interaction between sex and age since we wanted to estimate the extent to which females and males differed in their age-related behavioral trajectories (Bissonnette et al., 2009). If the interaction was not significant (p > .05) but the full-null model comparison (see below) was, we excluded the interaction and continued the analysis with the main effects. We fitted negative binomial GLMs with the function glm.nb of the package MASS (version 7.3-53; Venables & Ripley, 2002) and the beta model with the function betareg of the equally named package (version 3.1-4; Cribari-Neto & Zeileis, 2010; Grün et al., 2012). The analysis of degree revealed that a quadratic relationship produced a much better fit than the linear relationship. However, since this inclusion of age squared represents an a-posteriori hypothesis, the respective significance tests should be treated cautiously.

Before fitting the models, we z-transformed age and rank to achieve a more straightforward interpretation of the estimates (Schielzeth, 2010). Before fitting the beta model, we transformed the response according to the equation given in Smithson and Verkuilen (2006) to rule out that the response was zero or one. To rule out collinearity, we determined variance inflation factors (VIF), using the package car and the function vif (Fox & Weisberg, 2011) for models lacking the interaction. This revealed collinearity to be no issue (maximum VIF = 2.781). The stability of each full model was determined in terms of the model estimates using the function dfbeta or by manual case-wise deletion of data points (beta model). All models had good stability (see Supplementary Material).

In the negative binomial GLMs, we included focal observation hours (log-transformed) as an offset term to control for variation in observation effort (McCullagh & Nelder, 1989). In the models for degree and strength, we additionally included an offset term for the number of available interaction partners (i.e., group size −1; log-transformed). Similarly, we weighted the LMs and the beta model by the focal observation hours. Concerning the model assumptions, we checked the models for normality and homogeneity of residuals by visually inspecting a qq-plot, and a scatter plot of the residuals plotted against the fitted values (Zuur et al., 2010). These checks revealed no apparent violations of these assumptions. None of the GLMs was overdispersed (maximum dispersion parameter: 1.167). To avoid “cryptic multiple testing” (Forstmeier & Schielzeth, 2011), we conducted a full-null model comparison for each model to investigate whether the full model was significantly better at explaining the observed variation compared to the null model (lacking

| TABLE 1 Results of full-null model comparisons for the different response variables in the analysis |
|------------------------------------|------------------|-----------------|------------------|
| A. Linear models Response variable | Numerator d.f.   | Denominator d.f. | p                |
| Clustering coefficient | 1.353 | 3 | 78 | 0.263 |
| Proximity | 5.216 | 3 | 78 | 0.002 |
| B. Generalized linear models Response | $\chi^2$ | d.f. | |
| Indegree | 21.588 | 3 | <0.001 |
| Instrength | 60.596 | 3 | <0.001 |
| Outdegree | 21.329 | 3 | <0.001 |
| Outstrength | 69.854 | 3 | <0.001 |
| Centrality | 928.522 | 3 | <0.001 |
| Activity | 63.328 | 3 | <0.001 |
| Commenting | 11.070 | 3 | 0.011 |

Note: Test statistics ($F, \chi^2$), degrees of freedom, and p values are given.
age, sex, and their interaction) (Dobson, 2002). The analyzed data used for these models comprised 83 (clustering, outdegree, and out-strength) or 84 individuals (all others).

Data and code are available at https://osf.io/2wpr3. The authors declare no conflict of interest.

3 RESULTS

Except for the local clustering coefficient model, all models revealed a significant result in the full-null model comparison (Table 1). With two exceptions, neither the interaction between sex and age nor the interaction between sex and age squared were significant. We thus removed the interactions from the models. The exceptions were the centrality model (significant interaction: \( p < 0.001 \)) and the proximity model, which revealed a marginally nonsignificant interaction (\( p = 0.055 \); see Tables S14 and S17 for details).

Both age and sex influenced an individual’s position in the group. Figure 1 depicts social networks based on instrength (Figure 1a) and outstrength (Figure 1b) of study group PB. Young adult and old males occupied peripheral positions in both networks, while young adult and middle-aged females and middle-aged males were more central than older individuals. The highest interaction frequencies occurred between young females.

The number of partners that initiated an affiliative interaction with a given subject (indegree) showed similar age-related variation in males and females, though males were somewhat less frequently approached by other individuals than females. Indegree peaked at the age of ca. 10 years in females and ca. 14 years in males and was lower in older and younger individuals (significant effect of age: \( z = -2.81, p = 0.005 \); Figure 2a, see Tables S2-S5 for details). In-strength, the weighted measurement of indegree, was lower for older than for younger monkeys, and lower for males than for females (effect of age: \( z = -6.25, p < 0.001 \); effect of sex: \( z = -4.52, p < 0.001 \); Figure 2b; see Table S6 and S7 for details).

Across the entire age span, females were the target of affiliative interactions twice as often as males. Old monkeys were also less active in initiating affiliative interactions themselves. Middle-aged females and males at the age of ca. 15 years had the highest number of partners (outdegree, significant effect of age: \( z = -4.05, p < 0.001 \); Figure 3a), and females had more partners than males (\( z = -3.36, p < 0.001 \); see Table S8-S11 for details). In terms of the frequency of affiliative interactions given (outstrength), both sexes had the highest frequencies when young, with a steady decline with age (\( z = -6.13, p < 0.001 \), Figure 3b). To illustrate the results, young adult females initiated 2.64 affiliative interactions/h, middle-aged females 1.43, and old females 0.85 interactions/h on average. Young adult males initiated 0.83 affiliative interactions/h, middle-aged males 1.12, and old males 0.5 interactions/h. Overall, females initiated affiliative interactions significantly more frequently than males (\( z = -5.72, p < 0.001 \); see Tables S12 and S13 for details).

Concerning the indirect measurements, eigenvector centrality decreased with age in females but was low throughout in males, reflected by a significant interaction sex \( \times \) age (\( z = 13.94, p < 0.001 \), Figure 4a; see Table S14 for details). The clustering coefficient, in contrast, neither varied with age (\( t = 1.29, p = 0.22 \)) nor sex (\( t = -0.95, p = 0.35 \), Figure 4b; see Tables S15 and S16 for details).

![Figure 1](https://example.com/figure1.png)

**Figure 1** Social network based affiliative interactions (a: instrength, b: outstrength). Nodes represent individuals with circles showing females and squares showing males. Individuals under the age of 2 are excluded here for better visualization. In panel (a) we removed one individual that did not interact with any other individual. The color of the nodes indicates an individual’s age (color intensity increases with age, the darker, the older the individual). Lines between nodes depict an affiliative interaction between them, and the thickness of the line represents the frequency of interactions.
FIGURE 2  Number of partners and frequency of affiliation received in relation to age. (a) number of partners an individual received affiliation from (indegree). (b) frequency of interactions received from another individual in relation to age (instrength). The instrength is shown on a log-scale, due to four monkey’s large number of interactions. Dashed lines depict the fitted model (corrected for observation hours and with rank centered to a mean of zero), and polygons show their 95% confidence intervals. Females are depicted with circles in violet, males with triangle in green. The area of the points corresponds to the number of tied observations (1–3).

FIGURE 3  Affiliation given in terms of number of partners and frequency of affiliation in relation to age. (a) depicts the number of partners an individual actively affiliated with (outdegree). (b) depicts the frequency of interactions an individual gave in relation to age (outstrength). Females are depicted with circles in violet, males with triangle in green. The outstrength is shown on a log-scale, due to one monkey’s large number of interactions. Dashed lines depict the fitted model (corrected for observation hours and with rank centered to a mean of zero), and polygons show their 95% confidence intervals. The area of the points corresponds to the number of tied observations (1–2).

FIGURE 4  Two indirect social network metrics with regard to age. (a) eigenvector centrality (log-scaled) in relation to age. (b) clustering coefficient in relation to age. Females are depicted with circles in violet, males with triangle in green. Dashed lines depict the fitted model (with rank centered to a mean of zero), and polygons show the 95% confidence intervals.
For proximity, we found some marginal indication for an interaction between sex and age ($z = 1.95$, $p = 0.055$). Older females had fewer individuals nearby than younger ones, whereas, for males, no strong age-related pattern appeared (Figure 5a; see Tables S17 and S18 for details). Older monkeys were less active regarding energy-demanding behaviors like running, jumping, or climbing ($z = -9.62$, $p < 0.001$, Figure 5b). Males were slightly more active than females ($z = 2.12$, $p = 0.034$; see Tables S19 and S20 for details). Commenting behavior did not vary with age ($z = -1.24$, $p = 0.21$, Figure 5c). Overall, males commented less frequently than females ($z = -2.55$, $p < 0.011$; see Tables S21 and S22 for details).

4 | DISCUSSION

Males experienced similar age-related social changes as females: old males approached fewer partners for affiliation and initiated fewer affiliative interactions than middle-aged or young adult subjects. After a peak around the age of 15 years, the number of social partners that initiated affiliation with the subject decreased, and the amount of affiliation that an individual received also declined with age. Overall, males were less sociable than females. Old animals of both sexes were also spatially more reclusive than younger ones. Nevertheless, social interest remained high regardless of age, as evidenced by continual commenting on social interaction in the environment. In summary, the pattern we observed for males does not differ substantially from that we had previously reported for females (Almeling et al., 2016). Moreover, we replicated the previous findings for females here.

These findings refute our initial working hypothesis that some males continue to be important "players" in the social network into old age. Previous studies in this population reported that males differ in their infant carrying activities, impacting their position in the social network and that some old males were still highly active in this regard (Henkel et al., 2010). In another population of Barbary macaques, older males changed their competitive strategy from solitary aggression to coalitionary activity with other aged males (Rathke et al., 2017). These findings indicate that there may be variation in male sociality with group composition. A previous study found that males are more likely to partner up in coalitions with a male they affiliated with before (Berghänel et al., 2011). Future studies are needed to investigate if a previous history of mutual support affects partner choice in old age.
A study by Sosa (2016) in the population in Rocamadour also reported that males were less active in the affiliative network than females. However, males in that study did not experience a similar decline in social activity with age as females did (Sosa, 2016). The affiliative network in that study was based on grooming interactions, which are rare between males (Paul et al., 1996). In the present study, we included additional affiliative behaviors, such as contactsitting or triadic interactions, which provided a more nuanced picture of the changes in social behavior with age in males. In contrast to a previous study on the same population (Almeling et al., 2016), females in our study experienced a decline in partners affiliating with them. In the previous study, a drop in sociality was only found for females older than 25 years (Almeling et al., 2016). Such slight variations in patterns are likely to be stochastic and related to the composition of the relatively small number of subjects for the different age brackets.

We expected that when males are able to build a supportive network, they maintain central positions throughout adulthood and thereby show a different social aging pattern than females. Males had lower eigenvector centrality values than females, however. For both sexes, the eigenvector centrality value decreased with age. This finding indicates that older monkeys in this study appeared to play a less central role in the network, and males are less central than females irrespective of age. Other studies investigating eigenvector centrality with regard to age did not find this effect in rhesus macaques (Liao et al., 2017). That study was based on age classes (juveniles, sub-adults, adults) instead of individual ages and could not evaluate a potential age effect within the adult class.

We found that younger females exhibited the highest eigenvector centrality values, which indicates having many partners that are well-connected themselves. The matrilineal social structure in many primate societies is likely linked to those higher eigenvector centrality values in females than males. In vervet monkeys (Chlorocebus pygerythrus), females had higher eigenvector centrality values than males (Blaszczyk, 2018). In female baboons, a higher eigenvector centrality was linked to higher infant survival, potentially owing to a more central position in the group and a reduced risk of predation (Cheney et al., 2016). Contrary to our predictions, the clustering coefficient was neither affected by age nor sex. Older Barbary macaques did not cluster or affiliate in sub-groups more than younger conspecifics (see Sosa, 2016 for similar results).

The decrease in energy-demanding activities corresponds to the decline of physiological function in primates (Roth et al., 2004). Our results are in line with numerous studies that reported a decrease in activity (less running and climbing) in females (Almeling et al., 2017) and an increase in resting behavior in both sexes (Baker, 2000; Corr, 2003). Commenting behavior, the uttering of vocalizations towards conspecifics’ interactions was not affected by age—neither in females nor in males—and remained high throughout adulthood. This observation corroborates the view that older monkeys withdraw from active participation in interactions, although they do not lose social interest.

To date, only a few studies had investigated sex differences in social aging. In grey mouse lemurs (Microcebus murinus), older individuals from both sexes engaged less in affiliative interactions than younger individuals (Picq, 1992). In tufted capuchins (Sapajus sp.), affiliation decreased for females but not for males. Yet, male affiliation was generally low, resulting in a floor effect (Schino & Pinzaglia, 2018). In rhesus macaques (Macaca mulatta), older males received more affiliative behavior than younger males and had more individuals in proximity (Corr, 2003), a finding opposite from our results. A closer inspection of the results, however, showed that the majority of social partners were juveniles. Shifting towards interactions with infants might be a strategy to avoid costly interactions that could end in a physical confrontation. Thus, the decline of affiliative interactions in our study and the different composition of social partners in rhesus macaques may result from different strategies to reduce stressful social interactions. Overall, the comparison of the results emphasizes that more data is needed on male social aging in different nonhuman primate species and populations.

Our findings support the view that an awareness of one’s limited future time perspective is not the only factor driving changes in social behavior (Almeling et al., 2016; Schino & Pinzaglia, 2018). The present study adds to the existing literature by investigating physiological and social age-related changes in both sexes across adulthood. In old age, both male and female Barbary macaques were less sociable. Partly, this low social activity may be attributed to the waning of energy, as reflected in the lower amount of energy-demanding activities. Yet, when old females engaged in grooming interactions, these were longer than those of young females (Almeling et al., 2016), suggesting that the overall decrease of affiliative interaction is not just a result of physical weakness, but above all due to a change in motivation.

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Eva-Maria Rathke completed conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); visualization (equal); writing original draft (lead); writing review and editing (supporting). Julia Fischer completed conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal);
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DATA AVAILABILITY STATEMENT
Data and code are available at https://osf.io/2wpr3/

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